# REPORT FROM THE WORKSHOP ON <br> LAKE USE BY ATLANTIC SALMON IN NEWFOUNDLAND, CANADA 

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## Canadian Manuscript Report of

## REPORT FROM THE WORKSHOP ON

# LAKE USE BY ATLANTIC SALMON IN NEWFOUNDLAND, 

CANADA<br>by<br>P. M. Ryan, M. F. O'Connell, and V. A. Pepper<br>Science Branch<br>Department of Fisheries and Oceans<br>P. O. Box 5667<br>St. John's, Newfoundland A1C 5X1

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#### Abstract

Ryan, P. M., M. F. O'Connell, and V. A. Pepper. 1993. Report from the workshop on lake use by Atlantic salmon in Newfoundland, Canada. Can. MS Rep. Fish. Aquat. Sci. 2222: iv +54 p.

A workshop on lake use by juvenile Atlantic salmon (Salmo salar) was held at the Northwest Atlantic Fisheries Centre in St. John's, Newfoundland on April 23, 1993. Participants were the staff of the Salmonid and Habitat Science Division of the Science Branch, Department of Fisheries and Oceans. The workshop was held to review existing information on lake use by juvenile salmon, identify major gaps in our knowledge of the subject, and develop research priorities to remove those gaps. This report summarizes the workshop and is intended to assist in the development of necessary research pertaining to lake use by salmon. The report contains full formal papers on natural lake use by juveniles, experimental lake use by juveniles, and the current incorporation of lake use information into Atlantic salmon management. The recommendations for research made by workshop participants are also included.


## RÉSUMÉ

Ryan, P. M., M. F. O'Connell, and V. A. Pepper. 1993. Report from the workshop on lake use by Atlantic salmon in Newfoundland, Canada. Can. MS Rep. Fish. Aquat. Sci. 2222: iv +54 p.

Le 23 avril 1993, un atelier sur la fréquentation des lacs par les saumons de l'Atlantique (Salmo salar) juvéniles avait lieu au Centre des pêches de l'Atlantique du nord-ouest de St. John's (Terre-Neuve). Réunissant les employés de la Division des salmonidés et des sciences de l'habitat de la Direction des sciences de Pêches et Océans Canada, cet atelier avait pour but d'examiner les données connues sur la fréquentation des lacs par les saumons juvéniles, de cerner les principales lacunes dans nos connaissances sur le sujet et d'établir des priorités de recherche pour remédier à ces lacunes. Le présent rapport résume l'atelier et est concu pour soutenir l'élaboration des recherches nécessaires à l'étude de la fréquentation des lacs par le saumon. Il contient l'intégralité de rapports officiels sur la fréquentation naturelle des lacs par les juvéniles, sur les expériences d'empoissonnement des lacs avec des juvéniles, et sur l'intégration des connaissances actuelles en matière de fréquentation des lacs à des fins de gestion du saumon de l'Atlantique. Il comprend enfin des recommandations de recherche formulées par les participants à l'atelier.

## INTRODUCTION

This report presents the results of a workshop held by staff of the Salmonid and Habitat Science Division of the Science Branch, Department of Fisheries and Oceans, in St. John's, Newfoundland, April 23,1993. It is intended that this report will assist in the development of required research pertaining to lake use by Atlantic salmon (Salmo salar).

During the 1992 Program Review and Evaluation of Science Branch, staff of the Salmonid and Habitat Sciences Division initiated a number of discussions concerning our knowledge of the use of lakes by juvenile Atlantic salmon. Lake use by juvenile Atlantic salmon is a phenomenon common in Newfoundland, but less so elsewhere.

In Newfoundland, a substantial amount of Atlantic salmon smolt production occurs naturally in the abundant lakes which are locally referred to as ponds. Accordingly, knowledge of the production potential of lake habitat for salmon smolts is a requirement in setting catch quotas so that sufficient adults can escape to spawn and river systems are able to produce salmon to their full capacity. Additionally, knowledge of the potential of lakes to produce Atlantic salmon is a requirement for the recognition of biological changes brought about by environmental stressors such as acid rain, hydroelectric dams, and climate warming.

In the past 15 years, a considerable amount of information has been accumulated about lake use by Atlantic salmon and subsequently, this information has been practically applied. However, there are a number of unknowns concerning lake use which have necessitated approximations of production potential and spawner requirements in stock assessments and which have impeded the recognition of the causes of a variety of population changes.

As a result, a workshop was held to review existing information on lake use by salmon, identify major gaps in our knowledge of the subject, and develop research priorities to remove those gaps. This report summarizes the workshop and is intended to assist in the development of necessary research pertaining to lake use by salmon.

The format of the workshop consisted of three formal presentations, discussion, and the development of research recommendations with suggestions for implementation into the Division research program. Formal presentations were intended to review three main areas:

1/ Natural lake use by juveniles;
2/ Experimental lake use by juveniles; and
3/ Incorporation of lake use information into Atlantic
salmon stock assessment advice.
Following are the full texts of the formal presentations on lake use by salmon and the recommendations for research made by workshop participants.

# Natural Lake Use by Juveniles: A Review of the Population Dynamics of Atlantic Salmon in Newfoundland Lakes 

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Ryan, P. M. 1993. Natural lake use by juveniles: a review of the population dynamics of Atlantic salmon in Newfoundland lakes. p.3-14. In Ryan, P. M., M. F. o'Connell, and V.A. Pepper. 1993. Report from the workshop on lake use by Atlantic salmon in Newfoundland, Canada. Can. MS Rep. Fish. Aquat. Sci. 2222: iv + 54 p.

This paper reviews the population dynamics of juvenile Atlantic salmon (salmo salar) in two small, intensively studied lakes at the headwaters of the Gander River, Newfoundland. Atlantic salmon were censused, concurrently with brook trout (Salvelinus fontinalis), for density, biomass, and age composition in the spring and fall from 1978-92 in Spruce Pond and from 1979-92 in Headwater Pond using fyke nets and schnabel multiple mark-recapture techniques. Age-specific migrations to and from the lakes were calculated as the differences, by agegroup, between censuses. Densities of juvenile salmon ranged from 18.2-92.7 fish . ha ${ }^{\text {in }}$ spruce Pond and from 5.0-27.1 fish . ha ${ }^{-1}$ in Headwater Pond. References for corresponding data on salmon biomass were provided. Ages of salmon ranged from 1 to 7 years in both lakes with spruce pond fish tending to be younger; likely as a result of their proximity to the large downstream spawning area. Typically, the number of salmon increased in the lakes from fall to spring and decreased from spring to fall. The usual fall-to-spring increase in the number of salmon in the lakes was primarily due to a net movement into the lakes of agegroups 1, 2, and 3. The usual decrease in number over the spring-to-fall period was primarily due to a net loss from the lakes of individuals in age-groups 2, 3, 4, and 5. The calculated net downstream emigration from the study lakes over the spring-to-fall period was indicative of the magnitude and the age composition of the smolt run from the Gander River system. An inverse relationship between the average annual densities of trout and salmon in the lakes has been described. Mean annual total salmonid densities in both ponds as a whole ( 112.6 ha.) ranged from 40.0-74.9 fish . ha ${ }^{-1}$ and averaged 5 日. 2 fish . ha ${ }^{-1}$.

## INTRODUCTION

In insular Newfoundland, riverine portions of Atlantic salmon (Salmo salar) river systems are estimated to produce 2.8-8.9 million smolts . yr-1 (Pippy 1982). However, a substantial smolt production occurs naturally in Newfoundland's abundant lakes (Pepper 1976; Chadwick and Green 1985; Ryan 1986a; O'Connell and Ash 1989; Ryan 1993) which cover over $10 \%$ of the island's land mass (Whelan and Wiseman 1975). Accordingly, knowledge of the production potential of lake habitat for Atlantic salmon smolts is a requirement in setting catch quotas so that sufficient adults can escape to spawn and river systems are able to produce salmon to their full capacity.

This report is a review of the population dynamics of juvenile Atlantic salmon in two small, intensively studied lakes at the headwaters of the Gander River, Newfoundland. It is intended that this review will assist in the development of priorities for research pertaining to lake use by salmon.

## METHODS

## Study Area

Headwater and Spruce ponds are dilute (mean conductance $35 \mu \mathrm{~S}$. $\mathrm{cm}^{-1}$ ), brown-water lakes within the Department of Fisheries and Oceans' Experimental Ponds Area at the headwaters of the Gander River system (Ryan and Wakeham 1984). Their physical and chemical characteristics approximate the average descriptors of water quality in insular Newfoundland (Ryan et al. 1990). Headwater Pond ( 76.1 ha, maximum depth $=3.3 \mathrm{~m}$, mean depth $=1.1 \mathrm{~m}$ ) drains 3.5 km to the north into Spruce Pond ( 36.5 ha, maximum depth $=2.1 \mathrm{~m}$, mean depth $=1.0 \mathrm{~m}$ ) and the Spruce Pond outlet flows about 155 km northeast to the Atlantic Ocean. The closest major concentration of salmon spawning substrate is about 12 km downstream of Spruce Pond (Traverse 1972; Ryan and Wakeham 1984). In addition to anadromous Atlantic salmon, other fishes present in the lakes are the brook trout (Salvelinus fontinalis), the American eel (Anquilla rostrata), and the threespine stickleback (Gasterosteus aculeatus).

## Population Dynamics

Salmon were censused, concurrently with brook trout, for density, biomass, and age composition in the spring and fall from 1978-92 in Spruce Pond and from 1979-92 in Headwater Pond using fyke nets and Schnabel multiple mark-recapture techniques as detailed in Ryan (1984, 1990). The study was terminated by management in 1988, but subsequently reinstated in 1989. Fish were captured in fyke nets (Ryan 1984), measured for length, marked with fin holes or clips, released, and recaptured for the computation of population size. Weights and scale samples were obtained from a subsample of approximately 100-125 fish during each census.

The age composition of the population during each census up to 1983 was calculated from the ages and lengths of subsampled fish, the lengths of released fish, the computed population size, and their relative proportions using age-length keys (Ricker 1975).

Age-specific migrations to and from the lakes were calculated as the differences, by age-group, between censuses. Thus, the number of salmon smolts migrating out of the lakes each year up to 1983 has been calculated as the loss in numbers of salmon from each of the age-groups over the spring-to-fall period (Ryan 1986a). The calculated number of smolts in those years has been related to the number of salmon present in the lakes in the spring of the same year by least-squares regression to obtain a predictor of the smolt migration at given spring densities (Ryan 1986b).

Biomass data for salmonids in Spruce and Headwater ponds have been described in detail by Ryan (1986a, 1990). Density, rather than biomass data are reviewed here since smolt counts are typically reported as numbers rather than weights.

RESULTS
Population densities of salmon in Spruce and Headwater ponds in the spring and fall have varied, with highest densities occurring closest to the major spawning area downstream of Spruce Pond. Densities ranged from 18.2-92.7 fish . $h a^{-1}$ in Spruce Pond and from 5.0-27.1 fish. ha ${ }^{-1}$ in Headwater Pond over the entire study period (Fig. 1). Most dramatic fluctuations occurred in Spruce Pond after part of the upper watershed was burned in the spring of 1986.


Figure 1. Population densities of juvenile Atlantic salmon each spring and fall in Spruce Pond (upper panel) and Headwater Pond (lower panel), 1978-92.

Average annual salmon densities have been less variable and ranged from 27.0-70.5 fish . $\mathrm{ha}^{-1}$ in Spruce Pond and from 6.0-21.2 fish . $h^{-1}$ in Headwater Pond (Fig. 2). The greatest year-to-year variability occurred in Spruce Pond in the period after the fire of 1986.

Figure 2. Mean annual population densities of juvenile Atlantic salmon censused each spring and fall in Spruce Pond (upper panel) and Headwater Pond (lower panel), 1978-92.


The ages of salmon ranged from 1 to 7 years in both lakes with Spruce Pond fish tending to be younger; likely as a result of their proximity to the large downstream spawning area (Ryan 1986a). The typical variation in lacustrine age composition could be seen in the composition of ages each spring and fall from both lakes as a whole (Fig. 3). Combination of the data from both lakes compensated for lake-to-lake movements known to occur (Ryan 1986a). Typically, the number of salmon increased in the lakes from fall to spring and decreased from spring to fall.

The usual fall-to-spring increase in the number of salmon in the lakes (Fig. 1 and Fig. 3) was primarily due to a net movement into the lakes of age-groups 1, 2, and 3 (Fig. 4). Lesser numbers of fish were calculated to have entered the lakes as members of agegroups $0,4,5$, and 6 over the fall-to-spring period, but older fish usually decreased in number.


Figure 3. Age composition of Atlantic salmon in Headwater and Spruce ponds as a whole (112.6 ha.) at the end of censuses each spring and fall, 1979-83. Redrawn from Ryan (1986a).


Figure 4. Changes in the age composition of Atlantic salmon in Headwater and Spruce ponds as a whole ( $112.6 \mathrm{ha}$. ) between censuses each spring and fall, 197983. Based on data of Fig. 3. Redrawn from Ryan (1986a).

The usual decrease in the number of salmon over the spring-to-fall period (Fig. 1 and Fig. 3) was primarily due to a net loss from the lakes of individuals in age-groups 2, 3, 4, and 5 (Fig. 4). Lesser numbers of fish in age-groups 1, 6, and 7 were calculated to have left the lakes over the spring-to-fall period.

Changes in the numbers of fin-clipped salmon in the lakes provided further indication of the dynamic nature of their movements (Table 1). Few fish marked in the spring of 1982 were subsequently recovered. Three individuals marked in Headwater Pond were subsequently recovered in the fall downstream in Spruce Pond; an indication of interlake movements.

Table 1. Percentages of fin-clipped Atlantic salmon in the study lakes after marking in the spring of 1982. Percentages were calculated as the portion of each population clipped in the spring of 1982 and, subsequently, as the portion of clip recaptures in each catch. From Ryan (1986a).

|  | 1982 |  | 1983 |  |
| :--- | :---: | :--- | :---: | :---: |
|  | Spring | Fall | Spring | Fall |
| Headwater Pond | 57.4 | 2.9 | 0 | 0.6 |
| Spruce Pond | 65.3 | 0.2 | 0.0 | 0.0 |
|  |  |  |  | 0.0 |

a Does not include three fish recovered in Spruce Pond.

The calculated net downstream emigration from the study lakes over the spring-to-fall period has been considered to be indicative of the magnitude and the age composition of the smolt run from the Gander River system (Ryan 1986a). The calculated smolt migration rate from Headwater and Spruce ponds, 1979-83, averaged 13.4 smolts . ha ${ }^{-1}$. $\mathrm{yr}^{-1}$, ranged from 3.2 to 26.7 smolts . $\mathrm{ha}^{-1}$. $\mathrm{yr}^{-1}$, and was a significant ( $p<0.05$ ) correlate of spring salmon density in the lakes over the range of 14.2-42.8 salmon . ha ${ }^{-1}$ (Fig. 5). Residual salmon were always present in the lakes in the fall after the smolt run and these fish tended to be proportionately less at higher stock densities (Fig. 1 and Fig. 3).

Ratios of the abundance of salmon to trout were greater closer to the major salmon spawning area downstream of Spruce Pond (Fig. 6). Mean annual total salmonid densities in Spruce Pond ranged from 59.7-113.6 fish . $\mathrm{ha}^{-1}$ and in Headwater Pond ranged from 26.4-59.3 fish . ha' ${ }^{-1}$ (Fig. 6). Greatest year-to-year fluctuations, apparent in Spruce Pond but not in Headwater Pond, occurred in 1986 and 1989.

Figure 5. Smolt migrations (Sm) from Spruce and Headwater ponds as a whole ( 112.6 ha.) related to the spring densities (Sp) of salmon in the lakes in the same year. Years of census are indicated. Based on data of Fig. 3 and Fig. 4. Redrawn from Ryan (1986b).

Figure 6. Mean annual total salmonid densities in Spruce Pond (upper panel) and Headwater Pond (lower panel), 1978-92.



Mean annual total salmonid densities in both Headwater and Spruce Ponds as a whole (112.6 ha.) ranged from 40.0-74.9 fish . ha ${ }^{-1}$ and averaged 58.2 fish.ha ${ }^{-1}$ (Fig. 7). Based upon an inverse relationship between the average annual densities of trout and salmon in the lakes from 1979-83 (Ryan 1993), maximum spring densities of salmon in the absence of trout have been extrapolated as 90.3 fish . ha ${ }^{-1}$ with an associated smolt migration of 65.7 smolts . ha' ${ }^{-1}$ (Ryan 1993).


Figure 7. Mean annual total salmonid densities in Spruce and Headwater ponds as a whole (112.6 ha.), 1979-92.

## DISCUSSION

There are a number of factors which have affected the precision of the censuses and the calculation of smolt migration. These include the approximation of census requirements, an unknown mortality rate of parr, and the migration of precocious parr between spring and fall censuses. However, as discussed by Ryan (1986a; 1990), these factors do not preclude the application of the estimates for the practical purposes of monitoring the population.

The estimates of smolt migration rate from the study lakes are estimates of lacustrine smolt emigration rate rather than classical lacustrine production (weight produced in the lake environment per unit time) as a result of the use by young salmon of both lake and river environments. In the study lakes, the first lakeward migrations of salmon from streams most often occurs after the first year of life. Some of these fish may return to the streams for varying periods prior to reentering the lake environment (Ryan 1986a). This timing of first lake use appears to be a common one in insular Newfoundland (Pepper 1976; Hutchings 1986), although in some areas of the island lake use may occur earlier ( $0^{\prime}$ Connell and Ash 1989).

Generalized life histories of juvenile salmon using lake environments can be inferred from the present study. After hatching in stream spawning areas, juveniles disperse up and downstream with some entering lake environments, typically after the first year of life. These individuals remain for varying periods. They may subsequently return to stream environments prior to reentering lakes. They may mature as the precocious males often observed in the lakes in the fall, migrate to stream spawning areas and, subsequently, return to the lakes or remain in the streams. They may smoltify in the lakes as is observed in the spring, migrate to the ocean, and subsequently get captured in oceanic or riverine fisheries or return to the home spawning area. Similar life histories of lacustrine salmon on the northeast coast of insular Newfoundland have been inferred by Hutchings (1986).

The annual variation in calculated smolt migration rates from the study lakes, 3.2-26.7 smolts . ha $^{-1}$, appears to be representative of estimates of lacustrine smolt production for Newfoundland waters. In two other river systems comprised of 96 and $98 \%$ lake habitat, annual lacustrine smolt production was estimated as 10.1 smolts. $\mathrm{ha}^{-1}$ ( $96 \%$ of the total) ( $0^{\prime}$ Connell and Ash 1989) and 15.0 smolts . $h^{-1}$ (67\% of the total) (Chadwick and Green 1985), respectively.

Differing densities of salmon between the study lakes may result from a variety of factors. It seems probable that the proportion of naturally occurring lacustrine smolt production in watersheds is a function of the proportion of lacustrine habitat available, the degree of inter- and intraspecific competition, and the proximity of lakes to spawning habitat as evidenced by the work of Pepper (1976), Chadwick and Green (1985), Pepper et al. (1985), Rose
(1986), O'Connell and Ash (1989; 1993), Ryan (1993), and others. Accordingly, it can be expected that the densities of juvenile salmon will vary considerably among lakes for reasons other than innate differences in lacustrine carrying capacity. An ability to predict the proportion of Atlantic salmon and its variation in salmonid lakes remains to be developed.

Young salmon may benefit from entering lakes by increased growth and survival rates (Pepper 1976; Hutchings 1986). Lakeward movement may be a response to increased competition for food and/or space as parr get older and larger (see review by Bley 1987). Hutchings (1986) provided evidence that changing water temperatures and water depth are regulators of these non-random, directed movements, once they are initiated. He subsequently argued that lakeward movements have a genetic component.

Reasons for the differences in total salmonid densities and their variations between the study lakes are not completely understood. There is strong evidence that environmentally mediated interactions determine the varying proportions of each similar salmonid in a total potential salmonid biomass within individual river systems (Rose 1986; Ryan 1993). Variations in lacustrine carrying capacity, together with their probable causes, among other Canadian Shield lakes have been well documented (Ryder 1982). However, in Newfoundland, lakes typically possess unique limnological characteristics (i.e. high color, rapid water replacement, low depth) which are known to account for regional variations in previously documented relationships of fish production to lake descriptors. Thus, empirical relationships between lacustrine carrying capacity and other limnological characteristics in Newfoundland, both within and among lakes, remain undefined.

Atlantic salmon river systems in insular Newfoundland have a drainage area of $77,871.24 \mathrm{~km}^{2}$ and the riverine areas of these systems produce an estimated 2.9 - 8.9 million smolts . $\mathrm{yr}^{-1}$ (Pippy 1982). About 10 percent of the drainage area of these rivers, or $7,942.8 \mathrm{~km}^{2}$, is made up of standing waters with surface areas of 0.405 ha or greater (Whelan and Wiseman 1975). If 67.3 percent of this standing water were accessible to salmon, as is estimated for the riverine parr rearing areas (Anon. 1978), accessible standing waters would constitute $5,345.52 \mathrm{~km}^{2}$ of the drainage basins of insular Newfoundland's salmon rivers. At the calculated average annual smolt emigration rate of 13.4 smolts . ha ${ }^{-1}$ from standing waters in the Experimental Ponds Area, the calculated accessible standing waters in Newfoundland's salmon rivers would have a smolt emigration of 7.2 million smolts . $\mathrm{Yr}^{-1}$; approaching the estimated riverine production of 2.9-8.9 million smolts . $\mathrm{yr}^{-1}$ (Pippy 1982) in

[^0]insular Newfoundland. Accordingly, lacustrine production should be quantified and incorporated into estimated optimal escapement rates for river systems so that full salmon production potential can be realized.

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# Review of Experiments on Lacustrine Nursery Areas for Atlantic Salmon in Newfoundland and Identification of Further Research Opportunities. 

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#### Abstract

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Previous published documents on Newfoundland lacustrine experiments with stocking of Atlantic salmon (Salmo salar) juveniles are reviewed. Interpretations are updated by consideration of more recent data. Although the stocking sequence for this 25 year experimental design is now half completed, the number of adult escapements to the project is still insufficient to support quantitative analyses of adult salmon spawning returns. Interim results indicate that the stock characteristic of salmon from lacustrine stocking has shifted towards earlier smoltification and spawning escapement. The frequency of age 3 and age 4 grilse returning to the project reflects the proportions of age 2 and age 3 smolt emigrating from lacustrine habitat. Age 4 smolts, though they represent up to $2.76 \%$ of the smolts emigrating from a given year-class, rarely contribute to subsequent spawning escapement to this watershed. of the few instances in which post-smolt have been encountered in spawning escapements, most of those encountered are age 4 fish from the lacustrine experiment. These observations lead to the conclusion that the main response variable we have pursued in our analyses of lacustrine experiments is inappropriate and a better indicator of performance is instantaneous rate of mortality. In view of the revelations of this review, we present a discussion of research opportunities that would lead to a greater understanding of the ecological significance of lacustrine nursery areas for Atlantic salmon.

## INTRODUCTION

Atlantic salmon (Salmo salar) enhancement activities have been under way in Newfoundland since the mid-1950s (Farewell and Porter 1979). These activities have focused on low-technology approaches to biomanipulation of stocks to assure that salmon enhancement processes are founded on sound ecological and genetic principles.

Allendorf et al. (1987) cautioned that considerable care is required to prevent unwanted interactions between artificially propagated fish released to the wild and the natural populations of the release sites. McIntyre (1991) echoes this sentiment and indicates that stocking with fry or fingerlings must be with fish of appropriate genetic make-up that are no larger than fish in the supplemented population. Larger stocked fish have a competition advantage and can be expected to displace smaller wild fish, thereby increasing the risk of eroding the genetic fitness of the
wild stock. Clearly, effective enhancement requires understanding of the population dynamics and ecological constraints of the population. Newfoundland salmon enhancement projects have focused on broodstock that are chosen randomly from the wild stock being enhanced, so that the genetic composition of the population is changed as little as possible (Withler 1988).

It became apparent during early stocking activities that Newfoundland salmon stocking strategies were compromised by insufficient knowledge of the role lacustrine habitat plays in salmon ecology. Accordingly, biobaseline surveys of Atlantic salmon parr populations of natural lacustrine habitats were undertaken in 1975 and pursued during the next two years.

Results of this work (Pepper 1976; Pepper et al. 1985) revealed post-yearling salmon parr population densities of 55-66•ha' Conclusions of the initial survey work (Pepper 1976) are as follows:

1. Underyearling Atlantic salmon do not generally inhabit lacustrine areas.
2. Shallow rocky ponds with high dissolved oxygen and low predator/competitor pressure represent ideal rearing areas for Atlantic salmon parr.
3. Salmon parr survival is similar in pond and stream habitat. Survival within ponds is likely subject to less year to year variability due to a greater buffering of environmental parameters.
4. Salmon parr within a lentic environment are highly mobile, at least in littoral pond areas.
5.- "Territoriality", among juvenile Atlantic salmon, within pond environments, may occur for relatively short periods but is preceded by extensive swimming activity which results in circumnavigation of pond area.
5. Lacustrine insects comprise most of the Atlantic salmon parr food spectrum. Planktonic invertebrates are taken only incidentally during directed feeding activities.
6. Movement of stream-dwelling salmon parr to a lentic environment is mediated by unfavourable conditions within stream habitat.

In further studies of lacustrine habitats, it became apparent that, while these conclusions are generally applicable to ponds of Newfoundland, Atlantic salmon parr behaviour differed somewhat among different bodies of standing water. Mobility of parr within the ponds varied considerably, both seasonally and among different ponds. The extent of parr mobility is inversely correlated with mean depth. The tendency for parr to occupy a limited home range in ponds with greater mean depth was attributed to the tendency for larger brook trout to occupy deeper, cooler water and only venture into shallower, warmer water in search of prey (Pepper et al. 1985) .

On the basis of these survey results, a quest was undertaken for study ponds to subject to controlled releases of juvenile salmon. The search for candidate ponds was based on criteria of: accessibility; manageability; and, biological community simplicity. Briefly, ponds had to be readily accessible by surface vehicle to keep costs down; had to be large enough to provide significant production potential yet small enough to be studied with limited financial resources; and, have no natural salmon population that would confuse the assessment of survival of the year-classes released.

Between 1977 and 1979, fry stocking experiments were conducted within natural ponds of the Black Brook tributary of the Indian Brook watershed (Halls Bay, Newfoundland; Fig. 1 and Fig. 2).


Figure 1. Indian Brook watershed, Newfoundland.

Concurrent with these controlled releases of juvenile salmon, additional biobaseline studies were conducted on the anadromous salmon population of Indian Brook. These studies, plus historical data, indicate that Indian Brook smolt of riverine origin (i.e., prior to implementation of lacustrine experiments) averaged $10 \%$ age $2,75 \%$ age 3 , and $15 \%$ age 4 . Mean weight at age for these Indian Brook smolts was: 23.8 g age $2 ; 35.7 \mathrm{~g}$ age 3 ; and, 44.0 g age 4 . Of the brood salmon returning to Indian Brook from historical riverine salmon year classes, $2.1 \%$ were from age 2 smolts, $57 \%$ were from age 3 smolts and $40 \%$ were from age 4 smolts (Pepper and Oliver 1986).


Figure 2. Vertical configuration of Indian Brook watershed, Newfoundland.

With this as a biobaseline from which to document shifts in population structure, a more comprehensive experimental design for lacustrine stocking was implemented in 1982. A tentative stocking density of 1000 fry per hectare was adopted for the ponds of the Black Brook tributary. A deep-substrate incubator was constructed to provide in excess of one million salmon fry to support a more rigorous stocking study.

Evaluations of both freshwater and marine survival are essential components of analyses of the lacustrine nursery strategy. While sufficient data now exist on which to draw inferences of lacustrine ecology and smolt yield, interpretation of marine performance of lacustrine origin smolts is expected to require several more years of adult salmon returns to the project. This paper provides an overview of lacustrine performance of stocked year-classes and highlights research questions that should be addressed in the coming years of lacustrine salmon investigations.

## METHODS

The experimental design and required response variables for the lacustrine nursery project are described in detail by Pepper and Oliver (1986). The present lacustrine nurseries experiment is based on a long-term program to evaluate production benefits from different stocking strategies (i.e., consecutive vs. nonconsecutive stocking) and size/season at release (i.e., swim-up fry vs. 100 day, fed-fingerlings). These studies are designed to assure that juvenile salmon releases will not disrupt the natural salmon stock. This approach is founded on principles such as espoused by Bailey (1989), that selection for performance in a particular environment is most effective when conducted in that environment. The DFO Newfoundland enhancement strategy is to release juvenile salmon into natural habitat in which there are no existing populations of anadromous salmon. The Black Brook, incubation facility has provided swim-up salmon fry for lacustrine enhancement experimentation since 1984. Lake cages, as described by Pepper et al. (1987), have provided fall-fingerling parr.

Lacustrine nursery areas have been sampled only rarely after release of juveniles so as to avoid stress-related mortality. Limited lake trapping and inlet stream electrofishing have been done to document the incidence of precocious maturation subsequent to release. This sampling was conducted only in 1983 through 1985. Captured parr were anaesthetized, weighed, measured, and scale sampled. All were retained only long enough to recover from the anaesthetic, after which they were released back to the habitat from which they were captured. Precocity was identified by the ability to express sperm by applying gentle pressure on the vent area of the parr.

While we avoid intervention in the lacustrine ecology of juvenile salmon once they are released, the release program was closely
monitored to provide records of: juvenile survival (i.e., number of swim-up fry of each year-class released relative to number of smolts produced from each year-class; and, growth (i.e., mean weight of swim-up fry per year-class relative to the mean weight of each smolt age produced by the year-class). We emphasize that the calculated values for survival and growth are based on the number and weight of fry to the rearing strategy irrespective of whether the fry were distributed directly to the ponds or to lake cages before being released as fall-fingerlings. These two response variables provide the means to determine yield per year class for each pond stocked and instantaneous rate of change in bulk (Ricker 1975) per year class released. Details of these analyses are described by Pepper and Oliver (1986; Appendix 2).

## RESULTS

Between 1977 and 1979, initial fry stocking of the standing waters of Black Brook provided promising but variable smolt yields. Fry-to-smolt survivals varied considerably among release locations (0.9\% - 20\%; Pepper et al. 1985) and decreased with repeated consecutive fry releases. Fry-to-smolt survival in these initial experiments was $3.5 \%$.

As of 1992, 20 of the 40 juvenile salmon releases required by the current experimental design were complete. Complete smolt sequences have been achieved for only 13 of these releases. Pertinent data from completed smolt series are presented in Tables 1 to 3. Mean weight of smolts of each age group from completed emigration series (Fig. 3) has increased among consecutive annual releases. Year-class survival under consecutive releases has varied from decreasing to increasing (Table 3). Male precocity was observed but did not appear to represent a significant deterrent to fallfingerling survival to smoltification. Annual smolt yield (by yearclass) from stocking fall fingerlings ranged from 53 to $130 \cdot \mathrm{ha}^{-1}$ (mean $=77$ smolts $\cdot h^{-1}$ ). Survival, from fingerlings released until smolt emigration, ranged from 3.7 to $15.8 \%$ (mean survival $=11.2 \%$ ). These results are from stocking sequences for which smolt runs have been completed. Interim results from the single series of fry releases in Gull Pond do not appear to conform with the observed mean smolt yield from stocking of other ponds in this system.

Age 4 smolts from consecutive annual releases of fall-fingerlings had a greater incidence of males (Pepper et al. 1992). In contrast, from the single year-class released to Traverse Pond, there was a decreasing proportion of males among the older age groups.

Examination of smolt and adult characteristics has been informative in revealing shifts in population structure between lacustrine (Black Brook) and riverine (Indian Brook) components of this salmon stock. On completion of smolt emigration from the





Figure 3. Mean smolt weights by age, lacustrine study areas, Stocking sequences completed.

Table 1. Smott and adutt yields from Black Brook lacustrine areas

| Year | Smott Production | Grilse Returns |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  |  | IR Fishway Year +1 | Black Brook Year +1 | Return Year |
| 84 | 2061 | 2074 |  | 85 |
| 85 | 3993 | 2069 |  | 86 |
| 86 | 8081 | 407 | 59 | 87 |
| 87 | 25499 | 1460 | 238 | 88 |
| 88 | 22574 | 212 | 109 | 89 |
| 89 | 28604 | 1122 | 235 | 90 |
| 90 | 15877 | 711 | 112 | 91 |
| 91 | 18615 | 1315 | 457 | 92 |
| 92 | 9704 |  |  | 93 |

Table 2. Mean weights and sex ratios (\% female) for Black Brook lacustrine areas.

|  | Year Class |  | Fry <br> (g) | Smott |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | 2+ |  | 3+ |  | 4+ |  |
|  |  |  |  | Wt. | SR | Wt. | SR | Wt. | SR |
| Upper Micmac Consecutive FF |  | 1982 | 0.16 | 26.4 | 59 | 25.5 | 59 | 32.0 | 43 |
|  |  | 1983 | 0.14 | 23.9 | 74 | 31.0 | 59 | 56.2 | 41 |
|  |  | 1984 | 0.15 | 27.5 | 100 | 43.8 | 58 | 75.1 | 47 |
| Upper Micmac Non consecutive FF |  | 1988 | 0.17 | 24.6 |  | 43.3 | 29 | 87.3 | 47 |
| Traverse Pd. Consecutive FF |  | 1986 | 0.18 | 36.4 | 52 | 43.6 | 61.0 | 0 |  |
|  |  | 1987 | 0.16 | 35.4 | 58 | 54.2 |  | 114.0 |  |
|  |  | 1988 | 0.17 | 34.0 |  | 65.9 |  | 0 |  |
| Traverse Pond Non consecutive FF |  | 1982 | 0.16 | 36.5 | 47 | 48.8 | 61.0 | 83.9 | 70 |
| Micmac Lake Consecutive Fry |  | 1985 | 0.15 | 31.3 |  | 44.9 |  | 94.4 |  |
|  |  | 1986 | 0.18 | 30.7 |  | 50.1 |  | 97.4 |  |
|  |  | 1987 | 0.17 | 36.6 |  | 66.5 |  | 120.1 |  |
| Gull Pond Consecutive Fry |  | 1988 | 0.17 | 29.7 |  | 54 |  | 98.1 |  |
| Wolverine Non consecutive Fry |  | 1984 | 0.17 | 31.2 | 58 | 56.3 | 71.0 | 69.3 | 52 |

Table 3. Smoit survivals and instantaneous rate of change in biomass for Black Brook lacustrine areas.

| Location | Year Class | $\begin{aligned} & \frac{\text { R Value }}{\text { (from fry }} \\ & \text { stage) } \end{aligned}$ | Fingerling Stocking Waight | Smolt Survival (\%) |  |  |  | Total Survival to Smolt | Smolt Yield per ha. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | 2+ | 3+ | 4+ | 5+ |  |  |
| Upper Micmac | 1982 | 0.79 | 2.18 | 6.62 | 5.37 | 2.76 |  | 14.75 | 81.3 |
| (32 ha) | 1983 | 0.91 | 2.18 | 1.71 | 10.13 | 1.93 | 0.01 | 13.78 | 130.3 |
|  | 1984 | 1.08 | 2.31 | 0.93 | 9.87 | 0.18 |  | 10.98 | 103.0 |
|  | 1988 | 1.26 | 4.22 | 7.51 | 6.16 | 0.3 |  | 13.97 | 131.0 |
| Wolverine Pond (150 ha) | 1984 | 1.40 | 0.17 | 7.65 | 3.97 | 0.73 |  | 12.35 | 44.9 |
| Micmac Lake | 1985 | 1.51 | 0.15 | 9.76 | 1.9 | 0.27 |  | 11.93 | 30.6 |
| (790 ha) | 1986 | 1.10 | 0.18 | 4.39 | 1.58 | 0.2 |  | 6.17 | 30.0 |
|  | 1987 | 1.00 | 0.17 | 2.64 | 0.83 | 0.22 |  | 3.69 | 21.1 |
| Traverse Pond | 1982 | 0.72 | 1.94 | 1.87 | 5.3 | 0.16 |  | 7.33 | 53.0 |
| ( 66 ha ) | 1986 | 0.72 | 2.21 | 2.18 | 2.37 | 0 |  | 4.55 | 43.7 |
|  | 1987 | 1.57 | 4.83 | 12.82 | 2.76 | 0.18 |  | 15.76 | 159.4 |
|  | 1988 | 1.40 | 2.89 | 7.95 | 4.64 | 0 |  | 12.59 | 125.9 |
| Gull Pond <br> (1,000 ha) | 1988 | 0.85 | 0.17 | 0.81 | 2.64 | 0.24 |  | 3.69 | 9.1 |

lacustrine study areas in 1991, age at smoltification had shifted considerably relative to historical data for the Indian Brook stock (Table 4). Of considerable interest is a shift in sex ratio among smolts, from predominantly female (age 2) to predominantly male (age 4) as documented in Table 2. This trend is reversed for nonconsecutive stocking. Mean weight at age for these smolt runs is presented in Table 2. Variation in biomass of smolts produced from the various age classes is represented in Figure 4.

Table 4. Smolt age distributions, Indian Brook historical and Black Brook lacustrine areas

| Age | Indian Brook <br> Historical (\%) | Lacustrine <br> 1986-1991 |
| :---: | :---: | :---: |
| 2 | 10.0 |  |
| 3 | 74.0 | 65.9 |
| 4 | 15.0 | 30.7 |
| 5 | 1.0 | 3.4 |

${ }^{1}$ These smolts likely were predominantly from riverine habitat. Historical records do not document their origin. These data precede the lacustrine stocking experiments.


Smolt Biomass Production
Traverse Pond


Figure 4. smolt biomass production, consecutive stockings.

The number of spawning escapements to Black Brook from juveniles released to lacustrine habitat is too small to make statistically valid comparisons of performance of lacustrine smolts during their marine migrations. The limited grilse returns to date indicate that age distribution of spawners has shifted in concert with the change in age at smoltification for the lacustrine smolts (Table 5). Shift in age composition of the lacustrine smolts and adults, relative to the Indian Brook historical data, is evident (Figs. 5 and 6).

Table 5. Grilse age at smoltification, Indian Brook historical and Black Brook lacustrine areas.

| Smolt <br> age | Indian Brook <br> historical <br> (\%) | Lacustrine <br> (Black Brook <br> Swim-up brood) <br> (\%) |
| :---: | :---: | :---: |
|  | 2.1 | 52.8 |
| 2 | 57.1 | 46.2 |
| 3 | 39.7 | 1.0 |
| 4 | 1.2 |  |

Composition of the spawning escapement in 1991 and 1992 was altered by an unusual incidence of post-smolts. Of the 771 salmon counted at the fishway in 1991, 58 (7.5\%) were post-smolt. Incidence of post-smolt rose to $8.8 \%$ in 1992 (i.e., 127 of a total of 1445 fish). In 1991, 73\% of the post-smolt sampled from the fishway were age 4 fish. In 1992, 53 \% were age 4 . In both years, the remainder of the fish sampled were age 3. There were no age 2 post-smolt sampled in either year. Post-smolt were encountered only rarely prior to 1991.

## Age at Smoltification <br> Indian Brook Historical Data <br> 

Black Brook Enhanced 1986-1991

3 (30.7\%)


Figure 5. Age at smoltification. Indian Brook historical data and Black Brook lacuatrine enhanced.

## Age at Smoltification <br> Grilse Returns

Indian Brook Historical Data


Black Brook Enhanced 1986-1991


Figure 6. Age at amoltification of returning grilse. Indian Brook historical data and Black Brook lacustrine enhanced.

## DISCUSSION

Newfoundland salmon enhancement experiments on lacustrine nursery areas have utilized broodstock from the watershed that is under enhancement. Pepper et al. (1985) document the strategy for Black Brook incubation facilities regarding an effective population size of 900 for the broodstock population that contributes progeny to the lacustrine nursery experiments. This is consistent with subsequent guidelines presented by Tave (1986) that between 424 and 685 spawners/generation is a sufficient buffer to maintain genetic variability (i.e., heterozygocity) among fish released to the wild.

Throughout the history of the Lacustrine Nursery Areas experiments, attention has been focused entirely on release of juvenile salmon as dictated by the long-term (i.e., 25 year) experimental design, and monitoring of smolt emigration from the nursery areas. We have not attempted to monitor parr movements for evidence of transience of lacustrine habitation. We have no direct knowledge of parr movements during the summer. Parr scales do provide evidence of summer 'checks' in growth rate but it is unknown if this happens within the ponds or if it might be related to temporary forays into fluvial habitat.

Research results to date are consistent with predictions of smolt yield and biomass. Pepper and Oliver (1986) determined that annual smolt production potential for Indian Brook was 20000. Smolt runs from lacustrine habitats have more than doubled juvenile production from the Indian Brook system in some years (Table 1). Smolt emigration from Black Brook lacustrine nurseries has resulted in a downward shift in the age at smoltification of lacustrine smolts relative to that of the parent Indian Brook stock.

Indications are that marine survival is independent of smolt age (i.e., brood stock age distribution parallels smolt age distribution) for age 2 and 3 smolts. In comparison with the historical age distribution for grilse from Indian Brook (see above) lacustrine smolts demonstrate good survival for those that emigrate as age 2 and age 3. To date, there have been very few adult returns from age 4 smolts. This may be related to low survival potential once male parr have matured precociously. Completion of the lacustrine nurseries experimentation requires
analysis of Black Brook spawners as per the graphic illustration.
Smolt runs from these lacustrine habitats typically have contained more males than expected considering the incidence of precocious maturation that was noted in the autumn sampling surveys. Of the male smolts sampled, none had definitive evidence of previous gonad development. This suggests the following possibilities: a) precocious male parr died and therefore did not contribute to smolt runs; b) expenditure of energy on the maturation process precluded smoltification and hence, precocious males did not die but remained as parr; or c) that previously developed gonads regressed completely before smoltification and this previous sexual history delayed but did not significantly deter the subsequent smoltification process.

For the consecutive releases of fingerlings to Upper Micmac Pond, the frequency of males in the smolt samples increased with smolt age. This is in contrast to the single release of fingerlings to Traverse Pond for which the incidence of males decreased among the three smolt age groups produced. Precocity may have resulted in a delay in smoltification for Upper Micmac Pond smolts. However, this apparently was not the case for Traverse pond in which females predominated in later smolt runs.

Predominance of females among Atlantic salmon smolt runs has been documented by several researchers (Jones 1959; Osterdahl 1969; Gibson 1978). Considering that only 58\% of all of the smolt produced from the fall-fingerling releases were female, the incidence of male precocity overall either is low or does not result in significant mortality before smoltification. That the sex ratio was not more biased in favour of females is remarkable in that adult grilse spawning escapement to Black Brook, from 1984 to 1991, has averaged $76 \%$ female. It has been suggested (Dalley et al. 1983) that precocious maturation of male parr is a significant contributor to disproportionate sex ratios among Newfoundland spawning escapements .
M. F. O'Connell (Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, pers. comm.) has found an average incidence of female smolts of $83 \%$ from several ponds in Newfoundland. It currently is uncertain if male smolts from these lacustrine habitats have had any significant incidence of previous sexual development. We also do not know if previous sexual history has significance to the potential for survival during marine migrations as has been suggested by several authors where smolts were known to have matured prior to smoltification (Forsythe 1967; Osterdahl 1969; Leyzerovich 1973; Mitans 1973; Leyzerovich and Melnikova 1979; Dalley et al. 1983). Our data, indicating there are very few age 4 smolts returning as adults suggests that there is some disadvantage to smoltification at this age/size. We do not know if this is related to sex and/or precocity. This requires further investigation if we are to attempt to develop an optimal stocking strategy. Further sampling of precocious parr by stream
electrofishing and marking with fluorescent dye (Healey et al 1976; Gray et al 1978; Bandlow 1987; Negus et al. 1990) would provide further insight into this aspect of lacustrine population dynamics.

Until 1991, adult salmon returns to Indian Brook generally were increasing in parallel with lacustrine stocking intensity. The apparent marine mortality of smolts emigrating from Newfoundland rivers in 1990 is of concern. However, for Indian Brook, the marine mortality factor is made worse by natural catastrophes to the 1987 and 1989 salmon year-classes when the watershed rivers virtually dried up. It is apparent, from greater than 400 brood salmon that returned to the Black Brook facility in 1992, that lacustrine origin smolts do survive their marine migration and therefore have survival potential as they leave their lacustrine nursery areas.

There were numerous "post-smolt" among the 1991 and 1992 spawning escapements to Indian Brook. It is unlikely these specimens were in the sea for very long. As recorded by the International Council for Exploration of the Sea (ICES), catches of salmon on the northeast coast of Newfoundland in 1991 were the lowest ever recorded. This was attributed to "...Larger concentrations of ice persisting longer into the season and resulting in cold ocean water temperatures...". The increased incidence of "post-smolt" returning to Indian Brook in 1991 and 1992 gives further credence to the suggestion of poor marine environmental conditions as proposed by the ICES.

In view of apparently poor marine survival of age 4 smolts, and the incidence of post-smolts for this age class, it appears there may be a size threshold beyond which smoltification is either disadvantageous or dysfunctional. This observation casts considerable doubt on the initial choice of response variables as stated by Pepper and Oliver (1986). In their original EVOP design (Evolutionary Operations), these authors assumed that they should strive for maximum growth and survival (i.e., maximum $R$; instantaneous rate of change in biomass (Ricker 1975)) from lacustrine stocking. It now appears that mean $R$ values for a year class, that are inflated by very large size among age 4 smolts, provide no ecological advantage to the lacustrine salmon stock (i.e., larger smolts do not contribute to this gene pool, though they may contribute to the Indian Brook population) and therefore constitute a poor investment of lacustrine energy resources. Since smaller smolt have contributed virtually all of the subsequent spawning population in these experiments, it appears that analyses of experiments should focus only on survival. The apparent survival potential of the age 2 and 3 smolts suggests that growth, at least within the range of what has been achieved by these smolt ages, is relatively meaningless to the analysis. We propose that R now be replaced solely by $Z$ (instantaneous mortality (Ricker 1975)) in further analyses and that we aspire to minimal mortality among juveniles. We contend that a smolt of age 2 or 3 should be considered the unit of lacustrine production. Age 4 smolts appear to have little survival potential. If in fact the incidence of age

4 smolts can be demonstrated to be a significant function of previous male maturation, a strategy to deter precocity may improve smolt production benefits from lacustrine stocking.

Average survival of stocked juveniles to the smolt stage is somewhat greater for the fingerling release strategy (11.2\%) than for swim-up fry (3.5\%). Smolt production to date from fingerling releases appears to be less variable among years than production from swim-up fry releases. The primary advantage in improved salmon production from the lacustrine nursery experiments likely is due to improved fry to fall-fingerling survival through early rearing in the lake cages. Since there are no naturally occurring salmon parr in the ponds of this experiment, it is unlikely that this enhanced survival is due to a size advantage that displaces smaller wild salmon (McIntyre 1991) when the fall-fingerlings are released. We suspect the size advantage conveyed by release of fall-fingerlings confers a greater ability to avoid predation than any inter- or intraspecific competitive advantage. Alternatively, it may be that size is not the factor of greatest advantage. There are few predators of salmon parr in our study ponds. Since these fallfingerlings typically are released in October, when many of the larger brook trout are preoccupied with spawning and therefore have moved into streams, the number of brook trout left in the pond with sufficient size to ingest a fall-fingerling will be greatly reduced.

Our technique of rearing swim-up salmon fry in lake cages for release as fall-fingerlings has proven effective in producing the required numbers of fish. Other than for a brief period of elevated mortality at first-feeding, when fry are adapting to artificial food, there are few problems rearing salmon in lake cages. Survival during the 100 -day rearing interval in lake cages is within expectations (i.e., > 80\%). This is satisfactory in a fish-culture context. However, we have no knowledge of what happens with parr feeding subsequent to release. Our hypothesis is that, having been reared in a lake cage in which natural food is present, parr will have supplemented their diets with natural food items prior to release. Feeding of parr on zooplankton within our lake cages has been observed (Pepper et al. 1987). This "preconditioning" may help released parr to adapt quickly to natural food. Feeding behaviour of parr after release is a potential avenue for future research.

There are not yet sufficient data to define an optimal stocking level that will achieve lacustrine carrying capacity. In the more traditional releases of swim-up salmon fry to fluvial waters in Newfoundland, average fry density of $75 \cdot 100 \mathrm{~m}^{-2}$ has resulted in good yields of adults (O'Connell and Bourgeois 1987). This is equivalent to stocking 7500 fry ${ }^{-h a^{-1}}$ of littoral zone habitat. Assuming a mean fry weight of 0.18 g (Pepper and Stansbury 1985) at the time of release, Newfoundland fluvial habitats receive about $1.35 \mathrm{~kg} \cdot \mathrm{ha}^{-1}$. The lentic waters of this fall-fingerling stocking experiment received an average of $1.6 \mathrm{~kg} \cdot \mathrm{ha}^{-1}$ (i.e., equivalent to 8889 swim-up fry). Rate of increase in juvenile salmon biomass from lacustrine
habitat remained relatively stable over the duration of the study for the fall-fingerling release strategy (Pepper et al. 1992), suggesting that the average annual biomass of $1.6 \mathrm{~kg} \cdot \mathrm{ha}^{-1}$ of fallfingerling salmon released to natural lacustrine habitat did not exceed habitat carrying capacity. This suggests the biobaseline survey interpretation of potential stocking density (i.e., 10000 swim-up fry•ha- ${ }^{-1}$ Pepper et al. 1984), likely is within habitat carrying capacity for the standing waters of this Newfoundland experiment. However, we suspect our perception of what constitutes an effective stocking density will be challenged on completion of the smolt emigration series from Gull Pond.

As illustrated in Figure 2, there is considerable vertical (elevation) displacement of stocking locations. Gull Pond is the largest of our study ponds and has a relatively high elevation. We observe that the progression of environmental conditions from spring to summer in the lower part of the watershed, where our incubation facility is located, may be two to three weeks ahead of conditions at Gull Pond. Gull Pond, as the largest of our study locations, typically is the last to reach summer mean temperature. We suspect this may impose a significant constraint on operation of salmon enhancement facilities, especially those oriented to lacustrine stocking with swim-up fry.

These lacustrine stocking experiments were designed to examine smolt yield as a function of stocking sequence (consecutive vs. non-consecutive) and size/time at release (i.e., fry vs. fallfingerlings). Within the constraints identified above, pond morphometrics was not considered an experimental variable. However, present interpretation of preliminary results from Gull Pond suggests that the response variables are confounded by additional factors. Length of growing season may be one such factor. As an artifact of its elevation, the growing season for Gull Pond may be shorter (i.e., later summer and earlier winter) than for our other stocking ponds. This is of significant consequence to a stocking strategy.

Within the present experimental infrastructure, fry supply is limited to a two to three week interval in June. Due to deteriorating weather in the autumn, fall-fingerlings must be released by late October. Considering that September is the month of most rapid growth of parr in our lake cages, we have been reluctant to release parr before the end of this growth period. Relative to the conditions in Gull Pond during both spring and autumn, production characteristics in this pond may be well outside the optimum range. Accordingly, while we have been using a fixed strategy for fry and fingerling stocking, conditions in Gull Pond may warrant an alternative strategy. In a similar context, Upper Micmac Pond has the highest elevation of all of our study sites. It is the last of the study areas from which winter ice cover disappears each year. However, its smaller size and humic waters support rapid warming. We are aware of early plankton proliferation in this pond. In contrast, Gull Pond, with its large size and
transparent water, likely requires a greater interval to reach its maximum summer production. We suspect that early rearing in our lake cages for some four to six weeks may constitute a more effective approach to securing efficient smolt yields from Gull Pond.

Stocking experiments now await significant adult salmon spawning escapements to Black Brook to quantify marine survival of the various smolt age groups. Completion of the lacustrine nurseries sequence requires analysis of Black Brook spawners. In addition, analysis of scale characteristics is expected to quantify differences in early juvenile growth characteristics between lacustrine and riverine origin salmon.

## RESEARCH DEFICIENCIES

To date, we have demonstrated only that lacustrine stocking can work. We do not yet understand the biological basis of lacustrine parr population dynamics and therefore, are not in a position to predict what will happen when such stocking is undertaken in other locations. One very important consideration that is prerequisite to a predictive model of lacustrine stocking potential is the energy dynamics of the particular body of standing water.

## Lacustrine Nursery Production Dynamics

Comparison of the instantaneous rate of change in bulk (R) of year-classes released as swim-up fry, and those released as fallfingerlings, provides some insight into utilization of lacustrine food resources. $R$ values (Table 3) for fry releases have ranged from 1.00 to 1.51 . Fall-fingerling releases have resulted in biomass elaboration ranging from 0.72 to 1.57 but generally have been lower than for fry releases. There are too few data for the fry release strategy and too much variability among ponds to draw definitive conclusions of the relative merits of these two release strategies. It is apparent that food resources of the ponds for which stocking sequences have been completed are well suited to fry releases. Instantaneous growth from release to smoltification is as good for fry as for fall-fingerlings, thereby confirming that lacustrine food resources available to swim-up fry are at least as good as the artificial diets used for rearing in the lake cages. It appears that, at the present stocking density, there is no reason for concern about energy flow to the lower trophic levels that provide food to the early parr stages. Further attention is required to document growth through the later parr stages. A positive correlation between size of fish and size of food item has been well documented in the literature (Ivlev 1961; Kerr 1971; Thorpe and Wankowski 1979; Wankowski and Thorpe 1979). A more detailed food spectrum analysis is required to document prey selection (i.e., species and size of organism consumed) by the size range of parr within our lacustrine study areas.

Interpretation of the ecological significance of these observations requires further consideration of the energy dynamics
of our biomanipulations of lacustrine ecology. The scientific basis of this concern is contained within the cascading trophic interactions of Carpenter et al. (1985). Some limnologists advocate a "bottom-up-control" model of resource limitation for population growth. In this view of production, primary producers are limited by nutrients. An increase in nutrient availability will lead to an increase in primary productivity but will also affect grazers and carnivores. In contrast, other limnologists tend to favour a "top-down-control" notion that highlights the importance of predation (Kerfoot and Sih 1987; Carpenter 1988; Persson et al. 1988). We suspect our manipulations of parr populations have strong repercussions on the biomass, size structure and species composition of lower trophic levels. Strong predator-driven complex interactions can be important in determining benthic community structure (Kerfoot 1987; Carpenter et al 1987). Our interpretation of the $R$ values for fry releases is that fry are exerting predation pressure on the larvae of aquatic invertebrates but that this predation either does not have a significant impact on production of these food items or that the invertebrate populations are responding by increasing their rate of production. We feel this notion warrants further sampling similar to the multispecies research of Tyler (1986).

Confirmation of Suppositions
Biobaseline surveys of lacustrine habitats and Atlantic salmon populations have provided an interpretation of lacustrine morphometric characteristics that are desirable for rearing of juvenile salmon. These suppositions remain largely unchallenged. To document lacustrine nursery potential for development under active salmon enhancement, we have concentrated on ponds that conform with our perceptions of good rearing potential. Having demonstrated that cost-effective enhancement is possible, effort now needs to be applied to determine if our notions about poor rearing potential are appropriate. If we are to achieve this goal, we will have to attempt controlled releases of juvenile salmon to ponds that are judged to present poor rearing opportunities (i.e., large, deep lakes with little littoral area and a well-established population of piscivorous species).

## Predation and Competition

It is likely that benefits from stocking programs will be reduced in ponds containing landlocked salmon. These concerns need to be quantified if the lacustrine stocking strategy is to be advocated as a fishery development tool. As presented above, the present lacustrine experiments were designed to succeed. The biobaseline survey work conducted prior to implementing the stocking project documented use of our pond habitats by American eel and brook trout. All of the ponds of the present study area have significant brook trout populations, in the order of 270 individuals per hectare. Few of these trout are greater than 25 cm (fork length). This is consistent with Ricker's (1932) concept that the size attained by brook trout is positively correlated with the size of the water body in which it lives. The risk of heavy predation was
avoided by stocking ponds with relatively low predator potential. Production of salmon smolts from lacustrine areas with greater predation is likely to be lower than for the present experiment.

Considering the magnitude and apparent stability of $R$ values identified above, there seems to be little obvious evidence of either intra- or interspecific competition, at least during the underyearling interval. However, there may be some evidence of density dependence among older parr. Examination of mean size of different smolt age groups produced from the same year-class (Fig. 3) confirms that the largest smolts were produced consistently from the last of the three year-classes released to a stocking cycle. It is apparent that, as smolt leave the ponds, those parr that are left will have greater access to food resources remaining in the ponds. The generally larger size of smolts from later year-classes suggests that these fish have had access either to a greater food supply or to a better food supply. In consecutive annual releases during a three year stocking sequence, the numbers of juveniles in the pond increase throughout the first three years of release and then decline sharply in the fourth year (i.e., the first year after the stocking regime and the first of the age 3 smolt runs). The numbers of juvenile salmon left in the pond after the third year of stocking would be reduced (Table 6) to $30 \%$, $12 \%$, and $3 \%$ of the maximum juvenile salmon density (i.e., numbers) over the next three years before the last of the smolt emigrated from the pond. Clearly, juveniles of the last year-class stocked will have lower intraspecific competition to contend with in their foraging activity. While this conforms with general notions of density dependence, we can not rule out some form of "top-down" stimulation of rate of prey production in response to salmon parr predation pressure.

## Indian Brook Spawning Escapement

Indian Brook spawning escapement now consists of two groups of salmon, one destined to return to the Black Brook incubation facility, the other destined to remain in Indian Brook to spawn naturally. The Black Brook incubation facility has been provided with a salmon diversion fence that prevents migration of potential spawners upstream of the incubation site. Accordingly, the project is able to maintain detailed records of spawner numbers, morphometrics and age structure. Although we can subsample the spawning escapement to Indian Brook, we do not have the means to obtain comprehensive data that would be required for a river management program.

The Indian Brook fishway, located somewhat upstream from tidal influence, provides access to spawning escapement for both Black Brook and Indian Brook. Unfortunately, due to erosion of the stream obstruction, spawning escapement to Indian Brook is not obliged to use the fishway to achieve upstream passage. The proportion of the river escapement through the fishway is highly variable from year to year. Present experimental infrastructure allows us to determine spawning escapement to the Black Brook incubation facility.

Subtraction of the number of Black Brook spawners from the Indian Brook count provides an estimate only of the minimum number of spawners in Indian Brook. This is not very useful in monitoring status of the natural stock.

Table 6. Standing Stock of Lacustrine Parr Under Hypothetical Survival Values

Fry Stocking Strategy
SURVIVAL TO

| FRY INPUT | Fall-Fingerling | Age 1+ | Age 2+ | Age 3+ | Age 4+ |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: |
| 66000 | $50 \%$ | $50 \%$ | $50 \%$ | $70 \%$ | $20 \%$ |
| surviving | 33000 | 16500 | 8250 | 5429 | 543 |
| \% smoltifying | $0.0 \%$ | $0.0 \%$ | $6.0 \%$ | $50.0 \%$ | $50.0 \%$ |
| smolts | 0 | 0 | 495 | 2714 | 271 |
| remaining fish | 33000 | 16500 | 7755 | 2714 | 271 |
|  |  |  |  |  |  |
| TOTAL SMOLTS |  | 3481 |  |  |  |
| Survival from fry |  | $5.3 \%$ |  |  |  |
| \% smolt production by smolt age |  | $14.2 \%$ | $78.0 \%$ | $7.8 \%$ |  |


| YEAR | FRY INPUT | NUMBER Age 1 | OF FISH <br> Age 2 | REMAININ Age 3 | g AT Age 4 | TOTAL FISH | \% OF MAXIMUM NUMBER |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 86000 |  |  |  |  | 66000 | 73:13\% |
| 2 | 66000 | 16500 |  |  |  | 82500 | 91.41\% |
| 3 | 66000 | 16500 | 7755 |  |  | 90255 | 100.00\% |
| 4 |  | 16500 | 7755 | 2714 |  | 26969 | 29.88\% |
| 5 |  |  | 7755 | 2714 | 271 | 10741 | 11.90\% |
| 6 |  |  |  | 2714 | 271 | 2986 | 3.31\% |
| 7 |  |  |  |  | 271 | 271 | 0.30\% |

## Black Brook Stock Genetics

The Lacustrine Nursery Experiment has achieved a milestone in potential departure of salmon stock characteristics from those of the historical Indian Brook salmon population. We have documented many significant shifts in "stock" characteristics from those of the historical Indian Brook population. With the possible exception of salmon parr that utilize Indian Pond on the main stem of Indian Brook, juvenile salmon that are released to lacustrine habitats are subjected to very different habitat characteristics from those of the Indian Brook population. This provides a potentially useful and interesting mechanism for documenting divergence in population gene pool in reproductively "isolated" subunits of this salmon stock.

Blood sampling of Indian Brook and Black Brook spawners was undertaken in 1989 for possible application towards analysis of mitochondrial DNA. The technique of mtDNA analysis subsequently has proven inadequate to detect delicate shifts in gene pool structure. Further research work at Memorial University of Newfoundland now is focusing on the Atlantic salmon nuclear genome. This work has considerable potential for application to the river management concept and should receive further support. Additional sampling of Indian Brook and Black Brook spawners should be undertaken at least once every generation so that stored material can be used for genetic analysis once the Atlantic salmon genome has been sufficiently mapped to allow interpretation of the significance of gene sequences.

## SYNOPSIS OF REQUIRED STUDIES

Lacustrine enerqy dynamics.

1. A more detailed food spectrum analysis is required to document prey selection (i.e., species and size of organism consumed) by the size range of parr within our lacustrine study areas. The generally larger size of smolts from later year-classes suggests that these fish have had access either to a greater food supply or to a better food supply. Predation either does not have a significant impact on production of lacustrine food items or the aquatic invertebrate populations are responding by increasing their rate of production. We feel this notion warrants further sampling.
2. We have no knowledge of what happens with parr feeding subsequent to release of fall-fingerlings. Our hypothesis is that, having been reared in a lake cage in which natural food is present, parr will have supplemented their diets with natural food items prior to release. This may help released parr to adapt quickly to natural food.

## Carrying Capacity

3. Having demonstrated that cost-effective enhancement is possible, effort now needs to be applied to determine if our notions about poor rearing potential are appropriate. If we are to achieve this goal, we will have to attempt controlled releases of juvenile salmon to ponds that are judged to present poor rearing opportunities.
4. A tentative stocking density of 1000 fry $\cdot \mathrm{ha}^{-1}$ was adopted for these lacustrine experiments. This density was interpolated from observed standing stock of brook trout in the study areas and from literature on niche partitioning between Atlantic salmon and brook trout. Present results suggest that neither fry nor fall-fingerling releases, each at $1000 \cdot h^{-1}$, have exceeded carrying capacity in our study ponds. On the basis of biomass, fall-fingerling releases have exceeded fry biomass by a factor approaching 10. Some stocking at $10000 \cdot \mathrm{ha}^{-1}$ should be undertaken.
5. An a priori salmon release strategy for lacustrine habitat, based on performance elsewhere, may be inadequate. Consideration of prevailing habitat characteristics and progression of seasonal production is an important prerequisite to maximizing smolt yield. We suspect that early rearing in our lake cages for some four to six weeks may constitute a more effective approach to securing efficient smolt yields from Gull Pond because of a shorter growing season at this location. This aspect of lacustrine research needs considerable refinement.

## Significance of lacustrine ecology to salmon life-history

6. We have not attempted to monitor parr movements for evidence of transience of lacustrine habitation. We have no direct knowledge of parr movements during the summer. The opportunity for varying periods of fluvial residence may be an important component to optimal stocking density for lacustrine habitat.
7. Further sampling of precocious parr by stream electrofishing and marking with fluorescent dye would provide further insight into the significance of previous maturation on the sex and age composition of smolt runs and the survival potential of older/larger smolts.
8. Analysis of scale characteristics is expected to quantify differences in early juvenile growth characteristics between lacustrine and riverine origin salmon. Comparison of early rearing growth characteristics, as determined from smolt scales in comparison to adult scales, may provide evidence of survival advantages of different growth histories.

## Predation

9. It is likely that benefits from stocking programs will be reduced in ponds containing landlocked salmon. These concerns need to be quantified and could be addressed by closely monitored stocking of other watersheds.

## Genetics

10. Additional sampling of Indian Brook and Black Brook spawners should be undertaken at least once every generation so that stored material can be used for genetic analysis once the Atlantic salmon genome has been sufficiently mapped to allow interpretation of the significance of gene sequences.

River manaqement
11. Due to erosion of the stream obstruction of lower Indian Brook, spawning escapement is not obliged to use the fishway to achieve upstream passage. While we can subsample the spawning escapement to Indian Brook, we do not have the means to obtain comprehensive data that would be required for a river management program. Future management of this enhanced river system to maximize economic return on production benefits requires further adult salmon assessment infrastructure.

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# Atlantic Salmon Smolt Production and Corresponding Target Spawning Requirements for Newfoundland River Systems Characterized by Lacustrine Habitat: a Review 

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Atlantic salmon (Salmo salar) target spawning requirements for rivers in Newfoundland are currently calculated on the basis of the relative contribution of fluvial and lacustrine habitats to total production. Depending on the river, lacustrine habitat can account for a substantial proportion of production. The derivation of the interim model used at present and associated parameter values is reviewed and limitations are discussed. The potential impact of new information on egg-to-smolt survival on target egg requirement levels is addressed.

## INTRODUCTION

Anadromous Atlantic salmon (Salmo salar) are typically considered to be stream dwellers (Keenleyside 1962; Gibson 1966; Elson and Tuomi 1975; Symons and Heland 1978). While this applies to the species throughout most of its North American distribution, in insular Newfoundland juvenile salmon also make extensive use of lacustrine habitat for rearing (Pepper 1976; 0'Connell and Reddin 1983; Chadwick and Green 1985; Pepper et al. 1985; O'Connell 1986; Ryan 1986; O'Connell and Ash 1989; O'Connell et al. 1990). It is believed that the low fish species diversity in Newfoundland allows juvenile salmon to occupy a greater variety of habitats in comparison with other regions where Atlantic salmon occur (Gibson et al. 1993).

Within the lacustrine environment, studies have shown that most juvenile salmon were caught within the benthic littoral region including underyearling (0+) parr (O'Connell et al. 1990). However, juvenile salmon were also found in the nonlittoral benthic zone and in the pelagic environment (Table 1 and Fig. 1). Salmon parr caught in the latter habitats were typically older and larger in length than parr caught in littoral areas. Salmon were found in lacustrine areas during all seasons of the year.

Given the propensity for juvenile salmon to use lacustrine areas for rearing, it is inappropriate that these areas be excluded

Table 1. Distribution of Atlantic salmon parr in benthic and pelagic habitats of Junction Pond and Conne Pond, Newfoundland. Benthic zone stratified into littoral (depth 1-3 m for Junction Pond and 1-2 mor Conne pond) and nonlittoral (depth $>2 \mathrm{~m}$ or 3 m , respectively) zones. Pelagic habitat stratified into trophogenic and tropholytic zones according to the same depth partitioning. Data from o'connell et al. (1990)

| Habitat | Junction Pond |  | Conne Pond |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Number | \% | Number | \% |
| Benthic |  |  |  |  |
| Littoral | 301 | 59 | 130 | 72 |
| Nonlittoral | 147 | 29 | 23 | 13 |
| Subtotal | 448 | 88 | 153 | 85 |
| Pelagic |  |  |  |  |
| Trophogenic | 20 | 4 | 17 | 9 |
| Tropholytic | 43 | 8 | 10 | 6 |
| Subtotal | 63 | 12 | 27 | 15 |
| Grand Total | 511 |  | 180 |  |




Figure 1. Distribution of Atlantic salmon parr in benthic and pelagic habitats of Junction Pond and conne Pond, Newfoundland. See caption for Table 1 for further details on lentic zones.
from studies of the productive capacity of fish habitat or, more specifically, in defining juvenile salmon production in Newfoundland. O'Connell and Dempson (1990) have reviewed some approaches to solving this problem and discussed the inherent difficulties associated with it. Similarly, before the status of a salmon stock can be determined, a target spawning requirement has to be defined. The latter must factor in the potential contribution of both fluvial and lacustrine habitats.

The Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) currently accepts the use of 240 eggs/100 $\mathrm{m}^{2}$ of fluvial habitat, and 368 eggs/hectare (ha) of lacustrine habitat in establishing target spawning requirements in the context of conservation levels for Atlantic salmon (CAFSAC 1991). The following reviews the approach taken to establish target spawning requirements that incorporate both fluvial and lacustrine habitat. Current use, as well as limitations to the approach, are also discussed. Initially, estimates of smolt production are derived. From this, target spawning requirements in terms of numbers of eggs or adult fish can be obtained.

## DERIVATION OF SMOLT PRODUCTION PARAMETER VALUES

Figure 2 is a schematic representation of the main elements of the current model, which can be used in conjunction with the text.


Figure 2. Schematic representation of the model currently used to calculate target egg deposition requirements in Newfoundland rivers The values 0.0125 and 0.019 are egg-to-smolt survival rates.

Fundamental to the derivation of smolt production and spawning requirements for lacustrine habitat was the establishment of suitable values for the fluvial environment. O'Connell (1986) and $0^{\prime}$ Connell and Ash (1989) found that North Harbour River (Salmon Fishing Area (SFA) 9) and Bay du Nord River (SFA 11) were capable of producing 3 smolts/unit (a unit $=100 \mathrm{~m}^{2}$ ) of classical parr rearing habitat as defined by Elson (1957). These values were based on complete census of smolts obtained from fish counting fences in rivers characterized almost exclusively by fluvial habitat.

Estimates of smolt production from lacustrine areas in Newfoundland have been obtained using both direct and indirect methods (O'Connell and Dempson 1990). In some studies, estimates were for individual ponds while others pertained to production estimates for the entire river. CAFSAC considered the latter to be more appropriate. O'Connell (1986) and O'Connell and Ash (1989) determined smolt production in terms of lacustrine habitat for Northeast River (Placentia), and Beaver River, a tributary of Southeast River (Placentia). This was done by subtracting the number of smolts attributable to fluvial habitat from the total number of smolts censused. Lacustrine smolt production for Northeast River was 10.1 smolts/ha and for Beaver River it was 10.9 smolts/ha.

Similarly, estimates of smolt production from lacustrine habitat for Conne River (SFA 11) have been obtained by subtracting the estimated theoretical production of smolts from fluvial habitat ( 3 smolt/unit) from the total estimated number of smolts surveyed for the entire river (O'Connell et al. 1991). Details on the methodology used to survey the smolts is provided in Dempson and Stansbury (1991) and Schwarz and Dempson (1993). Point estimates of smolt production from lacustrine habitat ranged from 3.8 to 7.6 smolts/ha but could have varied from 2.8 to 10.4 smolts/ha if lower and upper confidence limits for smolt estimates were considered. CAFSAC currently uses the averaged values for Northeast River, Beaver River and Conne River, 7 smolts/ha, as an interim estimate for wild smolt production from lacustrine habitat. By comparison, Einarsson et al. (1990) had an average of 6.1 (2.1-13.0) smolts/ha from an Icelandic watershed. Two of their lower values, however, were considered to be underestimated because of incomplete smolt enumeration.

As stated above, the use of a fixed value of 3 smolt/unit for fluvial habitat is crucial to the derivation of lacustrine production estimates as currently used in insular Newfoundland. How does the value of 3 smolts/unit compare with other rivers and other regions? A search of the literature would suggest that 3 smolts/unit is certainly not inappropriate for use in Newfoundland. Elson (1957) estimated smolt production, derived from planting underyearlings in the Pollett River, at 6-7 smolts/unit and estimated an average production of 4.7 smolts/unit for the Miramichi River (Elson 1975). In Cove Brook, Maine, Meister (1962) found an average of 3.6 smolts/unit while Jessop (1975), for the

Big Salmon River, had a 6 -year mean production of 3.1 (1.7-4.4) smolts/unit. Gibson and Cote (1982) found a range of 0.5-2.6 smolts/unit at Matamek River, Quebec. In Newfoundland, Chadwick (1981) summarized the following values (in smolts/unit): Little Codroy River - 2.6; Long Harbour River - 7.6; Come by Chance River - 5.4; and Stoney Brook - 1.9. These values by Chadwick (1981) are overestimates since he attributed all production to fluvial habitat without deducting the contribution by lacustrine habitat. Gibson et al. (1987) found smolt production over three years in Highlands River to vary from 2.0-2.6 smolts/unit. In Europe, Gee et al. (1978) reported maximum smolt production at 4.3 (1.9-9.7) smolts/unit for the River Wye. Bagliniere and Champigneulle (1986) reported a density of 3.5 smolts/unit for the Scorff River, France, and Berg (1977) found a value of 2.9 smolts/unit in the Vardnes River.

## TARGET SPAWNING REQUIREMENTS

For those SFAs for which accessible habitat determinations have been made in terms of both fluvial and lacustrine area (SFAs 4, 5, 9, and 10, O'Connell and Dempson 1991a, 1991b), potential smolt production was determined by multiplying the amount of fluvial and lacustrine habitat by the respective production parameter values for each habitat. Target egg deposition requirements were then calculated from smolt production estimates using egg-to-smolt survival rates. For fluvial habitat, a rate of 1.25 \% was used. This value was derived by dividing 3 smolts/unit by 240 eggs/unit; the latter being the target egg deposition rate accepted by CAFSAC for fluvial habitat. For lacustrine habitat, a value of $1.9 \%$ derived for Western Arm Brook (SFA 14) by O'Connell et al. (1991) was used. To date, target spawning requirements in terms of adult fish have been expressed only in terms of small salmon.

To convert the target egg requirements into numbers of fish, information on the biological characteristics of the stock are needed:

$$
\begin{aligned}
& \text { Target no. of } \\
& \text { small salmon }
\end{aligned}=\frac{\text { Target no. of eggs }}{\text { Relative fecundity } \times \bar{x} \text { weight } \times \text { f female }}
$$

Target spawning requirements for SFAs 4, 5, 9, and 10, are summarized in O'Connell and Dempson (1991a, 1991b). Status of selected salmon stocks with counting facilities was reviewed for the period 1984-91 in O'Connell and Dempson (1992). In general, the approach taken to date provides a reasonable target for which to evaluate status of Atlantic stocks and for which managers can introduce measures, where necessary, to ensure targets can be achieved. Had derived targets been unrealistically too low or too high, then the utility of the method could easily be questioned.

## LIMITATIONS AND CONCERNS

The use of fixed parameter values such as 3 smolt/unit of fluvial habitat and 7 smolts/ha of lacustrine habitat to calculate smolt production for all rivers in an SFA has limitations in that there could be inter-river as well as inter-annual variation in such parameters. The same is true for the value of 240 eggs/unit used to calculate the egg-to-smolt survival of 1.25 f for fluvial habitat. The egg-to-smolt survival value of $1.9 \%$, chosen for lacustrine habitat, was calculated for Western Arm Brook (Chadwick et al. 1978). The dominant smolt age for rivers considered in the current review is $3+$ years. With one year less spent in freshwater, egg-tosmolt survival could be higher in these rivers than in Western Arm Brook and hence spawning requirements in terms of lacustrine habitat could be overestimated. The value of $1.25 \%$ for fluvial habitat is similar to one used by Symons (1979) for 3+ smolts with 'medium' survival. Should this value be too high for Newfoundland rivers, then spawning requirements could be underestimated.
o'Connell et al. (1992) have recently reviewed available data on egg-to-smolt survival for three Newfoundland rivers (Northeast Brook (Trepassey), Freshwater River, and Conne River) for which data are currently available for several year classes (Table 2). Based on ten point estimates, survival has varied from 0.28 to $0.79 \%(\bar{X}=0.48 \%)$; well below values currently being used. The impact of revising current target spawning requirements would be substantial.

Table 2. Egg-to-smolt survival values for Northeast Brook (Trepassey), Freshwater River (Cape Race), and Conne River.

| River | Brood Year | Egg-to-smolt Survival (\%) |
| :--- | :---: | :---: |
| Northeast Brook | 1984 | 0.50 |
|  | 1985 | 0.35 |
|  | 1986 | 0.45 |
| Freshwater River | 1987 | 0.46 |
|  | 1985 | 0.69 |
|  | 1986 | 0.79 |
|  | 1987 | 0.28 |
| Conne River | 1988 | 0.30 |
|  | 1986 | 0.50 |
|  | 1987 | 0.46 |

Ideally, stream production should be defined in terms of different types of fluvial habitat. As used here, smolt production was defined in terms of the amount of classical parr rearing habitat available, the relative proportion of which could be quite variable among rivers, thus confounding the estimates. Expressing lacustrine production in terms of total lake surface area, as opposed to production from different lentic habitats, poses similar problems and as well, variability in morphometric parameters affecting production are important considerations (O'Connell and Ash 1989; O'Connell and Dempson 1990).

The calculation of target spawning requirements assumes that the locations of spawning substrate and nursery areas are such that under natural mechanisms of distribution, juveniles will have access to all the specified fluvial and lacustrine habitat. This condition will likely be met to varying degrees on different rivers.

## WHERE DO WE GO FROM HERE?

Analyses of the data collected on the spatial and temporal use of lacustrine habitat is continuing. Relative abundance, based on an index of catch per unit effort, is being compared within and among ponds. Data on food and feeding characteristics are being compiled. Alternate methods to infer relative production of smolts from lacustrine habitat are presently being explored through the use of differences in scale characteristic patterns among fluvial and lacustrine parr. Proximate analyses are also currently being carried out to examine, from an energetic or nutritional state, any differences between fluvial and lacustrine parr that may confer a competitive advantage of one group over another.

There are still many unknowns pertaining to the ecology and production dynamics of juvenile salmon in lacustrine areas. For example, information on the extent and variability of movements within ponds is largely unknown. From our current studies it is known that single-point-in-time sampling can potentially provide misleading information on the distribution and relative abundance of parr in ponds. Additional data are required on the amount of smolts produced from lacustrine systems. In some cases, this information could be readily obtained, and suggestions to this end have been made on numerous occasions in the past. It is noted, that apart from our initial studies on spatial and temporal distributions of parr and the population assessments by Ryan (1986), there have been no directed studies by the salmonid research and assessment group on the lacustrine question. All work currently being carried out is done opportunistically in conjunction with other ongoing work.

## CONCLUSIONS

While there are a number of problems and weaknesses with the current assessment approach, it does provide a practical mechanism for us to manage and conserve our salmon stocks. Ultimately, smolt production parameter values and corresponding target spawning requirements will change. However, parameter values should not be modified haphazardly as incremental values are obtained annually. Only when sufficient information has been obtained to clearly warrant modification should the values be updated. This will avoid frequent changes to requirements and allow for some stability in the assessment and management of our salmon stocks.

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## Workshop Recommendations and Suggestions for Implementation

After the workshop presentations and discussion, participants recommended priorities for research addressing lake use by salmon. They suggested methods of incorporating this research into the existing Salmonid and Habitat Science Division program. Participants felt that the priorities developed could not be ranked due to the interdependence of all aspects of the research. Following are the non-prioritized recommendations with suggestions for their implementation.

1. Develop stock-recruit curves for Newfoundland salmon rivers.

Ideally, a curve should be developed for each river system in order to maximize knowledge about the individual runs. However, within present fiscal constraints, the development of stock-recruit curves for selected indicator river systems was recommended with a comparison of those curves for similarities and differences. Workshop participants considered that several data bases currently being developed (i.e. fence counts of Gander River adults and the census of juveniles in the Experimental Ponds Area, counts of adults and juveniles at Experimental Rivers, Conne River, and Western Arm Brook) would assist in the fulfilment of this goal. Additionally, the continuing education of local improvement groups conducting enhancement projects would contribute to the development of such curves as stocks grow.
2. Select the appropriate parameters for stock-recruit curves (i.e. smolts or smolt indices ?).

Workshop participants felt that, ideally, stock-recruit curves should encompass the full range of life stages possible (i.e. number of eggs related to fry, parr, smolt, and subsequent adults) with well-defined counts of each. However they judged that the acquisition of any subset would be beneficial. Additionally, participants considered that surrogates for those variables (i.e. angler CPUE as a measure of adult abundance) would provide useful insights into stock dynamics, especially in long-term continuing studies. Workshop participants recommended the continuation of long-term studies contributing in this regard (i.e. Gander River Assessments and the Experimental Ponds Area, Experimental Rivers Project, Conne River, and Western Arm Brook).
3. Conduct marking and hydroacoustic experiments to find the extent of salmon movements within lakes and as an aid in the estimation of parr and smolt production.

Participants suggested that continuing marking and recapture experiments in the Experimental Ponds Area would contribute in this regard and that a good potential exists for incorporation of such marking and hydroacoustic experiments in the Northeast River (Placentia) and Indian Brook studies.
4. Determine the timing of salmon movement into lakes, the associated life history characteristics of the lakeward miqrants, and the factors/mechanisms influencing the movement of the salmon into lakes.

Workshop participants considered that the mark-recapture and population age-structure studies in the Experimental Ponds Area contributed substantially in these regards as did continuing population monitoring in the Experimental Rivers Project. Additionally, the marking of stream fishes and subsequent tracking in Northeast River (Placentia) would contribute to the development of knowledge in these areas.
5. Conduct counting fence assessments of lacustrine smolt production.

Participants felt that counting fence assessments of natural smolt production from rivers dominated by lacustrine habitat such as Northeast River (Placentia) and Middle Brook should be initiated in an attempt to more adequately define the lacustrine production value used in the current CAFSAC model. The lacustrine smolt production value is critical to the assessment model but is presently based on very sparse information.
6. Determine the factors affecting the salmonid carrying capacity of Newfoundland lakes and develop an empirical relationship predictive of that capacity.

Participants judged that the continuation of long-term density monitoring studies and associated limnological documentation in Indian Brook, the Experimental Ponds Area, and the Experimental Rivers would contribute to the understanding of factors affecting carrying capacity as will lake fertilization research in the Experimental Ponds Area. However, they felt that the development of an empirical relationship predictive of carrying capacity for Newfoundland lakes would, in the near future, have to be obtained from a combination of studies. Participants suggested that this goal be publicized so that sufficient numbers of studies might contribute data over time and thus enable derivation of such a relationship.
7. Find the impact, if any, of inter and intraspecific competition on lake use by salmon and determine what food is used/preferred by various size classes of salmon in lakes.

Workshop participants agreed that the long-term documentation of species composition in the Experimental Ponds Area and the Experimental Rivers will contribute substantially to our understanding in this regard. Additionally, lake fertilization research in the Experimental Ponds Area will address some important aspects of these questions. Monitoring of the survival of salmon at different stock densities in Indian Brook will also contribute to our knowledge in this area. Workshop participants all understood
that the documentation of food preference and use by salmon in lakes was central to the understanding of lacustrine competition and carrying capacity. Participants felt that the analysis of existing stomach content collections and diet studies at different salmon/trout densities should be carried out.
8. Determine whether and how salmon movement within lakes is influenced by salmon density.

Participants agreed that knowledge of concurrent lake and stream population densities would be essential for the recognition of density influenced lakeward movement. Long-term studies at the Experimental Rivers have the potential to contribute greatly in this area. Additionally, combination of data from adult abundance at the Gander River counting fence with subsequent densities of resultant parr in the Experimental Ponds Area will contribute in this regard.
9. Promote a more effective sharing of resources within the Salmonid and Habitat Sciences Division to better develop an understanding of lake use by salmon.

Participants agreed that a greater interaction among project groups would contribute to a broader understanding of the work requirements and thus promote a more effective use of resources. Interactions could take the form of workshops, site visits, and combination of project groups during extensive work periods (i.e. stripping salmon, counting fence installation etc.).

## Comments from the Chairmen

The above recommendations, although not prioritized, are comprehensive and would require considerable resources if all were to be implemented. It is our view that the initial priority for extension of research on lake use by Atlantic salmon would be investigations of the movements of juvenile salmon into and out of lakes, as well as within-lake movements. This could be accomplished through the operation of fish counting fences concurrent with estimation of parr densities in lake and stream habitats and the application of discrete tags. Such work would allow for testable hypotheses on the factors limiting the salmon parr production and carrying capacity in lakes.

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[^0]:    ${ }^{a}$ Calculated from a total estimated smolt production of 37.3-114.6 smolts . $\mathrm{yr}^{-1}$. $\mathrm{km}^{-2}$ of drainage basin and an estimated 1.3-4.0 smolts . $\mathrm{yr}^{-1}$. $83.6 \mathrm{~m}^{-2}$ of accessible river (stream) area with gravel, boulder, or rubble substrate (Pippy 1982).

