TEMPORAL AND SPATIAL VARIABILITY IN DENSITY, RELATIVE CONDITION, GENDER COMPOSITION AND MATURITY STATUS OF ATLANTIC SALMON (Salmo salar L.) PARR IN THE HARRY'S RIVER DRAINAGE SYSTEM, INSULAR NEWFOUNDLAND

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Temporal and Spatial Variability in Density, Relative Condition, Gender Composition and Maturity Status of Atlantic Salmon (*Salmo salar* L.) Parr in the Harry's River Drainage System, Insular Newfoundland.

by

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A thesis submitted to the
School of Graduate Studies
in partial fulfilment of the
requirements for the degree of
Master of Science

Department of Biology
Memorial University of Newfoundland

December, 1999

St. John's Newfoundland

Abstract

Spatial and temporal variability in population densities and relative (length-specific) condition of Atlantic salmon parr in Harry's River were examined over the period 1987-1997. Apparent differences in growth allometry (slopes from log weight : log forklength regression) among sites and years were attributable to variability in stomach contents of the smaller fish and to sex and maturity status of the largest fish. Pooling of all weight : length data permitted identification of significant differences in relative condition factors (weight : length regression intercepts for specific sites/years) among all sites and years. No significant correlations were found between site-specific relative condition and parr density, food availability or physical habitat factors. The lack of correlation may be due to differences in the scale of the prey measurements versus parr feeding ranges.

A large proportion of males in the tributaries were sexually mature or "precocious" which corresponded with a preponderance of females (71%) in returning anadromous adults. There was a clear trend for increasing percentage male composition in the streams with age and even at age 1+ more than half of the males were precociously mature. The declining proportion of females with increasing age class in the streams suggests that females made greater use of pond habitat than males. Precociously maturing males had higher mean fork lengths and mean weights than immature males at age 1+ but growth rates decreased in the older age classes. The relative length-specific condition of precocious male parr was significantly higher than that of immature male and female parr at ages 1+ and 2+ while relative length-specific condition of 3+ female parr was very close to that of precocious males, indicating increased weight gain for females prior to smoltification.

Discriminant analysis was employed to construct a model that would predict sex and maturity status from the easily measured variables length and weight, and from length-specific condition which is calculated from these two parameters. The model was used to predict group membership for all unknown fish in 1997 to examine the relative distribution of precocious males throughout the watershed. The predictions of sexual maturity status provided by this model suggested that much of the historical variation observed in mean relative condition of parr populations among tributaries of Harry's River could be due to differences among sex and maturity status among sites.There was a positive correlation between predicted % precocity and observed site-specific condition. Those populations comprised of over 40% precocious males were mostly concentrated at sites above George's Lake, while the sites with the lowest (≤ 25.0%) proportion of mature male parr were located mostly in tributaries below George's Lake, suggesting that different life history strategies were being employed in the two regions. Such diversification should enable the population to adapt to a wider range of freshwater and marine habitat variation.

Acknowledgements

I would like to extend my gratitude to my Supervisor, Dr. Roy Knoechel, for his guidance and contributions throughout my research. I sincerely thank Conrad Mullins and the Department of Fisheries and Oceans for giving me the opportunity to begin this project, partial funding to complete it, and for providing me with historical data. I especially appreciate the assistance of DFO employee Don Caines for supervising electrofishing surveys as well as a number of summer students who worked with me in collecting the field data for 1996-1997. I would also like to thank Sean Clancy for assisting me in the lab with the dissection of parr salmon stomachs and with the identification of macroinvertebrates. Thanks are due to Brian Cook for providing me with maps of Harry's River using Geographic Information Systems.

I would like to thank Daniel Kearney, whose continual encouragement and love have been invaluable. Finally, I wish to dedicate this thesis to my mother, Madelyn FitzGerald who instilled in me a will to learn and the courage to try new things, and my late father, Bernard FitzGerald (1926-1996), who would have been beginning his Honour's degree when I was starting my Master's. I share this thesis with them.

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Chapter 1

General Introduction

Harry's River, SFA (Salmon Fishing Area) 13, is one of eight scheduled salmon rivers flowing into Bay St. George on the west coast of Newfoundland. The recreational catch of Atlantic salmon (*Salmo salar* L.) in this region declined from 1973 through 1991, with particularly strong declines since 1985 (Mullins et al., 1997). An assessment of the status of the salmon stock conducted from 1992-1997 indicated that stock had increased since 1992, but remained below required levels for stock conservation (Mullins et al., 1997).

Although considerable attention has been given to the status of the adult salmon population on Harry's River, relatively few studies have been conducted on the ecology of its parr population. A better understanding of how these future spawners are utilizing the river system is important to the evaluation of management strategies that have been implemented in recent years, and to the estimation of future conservation requirements.

The purpose of this study is to examine spatial and temporal variability in population densities and relative condition factors of Atlantic salmon parr in Harry's River. Relationships among these parameters and environmental conditions, habitat variables and food availability are investigated. The occurrence of sexually mature male parr is examined and its impact on the population dynamics of the stock is discussed.

Models that predict sex and maturity status from easily measured variables such as length, weight and length-specific condition are used to investigate spatial variability of these population characteristics and also to estimate the role that variability in sex and maturity may play in producing differences in length-specific condition among sites.

Chapter 2

Temporal and Geographic Variation in Parr Density, Relative Condition Factor, and Macroinvertebrate Abundance

Introduction

In this chapter, the spatial and temporal variability of salmon parr population densities in Harry's River is examined and its potential relationship with habitat variables is explored. The growth allometry of the weight : length relationship of salmon parr among sites is examined in relation to feeding and differences in sex and maturity. A potential relationship between variability in growth allometry and habitat conditions is investigated. Temporal and geographic variation in relative site-specific and length-specific condition of salmon parr is explored and potential relationships with environmental conditions are examined. The abundance of macroinvertebrates is examined at selected sites on the river to determine if there is a correlation between food availability and density or length-specific condition of salmon parr.

Methods

Location and Study Areas

Harry's River is located on the southwest coast of insular Newfoundland and drains into Bay St. George (48° 30' 45" N, 58° 25' 00" W). The river has a total drainage area of 816 km^2 and the watershed includes two major lakes: George's Lake and Pinchgut Lake. A general description of the river is given by Porter et al. (1974). Electrofishing surveys were conducted on tributaries and portions of the main stem of Harry's River in July and August from 1987 - 1989 and from 1992 - 1997 (Figure 2.1 , Table 2.1). A total of 28 sites, at each of which 300 m^2 was electrofished, were surveyed during the 8-year period, although only sites 3, 7, and 12 were surveyed consistently across years.

Salmon Parr Abundance

Salmon parr abundance was estimated using electrofishing removal techniques. Fish were removed from each sample site using a single anode Smith-Root, model VIII-A backpack electrofishing unit. Most sample sites were "closed" by barrier nets and surveyed by successive removal, with abundance estimated by the depletion method (Zippen, 1958) for both total and age - specific density (#/100 m^2). Other "open" sites

Figure 2.1: Sites Electrofished on Harry's River 1987 - 1989, 1992 - 1997.

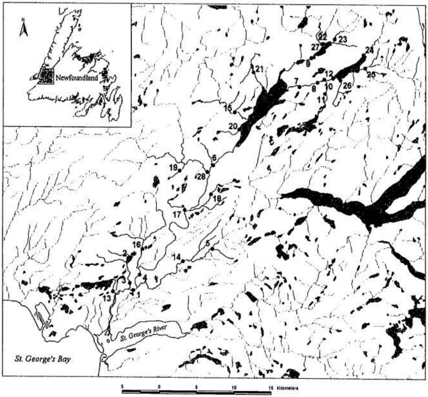


Table 2.1 Locations of electrofishing sites on Harry's River, 1987-1989, 1992-1997.

Site #	Site Name
1	Main Stem Lower
2	Black Duck Upper
3	Black Duck Lower
4	Main Stem Middle
5	Trout Brook A
6	Main Stem Upper
7	Pinchgut Brook A
8	Pinchgut Brook B
9	Stag Lake Brook
10	Pinchgut Brook C
11	Gull Pond Brook
12	Pinchgut Brook D
13	Long Gull Pond Brook
14	Trout Brook B
15	Spruce Brook
16	Crooked Brook
17	Jack Burke's Brook
18	Ahwhachenjeech Brook
19	North Brook A
20	Muskrat Brook
21	Beaver Brook
22	Stag Lake Trib. North A
23	Stag Lake Tributary South
24	Meadow Brook
25	Stag Hills
26	Camp 11 Brook
27	Stag Lake Trib. North B.
28	North Brook B

(no barrier nets) were electrofished for a period of 5 minutes. These catches were used as an index to estimate age-specific and total population density for that site using methods described by Strange et al. (1989) and Chaput and Jones (1992). Bycatch included brook trout (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*) and mummichogs (*Fundulus heteroclitus*) all of which were noted and released .

Growth and Condition

The fork length of parr captured at each site was measured to the nearest 0.1cm and whole weight was determined to the nearest 0.1g. Scale samples were removed from approximately three fish in each 0.5 cm length group for subsequent age and growth analysis. Back-calculated, age-specific lengths and growth rates were estimated for each fish using techniques described by Bagenal (1978). Approximately 2-3 fish from each age class at each site were sampled and preserved on ice for subsequent freezing and laboratory analysis. Lab weights (to the nearest 0.0001g) were determined for fish after removal of gonads and stomach contents. Gonads were weighed separately. All fish were categorized in terms of sex and reproductive status (mature male, immature male, immature female) and then dried to a constant weight in a convection oven at 60°C.

Growth rates were examined by comparing differences in length - specific weight among sites and rate of weight gain with increasing length among sites. This was explored using log weight : log fork length regression analysis. The y-intercepts were used as a measure of length-specific weight, while the slopes provided an indication of rate of weight gain with increasing length and the allometry of the weight : length relationship. Pearson correlation tests and chi-square tests were used to determine if the ranking of slopes of individual sites was consistent across years. All statistical tests were performed using the statistical software package SPSS 7.5 for Windows.

Stepwise multiple linear regression was used to fit a general log weight : log fork length relationship to the complete data base for all sites and all years and to then evaluate the relative condition of parr at individual sites and years relative to the overall relationship. A binary dummy variable (Norusis, 1988) was created for each site and year (e.g. 'Site387' = site 3 in 1987) and data from that site/year were coded as 1 with data from all other sites and years coded as 0 for that variable. Each site was tested in turn as a single additional independent variable in a stepwise multiple regression model:

$$\log \mathrm{Wt} = \mathrm{b}_1 \log \mathrm{Lt} + \mathrm{b}_2\ \mathrm{STYRx} + \mathrm{a}$$

'STYRx' is the site/year dummy variable being tested. When STYRx has a value of zero, $10^{(\mathrm{STYRx} * \mathrm{b2})}$ has a value of 1.0 and thus does not modify the calculated weight. When converted back to linear form, the regression coefficient for the site/year dummy variable (STYRx) gives a quantitative estimate of the length-specific weight of parr for that site and year relative to that of the complete data set:

$$\mathrm{Wt} = (10^{\mathrm{a}}) * \mathrm{L}^{\mathrm{b1}} * 10^{(\mathrm{STYRx} * \mathrm{b2})}$$

This will henceforth be referred to as 'relative site-specific condition'.

The regression equation from regression analyses that incorporated data from all sites and years was used to calculate 'relative length-specific condition' for individual fish as the ratio of the actual weight of the individual to its predicted weight calculated from the general (all data) log weight : log length regression.

Parr Habitat

Site descriptions for each location included such habitat variables as area, mean depth (m), maximum depth (m), habitat type (riffle, run, pool), substrate composition (% rubble, cobble, etc.) and vegetation (% overhang). In addition, air and water temperatures (°C) were recorded as well as water flow velocity (m/s), conductivity (umhos) and salinity (ppm). Principal Component Analysis (PCA) was used to condense these variables into a smaller, more manageable number of composite habitat components (Norusis, 1988). Variations in density and condition were related to habitat characteristics using stepwise multiple regression analysis which was performed using site component scores as independent variables to explain variation in density, regression slopes and condition coefficients.

Macroinvertebrate Abundance

An index of macroinvertebrate abundance was obtained using artificial substrates (rock bags, Clarke et al., 1998). Five rock bags were placed approximately 20 m upstream from electrofishing sites and were left for a period of two weeks during late July to early August. Each bag consisted of approximately 1.5 kg of coarse road gravel contained in plastic bait bag netting with 1.25 cm mesh. Invertebrates that had colonized the rocks inside the mesh bags were removed using a washing - sieving method (Clark et al., 1998) and all organisms were preserved in alcohol for future examinatiön. Rock bags were examined from four sites in 1996 and 1997 : sites 7, 8, 13, and 24. These sites were chosen because they represented a wide range in relative length-specific condition. Organisms were counted and categorized by taxonomic family and, in two cases, by taxonomic order. The most abundant taxa of those present in the stomachs of sampled fish were used for subsequent analysis. These were the Ephemeroptera (mayfly larvae), Trichoptera (caddisfly larvae), and two Dipteran families : Chironomidae (chironomids) and Simulidae (blackfly larvae). The five replicate counts for each group in 1997 were subjected to 1250 randomization trials to generate a distribution of means from which to estimate the standard deviation of the mean. Total counts for each group in 1996 were divided by five to calculate a comparable mean; all five bags were unfortunately combined prior to counting, thus a valid standard deviation could not be estimated.

Spawning Survey

A spawning survey was conducted on Harry's River from November 12-19 in

1996. The survey started at the headwaters of each tributary and covered a total 112.7 km. Survey crews of two walked downstream on both sides of the tributaries recording the distance surveyed, the location and number of redds, and the location of impassible obstructions.

The number of redds attributable to each electrofishing site was determined from sightings recorded on that section of tributary during this survey.

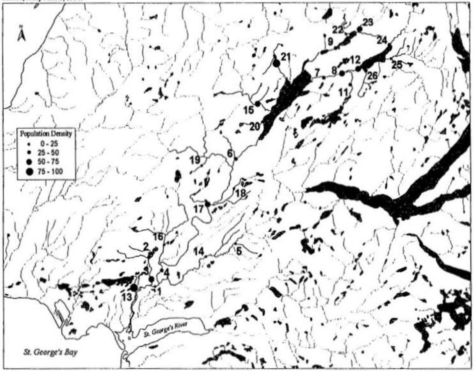
Results and Discussion

The spatial and temporal variability of salmon parr population densities and the potential relationship with habitat variables will be explored in this section. The growth allometry of the weight-length relationship of salmon parr among sites will be examined in relation to feeding and differences in sex and maturity status. Variability in relative site-specific condition as well as length-specific condition of salmon parr will be explored to reveal potential relationships with physical habitat variables. Macroinvertebrate abundance at selected sites in the river will be examined to determine if there is a correlation between food availability and density or length-specific condition of salmon parr.

Parr Density

Parr population densities on Harry's River varied widely among sites in 1996 (Figure 2.2) and displayed a contagious or "patchy" distribution with high variability relative to the mean density (coefficient of dispersion > 1). Long-term data for sites 3, 7, and 12 permit a comparison of parr densities among sites during pre (1987-1989) and post-moratorium (1992-1997) years (Figure 2.3). Young of the year (0+) densities did not vary consistently among sites, suggesting equivalent levels of "seeding" at this early life

Figure 2.2 Total population density (#/100sq.m), juvenile Atlantic salmon, Harry's River, 1996.



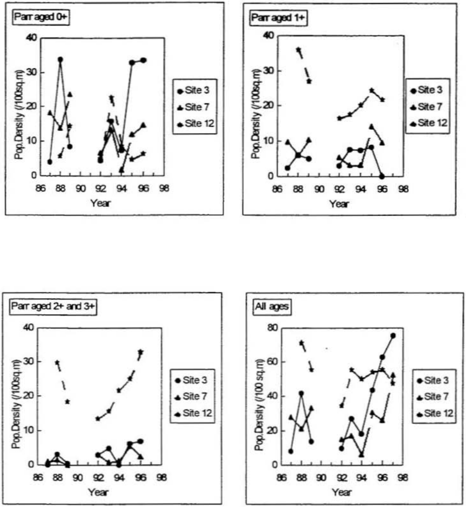


Figure 2.3 Total and age-specific population densities (#/100sq.m) for Atlantic salmon parr. Sites 3, 7, and 12, Harry's River, 1987-1997. Note : Site 12 was not electrofished in 1987.

stage (Figure 2.3, upper left panel). In contrast, parr densities for 1+, 2+ and 3+ age classes were consistently higher at site 12 during pre-moratorium years (1987-1992), suggesting that it was a preferred habitat. The moratorium on commercial salmon fishing instituted in 1992 was expected to result in higher parr densities in subsequent years, starting with age 0+ in 1993. By 1997, total densities at all three sites exceeded those observed in 1992 (Figure 2.3, lower right panel). Total parr densities at sites 3 and 7 approached or exceeded those at site 12 by 1997. Total densities for six of seven "closed" (with the use of barrier nets) sites in 1997 were higher than those observed in 1996 (Figure 2.4), suggesting that the parr populations were still increasing.

Potential relationships between parr density and habitat conditions in 1996 and 1997 were investigated using stepwise multiple regression analysis. Analyses using individual habitat variables revealed no statistically significant relationships between total and age-specific density and habitat data for both years. Gibson (1993) suggested that habitat choice results from a complex of factors which may interact synergistically, and that the importance of one habitat variable such as substrate is dependent on interactions with other habitat variables such as water velocity, depth, light and cover. Stepwise multiple regression analysis using Principal Component scores (used to condense these variables into a smaller, more manageable number of related habitat components) as the independent variables revealed only weak, non-significant relationships with the exception of one age class. There was a negative correlation between principal component 2 (which was characterized by the site description "wide and deep") and

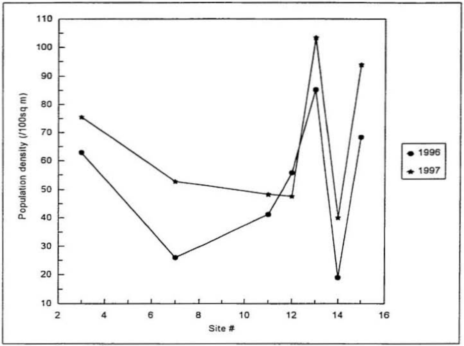


Figure 2.4 Population estimates for 7 'closed' electrofishing sites. Atlantic salmon parr, Harry's River, 1996-1997.

population density of 0+ salmon fry (p-value = 0.006). This would suggest that young-of-the-year salmon prefer those habitats that are narrow and shallow rather than those with wider deep pools. Egglishaw and Shackley (1982) noted that the highest densities of salmon fry were found in stream sections where the proportion of shallow water was the highest and, in a Northern Ireland stream, Kennedy and Strange (1982, 1986) captured more than 75% of salmon fry at sites with mean depths of less than 20cm.

The lack of significant relationships may reflect the fact that sampling sites were not randomly selected; they were chosen on the basis of having "good" parr habitat and thus contained less variability than the entire river system. Sites were initially selected, however, to provide a representative overview of salmonid habitat in the whole system and, as a result, there appeared to be sufficient heterogeneity among sites to reveal any significant relationships between parr density and habitat conditions. A second, more likely possibility is that habitat selection may occur on a finer scale than the spatial scale of the sample sites which consisted of 300 m^2 of stream varying in width from 2.5 m - 22.0. The habitat data collected at each site may have simply represented too broad a range for any significant relationships to be detected. Bult et al. (1999) suggest that parr may select habitats on a much smaller spatial scale than that which is used to record habitat observations and that macrohabitat modelling is likely to explain only a limited portion of variation in parr density.

There was no correlation between the number of redds observed in the tributaries in 1996 and subsequent population density for fry (aged 0+) at those sites in 1997 (Figure

2.5). It is thus evident that sites with high fry density cannot be attributed to their proximity to spawning redds alone. It is likely that high density sites provide favourable conditions for parr aged 0+, which migrate to those locations after emergence from the redd.

Growth Allometry

There were significant differences in the log weight : log fork length regression slopes among sites in 1996 (Figure 2.6) which would suggest that the allometry of the weight-length relationship varied among locations. The differences in slopes would also have an influence on the y-intercepts and complicate interpretations of the "relative condition factor". To test for relationships among the data, slopes were plotted against mean weights, mean fork lengths, y-intercepts, and density for each site. No pattern was found which suggested that there was no significant bias in the slopes due to relationships with these variables. Log weight : log fork length regression was also performed on data collected for all years. Slopes were found to differ significantly among sites in 1987, 1988, 1993, 1994, and 1996 which again suggested that the allometry of weight versus length varied among sites. Differences in weight at length might be related to varying food availability or to environmental conditions among sites.

Relationships between regression slopes and habitat conditions for 1996 and 1997 were investigated using stepwise multiple regression analysis. Analysis using individual

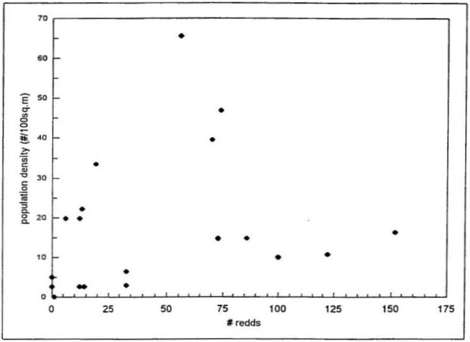


Figure 2.5 Population density of 0+ parr at sites in 1997 vs. number of spawning redds at those locations in 1996. Atlantic salmon parr, Harry's River.

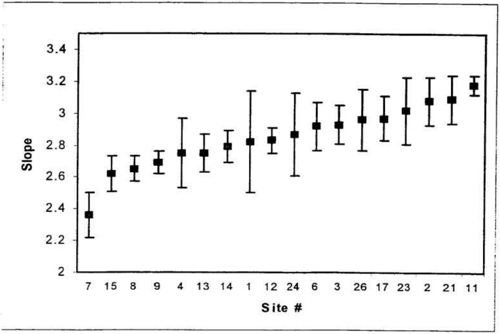


Figure 2.6 Slopes from log field weight : log field fork length regression analysis for Atlantic salmon parr from individual sites, Harry's River, 1996. Bars represent 95% confidence limits. Sites were ranked in order from lowest to highest slope.

habitat variables revealed that there was a significant negative relationship between the width of the stream and the weight - length regression slopes (p-value = 0.03). The addition of flow increased the significance of the model and revealed that water flow velocity had a significant positive effect on the weight-length regression (p-value = 0.02). This analysis suggests that growth conditions are more optimal at those sites on Harry's River which are narrow and/or have high water flow velocity. The addition of the other variables to the analysis did not increase the significance of the model. Analyses using principal component scores revealed only weak, non-significant correlations among the regression slopes and the habitat data (FitzGerald et al., 1998). Furthermore, there was no relationship between the slopes and parr population density. A Spearman rank correlation test indicated that there was no significant correlation between the ranking of the regression slopes for all sites in 1996 versus that in 1997. Similarly, a chi-square test revealed that there was no significant correlation in the ranking of slopes from sites 3,7, and 12 (the only sites with a long data record) for years 1988-1997 (1987 was excluded because site 12 was not electrofished that year); the site with the highest slope one year could have the lowest slope the following year. These observations raised further questions about the biological basis of the apparent variation in the growth allometry among sites.

Scales were analysed to determine if the apparent differences in growth allometry among sites were reflected in the growth patterns of individual fish at those sites. Analysis revealed that growth rates for the year of capture did not differ significantly among sites in 1996 (independent sample t-test). As a result, it could be concluded that the differing growth allometry inferred from the weight - length regression analysis was not supported by scale analysis. Further investigation into the observed variance in the weight - length data was required.

Inspection of log weight : log length field data for the two most divergent sites (sites 7 and 11 in Figure 2.6) revealed that most of the variance was associated with fish less than 6.0 cm fork length (-0.22 on log scale) (Figure 2.7). Removal of stomach contents from the weights of fish collected in 1997 eliminated the differences in weight of small fish among sites. Visual inspection of the stomach contents from fish of the same length but with differing weights from several sites confirmed that the heavier fish had eaten a larger amount of food, compared to the lightest fish whose stomachs contained little more than mucous. Thus the previously observed variation among small fish weights reflected their recent feeding history rather than true differences in growth allometry.

Removal of small fish (< 6.0 cm) from the 1997 field weight : length data left only a few sites with significantly different slopes (Figure 2.8). Plots of log weight vs. log length for the most extreme of these sites revealed that the differences were now due to variation in the weights of the largest fish and were related to differences in sex and maturity status (Figure 2.9). Analysis using all 1997 data for fish > 5.9 cm (all ages) revealed that precocious males were significantly (p-value < 0.001) heavier at length than immature males which, in turn, were significantly heavier than immature females (p-

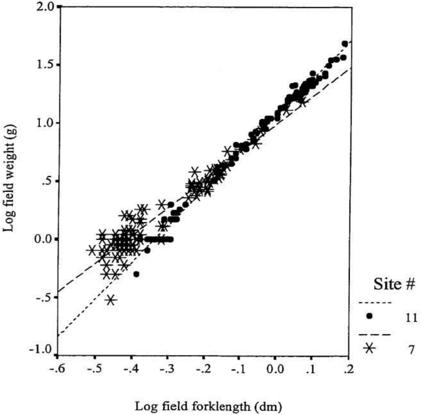


Figure 2.7 Log field weight (g) vs log field fork length (dm) for Sites 7 and 11, Harry's River, 1996.

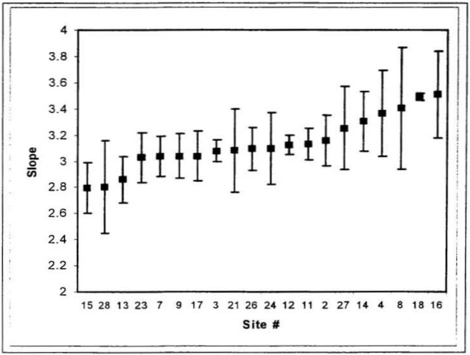


Figure 2.8 Slopes from log field weight : log field fork length regression for Atlantic salmon parr from individual sites, Harry's River, 1997. Fish < 6.0 cm were excluded from the analysis. Sites were ranked in order from lowest to highest slope.

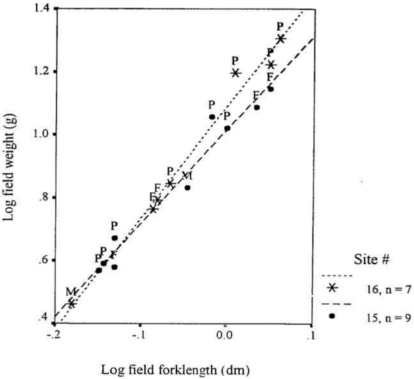


Figure 2.9 Log field weight (g) vs. log field fork length (dm) and sex and maturity status for Atlantic salmon parr from Sites 15 and 16, Harry's River, 1997.
P = Precocious male M = immature Male F = Female

value <0.001). This variation could produce artifactual significant differences in regression slopes in small samples wherein the sex/maturity classes may not be equally represented among sites. It was concluded that a single fundamental allometric relationship could thus be applied to field data from all sites and years once small fish (< 6.0 cm) were removed from the population. This permitted pooling of data for further analysis of relative parr condition.

Relative Site-Specific Parr Condition (regression intercepts for sites/years)

Relative site-specific condition of parr salmon on Harry's River varied significantly among sites and years, ranging from a maximum 15 % above mean condition to a minimum of 40 % below mean condition. Inspection of log weight : log length plots for sites with the most extreme differences in site-specific condition (site 7, 1987 and site 8, 1996; Figure 2.10) revealed a clear separation of weight-at-length between the sites across all lengths (and thus all ages). Such variation might possibly be related to environmental conditions. However, stepwise multiple regression analysis using 1996 condition coefficients as the dependent variable and the habitat factor scores generated by PCA as the independent variables revealed no significant relationships. There was also no significant relationship between relative parr site-specific condition and site population density over all years (Figure 2.11).

The method of habitat sampling used in this study, however, relies on the implicit

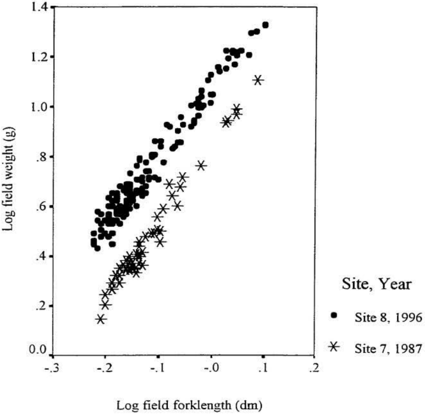


Figure 2.10 Log field weight (g) vs. log field fork length (dm) for Atlantic salmon parr from Site 7, 1987 and Site 8, 1996.

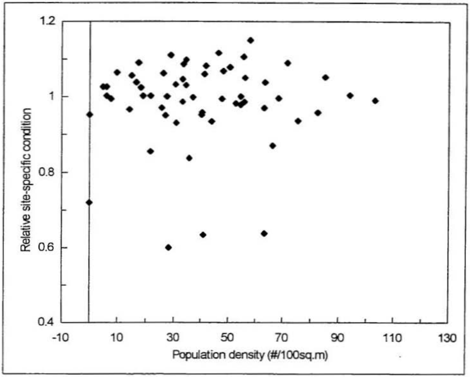


Figure 2.11 Population density (#/100m^2) vs. relative site-specific condition. Atlantic salmon parr, Harry's River, 1987-1997. Note : Pearson correlation coefficient = 0.041, p-value = 0.759.

assumption that there is restricted movement of salmon in the stream and that different stream reaches can be considered independent units. Gowan et al. (1994) suggest that if, as a result of movement, the fish population being modelled is affected by unmeasured habitat conditions in *other* stream reaches, then the habitat models developed from a single reach become less useful. They suggest that researchers should first attempt to determine the extent of fish movement in the study area by sampling many short reaches throughout a system, individually marking fish at the exact location of release, and sampling during different times of the year. In this study, it would have been useful to have applied such methods before attempting to extrapolate the results of potential habitat variation from relatively small sample sites (~300 m^2) to the entire population which exists at a larger scale.

Water discharge levels monitored near Site 12 provide an opportunity to explore potential relationships between discharge and parr condition. The relative site-specific condition of parr at Site 12 was unusually low in 1989 (Figure 2.12), coincident with unusually high water discharge (Figure 2.13) from the week of August 8th through early September (the time period in which the majority of electrofishing was conducted for that year). However, relative condition of parr at site 12 was also low in 1995 when discharge levels were not unusual.

Overall there appears to be little correlation between site-specific condition and mean water discharge for up to 4 weeks prior to sampling (Figure 2.14). This may be misleading, however, in that it is difficult to determine which time period to consider

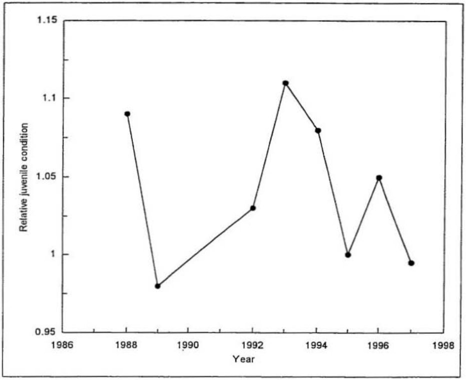


Figure 2.12 Relative site-specific condition of Atlantic salmon parr, Site 12, Harry's River, 1988-1997.

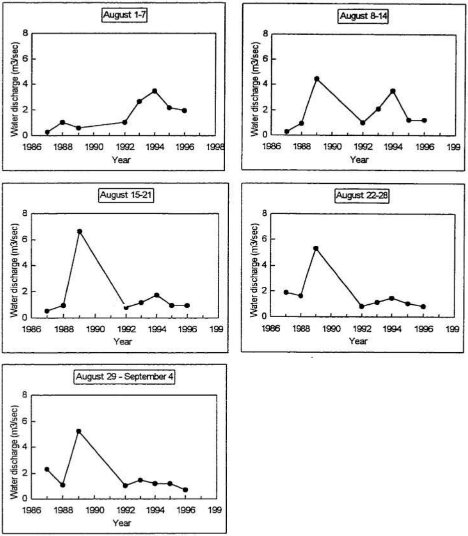


Figure 2.13 Mean weekly water discharge (m^3/sec) at Site 12, Pinchgut Brook, Harry's River, 1987-1997.

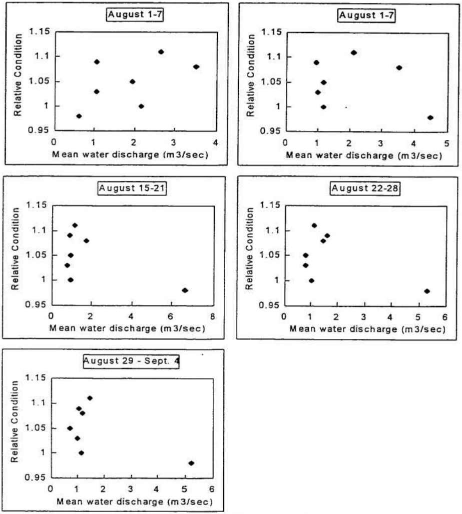


Figure 2.14 Mean weekly water discharge (m^3/sec) vs. relative site-specific condition. Atlantic salmon parr, Pinchgut Brook, Harry's River, 1988-1996. The majority of electrofishing was conducted throughout the last two weeks of August each year.

because it is not known how quickly relative condition of the fish can be affected by unusual water levels. It is also unclear what the mechanisms affecting the fish might be; for example, feeding actually might decline at low water level while energy expenditure might increase at high discharge rates. A temporal series of repeated measurements during a single season might help resolve these questions.

Temporal Variation

The long-term data series for sites 3, 7, and 12 permits a comparison of temporal variation in relative site-specific condition among sites (Figure 2.15). These sites displayed similar temporal trends during the post-moratorium years. For example, from 1994 through 1997, the year-to-year pattern was down, up, down at all sites. This observation is suggestive of broad spatial influences at scales as large as or larger than that of the entire watershed. The observation that site 12 always had fish with a relative condition at or above average (Figure 2.15), despite its relatively high densities (see Figure 2.3), suggests the effects of localized factors such as food supply.

Geographic Variation

There was also evidence for significant within-watershed variation in body condition. The four occurrences of extremely low condition (see Figure 2.11) were all recorded in 1987. These sites (sites 7, 8, 9, and 10) are located in the upper reaches (● symbols, Figure 2.16) of the watershed in the Pinchgut Lake area. Unusually low stream

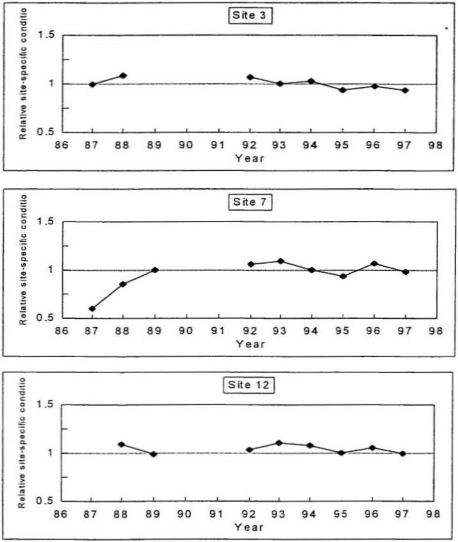
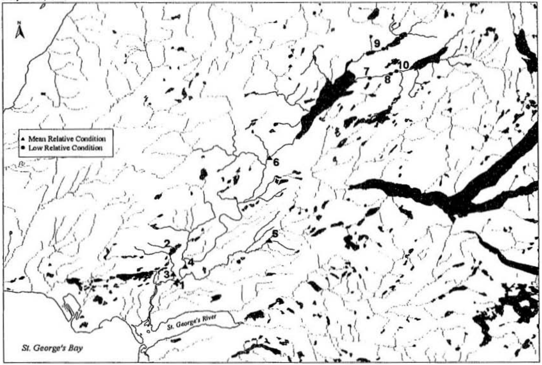


Figure 2.15 Relative site-specific condition of Atlantic salmon parr from Sites 3, 7, and 12, Harry's River, 1987-1997.

Site 2.16 Relative site-specific condition, juvenile Atlantic salmon, Harry's River, 1987.



water levels during the first three weeks of August in 1987 (Figure 2.13) should have affected these headwater sites more than those located further downstream. The fact that fish at all lengths (and consequently ages) displayed unusually low relative condition is suggestive of severe stress. Relative site-specific condition at site 7 rebounded in 1988 and returned to the long-term average in 1989 (see Figure 2.15), indicating that surviving fish had recovered the lost weight, and/or had been replaced by younger cohorts of average relative condition.

Food Availability

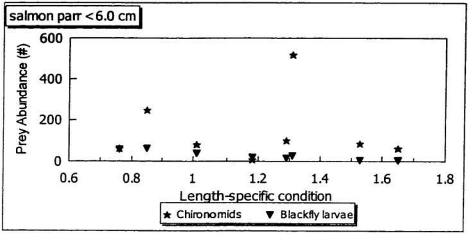
In this section, mean length-specific condition will be examined in relation to the abundance of macroinvertebrates to explore the potential relationship with food supply. Examination of the stomach contents of small fish (<6.0cm) revealed that their diet consisted mainly of small prey items, primarily chironomids and blackfly larvae, while the larger fish ate larger prey, primarily caddisfly and mayfly larvae. Those sites with higher length-specific condition would be hypothesized to have a greater abundance of invertebrates of the appropriate prey. Four sites (sites 7, 8, 13, and 24) that exhibited relatively large changes in length-specific condition over the 1996-1997 period were selected for analysis.

There appears to be no overall relationship between relative length-specific condition of small fish (<6.0cm) and small prey (chironomids and blackfly larvae), or between large prey (mayfly and caddisfly larvae) and the length-specific condition of the larger fish (Figure 2.17). This indicates that relative conditions of parr salmon at these sites do not vary consistently relative to the abundance of important prey items. It is possible, however, that relationships could vary among sites due to other variables such as stream size, average water velocity, etc. Analysis of temporal variability in mean length-specific condition at individual sites should help minimize this source of variation.

Relative condition of small fish from Site 13 decreased from 30% above mean condition in 1996 to 15% below mean condition in 1997 (Table 2.2), coincident with a significant decrease in chironomids (as evidenced by the lack of overlap between the 1997 confidence interval and the 1996 mean) (Figure 2.18).There was also a small decline in the relative condition of the large fish, coincident with a large decline in the abundance of caddisfly larvae.

The length-specific condition of small fish at Site 24 increased from 1996-1997 (Table 2.2), consistent with a large increase in chironomid abundance, however large fish length-specific condition declined over the same period despite a significant increase in mayfly larvae and a smaller, non-significant increase in caddisflies.

Relative length-specific condition of all fish at Site 7 decreased from 1996 to 1997 (Table 2.2). Contrary to expectation, there was an increase in abundance for all four invertebrate prey groups at Site 7 from 1996 to 1997 (Figure 2.17), although only the increases in mayflies and blackflies were statistically significant . Relative length-specific



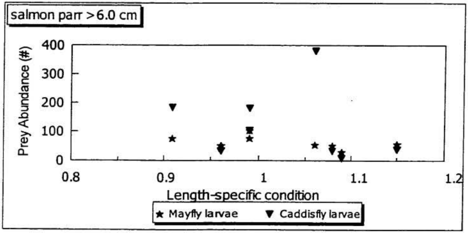


Figure 2.17 Relative length-specific condition of small (<6.0cm) and large (>6.0cm) Atlantic salmon parr vs. macroinvertebrate abundance, Harry's River, 1996-1997.

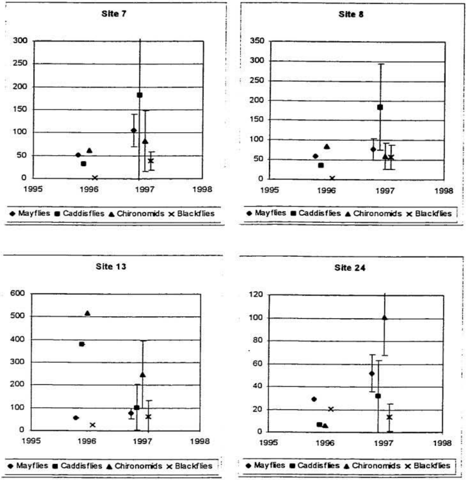


Figure 2.18 Macroinvertebrate abundance at four selected sites on Harry's River, 1996-1997. Bars represent 95% confidence intervals.

Table 2.2 Relative length-specific condition of small (<6.0cm) and large Atlantic salmon parr, sites 7, 8, 13, and 24, Harry's River, 1996-1997.

SITE 7	**1996**	**1997**
Small fish condition	1.655	1.006
Large fish condition	1.076	0.991

SITE 8	**1996**	**1997**
Small fish condition	1.529	0.758
Large fish condition	1.153	0.905

SITE 13	**1996**	**1997**
Small fish condition	1.307	0.849
Large fish condition	1.06	0.999

SITE 24	**1996**	**1997**
Small fish condition	1.183	1.286
Large fish condition	1.093	0.964

condition of both small and large fish at site 8 also decreased from 1996 to 1997 (Table 2.2), even though there was a significant increase in caddisflies and blackflies at this site from 1996-1997, while the other two prey categories were not significantly different (Figure 2.17).

Single-site contrasts across years are thus contrary to the expected positive relationship between prey abundance and length specific fish condition in 5 of 8 comparisons. This suggests either that variability in fish condition is primarily attributable to factors other than prey abundance such as sex composition and maturity status (see Chapter 4) or that the prey abundance measures chosen were insufficient to demonstrate the relationship. Prey abundance was estimated from five rock bags set across the stream upstream from the electrofishing site and retrieved in August, while August parr condition reflects the integration of feeding history and habitat variables over a broader spatial / temporal scale. Fish condition might be affected by previous insect emergences not reflected in the August invertebrate community sampled by the rock bags. A method of invertebrate collection more representative of available prey abundance would be to place the rock bags at more than one transect throughout the sampling reach, and to set and collect them during different seasons of the year. In addition, more sites should be included for analysis to better represent variability in fish condition among years and among sites throughout the watershed.

Chapter 3

Gender Ratio and Maturation Status of Stream-Dwelling Atlantic Salmon Parr and Their Ecological Implications

Introduction

Sex ratio and sexual maturity

In the Atlantic salmon life cycle, alevins emerge from the spawning redd, spend 1-5 years in the freshwater river environment, then smoltify and emigrate to sea where they mature after 1-4 years. They then return to the freshwater environment from which they emigrated to spawn as adults. Insular Newfoundland populations differ from this pattern in two respects. Firstly, parr make extensive use of lake habitat (Hutchings, 1986; Ryan, 1986; O'Connell and Ash, 1993; O'Connell and Dempson, 1995) and secondly, the sex ratio of returning adults is strongly biased in favour of females. The objective of this chapter is to examine the sex ratios and maturation status of Atlantic salmon parr salmon in the lotic environment to determine how the Harry's River population compares with the life cycle reported for salmon elsewhere in its range. The implications of these differences are also explored.

If all parr followed the life pattern described above, the sex ratio of returning adults should be 1 : 1, assuming no sex-biased mortality. Adult returns to insular Newfoundland rivers are in fact highly biased in favour of females. For example, adult returns on Harry's River have been predominantly female over the last two decades, with a mean of 71% female from 1992-1997 (Mullins et al., 1997). It is well documented that a variable proportion of males mature as parr in freshwater without ever having been to sea (Jones, 1959), while other mature males smoltify and emigrate, and yet others remature as residents (Leyzerovich, 1973).

The spawning population of Atlantic salmon is thus composed of returning anadromous adults (male and female) as well as sexually mature or "precocious" male parr (Jones, 1959; Leyzerovich, 1972; Sutterlin et al., 1978; Dalley et al., 1983; Moran et al., 1996). Precociously mature males occur both in nature and in hatchery-reared stocks and are capable of fertilizing adult salmon eggs (Jones and King, 1952). These precocious male parr have acquired the name "sneakers" because of their behaviour on the spawning grounds. They approach a spawning pair when the female is shedding eggs and fertilize a proportion of them in the process. Myers and Hutchings (1987) showed that precocious males can stimulate females to spawn in the absence of anadromous males and Hutchings and Myers (1988) showed that Atlantic salmon precocious male parr were able to mate with adult females.

Although the incidence of sexual maturation of male Atlantic salmon parr varies among stocks of Atlantic salmon (Dalley, 1983), it is a common phenomenon which occurs over the geographic range of the species (Jones, 1959; Leyzerovich, 1972;

Sutterlin et al., 1978; Dalley et al., 1983; Moran et al., 1996). In some Atlantic salmon populations, as high as 80% of male parr can reach maturity during the first and second year of life (Myers, 1984; Myers et al. 1986). Dalley et al. (1983) found precocious male parr in all areas sampled in insular Newfoundland, although the percent occurrence was variable depending on age and location, ranging from 12.3% to 100%.

Fishery effects

Myers (1983) suggested that changes in the proportion of precociously maturing male parr can have an effect on the yield of a fishery and that human-induced changes in this proportion can result from an evolutionary response to fishing pressure. Population size estimates or projections based solely on the biological characteristics of returning adult salmon do not take into consideration the spawning capabilities of these sexually mature male parr which contribute to the reproductive population size (Myers, 1983). From a management perspective, it is necessary to take into account this contribution in order to implement the most productive conservation strategies.

Methods

Parr from each of 28 sites on Harry's River sampled by electrofishing during the month of August (see Chapter 2, Table 2.1, and Figure 2.1) in 1997 were measured for fork length (to the nearest 0.1cm) and whole weight (to the nearest 0.1g) Approximately 2-3 fish from each age class at each site were randomly sampled and frozen. All fish were examined internally in the laboratory and categorized in terms of sex and reproductive status (mature males, immature males and immature females).

Sex and reproductive status were then related to differences in fork length, whole weight, and relative length-specific condition (one-way Anova with a Student-Newman-Keuls multiple range test). The regression equation from regression analysis using length and weight data from all sites and years was used to calculate 'relative length-specific condition' for individual fish as the ratio of the actual weight of the individual to its predicted weight calculated from the general (all data) log weight : log length regression. All statistical tests were performed using the statistical software package SPSS 7.5 for Windows.

Results and Discussion

Sex ratio and maturation status of stream parr

The majority of the sampled parr in Harry's River were males and a majority of the males were precocious (Tables 3.1 and 3.2). This indicates that most of the males remaining in the streams mature precociously rather than migrating to sea as smolts and suggests that females are disproportionately entering pond environments to continue their growth prior to smoltification. The percentage female population composition declined from 42.9% at age 1+ to 14.3% at age 3+ (Tables 3.2 and Figure 3.1). There is a clear trend for increasing percentage male composition in the streams with age (from 57.1% at age 1+ to 85.7% at age 3+) and even at age 1+ more than half of the males were precociously mature (Table 3.2). Although it has been reported that Atlantic salmon may deviate from a 1:1 sex ratio at various life stages, it is generally accepted that there is a 1:1 ratio at hatching (Osterdahl, 1969). The percentage female composition for age 1+ is within 2 standard deviations of 50% (Table 3.2) which agrees with the assumption of 1:1 male : female young of the year production. The percentage female composition for 2+ and 3+ parr, however, is significantly less than 50% which indicates a skewed sex ratio in favour of males. Dalley et al. (1983) found that in almost

Table 3.1 Age-specific sex and state of sexual maturity of sampled Atlantic salmon parr, Harry's River, 1997.

Age	**# immature females**	**# immature males**	**# precocious males**	**#indeterminate**
1+	36	19	29	4
2+	16	5	35	
3+	2	3	9	
Total	54	27	73	4

Table 3.2 Age-specific sex composition (%) and state of sexual maturity of sampled Atlantic salmon parr, Harry's River, 1997. The four fish whose sex could not be determined were not included in the percent composition analysis.

Age	% female	std. dev. (%)	% male	% males that are precocious	std. dev. (%)	N
1+	42.9	5.4	57.1	60.0	7.1	84
2+	28.6	6.0	71.4	88.0	5.1	56
3+	14.3	9.4	85.7	75.0	12.6	14
Total						154

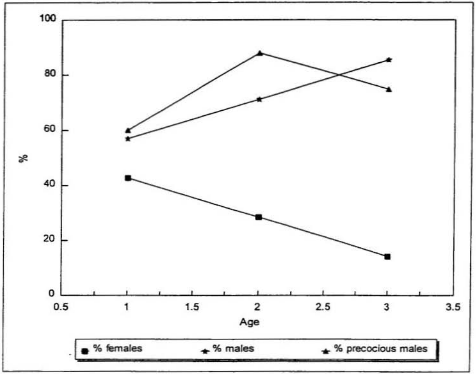


Figure 3.1 Age-specific sex composition of sampled Atlantic salmon parr, and % of males which were precociously mature, Harry's River, 1997

all cases, sex ratios of parr in various Newfoundland streams deviated significantly from 1:1 in favour of males, as is the case in Harry's River. Hutchings (1986) found that parr undertook lakeward migrations in an eastern Newfoundland River (Wings Brook system) where he found that they largely remained in the lakes where the males matured as parr and the females smoltified before going to sea.

Lake use by salmon parr

Atlantic salmon parr are considered mainly to be a riverine species, although it is well documented that a portion of their juvenile life in insular Newfoundland can be spent in lacustrine habitats (Hutchings, 1986, Ryan, 1986, O'Connell and Ash, 1993). In Newfoundland, parr salmon make widespread use of lacustrine habitat for rearing and lake habitat can account for a substantial proportion of total production in river systems with extensive pond environments (O'Connell and Dempson, 1995).

It has been suggested that lakes provide conditions for increased parr growth and survival to the smolt stage relative to the riverine environment and provide important overwintering habitat (Hutchings, 1986). There is evidence that the majority of smolt production occurs in lacustrine habitat in at least two Newfoundland river systems (Chadwick and Green, 1985; Hutchings, 1986). Studies have shown that increased growth early in the life stages of salmon parr is correlated with precocious sexual maturity (Dalley et al. 1983; Simpson 1992; Bailey et al., 1980; Saunders et al., 1982). It has been hypothesized that lakes may provide the necessary conditions for higher growth and may thus play a role in the occurrence of precociously mature individuals in salmon populations.

Hutchings (1986) suggested that lakeward movements had an adaptive basis and could be explained as an evolutionarily stable reproductive tactic. He suggested that if size is positively correlated with fitness, a proportion of the parr population could be expected to adopt behaviours that would enhance growth and thus survival. Because the lakes provide conditions for increased growth, parr would emigrate from streams to reduce size-specific mortality and increase growth. Thus movements into the lakes, rather than maintaining residency in lotic habitat, could represent one part of an alternative reproductive tactic (Hutchings, 1986).

Costs and Benefits

The net effect of male precocity on reproductive success is the sum of benefits such as earlier age of maturity and avoidance of marine mortality as well as costs which might include faster consumption of energy reserves and fewer sperm to fertilize eggs due to lower body mass at maturity. The cost of sexual maturation in males also includes a higher mortality rate than for immature male parr (Myers, 1984). In natural environments the risk of damage to the precocious parr during spawning is an additional hazard (Saegrov and Urdal, 1993); when more than one adult male is interested in the same female, these adult males may chase parr swimming in the vicinity of the female (Hutchings and Myers, 1987). Maturation also consumes energy reserves in the form of fat which may reduce the ability to survive stress.

Leyzerovich (1973) and Hansen et al. (1989) found that sexual maturation of salmon parr reduces the probability of a future seaward migration. It was suggested that a portion of mature males do actually smoltify and emigrate, while the remainder remature as residents. The benefits of emigration to the sea would be improved feeding opportunities, increased body size and therefore increased fecundity, and supposed increased mating success. However, if the chance of mortality is increased at sea or during emigration, the benefit of migration would obviously be reduced.

It has been suggested that the proportion of mature male parr should increase in those populations that experience high mortality at sea (Gibson, 1978). Intense fishing pressure may contribute to high levels of precocity by favouring those genotypes that mature in freshwater, and therefore avoid mortality at sea (Myers. 1983). Myers et al. (1986) found no evidence, however, to support this evolutionary theory in their analyses of data on the Matamek and Little Codroy River salmon populations.

If the sex ratio at hatching was 1 : 1, the observed 71% returning female adults to Harry's River from 1992-1997 (Mullins et al., 1997) would require a smolt sex ratio of 1 : 0.4 (females : males) which would in turn imply that 60% of the males mature precociously and do not emigrate to sea. The stream data for age 2+ and 3+ males presented here indicate that 85% of the males matured precociously and stayed in the river. This should produce a smolt sex composition that is 85% female. The stream data thus predict a higher adult % female return than actually observed. This could be reconciled either by higher female mortality at sea, by some smoltification and subsequent return to sea of precocious male parr, or by a disproportionate number of immature males utilizing lake habitat prior to smoltification and thus not being represented in the stream samples. Unfortunately there are no data for lake habitat parr in the Harry's River system.

Adult salmon

The adult salmon runs returning to Harry's River are characterized by a high proportion of grilse (fish < 63.0 cm) (Mullins et al., 1997) and a sex ratio highly biased in favour of females. Adult returns on Harry's River from 1992-1997 were comprised of a mean of 95% grilse of which 71% were female (Mullins et al., 1997).

It has been suggested that high proportions of precocious males in a salmon population can result in a decrease in those males that smoltify and go to sea. In Harry's River, a large proportion of males in the tributaries were precocious (Table 3.2) which suggests that only a small proportion of precocious male salmon parr actually smoltified upon reaching the stage of potential smoltification.

Marine survival rates on the Conne River (south coast of the island) decreased from a high of ~10% in 1988 to a low of ~2.5% in 1994 (Dempson and Furey, 1997).

Smolt survival in Western Arm Brook (Northern Peninsula) decreased from 6.8% in 1971 to a low of 2.1% in 1987 and then increased to 8.1% in 1996 during the commercial fishing moratorium (Mullins et al., 1998). However, there is no information regarding the proportion of sexually mature parr on these rivers.

There are other factors which may potentially affect the proportion of precocious males in the river and the number which survive to smoltify and return to Harry's River. Such factors as food availability, environmental conditions, and habitat quality can influence growth (length and weight) and condition (weight at length) and, as a result, sexual maturation.

Length, weight, and sexual maturation

Previous studies suggest that precocious males can be distinguished by above-average weight and length in 1+ fish but that differences disappear at older ages. In this section the ability to distinguish precocious males from immature males and females on the basis of length, weight and relative condition factor, as determined from length-specific weight analysis, is examined.

Length

Comparisons of mean length at age support the conclusion that precociously maturing males have higher mean fork lengths than immature males at age 1+ but that growth rates tend to decrease in the older age classes.

A one-way Anova with a Student-Newman-Keuls multiple range test determined that there was no significant difference in mean field fork lengths among the three groups of parr (immature female, immature male, sexually mature male) at ages 3+ and 2+ ($p = 0.506$ and 0.093 respectively) (Table 3.3 and Figure 3.2). However, age 1+ females and precocious males had significantly higher mean fork lengths than immature 1+ males ($p = 0.034$). An independent sample t-test revealed that precocious males had significantly longer fork lengths than immature males in this age group ($p < 0.001$). Mean lengths of males that matured at age 1+ ranged from 6.7 to 9.7 cm and the smallest precocious parr taken from any of the sites was 6.5 cm (not aged) (Table 3.4). These results are consistent with observations by Dalley et al. (1983) in various rivers in insular Newfoundland who reported that mean lengths of precocious 1+ males were greater than those of immature males in all samples but that there were no such trends for older age groups.The fact that precocious parr are longer at age 1+ but not at ages 2+ and 3+ indicates that growth rates of sexually mature males decline relative to immature males. As a result, length alone cannot be used as a discriminating factor between mature and immature parr after the age of 1+. Leyzerovich (1973) also found that the mean growth rate (length increment) of hatchery reared mature male parr during maturation is greater than the mean growth rate of immature individuals, in the first year of life and the beginning of the second year. Bailey et al. (1980) found that larger parr within an age group would mature earlier and Saunders et al. (1982) found that faster growing individuals tend to mature early. Daley et al. (1983) however, found that age-specific

Table 3.3 One-way Anova results with Student-Newman-Keuls (S-N-K) multiple range test for differences in mean fork lengths (cm) among sex categories of Atlantic salmon parr, Harry's River, 1997.

AGE 1+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between groups	7.238	2	3.619	3.520	0.034
Within Groups	83.280	81	1.028		
Total	90.518	83			

S-N-K	N	Mean Fork length
Precocious Males	29	7.9379
Immature Males	21	**7.2048**
Immature Females	34	7.8147
Sig.		<0.001

AGE 2+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	6.564	2	3.282	2.482	0.093
Within Groups	70.082	53	1.322		
Total	76.646	55			

S-N-K	N	Mean Fork length
Precocious Males	35	10.5971
Immature Males	5	10.56
Immature Females	16	11.35
Sig.		0.272

Table 3.3 (continued)

Age 3+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	1.567	2	0.784	0.724	0.506
Within Groups	11.902	11	1.082		
Total	13.469	13			

S-N-K	N	Mean Fork length
Precocious Males	9	13.2556
Immature Males	3	12.6
Immature Females	2	12.5
Sig.		0.642

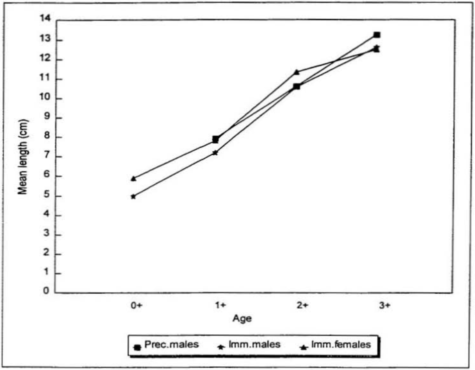


Figure 3.2 Mean length (cm) at age for sexually mature and immature Atlantic salmon parr, Harry's River, 1997.

Table 3.4 Descriptive statistics of fork length (cm) from Atlantic salmon parr populations categorized in terms of age-specific sexual maturity, Harry's River, 1997.

Age	Sex	N	Mean	St.dev.	Min.	Max.
0+	Precocious Males	0	N/A	N/A	N/A	N/A
	Immature Males	3	4.9667	0.6351	4.6	5.7
	Immature Females	2	5.9000	0.4243	5.6	6.2
1+	Precocious Males	29	7.9379	0.8662	6.70	9.70
	Immature Males	21	7.2048	0.847	5.70	8.8
	Immature Females	34	7.8147	1.2051	6.20	12.0
2+	Precocious Males	35	10.5971	1.2087	8.70	13.50
	Immature Males	5	10.56	1.5502	9.0	13.10
	Immature Females	16	11.35	0.8485	10.0	12.70
3+	Precocious Males	9	13.2556	1.0737	11.0	14.0
	Immature Males	3	12.6	1.044	11.90	13.80
	Immature Females	2	12.5	0.7071	12.0	13.0

lengths of parr salmon populations in Newfoundland did not consistently correspond with high percentages of sexually mature parr and suggested that other factors were necessary for maturation.

Several studies suggest that environmental cues can influence the "decision" to mature. Evidence from field studies suggest that rate of increase in fork length during the first year of life is positively correlated with the proportion of males maturing at age 1+ (Myers et al., 1986). Berglund (1991) suggested that both the size at age 1, resulting from the growth rate during the first summer (age 0+), and the opportunity for growth during the period preceding the onset of gonadal growth affect the incidence of maturation in male parr of age 1+. Bailey et al. (1980) and Saunders et al. (1982) found that the "decision" of the individual parr whether to mature or not was made some weeks or months before observable growth of the testes and that the individual fish had to "make" this decision in response to environmental cues. It has been suggested that favourable growth conditions prior to maturation of the gonads increases the incidence of parr maturation (Saunders et al., 1982). The quality of growth at this time may be affected by many different factors, such as temperature, food supply and habitat quality. It would be valuable to further investigate this issue.

Weight

Comparisons of mean weight-at-age support the conclusion that precociously maturing males have higher mean weights than immature males at age 1+ and that growth rates tend to decrease in the older age classes. A one-way Anova with a Student-Newman-Keuls multiple range test determined that there was no significant difference in mean field weights among the three groups of sexed parr at age 3+ and 2+ ($p = 0.224$ and 0.720 respectively) (Figure 3.3 and Table 3.5). However, precocious males and immature females had significantly higher field weights than immature males at age 1+ ($p = 0.01$) (Table 3.5). An independent sample t-test revealed that precocious males had significantly higher mean weights than immature males at this age ($p = 0.005$). Weights of males that matured at age 1+ ranged from 3.1 to 11.6 g (Table 3.6).

Relative length-specific parr condition

Relative length-specific condition factor varied more consistently among the sex and maturity groups. The relative length-specific condition of precocious male parr was significantly higher than that of immature male and female parr at ages 1+ and 2+ (there were no 0+ precocious males in the sample). The relative length-specific condition of 3+ female parr was very close to that of precocious males indicating increased weight gain prior to smoltification; most 3+ females would smoltify and leave the river the following spring. An independent sample t-test revealed that there were significant differences in length-specific condition between the precocious parr and the immatures (both sexes) ($p<0.001$) as well as significant differences in condition across all age classes between mature and immature males. Relative condition in precocious male parr ranged from 0.8912 to 1.2990 across all age groups (Table 3.7 and Figure 3.4).

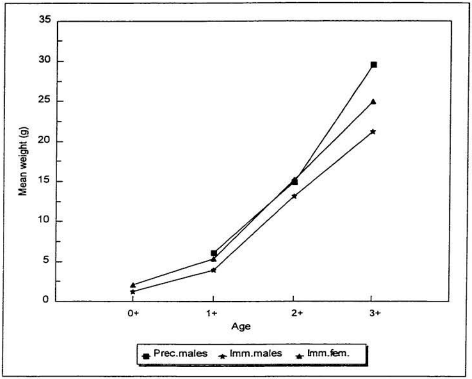


Figure 3.3 Mean weight (g) at age for sexually mature and immature Atlantic salmon parr, Harry's River, 1997.

Table 3.5 One-way ANOVA results with Student-Newman-Keuls multiple range test for differences in mean whole weights (g) among sex categories of Atlantic salmon parr, Harry's River, 1997.

AGE 1+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between groups	53.491	2	26.745	4.849	0.010
Within Groups	446.759	81	5.516		
Total	500.250	83			

S-N-K	N	Mean Weight
Precocious Males	29	6.0276
Immature Males	21	**3.9429**
Immature Females	34	5.3176
Sig.		<0.001

AGE 2+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	16.982	2	8.491	0.330	0.720
Within Groups	1363.406	53	25.725		
Total	1380.388	55			

S-N-K	N	Mean Weight
Precocious Males	35	14.8771
Immature Males	5	13.10
Immature Females	16	15.1813
Sig.		0.623

Table 3.5 (continued)

Age 3+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	166.194	2	83.097	1.719	0.224
Within Groups	531.701	11	48.336		
Total	697.894	13			

S-N-K	N	Mean Weight
Precocious Males	9	29.4889
Immature Males	3	21.1667
Immature Females	2	24.95
Sig.		0.324

Table 3.6 Descriptive statistics of whole weight (g) from Atlantic salmon parr populations categorized in terms of age-specific sexual maturity, Harry's River, 1997.

Age	Sex	N	Mean	St.dev.	Min.	Max.
0+	Precocious Males	0	N/A	N/A	N/A	N/A
	Immature Males	3	1.1667	0.6351	0.80	1.90
	Immature Females	2	2.0	0.2828	1.80	2.20
1+	Precocious Male	29	6.0276	2.2846	3.10	11.60
	Immature Male	21	3.9429	1.4593	1.60	7.30
	Immature Female	34	5.3176	2.7963	2.30	16.60
2+	Precocious Male	35	14.8771	5.3989	7.40	29.50
	Immature Male	5	13.1000	6.6832	6.80	24.30
	Immature Female	16	15.1813	3.5937	10.50	22.10
3+	Precocious Male	9	29.4889	6.9276	16.40	35.40
	Immature Male	3	21.1667	6.0053	17.60	28.10
	Immature Female	2	24.9500	8.6974	18.80	31.10

Table 3.7 Descriptive statistics of relative condition from Atlantic salmon parr populations, categorized in terms of age-specific maturity, Harry's River, 1997.

Age	Sex	N	Mean	Std. Dev.	Min.	Max.
0+	Precocious Male	0	N/A	N/A	N/A	N/A
	Immature Male	2	0.8173	0.1014	0.7587	0.9344
	Immature Female	3	0.8854	0.0695	0.8362	0.9345
1+	Precocious Male	29	1.0271	0.0833	0.8912	1.2297
	Immature Male	21	0.9006	0.0672	0.7869	1.0038
	Immature Female	34	0.9283	0.0556	0.8221	1.0194
2+	Precocious Male	35	1.0533	0.0753	0.9230	1.2990
	Immature Male	5	0.9292	0.0929	0.8255	1.0756
	Immature Female	16	0.8914	0.0584	0.7430	0.9518
3+	Precocious Male	9	1.0713	0.0371	1.0164	1.1407
	Immature Male	3	0.9006	0.0251	0.8726	0.9211
	Immature Female	2	1.0847	0.1969	0.9455	1.2239

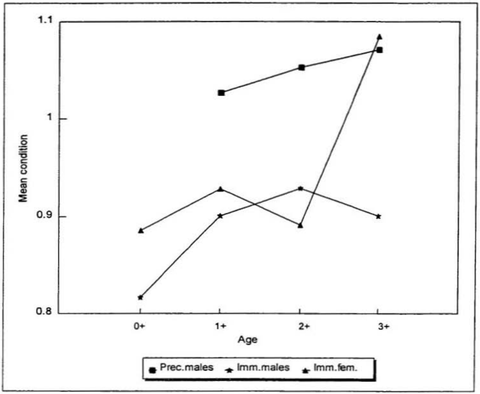


Figure 3.4 Mean relative length-specific condition at age for sexually mature and immature Atlantic salmon parr, Harry's River, 1997.

Precocious males and immature females aged 3+ had significantly higher relative length-specific condition than immature males ($p = 0.008$, one-way Anova with a Student-Newman-Keuls multiple range test). Precocious males had significantly higher relative condition than immature males and females aged 1+ and 2+ ($p < 0.001$ in both cases) (Table 3.8). It is interesting to note that the mean fork length of immature female parr was higher than that of precocious males at age 3+.

The significant differences in relative length-specific condition among sex and maturity classes could play a role in the previously identified (Chapter 2) differences in mean relative condition of parr populations among tributaries on Harry's River if there were differences in sex ratio among sites.. Discriminant analysis provides a tool for investigating such differences.

Table 3.8 One-way ANOVA results with Student-Newman-Keuls multiple range test for differences in relative condition factor among sex categories of Atlantic salmon parr, Harry's River, 1997.

AGE 1+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between groups	0.234	2	0.117	24.483	<0.001
Within Groups	0.382	80	0.004778		
Total	0.616	82			

S-N-K	N	Mean Condition
Precocious Males	29	**1.027117**
Immature Males	20	0.90069
Immature Females	34	0.928288
Sig.		<0.001

AGE 2+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	0.312	2	0.156	29.810	<0.001
Within Groups	0.277	53	0.005236		
Total	0.590	55			

S-N-K	N	Mean Condition
Precocious Males	35	**1.053254**
Immature Males	5	0.929240
Immature Females	16	0.891375
Sig.		<0.001

Table 3.8 (continued)

Age 3+

ANOVA	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	0.07093	2	0.03547	7.642	0.008
Within Groups	0.05105	11	0.004641		
Total	0.122	13			

S-N-K	N	Mean Condition
Precocious Males	9	1.071267
Immature Males	3	**0.9006**
Immature Females	2	1.0847
Sig.	.	<0.001

Chapter 4

Discriminant Analysis : A Tool For Predicting Sex and Maturity Status of Atlantic Salmon Parr

Introduction

The objective of this chapter is to examine models that predict sex and maturity status from easily measured variables such as length and weight. These models could be used to investigate spatial and temporal variability of such population characteristics and also to estimate the potential role of this variability in the previously observed differences in parr condition among sites (Chapter 2). The approach taken was to begin with salmon parr classified as to sex and maturity status based on internal examination and then to use discriminant analysis to build predictive models based on the externally measurable characteristics of length and weight, as well as relative condition which is calculated using these parameters (actual weight / predicted weight).

Methods

Length (to the nearest 0.1cm) and weight (to the nearest 0.1g) were determined for parr specimens from each of 28 sites sampled by electrofishing (see Chapter 2, Table 2.1, and Figure 2.1) in 1997. Approximately 2-3 fish from each age class at each site were examined internally in the laboratory and categorized in terms of sex and reproductive status. Discriminant analysis (Norusis, 1988) was employed to build a predictive model of group membership (sex and maturity status) based on independently observed characteristics of length and weight, and on relative condition which is calculated from these parameters. The procedure generated a set of discriminant functions based on linear combinations of the predictor variables which provided the best discrimination among the groups. The functions were generated from a sample of cases for which group membership was known; the functions could then be applied to new cases with measurements for the predictor variables but unknown group membership. The smallest parr of known sexual status was 4.6 cm so all subsequent analyses excluded fish smaller than this size.

All statistical tests were performed using the statistical software package SPSS 7.5 for Windows.

Results and Discussion

Discriminant Analysis

Discriminant analysis was first used to construct a model to predict both sex and maturity status (precocious males, immature males and immature females), hereafter referred to as Model 1. The same procedure was then used to construct a model to predict maturity status only, i.e., to distinguish precocious males from all other parr, hereafter referred to as Model 2.

Model 1 included relative condition, field-measured fork length (cm), and whole field-measured weight (g) as the predictor variables in a stepwise model. The dissected fish were placed into 3 categories : (1) precocious male, (2) immature male, and (3) immature female. Relative condition factor alone was a significant variable (Table 4.1), and yielded a model (1a) that correctly classified 61.1% of the original grouped cases (Table 4.2). Relative condition alone was effective at classifying precocious males (76.3% correct) but made numerous errors in classification of the immature individuals.

The addition of fork length to the analysis as a predictor variable was statistically significant at the 10% level (p=0.098) and yielded a model (1b) which correctly classified 65.4% of the original grouped cases as well as a slightly higher correct prediction rate for precocious males (Figure 4.1). The percentage of correctly grouped cases for immature females increased from 41.8% in Model 1a to 49.1% in Model 1b.

Table 4.1 Results from stepwise discriminant analysis Model 1 using relative condition, fork length (cm), and whole weight (g) as predictor variables to estimate group membership based on state of sexual maturity of Atlantic salmon parr, Harry's River, 1997. Known group categories were sexually mature males, immature males, and immature females.

Step	Predictor Variable	P
Model 1a	Relative condition	<0.001
Model 1b	Relative condition	<0.001
	Fork length	0.098
Model 1c	Relative condition	<0.001
	Fork length	0.012
	Whole weight	0.044

Table 4.2 Predicted group membership generated from discriminant analysis Model 1, using relative condition, fork length, and whole weight additively as predictor variables. Known group categories were sexually mature males, immature males, and immature females. The percentage data in bold type represents the percentage of correctly classified cases.

Model 1a

		Predicted	Sex	Category	
	Sex Category	Imm. Female	Imm. Male	Prec. Male	Total
Count	Imm. Female	23	23	9	55
	Imm. Male	10	18	3	31
	Prec. Male	17	1	58	76
Percentage	Imm. Female	**41.8**	41.8	16.4	100.0
	Imm. Male	32.3	**58.1**	9.7	100.0
	Prec. Male	22.4	1.3	**76.3**	100.0

* 61.1% of original grouped cases correctly classified.

Model 1b

		Predicted	Sex	Category	
	Sex Category	Imm. Female	Imm. Male	Prec. Male	Total
Count	Imm. Female	27	21	7	55
	Imm. Male	8	20	3	31
	Prec. Male	10	7	59	76
Percentage	Imm. Female	**49.1**	38.2	12.7	100.0
	Imm. Male	25.8	**64.5**	9.7	100.0
	Prec. Male	13.2	9.2	**77.6**	100.0

* 65.4% of original grouped cases correctly classified.

Table 4.2 (continued)

Model 1c

		Predicted	Sex	Category	
	Sex Category	Imm. Female	Imm. Male	Prec. Male	Total
Count	Imm. Female	33	15	7	55
	Imm. Male	11	17	3	31
	Prec. Male	11	7	58	76
Percentage	Imm. Female	**60.0**	27.3	12.7	100.0
	Imm. Male	35.5	**54.8**	9.7	100.0
	Prec. Male	14.5	9.2	**76.3**	100.0

* 66.7% of original grouped cases correctly classified.

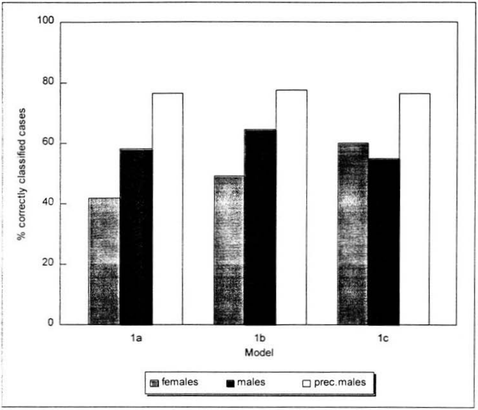


Figure 4.1 Predicted sex category generated from discriminant analysis Model 1 using relative length-specific condition, fork length (cm), and weight (g) additively as predictor variables.

The percentage of correctly grouped cases for immature males increased from 58.1% in Model 1a to 64.5 % in Model 1b (Table 4.2).

Adding whole weight as a third variable (Model 1c) to predict state of sexual maturity produced a model in which all factors were significant at the 5% level and generated the highest percentage (66.7%) of correctly classified cases. This analysis placed 76.3% of the precocious males into the correct group and correctly classified 60% of immature females and 54.8% of immature males (see above Figure 4.1 and Table 4.2).

Most of the classification errors in Models 1a, 1b, and 1c were within the immature categories, suggesting that a simpler, two-category model might be more effective. Discriminant analysis was therefore employed to generate a similar stepwise model (Model 2) with the only difference being that the previously grouped salmon parr were classified into two categories : (1) mature parr (precocious males) and (2) immature parr (males and females). Relative condition alone as a predictor variable generated a highly significant model ($p < 0.001$) (Table 4.3) which correctly classified 77.6% of the mature males and 86.0% of the immature parr (Table 4.4).

The addition of length to the model did not yield a statistically significant increase in predictive power ($p = 0.169$) but yielded a model (2b) which correctly classified a higher percentage of grouped cases overall (83.3%) as well as a slightly higher correct prediction rate for precocious parr (Table 4.4).

The model which used all three predictor variables (Model 2c) in the analysis

Table 4.3 Results from stepwise discriminant analysis Model 2 using relative condition, fork length (cm), and whole weight (g) as predictor variables to estimate group membership based on state of sexual maturity of Atlantic salmon parr, Harry's River, 1997. Known group categories were sexually mature males and immature parr (males and females).

Step	Predictor Variable	P
Model 2a	Relative condition	<0.001
Model 2b	Relative condition	<0.001
	Fork length	0.169
Model 2c	Relative condition	<0.001
	Fork length	0.390
	Whole weight	0.644

Table 4.4 Predicted group membership generated from discriminant analysis Model 2 using relative condition, fork length, and weight additively as predictor variables. Known group categories were placed sexually mature males and immature parr (males and females).The percentage data in bold type represents the percentage of correctly classified cases.

Model 2a

		Predicted	Sex	Category
	Sex Category	Immature Parr	Precocious Parr	Total
Count	Immature Parr	74	12	**86**
	Precocious Parr	17	59	76
Percentage	Immature Parr	**86.0**	14.0	100.0
	Precocious Parr	22.4	**77.6**	100.0

* 82.1% of original grouped cases correctly classified.

Model 2b

		Predicted	Sex	Category
	Sex Category	Immature Parr	Precocious Parr	Total
Count	Immature Parr	75	11	86
	Precocious Parr	16	60	76
Percentage	Immature Parr	**87.2**	12.8	100.0
	Precocious Parr	21.1	**78.9**	100.0

* 83.3% of original grouped cases correctly classified.

Model 2c

		Predicted	Sex	Category
	Sex Category	Immature Parr	Precocious Parr	Total
Count	Immature Parr	75	11	**86**
	Precocious Parr	13	63	76
Percentage	Immature Parr	**87.2**	12.8	100.0
	Precocious Parr	17.1	**82.9**	100.0

* 85.2 of original grouped cases correctly classified.

improved the correct prediction rate even though the addition of weight was not significant ($p = 0.644$). This model yielded the highest overall correct prediction rate (85.2%) as well as the highest percentage of correctly classified precocious parr (82.9%) (see above Table 4.4).

Predicted Sexual Status of Parr for 1997

The classification coefficients from Model 2a (see Appendix A) were applied to the full 1997 field data set ($n= 1147$) to predict percent composition of precocious males, which was then evaluated to determine if it was related to variability in site-specific condition of salmon parr, as noted in Chapter 2 and hypothesized in Chapter 3.

Examination first of the predicted occurrence of precocious male salmon parr at sites on Harry's River and their corresponding relative condition factor revealed that there was a positive correlation between predicted % precocity and site-specific condition ($r^2 = 0.62$, Figure 4.2). Salmon parr at Sites 3 and 14 were significantly lower in site-specific condition in 1997 (condition = 0.9366 and 0.9521, respectively). Each of these sites was predicted to be comprised of less than 25 % precocious males. Conversely, Site 11 was significantly higher in site-specific condition by approximately 7 % in 1997 and was predicted to be comprised of over 55 % precocious males. These observations suggest that some of the previously documented variability in site-specific condition (see Figure 2.11) could result from variability in sex and maturity status in the

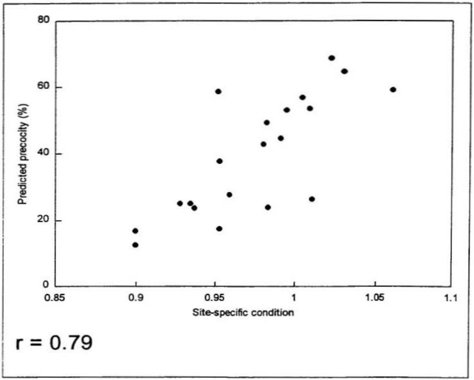


Figure 4.2 Precocity (%) predicted by applying Model 2a to the entire field weight : length data set vs. relative site-specific condition for each field site, Harry's River, 1997.

sample.

Geometric mean regression was used to fit a relative condition : % precocity relationship to the 1997 data and the regression equation was then used to predict mean site-specific condition for hypothetical populations with varying percentages of mature males. A population with 0% precocious males was calculated as having 0.87 mean relative condition while a population with 100% precocious males would have a mean condition of 1.12 (Figure 4.3). This range contains most of the previously calculated site-specific condition values for salmon parr populations on Harry's River from 1987-1997 (see Figure 2.11) which ranged from a low of 0.60 to a high of 1.15. It is, therefore, plausible to suggest that much of the previously observed variability in site-specific condition (Figure 2.11) could potentially be explained by differences in sexual maturity of fish among sites and years with only the most extreme observations requiring extraordinary environmental conditions.

The classification coefficients from Model 2a were used to predict group membership for all unknown fish in 1997 (Table 4.5) to examine the relative distribution of precocious males throughout the watershed. Nine of the ten sites predicted by the model to be comprised of over 40% precocious males were concentrated at sites above George's Lake with the exception of Site 13 found at the lower end of the system (Table 4.5 and Figure 2.1). Site 13 is located just below a relatively large pond (Long Gull Pond), however, and is likely the exception that proves the rule. Six of the seven sites with the lowest ($\leq 25.0\%$) proportion of mature male parr were located in tributaries

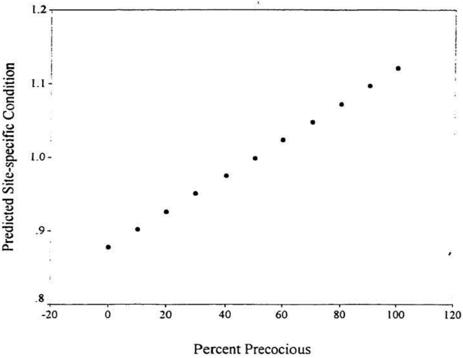


Figure 4.3 Site-specific condition, as predicted from geometric means regression, for hypothetical populations of precocious salmon parr, Harry's River, 1997.

Table 4.5 Results from applying discriminant analysis Model 2a to field weight : length data from 1997 to predict state of sexual maturity of Atlantic salmon parr. The model was applied to the whole sample excluding fish < 4.6 cm for 1997.

	Percentage				
Site	Immature (males and females)	Mature (males)	Sample Size	Above George's Lake	Site Condition Factor
2	76.1	*23.9*	109		0.9836
3	76.3	*23.8*	80		0.9366
4	83.3	*16.7*	6		0.8992
7	50.7	**49.3**	69	Yes	0.9827
8	87.5	*12.5*	8	Yes	0.8992
9	46.3	**53.7**	41	Yes	1.0091
11	40.8	**59.2**	130	Yes	1.0683
12	46.9	**53.1**	130	Yes	0.9952
13	55.2	**44.8**	67		0.9917
14	82.6	*17.4*	132		0.9521
15	43.1	**56.9**	51	Yes	1.0047
16	73.5	26.5	34		1.0110
17	72.2	27.8	72		0.9589
18	75.0	*25.0*	4		0.9342
21	35.3	**64.7**	34	Yes	1.0299
23	57.1	**42.9**	49	Yes	0.9806
24	41.2	**58.8**	17	Yes	0.9511
26	62.2	37.8	45	Yes	0.9525
27	31.3	**68.8**	16	Yes	1.0224
28	75.0	*25.0*	12		0.9272

below George's Lake, Site 8 being the exception. The upper watershed contains George's Lake and Pinchgut Lake which comprise the major portion of the lacustrine habitat on Harry's River. It thus appears that the upper watershed of the Harry's River system had a higher incidence of precocity than the lower watershed in 1997. Results from this study (see Chapter 3) suggest that faster growing males mature precociously; thus males from the upper watershed of Harry's River are likely growing faster. Faster growth could be related to food availability. Unfortunately, the only prey data examined from the lower portion of the river system were collected at Site 13 which was the outlier (the only site in the lower watershed with a high occurrence of precocious males).

Faster growth may also be due to the presence of lacustrine habitat if fish move back and forth between streams and lakes. Hutchings (1986) reported that lakeward movement of parr salmon in a Newfoundland stream occurred from May through September and that parr remained in the lakes until they either matured (usually males) or smoltified (usually females) before returning to the streams. The benefits from this lakeward migration can be enhanced growth, increased reproductive success, or avoidance of unfavourable environmental conditions (Northcote 1978; Godin 1982). Lake use by these parr would support my previous findings that the faster growing individuals, at least to age 1+, mature earlier.

Overall there appears to be a difference in life history strategies between the upper and lower portions of the watershed. If females homed to their natal area of the watershed, then upstream and downstream populations could diverge genetically and display different adaptive strategies. This range in strategies may enable the population to cope with a wide range in environmental variability during the freshwater and marine portions of the life cycle.

General Conclusions

Parr population densities on Harry's River varied widely among sites in 1996, and populations of all age classes of parr (0+, 1+, 2+ and 3+) displayed a contagious or "patchy" distribution with high variability relative to the mean density (coefficient of dispersion > 1). There was a significant negative relationship between population density of 0+ salmon fry and wide, deep sites. No significant relationship between density and habitat variables was evident in the other age classes. There was also no relationship between number of nearby redds in 1996 and population density of fry (aged 0+) at sites in 1997.The moratorium on commercial salmon fishing instituted in 1992 was expected to result in higher parr densities in subsequent years, starting with age 0+ in 1993. Total densities at three sites in 1997 for which long term data were available exceeded those observed in 1992.

There were significant differences in the log weight : log fork length regression slopes among sites in 1996 which would suggest that the allometry of the weight-length relationship varied among locations. Relationships between regression slopes and habitat conditions were investigated using stepwise multiple regression analysis. Analysis using individual habitat variables revealed that there was a significant negative relationship between the width of the stream and the weight - length regression slopes. The addition of flow increased the significance of the model and revealed that water flow velocity had a significant positive effect on the weight-length regression. Analyses using principal component scores revealed only weak, non-significant correlations between the regression slopes and habitat variables. The differing growth allometry inferred from the weight : length regression analysis was also not supported by scale analysis. Inspection of log weight-log length field data for the two most divergent sites (Sites 7 and 11) revealed that most of the variance was associated with fish less than 6.0 cm. The previously observed variation among small fish weights seemed to reflect their recent feeding history rather than true differences in growth allometry. Plots of log weight vs. log length excluding small (<6.0cm) fish revealed that the remaining differences were largely due to variation in the weights of the largest fish and were related to differences in sex and maturity status. It was concluded that a single fundamental allometric relationship could be applied to field data from all sites and years once small fish (< 6.0 cm) were removed from the population. This permitted pooling of data for analysis of relative parr condition.

Relative site-specific condition of parr varied significantly among sites and years on Harry's River ranging from a maximum 15 % above mean condition to a minimum of 40 % below mean condition. Water discharge data for Harry's River suggested that there was little correlation between high and low water levels and site-specific condition factor of salmon parr, except at the extreme, which was evidenced by unusually low water levels in 1987. There was evidence of significant within-watershed variation associated with extremely low site-specific condition at four sites in 1987.

These four sites (Sites 7, 8, 9, and 10) were all located in the upper reaches of the watershed in the Pinchgut Lake area. Unusually low stream water levels in 1987 should have affected these headwater sites more than those located further downstream. The fact that fish at all lengths (and consequently ages) displayed unusually low relative condition is suggestive of severe stress. Relative site-specific condition at Site 7 rebounded in 1988 and returned to the long-term average in 1989, indicating that surviving fish had recovered the lost weight and/or been replaced by younger cohorts of average relative condition.

There appeared to be little relationship between relative length-specific condition of both small (<6.0cm) and large fish, and abundance of appropriate-sized prey, i.e., chironomids and blackfly larvae for small fish and mayfly and caddisfly larvae for the larger fish. The lack of correlation might be due to differences in the spatial scales of the prey measurements versus parr feeding ranges.

Parr sex data suggested that females were disproportionately entering pond environments prior to smoltification to continue their growth. There was a clear trend for increasing percentage male composition in the streams with age (from 57.1% at age 1+ to 85.7% at age 3+) and even at age 1+ more than half of the males were precociously mature. Most of the males remaining in the tributaries mature precociously rather than migrating to sea as smolts.

Mean lengths of precocious 1+ males were greater than those of immature males in all samples but there were no such trends for older age groups. The fact that precocious parr are longer at age 1+ but not at ages 2+ and 3+ indicates that growth rates of sexually mature males decline relative to immature males. As a result, length alone cannot be used as a discriminating factor between mature and immature parr after the age of 1+. Comparisons of mean weight at age support the conclusion that precociously maturing males have higher mean weights than immature males at age 1+ but growth rates tend to decrease in the older age classes. There were significant differences in length-specific condition between the precocious parr and the immatures (both sexes) as well as significant differences in condition across all age classes between mature and immature males.

Discriminant analysis was employed to successfully predict sex and maturity status of Atlantic salmon parr. The classification coefficients were then used to predict group membership for all fish of unknown sexual status in 1997, revealing that those populations comprised of over 40% precocious males were concentrated at sites above George's Lake while sites with < 25% precocious male parr were located mostly below the lake. This observation indicates that there is a wide range of life history strategies within the watershed, and this diversity may be related to differences in the availability of lacustrine habitat. A wide range in life history strategies may help the population respond to environmental variability encountered in both the freshwater and marine portions of the life cycle.

In summary, Atlantic salmon parr in regions of the Harry's River watershed vary widely in terms of density, relative condition, and sexual maturity. Information gathered during this study will provide a better understanding of how these future spawners are utilizing the river system. The analysis of relative condition factor presented in Chapter 2 provides a rapid means of evaluating parr condition in the field. This could be a useful technique for identifying periods of unusual stress in real time so that the underlying causes could be identified more readily.

Further study on the use of lacustrine habitat by salmon parr would be useful as it may play an influential role in their growth and survival, particularly for females. Variation in population characteristics such as sex ratio and sexual maturity of Atlantic salmon parr may have an impact on the management strategy of Harry's River. For example, if adult salmon home to their natal areas of the system, then the present study suggests that most adults returning above George's Lake will be females while adults returning to the lower portion of the watershed will have a more balanced sex ratio. If this is actually the case, then a recreational fishery in the lower watershed would have less impact on egg deposition than one in the upper watershed. The mechanisms which produce the variation in population characteristics are worthy of further study and will contribute to the evaluation of future conservation strategies.

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Appendix A

Discriminant Analysis Model 2a Coefficients

	Coefficient
Relative Condition	13.546
Constant	-13.204

Discriminant Coefficient:

Score = 13.546 *(relative length-specific condition) - 13.204

Individuals with scores > 0.05 were classified as mature precocious males.