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Life History Strategies Of A North Temperate Salmonid, Salvelinus Fontinalis, In Polar Bear Provincial Park, Ontario

Peter Owen Steele

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LIFE HISTORY STRATEGIES OF A NORTH TEMPERATE SALMONID, *SALVELINUS FONTINALIS*, IN POLAR BEAR PROVINCIAL PARK, ONTARIO.

by

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Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

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Abstract.

A northern anadromous population of brook trout (*Salvelinus fontinalis*), from the Sutton River, in the Ontario Hudson Bay Lowlands, was examined to determine if its life history differed from that reported for the species elsewhere. The Sutton River population was similar to historical anadromous populations native to North America 200 years ago. Only minor differences were discernible between the life histories of brook trout from Sutton River, Ontario, Nelson-Hayes River, Manitoba, and Richmond Gulf, Quebec. All of these populations differed from populations in Canadian Maritime Provinces, in that the northern trout migrated to saline water earlier, matured later and at a larger size. They also had greater longevity and life time fecundities.

These differences in life history were interpreted in light of resource allocation models developed for other anadromous salmonids and the peculiarities of the southwest coast of Hudson Bay.

A comparison of the suitability of scales, fin ray sections and otoliths as ageing structures was undertaken. Scales were the least reliable and accurate due to problems of resorption that were aggravated by the trout's anadromous habits. Fin ray sections and otoliths were of similar accuracy and reliability.

In spite of low marine temperatures, immature trout grew 3.3 cm/month. This exceeds reported growth estimates for anadromous brook trout. The fast growth rate was the result of abundant forage and a sustained production of growth hormone (GH) while resident in the isosmotic waters of Hudson Bay. Sustained GH production also caused reductions of the weight on length regression slope. Slopes stabilized with sexual maturity; mature trout spent less time in the Bay and had slower growth rates.

The blood of trout returning from Hudson Bay did not coagulate. Even minor injuries (e.g., those caused by angling or tagging) resulted in death. This phenomenon was temporary, and may have been induced by the same enzymes responsible for the rapid degradation of GH on re-entry to fresh water. The lack of coagulative ability has profound consequences for the catch and release fishery of the area. As a result the legislation enacted to regulate and protect the fishery is being changed.

ACKNOWLEDGEMENTS

I am indebted to a great number of individuals and organizations for assistance, encouragement and funding during the preparation of this thesis.

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Second, I wish to acknowledge the input of the many people of the Ontario Ministry of Natural Resources that made this study possible. Mr. J. Weir introduced me to the beauty and the fauna of the Hudson Bay Lowlands. Mr R. Stit taught me how to survive and live in style on the Lowlands; in return I introduced him to drinking tea with the tea bag in the mug. The Ministry's Air Service ferried myself, my dog Cody and countless tons of equipment and supplies back and forth across the Lowlands. Pilots 'One Cloud Eddie' and Johnny Bell flew tremendous loads through hideous weather to keep things running smoothly. Thank you.

A special vote of thanks goes to Mr. B. Lannin, whose patience I tested continually. Bill went to bat often for me and the Sutton River Trout Study. He planned aircraft

schedules and made sure that food and supplies were bought as well as loaded on the planes. Without Bill's input and advice this study would never have been successful.

District Manager S. Toole had enough confidence in my abilities to give me a free rein while in Moosonee District and support my proposal to the Region and finally Queen's Park. Dr. D. Dodge and Dr. R. Biette made the study possible and encouraged the investigation of different aspects of the study that were not included in the original plan.

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I owe my greatest debt to my wife Ann. She nurtured, encouraged, and coaxed me through this thesis although it meant sacrificing some of her own dreams. She patiently sat at home while I spent the summers away and the evenings at work. She supported us financially while I studied and spent her holidays travelling to visit me when I was in the field. Towards the end of the thesis, she accompanied me into Collip in the evenings to sit with the cockroaches while I pounded words out on the keyboard. Without her undying devotion and love I would have never been able to complete this thesis.

This work was funded by the Ontario Ministry of Natural Resources through Moosonee District and grants to the University of Western Ontario. Grants from the Northern Scientific Training Program, Department of Indian Affairs and Northern Development helped offset the high cost of operating in a remote area. Natural Science and Engineering Research Council grants to M.H.A. Keenleyside paid for numerous incidentals that were necessary during the study and writing of the thesis.

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1. INTRODUCTION.

1.1 General.

Life history strategies of northern fish populations express latitudinal trends (Leggett, 1969). Carscadden and Leggett (1975) observed latitudinal trends in the percent of the population that was iteroparous, the relative and absolute fecundities, and the age of first reproduction in Atlantic coast populations of American shad (*Alosa sapidissima*). Power (1981) correlated several life history variables with the latitude of maternal rivers for Atlantic salmon (*Salmo salar*). Even the variability about the mean age of first reproduction reflects a latitudinal trend in Atlantic salmon (Schaffer and Elson, 1975).

These trends "were predictable and arise because many environmental variables are arranged on a north-south gradient" (Power, 1981, p. 1603). Life history features such as 'run' characteristics (peak date of migration, start and end of run), percent grilse, smoltification age, length of time spent at sea, percent repeat spawners, length of smolts and sea age fish for Atlantic salmon are correlated ($p<0.002$) with such environmental parameters as mean air temperature, length of growing season and river discharge (Power, 1981). In all cases, correlations with environmental variables exceeded that with latitude indicating the causative agents to be environmental (Table I, Power, 1981).

Hence, the life history strategies of northern fish populations are dictated by the rigors of their environment (Stearns, 1976).

Life history strategies are assumed to be adaptive for each of the populations as they represent the outcome of selection operating on a 'complex of resource allocation alternatives' (Shoubridge & Leggett, 1978). Organisms are faced with fixed time and energy budgets. These budgets must be divided between growth, maintenance and reproduction (Cody, 1966). Hence, the allocation of resources to one activity is not independent of the allocation to the other two. An increase of resources to present reproduction reduces resources available for allotment to maintenance and growth. Reducing the allotment to maintenance may increase the probability of post-breeding mortality; reducing the allotment to growth may reduce subsequent growth rates and future fecundity if fecundity is size dependent. Therefore, the optimum life history strategy is one that will divide the available resources in such a way as to maximize the total reproductive value of the individual (Fisher, 1930). This is equivalent to maximizing 'r', the intrinsic rate of increase, for the population (Williams, 1966; Goodman, 1974; Schaffer, 1974).

The energy budget of the ectothermic organism is generally controlled by temperature, with low temperatures depressing the total budget (Fry, 1971; Brett, 1979). The 'scope of activity', and hence allotments available to growth and reproduction, is reduced at low temperatures (Beamish, 1964; Fry, 1971; McCormick et al., 1972; Brett, 1974, 1976, 1979; Elliot, 1976). As such, size dependent processes (e.g., smoltification, maturation, and fecundity) are often delayed or reduced, decreasing the individual's reproductive value. A delay in maturation is advantageous only if an increase in fecundity can offset the combined disadvantages of time and mortality. With slow growth rates this is unlikely, as fecundity is closely correlated to body size (Carlander, 1969; Power, 1980). Since the increase in body size is reduced at slow growth rates so is the increase in fecundity. Moreover, a high cost of reproduction for iteroparous salmonids (44 -79% of growth for that year in Atlantic salmon (Schaffer & Elson, 1975)) precludes pursuing both strategies, namely early and late reproduction, in all but the fastest growing individuals. This cost of reproduction is attributable to the sum of the many costs associated with reproduction in anadromous salmonids including that of forming and carrying gametes, development of secondary sexual characteristics, an often lengthy and rigorous spawning migration and physiological adaptations that accompany changes in environment salinity.

A reduced scope of activity at low temperatures increases the relative cost of reproduction for fish that attempt to breed at those temperatures. During conditions of resource limitation, regardless of whether externally caused (e.g., scarcity of prey) or internally caused (e.g., reduced metabolic rate), individual reproductive efforts must either 1) be further separated in time, in comparison with southern, warm-water, stocks; 2) consist of reduced individual efforts (either reduced fecundity or reduced gamete quality/size); or, 3) be a combination of both. Since total egg (ovary) volume and body size are strongly correlated in Canadian species of fish (Wootton, 1984) there is restricted scope for independent variation of fecundity and egg size. Fecundity is generally fixed by body size and is consistent regardless of habitat for salmonids (Power, 1980). This is also true of egg size for at least some salmonids (e.g., brook trout, *Salvelinus fontinalis*: Ricker, 1932; Wydoski and Cooper, 1966). Hence, the option of reducing individual effort per spawning does not seem to be widely employed by these teleosts. Instead, iteroparous salmonids such as brook trout vary the time between reproductive efforts from yearly intervals in temperate environments, to twice every three years, or to alternate years for northern populations (Power, 1980). Widely spaced reproductive efforts which involve missing or skipping breeding seasons have been suggested as a possible mechanism whereby semelparous reproduction has arisen (Schaffer, 1974).

Northern latitudes are characterized by short summers to which growth and reproduction in fishes are restricted. This season is accompanied by an increased number of daylight hours (max. of 20 hr) that accelerate the heating of surface waters, thereby forcing stenothermic species to flee into cooler waters (eg., deep lakes or marine waters). Possibly for this reason, many northern fishes (eg., members of the genus *Salvelinus* and *Coregonus*) are anadromous - the usual pattern is one of spending the summer in the cooler marine waters and the winter in the warmer (0 - 4°C) fresh waters. However, it is not known if summer river temperatures exceed the upper lethal temperature of Hudson Bay Lowland fish hence forcing them to be anadromous or if anadromy is favoured for other reasons. Summer river temperatures will be discussed as a reason for the anadromy of the Sutton River brook trout.

Low temperatures and slow growth rates have specific consequences for anadromous fish. First, the marine portion of their life history is delayed as 'smoltification' is a size dependent process (Folmar & Dickoff, 1980). This results in a longer freshwater residency before migrating for the first time. Second, a greater number of seasons is needed to achieve initial physiological reproductive capability (Schaffer & Elson, 1975). As previously noted, little is gained by delaying reproduction beyond the attainment of reproductive capability under conditions of slow growth, and the return to freshwater to spawn should occur soon afterwards (Schaffer & Elson, 1975). Faster growing anadromous stocks may increase the number of seasons at sea after the physiological attainment of reproductive capability, delaying reproduction to take advantage of rapid sea growth (attaining a large body size) and thereby increasing fecundity and egg size. These predictions are summarized below.

1.2 Summary of Predictions for the Sutton River Brook Trout.

1. All ages will be characterized by low growth rates.

2. Parr will not 'smoltify' till 4 to 6 yrs of age.

3. 'Smolts' will migrate to Hudson Bay for several seasons before they attain the physiological capability to spawn.

4. Trout will return to Sutton River to spawn the first year that they are capable of doing so. (Short time at sea after attainment of physiological capability to spawn).

5. Maturation will occur at a small size.

6. Reproduction will be costly; little somatic growth will occur after maturation.

7. Individuals will skip years between reproductive attempts. The population will tend towards semelparity or infrequent iteroparity.

The severity of the climate of the Sutton River region allows the formulation of these predictions. Fish of cold (northern) habitats should express an extreme life history strategy as described. The life history strategy will reflect the harshness of the abiotic environment.

1.3 Additional studies.

During the course of this study it was observed that Sutton River brook trout became leaner with age instead of fattening as is usual for fish. This resulted in mature fish that were thicker-bodied but less deep (i.e., torpedo-shaped). These fish also were producing copious quantities of mucous which is unusual for trout. After the first field season was completed it was apparent that these fish were growing at a phenomenal rate. Rapid growth, especially of the longitudinal axis, and excessive mucous production was consistent with the prolonged stimulation of the growth hormone (GH) axis. Accordingly, experiments were undertaken to determine if these fish were secreting large quantities of GH. These experiments are included as Appendix I.

During the course of the GH study, irregularities of the clotting system of brook trout blood were noted. These irregularities were also pursued as a separate study and appear as Appendix II.

1.4 Species Description.

The brook trout is the best known and most studied species of the genus *Salvelinus*. Although it exhibits considerable variation throughout its range it is a stable and well-defined species (Scott and Crossman, 1973). Morphology and meristic descriptions for both native and introduced populations are available in Vladykov (1954), Bigelow (1963), Scott and Crossman (1964, 1973), and selected works edited by Balon (1980). The morphology and meristics of anadromous and non-anadromous forms of brook trout were compared by Wilder (1952), McGlade & MacCrimmon (1979) and McGlade (1981).

Brook trout hybridize with other species of charr, trout and salmon (Schwartz (1972) provides a bibliography to the literature). The best known of these hybrids is the 'splake' (male *S. fontinalis* x female *S.namaycush*) and the tiger trout (*S. fontinalis* x *Salmo trutta*). Hybridization with species outside the Salmonidae is probably prevented by the tetraploid nature of this family (Allendorf and Thorgaard, 1984).

Brook trout are endemic to northeastern North America, penetrating as far as 60°N latitude in Ungava, as far west as the Upper Mississippi watershed and as far south as Georgia in the Appalachian Mountains. The Atlantic Ocean, from Port Burwell, Labrador to Cape Cod forms the easterly boundary to the native range of this potentially anadromous species (Scott and Crossman, 1973). Successful introductions of the species to every continental landmass (with the exception of the Antarctic) have been made in recent years (MacCrimmon and Campbell, 1969; MacCrimmon et al., 1971). Prevailing water temperature seems to be the most limiting condition for further extension of the brook trout's range (MacCrimmon and Campbell, 1969).

Brook trout have a final preferred temperature of between 14.0 and 16.8°C (cf. Houston, 1982) and a preferred range between 4 and 20 °C (Power, 1980). The upper incipient lethal temperature for yearling brook trout approaches 25.5 °C (Fry et al., 1946) for larval trout (eleutheroembryos) it is 20.1°C (McCormick et al., 1972), and for eggs it is 18°C (Hokanson et al., 1973). The lower incipient lethal temperature for brook trout is 0°C in freshwater and probably -0.7°C in 30 °/oo sea water (Saunders et al., 1974, 1975). Spawning only occurs at temperatures of 16°C or less, with temperatures below 12°C preferred (Hokanson et al., 1973).

Lethal pH conditions for brook trout as determined by acute exposure experiments are 3.5 and 9.8 (Daye and Garside, 1975) although a pH of 5.0 was lethal to eggs (Menendez, 1976) and superficial gill damage occurred in adults at a pH below 5.2 and above 9.0 (Daye and Garside, 1976).

Similar to other *Salvelinus* species, brook trout are fall spawners, depositing large eggs (3.5 – 5.0 mm dia.) in gravel redds excavated by the female. The number of eggs deposited depends on the size of the female, her state of nutrition and probably heredity (Power, 1980). Gibson et al. (1976), however, found that nutritional state was not a determinant in fecundity of Matamek River brook trout. Fecundity varies considerably in wild populations and there has been much discussion of this variation in the literature. However, the differences result mainly from comparing different sized fish. When fecundity is plotted against length for the entire spectrum of brook trout stocks, there is a general consistency in form and proportions over a range of habitats (Power, 1980).

Eggs hatch in 28 to 150 days post-fertilization depending on temperature (Embody, 1934) and oxygen tensions (Garside, 1966). The eleutheroembryos remain protected in the gravel till the yolk has been absorbed and feeding has begun. Dispersal and/or migration to nursery grounds occurs soon afterwards; the parr become territorial with age (Power, 1980). If the trout are going to move to lotic environments they usually do so during their second or third summer at a size of 80 – 150 mm (Saunders and Power, 1970). If they become anadromous, smoltification occurs at 140 mm or longer (Wilder, 1952; Smith and Saunders, 1958; Saunders et al., 1974, 1975; Dutil, 1976). Under exceptional conditions first reproduction may occur at 0+ yr (Wydoski and Cooper, 1966) but more usually it occurs at age 2+ yr (Scott and Crossman, 1973) or at a size of 137 - 140 mm (Ricker, 1932; Frost, 1938). As in other salmonids, males mature earlier than females. Both sexes are iteroparous. In the southern and intermediate part of their range mature individuals spawn every season. In the north where resources are limited, females may only spawn in alternate seasons (Vladykov, 1956; Power, 1980).

Anadromous brook trout descend rivers during April and May in Maritime Canada (White, 1940, 1941, 1942; Smith and Saunders, 1958). Dutil and Power (1977) reported that trout had moved into saline water by May 26 in the Richmond Gulf area (east of Hudson Bay). Return migration occurs in June - July in the Maritimes (White, 1940, 1941, 1942; Smith and Saunders, 1958; Castonguay et al., 1982) and July - August further north (Coleman, 1970; Dutil and Power, 1977). Maritime trout also migrated out of the river during late fall (October - December) and returned in early spring (Smith and Saunders, 1958). Experimental work by Saunders et al. (1974, 1975) indicates that low temperatures (<0°C) and full seawater (30 °/₀₀ salt) are a lethal combination for brook trout, suggesting that the winter migrations are only to brackish waters. Towards the southern extent of their range, brook trout migrate to sea after spawning, spend the winter in marine waters (winter sea temperatures remain well above zero at these latitudes) and return to the cooler freshwater during summer (Mullen, 1958 from Power, 1980).

Growth rate is variable throughout the species range; Carlander (1969) summarized much of the early literature. Hazel (1976) provides growth curves for 50 populations, many from introduced populations that Power (1980) suggests "represent an artificial, somewhat temporary, condition" (p. 163). Growth rates for natural populations tend to range from 3 to 7 cm/yr, with asymptotes of less than 40 cm for freshwater fish if they survived 10 years and perhaps 60 cm for anadromous trout that survived 15 years (Fig 12 in Power, 1980). Fish of these ages are seldom found. Unlike lake trout (*S. namaycush*) and arctic charr (*S. alpinus*), brook trout are short-lived and rarely exceed 5 yrs of age except in the extreme northern part of their range (Scott and Crossman, 1973). Power (1980) provides a list of authors who found trout of ages greater than 6+ yrs.

Anadromous trout not only grow larger but also are of a different shape than freshwater residents. "Salters are thicker-bodied but less deep than freshwater trout and tend to be somewhat heavier at similar lengths (Bigelow,1963), but these differences did not seem statistically significant (Wilder, 1952)" (Carlander, 1969; p. 247). Wilder (1952) found more variation (both meristically and morphologically) within a habitat than between habitats in his attempts to elucidate differences between resident and anadromous trout. Carlander (1969) verifies that length weight relationships and condition factors vary much more locally than by region or major type of habitat (p. 247). Shapes of *Salvelinus* species were best described by weight-on-length regression slopes of 3.15 but brook trout varied from 2.781 to 3.213.

Brook trout are insectivorous (especially drift) when young and become piscivorous with age. Their habitat determines diet as well as major predators (usually avian or mammalian). Brook trout are host to many parasites (Power (1980) provides a recent list) but the host and parasite seem well adapted to each other as serious deleterious effects of infestation are rare. When sympatric with other salmonids, competition is reduced by habitat segregation, (Keenleyside, 1962; Gibson and Keenleyside, 1966; Gibson, 1966) but Atlantic salmon and lake trout may both displace brook trout (Gibson, 1973). Brook trout may be able to displace arctic charr (Power, 1980). Little information is available on interactions with non-salmonids.

1.5 Study Site Description.

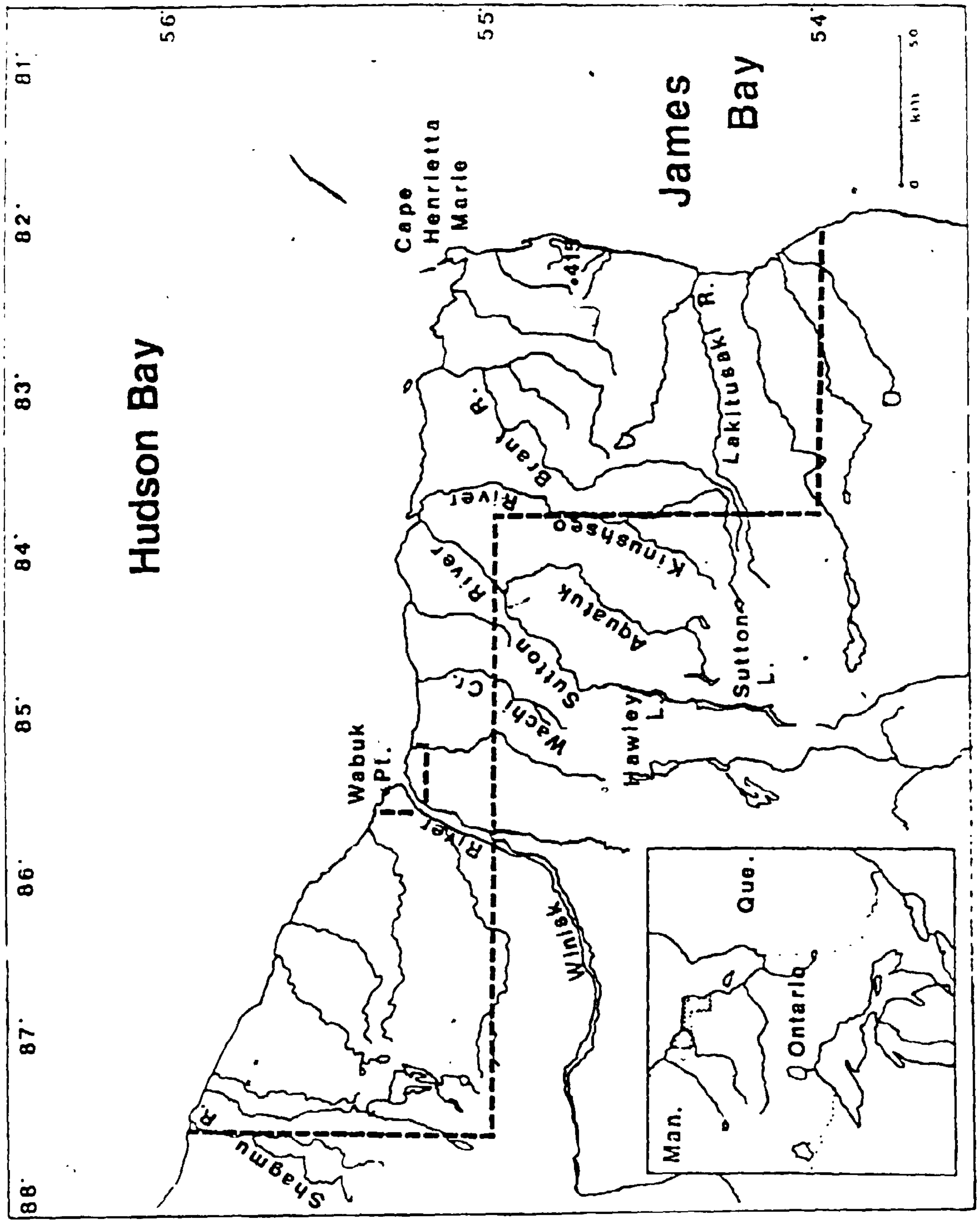
1.5 a) General.

The Hudson Bay Lowland is a low lying, poorly drained sub-Arctic wetland that stretches along the James Bay and Hudson Bay coastline from Quebec to Manitoba and inland a distance of 200 km. These lowlands comprise 1/4 of Ontario by area. One of the largest parks in the world, Polar Bear Provincial Park (24,087 km^2), is situated within this area and along part of this 6000 km marine coast of Ontario.

Polar Bear Provincial Park (P.B.P.P.) was chosen as a study area as it is one of the more northerly boundaries of the range of anadromous brook trout in the world (Scott and Crossman, 1973) and climatically may represent the species' most northerly habitat (Ministry of Natural Resources, 1977). Also advantageous is that the brook trout in this area have till now been relatively free of exploitation, due to the inaccessibility of the park area. The area is accessible only by air (4 1/2 hr flight from either Moosonee or Hearst, Ontario) and has a population density of 5 people per 1000 km^2. However, recent increases in the number of aircraft landing permit applications and non-native park use suggest that this is changing and that the fishery resources of the area will come under increasing exploitation in the near future. In response to this anticipated change, Ontario's Ministry of Natural Resources (M.N.R.) has undertaken research to allow the formulation of a fisheries management plan that will retain pre-exploitation aspects of the fish populations. It is of further interest to determine what is unique to this area that allows P.B.P.P. to be a consistent producer of trophy sized brook trout.

Central to the park, and 100 km east of Winisk, is Sutton River (Fig. 1). The Sutton River originates south of P.B.P.P. as the outflow of Hawley Lake (54°30′ N, 83°40′ W) and flows northward for 120 km to empty into Hudson Bay (55°15′ N, 83°45′ W). The river has one major tributary, the Aquatuk River that enters the Sutton 45 km upstream from the coast. Most of the tributaries of the Sutton river are intermittent creeks that drain the surrounding bog. These creeks seldom exceed 500 m in length and often enter the river by seepage through the gravel river banks. The river between Hawley Lake and Aquatuk River alternates between slow (<1 m/s) and shallow (<1 m) meandering stretches and fast flowing riffles (average gradient, 0.9 m/km). Downstream of the Aquatuk, there are few fast stretches (average gradient, 0.6 m/km). Accompanying the decrease in gradient is a general increase in river width from an average of 300 m upstream of the Aquatuk to an average of 1000 m downstream of the Aquatuk. The river bottom varies with current velocity from coarse rubble to fine sand. Only immediately downstream of Hawley Lake is there any organic substrate (mud and ooze). This coincides with the site of a native family's traditional camp (which may be approx. 1000 yr.s

Figure 1. Map of the Sutton River watershed and vicinity indicating locations of major rivers and lakes.


Hudson Bay
James Bay
Cape Henrietta Marie
.415
Brant R.
River
Lakitusaki R.
Kinushseo
River
Aquatuk
Sutton
Sutton L.
Hawley L.
Wachi Cr.
Wabuk Pt.
River
Winisk
Shagamu R.
56°
55°
54°
81°
82°
83°
84°
85°
86°
87°
88°
0
km
50
Que.
Ontario
Man.

old) and thick stands of aquatic macrophytes such as *Hippuris vulgaris, Potamogeton spp.* and *Myriophyllum spp.*.

Spring flooding (late May, early June) is severe for the Sutton River. The rivers "overflow their inadequate banks, turning the surrounding land into a veritable silt-laden lake" (M.N.R., 1977, p. 19.). Ice scour up to 8 m above the summer river level south of the tree line can be observed as well as transported river debris that has been left on the tundra hundreds of metres from the river. In addition, coastal areas are frequently flooded by spring and storm tides.

1.5 b) Base Camp Location.

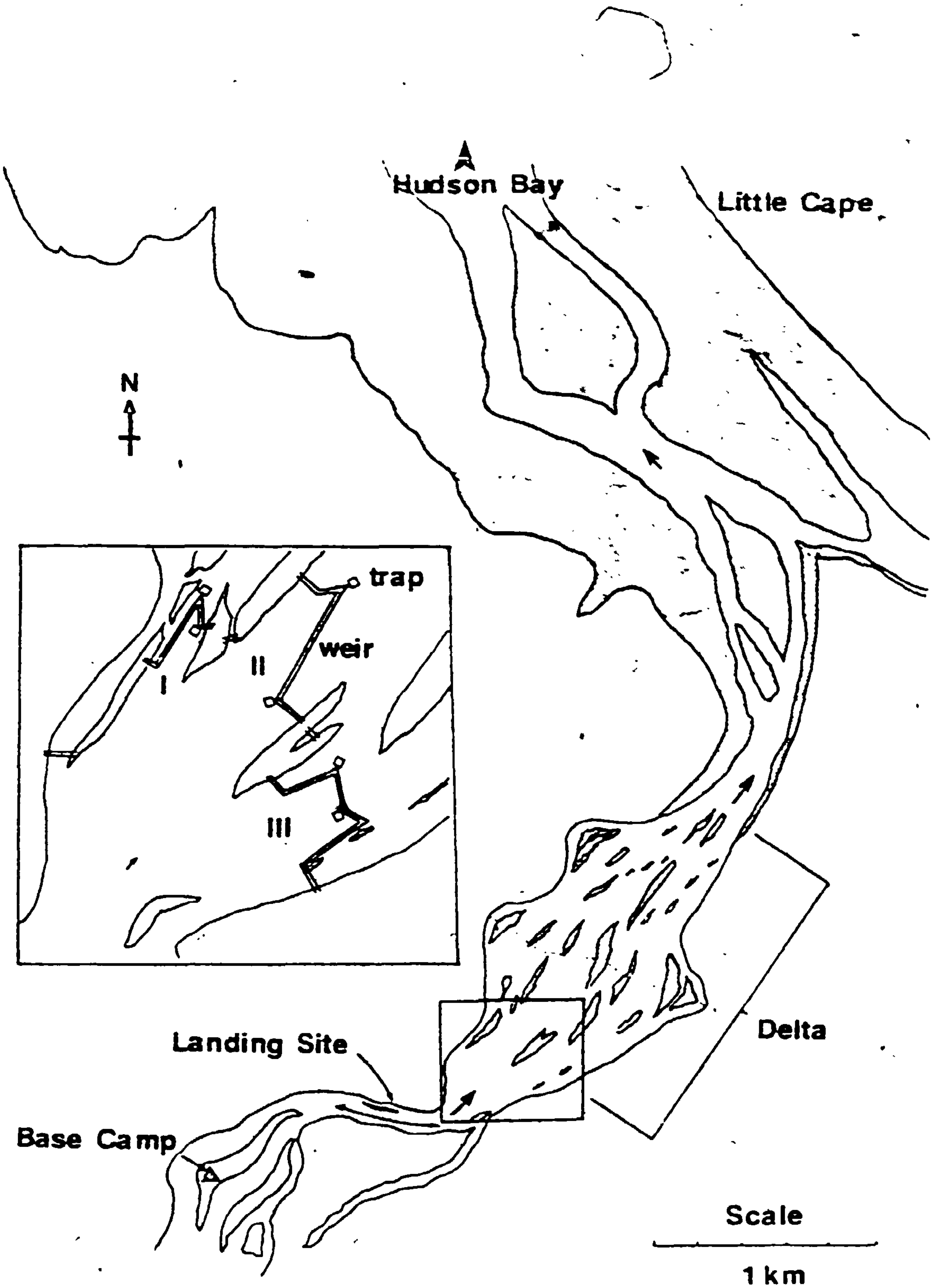
To verify the predictions about the life history of these trout it was necessary to study the fish as they migrated in and out of the Sutton River. This required locating as close to the tidal zone as logistically feasible. The summer high tide mark is in the delta, a 3.7 km stretch of shallow (<20 cm) river (Fig. 2). Islands in the delta were of low relief and frequently flooded during storm tides. A weir was built at the head of the delta and above tidal influences. Immediately above the weir was the only stretch of the river that was deep enough and straight enough to land float planes on during high water. The first sizeable island above the Landing Site that was dry and was not likely to flood, was chosen to establish the Base Camp.

This island was 2.2 km above the weir site (Fig. 2). Base Camp was occupied from June 10 to September 28, 1983 and May 24 to September 30, 1984.

1.5 c) Regional Geology.

The headwaters of the Sutton River are situated on a Precambrian rock outcropping that is bisected by a north-east south-west fault (Hawley and Sutton Lakes). The rest of the area's bedrock is a limestone, dolomite, siltstone, shale, mudstone, sandstone and chert mixture that when exposed to the river renders the water alkaline (pH = 9.0). Prior to 7000 years ago, the area was covered with 3000 m of ice that depressed the land by 550 m. Since then the land has been isostatically rebounding at rates faster than 1.2 cm/yr. This results in an additional 20 cm of beach each year at the coastline. After the glacial retreat, the area was covered by the Tyrrell Sea. The Tyrrell Sea receded from the area of the headwaters of the Sutton River approximately 4000 years ago, from the area of the tree line 2000 years ago, and from the coastal plain 1000 years ago (M.N.R., 1977). It left behind a 3 to 11 m deep layer of impervious marine clay which is responsible for the inadequate drainage of the area. This area "has a greater percentage [75%] of surface water than any other section of land of similar size on the North American continent" (Coombs, 1954, p. 69 in M.N.R., 1977). Only 10 percent of the area is sufficiently drained to support tree growth.

Figure 2. Detailed map of the Sutton River mouth and vicinity indicating locations of the weir and Base Camp. Weir channels are denoted with roman numerals in the insert. Shaded areas are submersed at high tide (indicated by dotted line).


Hudson Bay
Little Cape
N
trap
weir
I
II
III
Landing Site
Base Camp
Delta
Scale
1 km

1.5 d) Regional climate.

The climate of this region is extreme with daily temperature fluctuations of up to 45°C within 12 hrs and wind speeds of up to 170 km/hr. The area is overcast 80% of the year and receives greater than 20 cm of rain and 200 cm of snow yearly. Permafrost is seldom more than 1 m below the surface of the ground.

Spring does not arrive till late May or early June. This is also the time of the last major snowfall and when the ice starts to break up on the Sutton River. The mean April temperature is -9.4°C and the prevailing winds are from ice-covered Hudson Bay.

Summers are cool (mean July temp., 11.7°C) due to the sea ice which remains till mid-August (Plate 1). Although prevailing winds are still from the north-east, low pressure cyclonic activity invades the area from the southwest at intervals of 3 to 4 days. Hence it rains 1 of every 3 days. Summer is also the time of extensive fog which makes air travel difficult.

The rain turns to snow by September and is accompanied by freezing temperatures and severe wind storms from the high Arctic. Lakes start to freeze in October as does Hudson Bay. The mean temperature in October is -1.6°C. Autumn ends with a mean snowfall of 34.3 cm during November.

Plate I. Aerial view of the mouth of Sutton River at low tide, mid-June, 1984. The river had been ice-free for two months at this time. The Bay ice persisted for an additional 1.5 months (till August).

[redacted]

Winter is cold and harsh. The winds remain severe and temperatures may plummet to -50°C for weeks on end. Snow often accompanies the gale force winds causing severe and prolonged blizzards. As such, "Polar Bear Provincial Park is part of one of the windiest areas of Canada ... continual brisk winds and cold temperatures make the Hudson Bay area the coldest place in North America on the basis of wind chill" (M.N.R., 1977, p. 12). During winter, tundra and Hudson Bay are indistinguishable and the rivers freeze to the bottom in all but the deepest pools.

1.5 e) Regional Flora and Fauna.

Although over 33 vegetational patterns have been identified in the Park (M.N.R., 1977), only two major classifications need be considered; transitional forest and tundra. Transitional forest is restricted to drained areas such as river banks. The dominant species of this type of boreal forest include black spruce (*Picea mariana*), larch (*Larix laricina*), balsam popular (*Populus balsamifera*), dwarf birch (*Betula glanulosa*) and a variety of willows (*Salix spp.*). Growth can be extremely slow (7 mm/yr) near the coastal plain were there is little protection from the elements; trees often grow in candelabra formations.

Tundra includes both bog (treeless fen), coastal plain and raised beach ridges. The vegetation is typical of low Arctic with plants such as sedges (*Carex spp.*), horsetails

(*Equisetum spp.*), Lapland rosebay (*Rhododendron lapponicum*), and saxifrax (*Saxifraga spp.*). In muskeg bogs sphagnum (*Sphagnum spp.*) may accumulate at rates of up to 1 cm/yr (M.N.R., 1977).

The dominant fauna are the blood sucking insects for which the Lowlands are infamous. Mosquitos alone may exceed densities of 12 million per hectare (M.N.R., 1977). In addition to mosquitos, there are numerous members of the blackfly family, (Simuliidae) and of the tabanid tribes (biting midges, deerflies, horseflies). During summer, migratory birds (only a half dozen species remain during winter) including insectivorous warblers, birds of prey and waterfowl nest in the area. Mammals are comparatively scarce with polar bears, timber (Arctic) wolves, caribou, seals and whales being most noticeable.

Surveys of the Lowland fish populations have been infrequent and incomplete. Scott and Crossman (1973) listed 1 acipenserid, 6 salmonids (3 charrs including brook trout and 3 whitefish), 1 esocid, 6 cyprinids, 3 catostomids, 1 gadid, 3 gasterosteids, 1 percopsid, 3 percids and 3 cottids as native species in the Sutton River area. Zalewski and Weir (1981) added 15 species to the species list of which two were from Sutton River (a cyprinid and a percid). Steele (in ms) added a new family to the list (Petromyzontidae). Less is known about the near-shore marine environment of

Hudson Bay (Bajkov, 1975; Beals, 1968; Morin et al., 1980; and Leim & Scott, 1966). It is apparent that much work needs to be done before a complete list can be published.

2. METHODS.

2.1 Physical Characteristics.

2.1 a) Water Levels.

Water levels were monitored at least once daily at both Base Camp and at Landing Site. The water gauge at Base Camp was upstream of the camp at the head of the central river channel in slow (<1 ms^{-1}) flowing water and was therefore uninfluenced by either the weir or camp. Data from this gauge were used for within and between year comparisons. The water gauge at Landing Site was 350 m upstream of the weir and was influenced by weir operation. Elevated water levels at the weir were reflected by elevated water levels at this gauge. Data from this gauge were not used for comparison but rather as indicators of weir maintenance and the condition of the Landing Site for float planes.

2.1 b) Water Temperature.

A continuous recording submersible thermograph (Model J, Peabody Ryan Inc., Seattle, Washington, U.S.A) was stationed upstream of Base Camp for the duration of field operations. The instrument was submerged 20 cm below the surface, 80 cm above the bottom, and in a moderate (1 ms^{-1}) current. Once monthly the instrument was recovered, charts and batteries replaced and the clock checked. Data recorded from this instrument were used for comparisons within and between years.

In addition to the thermograph, minimum-maximum thermometers were used at each water level gauge to monitor river temperature. The thermometers were read and reset each morning when water levels were recorded. Minimum-maximum thermometers were also maintained at each upstream trap of the weir during 1983. This was discontinued for 1984 as temperatures at the weir were influenced (+/- 2°C) by weir operation.

2.1 c) Discharge estimates.

Discharge rates were estimated from depth profiles and surface current velocities. Depth profiles were constructed by erecting a line across the river at the water level gauge at Landing Site and determining at 5 m intervals, the river depth to the nearest 0.5 cm. Surface velocities were estimated by averaging the time that it took for a plastic practice golf ball to drift 10 m during three trials. Surface velocities were measured on July 11 and August 7, 1984 when water levels were 56 and 46 cm respectively.

2.2 Pre-weir.

Previous to weir construction each year attempts were made to recover trout from Sutton River. Angling was also employed during the week of March 24, 1983 to capture fish under the ice at a site immediately above the Base Camp. Angling (spin casting and fly fishing), gillnetting (standard survey meshes) and electrofishing (7.5 kilowatt unit) were employed to capture fish within the river during June, 1983. Angling alone was used during May 25 to June 21 of 1984. Numerous locations from 1 km downstream of the weir site to 8 km upstream of the weir were fished both years. These fish were treated in a manner similar to fish killed at the weir (see 2.3 d).

2.3 Weir.

2.3 a) Weir Location.

Factors that determined the site of the fish weir included: distance above high tide mark, river width, river bed composition, river bed topography, prevailing current velocities, river bank development, potential for the containment of flood waters, availability of 'deep' holes, location of potential spawning sites, and proximity to both aircraft landing sites and dry ground for camping.

Logistical problems were reduced by locating the weir close to an aircraft (float) Landing Site and Base Camp. This reduced the distance that gear, construction materials and supplies were carried over the muskeg and bogs. The weir was located upstream of the influence of the tide to minimize rotation of stress vectors on the weir and to ensure that any trout caught at the weir were in fresh and not brackish water. Logistical and maintenance concerns were minimized by avoiding extreme river widths and current velocities. Bank development at the site was sufficient to allow the weir to butt onto the banks, but not so much as to contain and funnel flood waters onto the structure; it was preferred that flood waters were diverted elsewhere (i.e., into dry riverbeds and onto the flood plain). The absence of deep water downstream of the weir, that may have supported a resident trout population, ensured that all upstream swimming trout were from Hudson Bay and not residents of the river. All potential spawning sites were upstream of the weir ensuring that migrating spawners would pass the weir. The riverbed at this site was a marine clay covered with gravel and boulder.

2.3 b) Weir Construction.

The weir was constructed across the entire width of the river (700 m) so as to form a 'Z' or 'W' shape within each of the three major channels (Fig. 2). Traps facing either upstream (3) or downstream (3) were placed at each apex. Lesser channels were blocked by weirs perpendicular to the current; no traps were placed in these channels.

The basic components of the fish weir were steel snow fence stakes (2 m long), lumber (5 cm x 10 cm), and welded wire fabric (2.5 cm square). The snow fence stakes were driven by sledge hammer into the gravel clay river bed to a depth of approximately 0.5 metre. A lumber frame was constructed in place and wired onto the steel stakes; wire fabric was nailed on the upstream side of the lumber so that a minimum of 35 cm of overlap with the river bed existed. Rocks were placed on top of the fabric to ensure a 'fish tight' seal with the river bed (Fig. 3).

The fish traps were constructed from lumber (both 2.5 cm x 5 cm and 5 cm x 10 cm pieces), plywood (8 mm) and wire fabric (1.2 cm square). The traps were wired directly into the wire fabric of the weir and the positions stabilized against the current with snow fence stakes (Fig. 3).

2.3 c) Weir Operation.

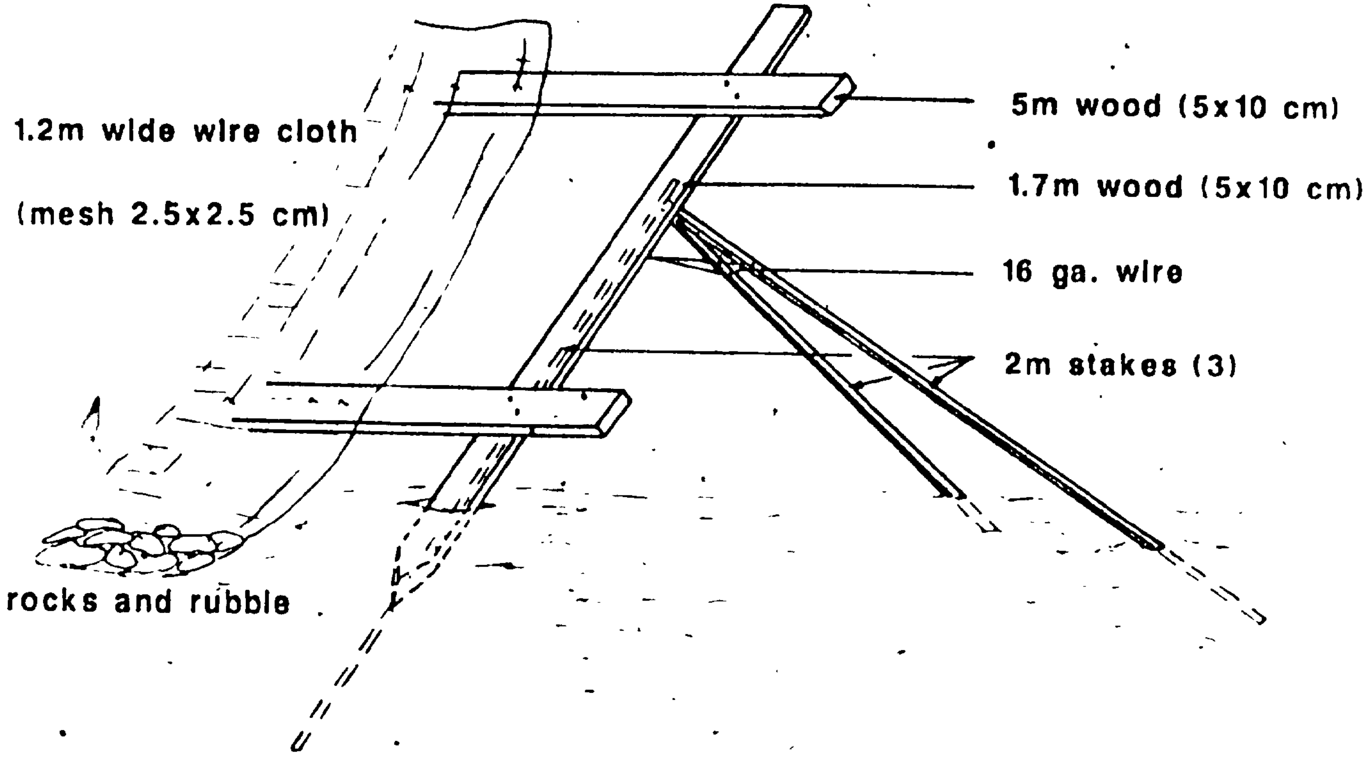
The weir was cleared of debris at least once daily, and was scrubbed with wire rakes and/or wire bristled brooms as required (every 6 to 48 hrs) to prevent the accumulation of a head of water. Damage or erosion noted during cleaning was repaired immediately. During high water, the weir was checked, cleaned, and repaired by snorkelling.

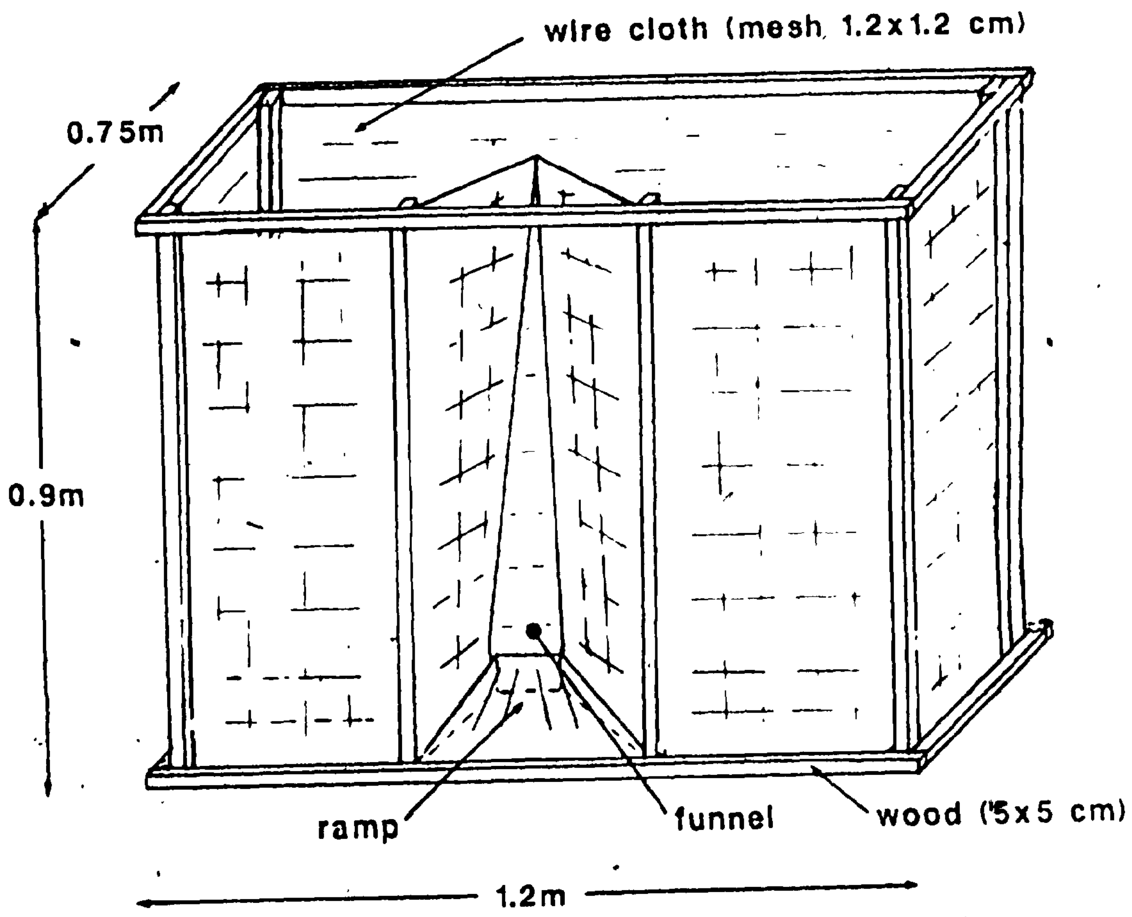
All traps were checked and emptied of fish every morning and if necessary again in the evening. Non-trout species were identified, counted, and passed over the weir.

2.3 d) Handling and tagging of fish.

All live trout were measured (total and/or fork length) to the nearest mm and tagged with a numbered oval plastic tag that was attached to the fish either by a *Floy* double anchor dart tag or sutured to the base of the dorsal fin with 4.5 kg test monofilament. Fish were tagged so that the population size and age specific mortality rates could be estimated, spawning frequency and migration routes determined, and ageing and length at age estimates verified.

Figure 3. Detail of weir and trap construction.


1.2m wide wire cloth
(mesh 2.5x2.5 cm)
rocks and rubble
5m wood (5x10 cm)
1.7m wood (5x10 cm)
16 ga. wire
2m stakes (3)



N.B., Plywood top not shown.

They were weighed (+/- 1%), and released on the opposite side of the weir. Trout captured in July of 1983 were anesthetized with Tricanine methane sulfonate (MS 222), before being handled. This was found to be unnecessary and was discontinued during early August; for the remainder of the project, handled trout were placed inside a wet wool sock to placate them. Trout tagged with *Floy* tags during 1983 were tagged ventral to the adipose fin; all other fish were tagged ventral to or anterior and ventral to the dorsal fin. The date, weir channel, direction (upstream or downstream), presence of lamprey or other marks, as well as general remarks about the individual fish were recorded on a numbered scale sample envelope along with other pertinent information. Scales or other material for ageing were not taken from fish that were to be released.

Sacrificed trout were placed in plastic gillnet boxes and brought back to the Base Camp for examination. In addition to recording the above information, scales, pectoral fin rays and sagittal otoliths were removed for later analyses. The fish were dissected so that sex and state of gonadal maturation could be determined. All trout identified as females were further assigned to one of seven maturity stages (Table 1). Stage three did not discriminate between immature fish with large gonads and mature (previously spawned) fish with gonads that were at the minimum annual size. Hence, mature trout sampled during spring or early summer were classified to the same stage of

Table 1. Classification stages used to describe female maturation. This scheme is similar to that used by some Ontario M.N.R. creel survey crews.

Stage		Description.
1	Immature	Gonads are just visible to the naked eye. Sex determination is not possible.
2		Gonads are visible, but very small. Sex determination is difficult and unsure.
3		Gonads are easily visible, sex determination is distinct, atretic eggs may be present in fish that have spawned before. This is the minimum annual gonad size attained by mature fish and the maximum gonad size attained by immature fish.
4	Mature	Gonads are under going rapid expansion in preparation for reproduction. Individual eggs are readily visible by the end of this stage.
5		Prespawning stage, gonads are at maximum size for this reproductive event but the eggs are still contained within the ovary.
6		'Ripe and runny'. The eggs have been liberated from the ovary into the body cavity. Spawning will take place within two or three days.
7		The female is spent. A few eggs may remain in the body cavity but the majority have been extruded. Blood is evident throughout the ovary.
8	Other	Abnormal ovarian state: there may be a restriction in the ovary, tumour growth or some other condition that distinguishes this fish's ovaries from the rest of the population.

maturity as fish that had never spawned. This classification system, therefore, under-estimates the number of mature females in a sample. This under-estimation approaches 100% in April through early-July, and 0% during August to October. Stomachs were examined for contents (presence or absence). Stomach contents were identified and the presence of any macro parasites or internal abnormalities noted.

The area between the weir and Base Camp was examined daily for dead fish. Any carcasses that were discovered were recovered, identified as to species and if they were trout were examined for tags. Any additional information that could be obtained from the carcasses was recorded. All recovered carcasses were buried to prevent attracting skunks and polar bears.

2.4 Ageing.

Scales, fin rays and otoliths were collected from dead trout for the purpose of ageing the fish. Although numerous trout were sampled, only a proportion of material collected was aged; selected samples were aged by each of these three methods and the results compared by ANCOVA.

Scales were removed from dead fish from the left lateral area dorsal to the lateral line, anterior to the dorsal fin, and caudal to the pectoral fin. At least 12 scales were removed from each fish with either forceps or a sharp knife; instruments were rinsed after each use to avoid contaminating the next sample with excess scales from previous samples. Scales were placed in numbered paper M.N.R. scale envelopes to dry. Cellulose acetate impressions rolled from cleaned and dried scales were projected on a trichinoscope for reading.

Leading left pectoral fin rays were disarticulated and dissected away from the fin membrane. The rays were stored and dried in numbered scale envelopes. Dried fin rays were mounted in an epoxy resin, thin sectioned with a jeweller's saw, mounted on a glass slide and examined with a microscope under low power.

Sagittal otoliths were collected from trout by a sagittal incision that bisected the cranium. The sagittae were removed by knife point, separated from the sacculus on the back of the opposing hand, and placed in the numbered scale envelopes to dry. Dried otoliths were fractured through the nucleus, burnt in a flame, and mounted in plasticine. The otoliths were read with a dissecting scope and reflected light.

Scale impressions, fin ray sectioning and otolith burning were performed and read by Jon Tost; his results were verified by Dr. J. Casselman (Fisheries Research Branch, M.N.R.).

Notation used for ages was that commonly used (Tesch, 1971); the number indicates the number of annuli that are present on the ageing structure (i.e., scales, fin rays, otoliths) and the "+" indicates growth that has occurred since annulus formation.

2.5 Parr.

One thousand parr were seined from waters upstream of Base Camp between July 16, and August 13, 1984. Dependent on the area from which the parr were captured, either a pectoral, pelvic, or adipose fin, or a combination was removed before the fish were released into the same waters from which they were captured. After August 15, downstream of the weir was seined in an attempt to recover fin clipped parr.

In addition, parr were measured (total and fork length) to the nearest millimeter at arbitrarily chosen times throughout the summer of 1984. A few were preserved in 70% ethanol or 10% formalin.

Parr behaviour and interactions were observed *in situ*, by snorkelling, at irregular intervals throughout the summer of 1983 and 1984. Larger fish were not observable by snorkelling; they were too skittish and fled at a swimmer's approach. Larger trout however, could be observed from boats or by wading (within 2m).

2.6 Salinity Bioassay.

Static bioassays were used to determine the salinity tolerance of trout parr. The parr were seined from waters around the Base Camp three days prior to testing and were maintained in 45 litre plastic pails of river water at prevailing river temperatures.

Salt solutions used for the assays were made by adding a commercial sea salt composition (Instant Ocean, Aquarium Systems, Ohio) to unfiltered river water. Test fish were placed directly into the solutions without acclimation, at a density of one fish per 4 l. Temperature and photoperiod were allowed to vary with prevailing natural conditions in the river during the assays.

Assays were initiated in the mornings and continued for 132 hrs. Observation times were those suggested by Sprague (1973). Dead fish were removed, blotted dry, measured (total and fork length), weighed and preserved. At the end of each assay, all remaining fish were killed and treated similarly.

2.7 Fecundity.

Ovaries were collected from ripe or almost ripe females that were killed for blood analysis in 1985. The dead fish were measured and weighed before the ovaries were removed and preserved in 10% formalin. In the laboratory, the number of eggs in each ovary was counted and the egg number of the two ovaries from each fish was regressed. Outlying points of the regression were discarded as abnormal and the log total number of eggs for each female was regressed (geometric mean regression, Ricker; 1973) against the log of the corresponding fork length.

3. RESULTS.

3.1 Physical Characteristics.

3.1 a) Water levels.

Water levels between years were not comparable due to ice damage to measuring gauges during the winter of 1983 - 1984. Gauge replacement may account for differences of up to 5 cm between years in mean water height. Measurement of water fluctuations within years was not affected by annual replacement of gauges. Water levels during 1983 were more variable than in 1984 (Table 2). This was a result of frequent convectional thunderstorms that dominated the weather in 1983. Rain was scarce and spring runoff was early during 1984. Furthermore, snow cover was sparse (<1 m) during the winter of 1983 - 1984 and the Sutton River was ice free 1.5 months earlier than usual in 1984 (pers. comm., Ontario Ministry of Natural Resources, Moosonee District). Water levels declined continuously during July and August of 1984 with the exception of a single event on July 23 (Fig. 4).

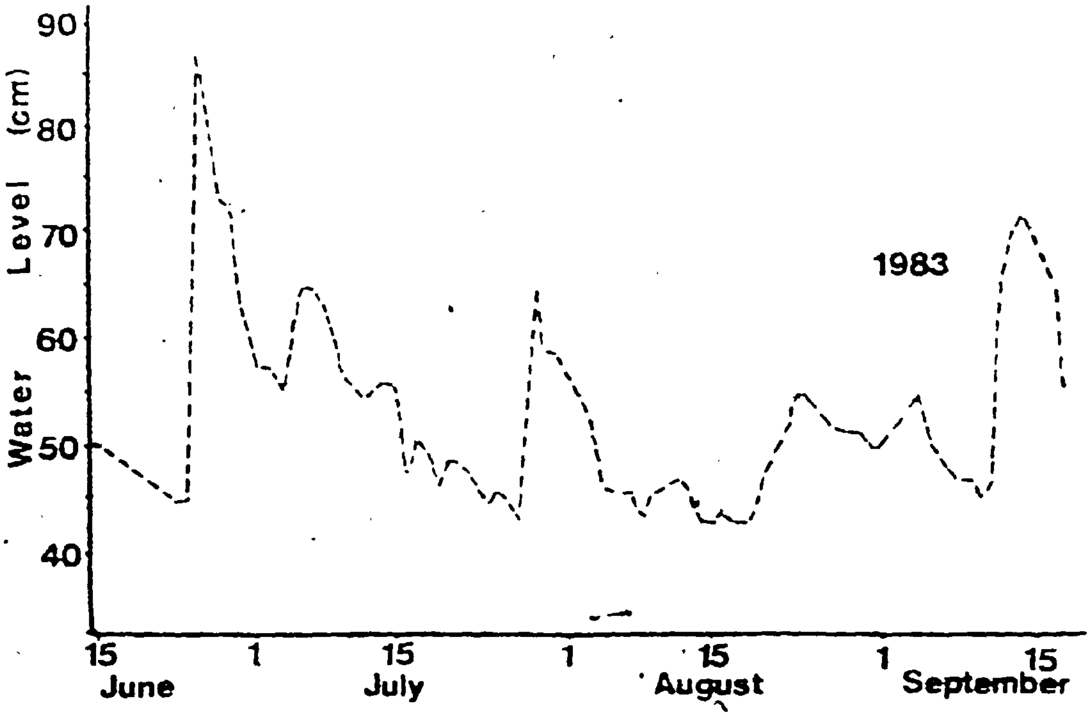
3.1 b) Water temperature.

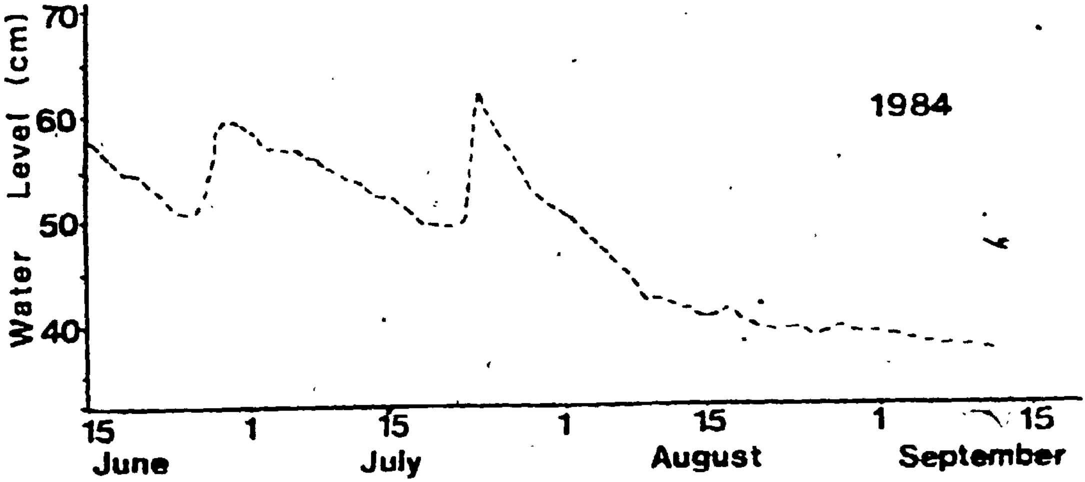
Malfunctions of the continuous recording thermometer during 1984 caused a loss of data. On June 10, 1984 the charting mechanism jammed and this was not discovered until

Table 2. Water level fluctuation at Base Camp on the Sutton River, 1983 and 1984.

Year	Seasonal		Daily Fluctuations		
	Mean (cm)	Range (cm)	Mean (cm)	Range (cm)	S.D. (cm)
1983	54.3	45.0	2.88	42.5	5.54
1984	49.0	23.5	0.89	8.0	1.29

Figure 4. Daily water levels of the Sutton River measured at Base Camp. Levels are not comparable between years due to gauge replacement.


90
80
70
60
50
40
Water Level (cm)
1983
15
June
1
15
July
1
15
August
1
15
September


70
60
50
40
Water Level (cm)
1984
15
June
1
15
July
1
15
August
1
15
September

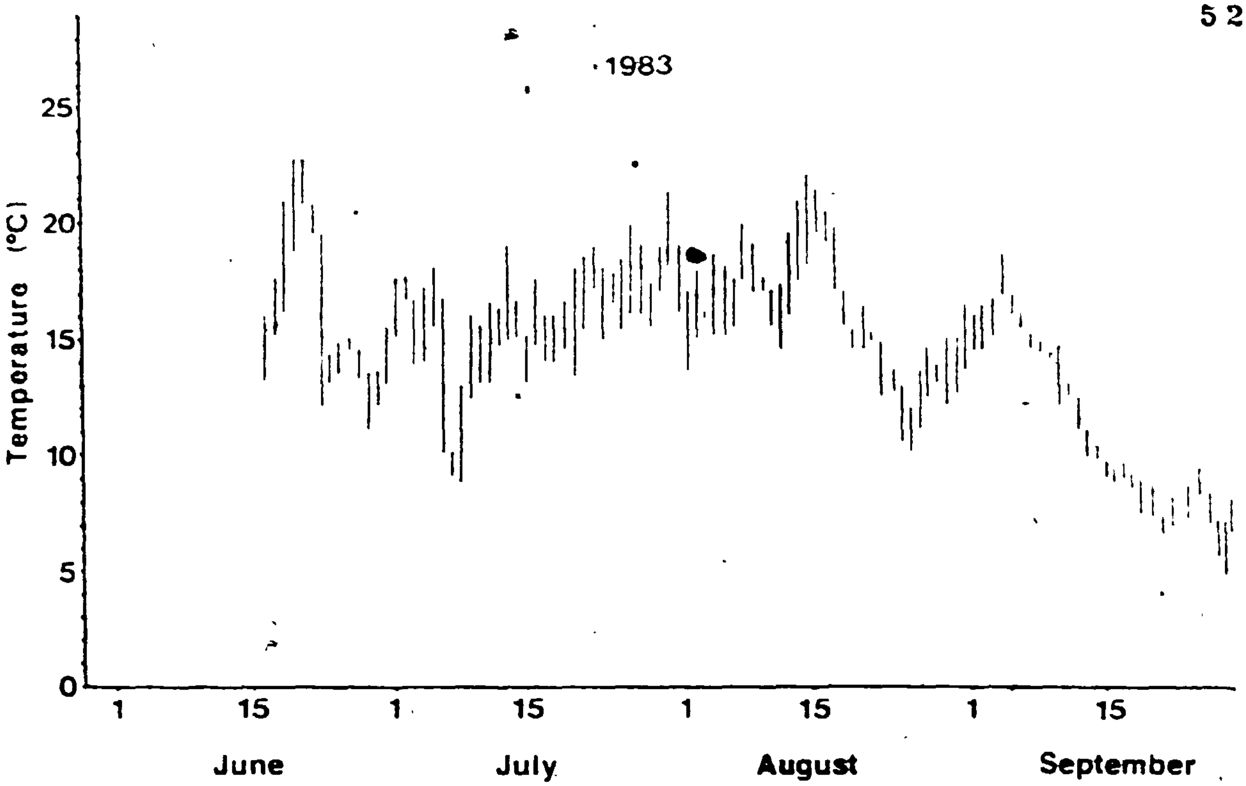
June 18; and on August 15, 1984 the chart mechanism jammed and disintegrated rendering the instrument useless for the rest of the season.

Lower water levels during 1984/were coupled with greater fluctuations in water temperature (Fig. 5). Daily water temperature fluctuations during 1984 were twice those observed in 1983 (Table 3). However, mean temperatures were similar (15.6°C and 15.2°C respectively).

3.1 c) River discharge estimates.

Discharge estimates were available for only two water levels during 1984 (Table 4). These estimates assumed constant velocities irrespective of depth. This is not a valid assumption as surface currents were positively correlated with location depth (Table 4). Hence, reported discharge estimates are probably greater than true values.

Figure 5. Daily water temperature of the Sutton River as measured at Base Camp. Data collected by minimum-maximum thermometers represented by dashed line.


1983
Temperature (°C)
0
5
10
15
20
25
1
15
1
15
1
15
1
15
June
July
August
September

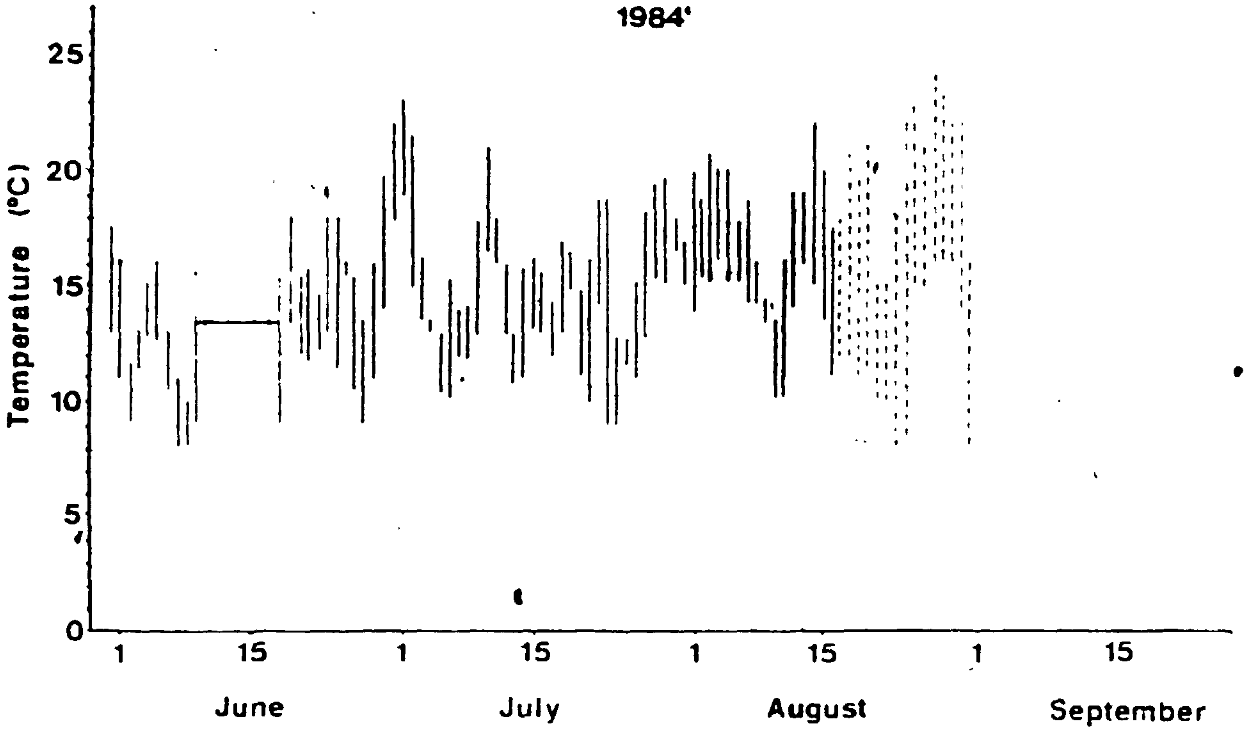

1984
Temperature (°C)
0
5
10
15
20
25
1
15
1
15
1
15
1
15
June
July
August
September

Table 3. Daily water temperature fluctuation at Base Camp on the Sutton River, 1983 and 1984.

Year	Daily Mean High (°C)	Daily Mean Low (°C)	Daily Fluctuation Mean (°C)	Daily Fluctuation Range (°C)	Daily Fluctuation S.D. (°C)
1983	16.9	14.4	2.5	5.1	1.1
1984	17.6	12.9	4.6	9.5	2.4

Table 4. Discharge estimates and current depth regressions for two water levels of the Sutton River, 1984.

Water Level (cm)	Discharge Estimate ($m^3 s^{-1}$)	Maximum Current ($m\ s^{-1}$)	Depth Current Regression	r^2 (adj.)
46.0	13.3	0.23	C=0.01 + 1E-4(D)	0.69
56.0	192.1	0.49	C=0.07 + 2E-4(D)	0.74

3.2 Weir.

3.2 a) Construction and operation.

The weir was operated at different efficiencies during the two seasons (Table 5). In 1983 high water, inexperience, and lack of manpower delayed construction. The 880 m weir was brought on line at 100% efficiency on the morning of July 17. Ten days later flood waters removed the weir on Channel I and caused extensive erosion deepening the channel by 2 m. The weir across Channel I was beyond repair for the rest of 1983. The 10 m portion of the weir furthest downstream on Channel II was also damaged beyond repair. The river bed at this site was so altered that it would no longer support the weir. Damage to the rest of the weir across Channel II and III was minimized by removing strategic portions of the weir with an axe at the peak of the flood. Repairs were quickly effected to the weir across Channel III and then Channel II. To prevent a similar occurrence in 1984, the weir was built with numerous removable gates to spill flood waters should high water levels occur. Previously, each channel had only one gate to allow boats to pass through.

Low water levels were a problem in 1984. Much of the weir (up to 50%) was out of water by the end of August. This reduced maintenance but also concentrated fish into several small shallow areas, stressing both whitefish and trout.

Table 5. Effectiveness and duration of weir operation during 1983 and 1984.

Year	Date (start) (end)	Duration (hr)	River blocked (%)
1983[1]	July 17 to July 27	240	100
	July 27 to July 31	96	0
	July 31 to Aug. 8	192	30
	Aug. 8 to Sept 12	840	60
1984[2]	June 20 to Sept 11	2016	100

[1] ice out June 1st.

[2] ice out last week of April.

While no trout were observed to jump the weir which often extended less than 20 cm above the surface in 1983, numerous trout jumped 1 m high sections of the weir at night during 1984. It is not known if low flow rates and water levels increased the likelihood of the trout to jump.

3.2 b) Trout migrations.

A total of 1381 trout was captured at the weir during 1983 and 3891 trout during 1984 (Table 6). Most of these trout were tagged (81% and 88% respectively), a few were killed for dissection (8% and 15% respectively) and a similar number died from unknown causes (11% and 14% respectively).

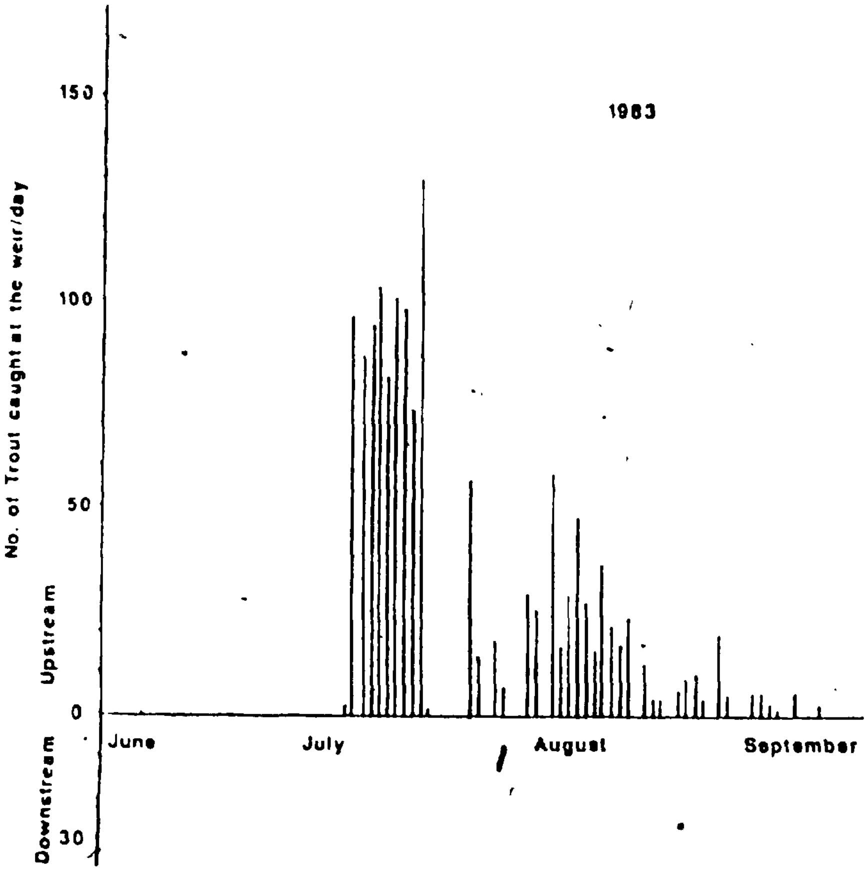
Trout entered the weir only during the night. There was little movement, especially in the delta, during the day. Movement of trout in the river occurred as discrete events or 'runs' lasting approximately two weeks each (Fig. 6). Attempts to describe the runs using two types of frequency analysis programs were unsatisfactory. Both of these programs rely on a defined number of normal distributions contained within the data set; they then attempt to optimize peaks and distribution widths. The methods are susceptible to outliers (days with few fish surrounded by days with many fish or vice versa), and do not always provide results that are intuitively satisfactory or biologically sensible. Statistically significant (p<0.05) results may be obtained

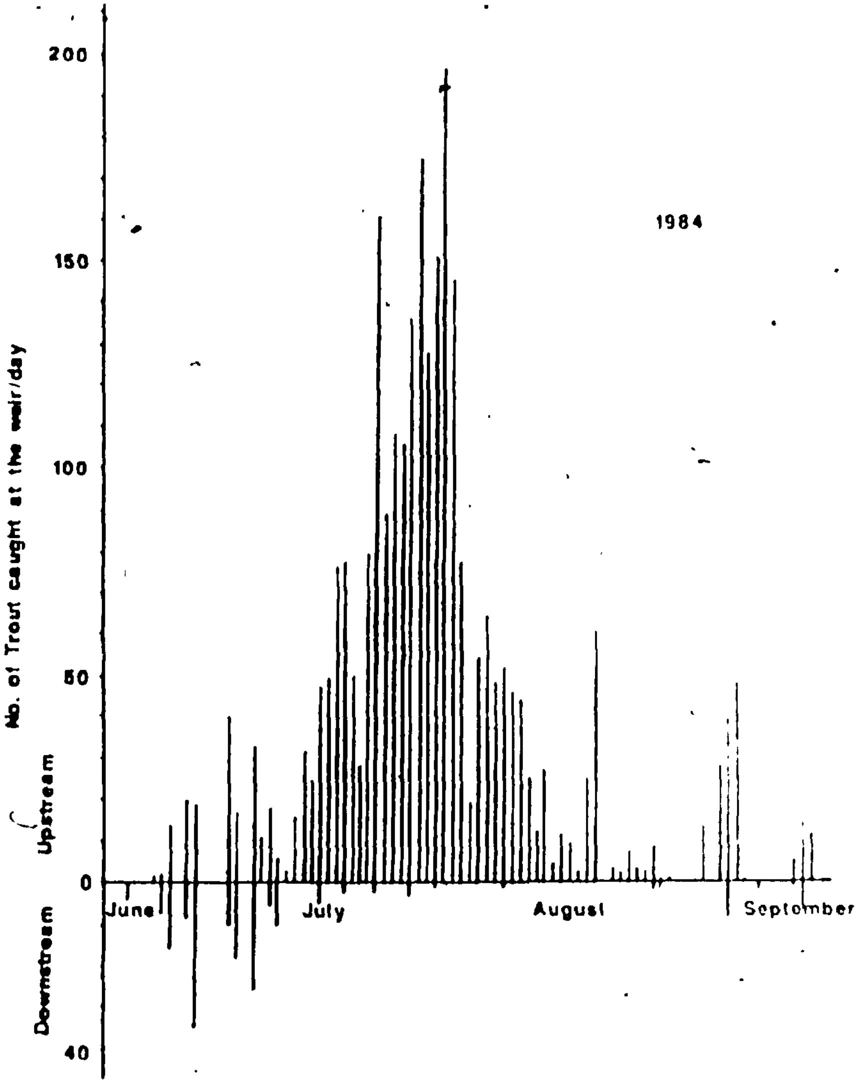
Table 6. Numbers of trout handled at the weir during 1983 and 1984.

Year	Killed	Tagged	Recapt.	Dead	Escaped	Other	Total
1983	109	1118	17	154	--	--	1398
1984	604	2649	37[1]	556	36	24	3906
Total	713	3767	54	710	36	24	5304

[1] 22 of which were tagged in 1983.

Figure 6. Number of brook trout passed through the weir for each day of operation during 1983 and 1984.


1983
No. of Trout caught at the weir/day
Upstream
Downstream
150
100
50
0
30
June
July
August
September


1984
No. of Trout caught at the weir/day
Upstream
Downstream
200
150
100
50
0
40
June
July
August
September

for differing numbers of distributions for the same data set. Attempts to redesign these tests to reduce their sensitivity to outliers and departures from normality severely handicapped their use without providing results any more satisfactory than commercially available programs. For these reasons frequency analysis approaches were abandoned in favour of less sophisticated methods of describing runs by direction, start, end and peak dates (Table 7).

Peak dates of runs occurred at similar times during 1983 and 1984 even though ice-out was 6 weeks early in 1984. The major run in both years occurred in July and was followed by runs of decreasing size as the year progressed (Table 7). The shorter and less efficient weir operation time in 1983 meant that runs that occurred earlier than July 17 or later than Sept. 12 were not detected. Few trout were observed to migrate downstream once upstream migrations started (Fig. 6).

Mean fork length of all trout caught in the weir decreased after the major run in July (Fig. 7). This was consistent for both years.

3.2 c) Channels.

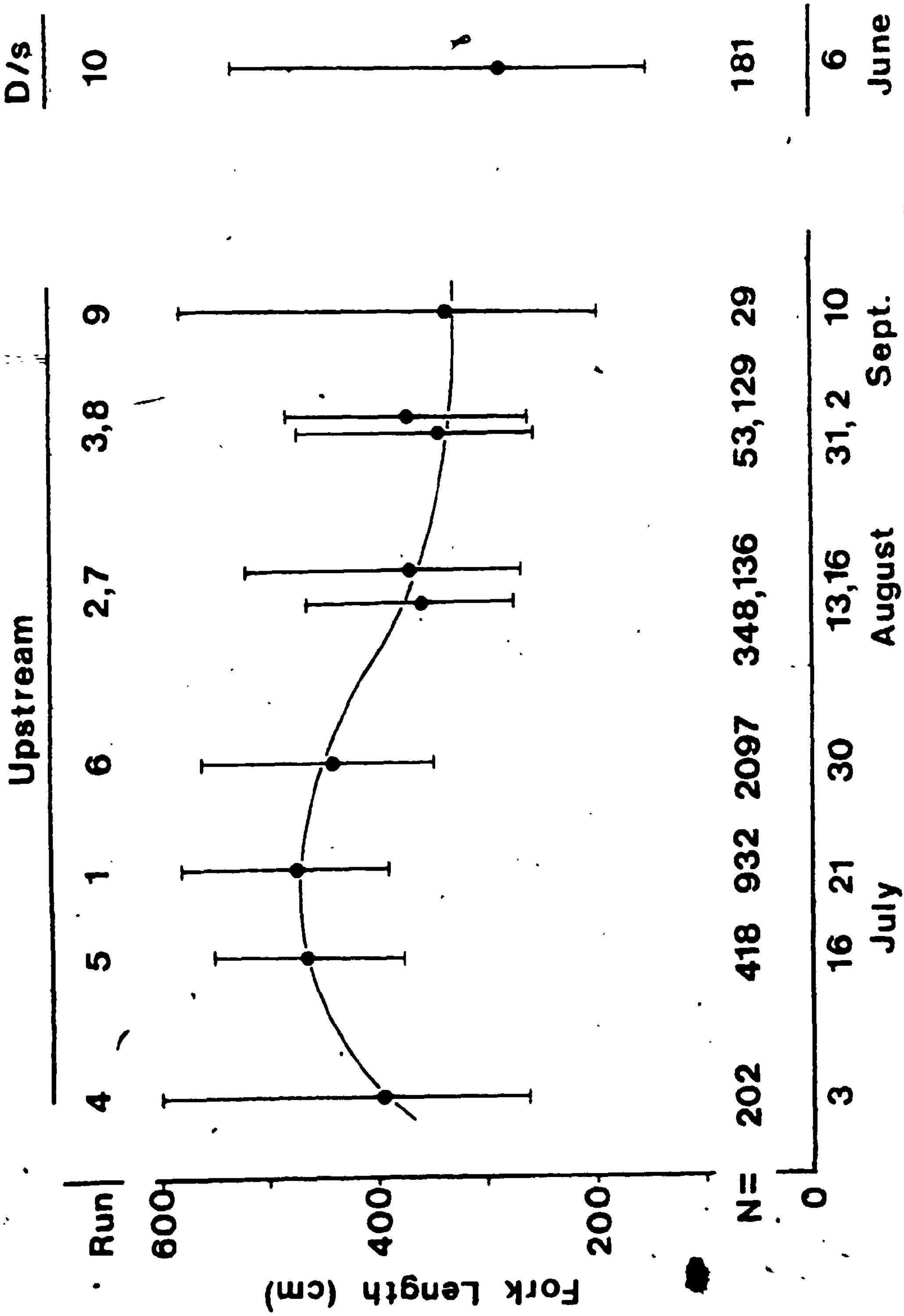
Preference for channels during 1984 was tested with a randomized complete block (day) design of ANOVA. The effect of channel was highly significant ($p<<0.001$) with more trout

Table 7. Date and direction of trout runs in the Sutton River.

Year	Run No.	Direction[1]	Date Start	End	Peak Date	No. of Trout
1983	1	U/S	July 17	Aug. 6	July 21	932
	2	U/S	Aug. 7	Aug. 23	Aug. 13	349
	3	U/S	Aug. 24	Sept. 7	Aug. 31	53
1984	4	U/S	June 23	July 10	July 3	202
	5	U/S	July 11	July 19	July 16	418
	6	U/S	July 20	Aug. 11	July 30	2097
	7	U/S	Aug. 12	Aug. 23	Aug. 16	136
	8	U/S	Aug. 24	Sept. 3	Sept. 2	129
	9	U/S	Sept. 4	Sept. 15	Sept. 10	29
	10	D/S	June 5	July 19	June 6	181

[1] U/S - Upstream, D/S - Downstream.

Figure 7. Mean fork length, with 95% confidence limits, of the trout in each of the 10 'runs'. Direction of the run and the run number appears at the top of the graph. The number of trout measured in each run (N) appears above the abscissa.


Upstream
D/s
Run
4
5
1
6
2,7
3,8
9
10
Fork Length (cm)
600
400
200
0
N=
202
418
932
2097
348,136
53,129
29
181
3
16
21
30
13,16
31, 2
10
6
July
August
Sept.
June

ascending Channel II than Channels I and III combined in 1984 (1772, 673 and 579, respectively). This was most noticeable in July ($p<<0.001$) and less so in August ($p=0.06$) and September ($p>0.1$). The number of trout ascending one channel could be predicted from the number of trout ascending either of the other channels (Table 8). Channels I and III did not differ. It was not possible to test for channel preference in 1983 due to the incomplete blocking of the river after the July 27 flood.

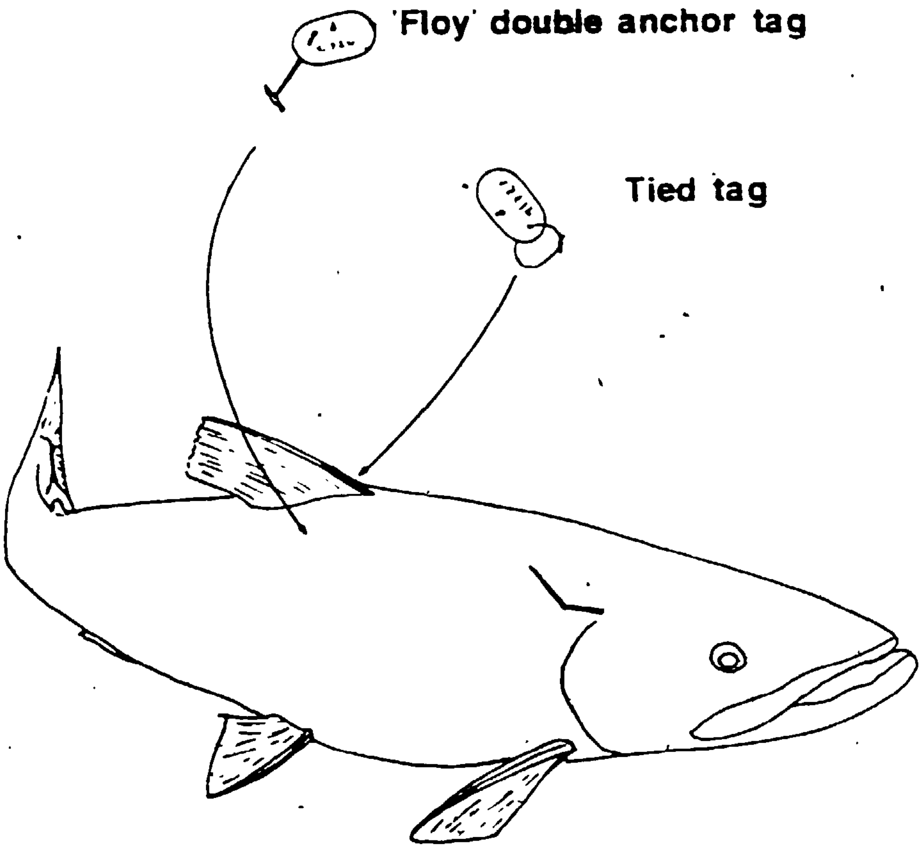
3.2 d) Tagging.

Two types of tagging techniques were used to attach Ontario Ministry of Natural Resources numbered oval tags to trout (Fig. 8). The first technique, a *Floy* double anchor tag, was used during 1983 and infrequently during 1984. This technique was abandoned as the plastic stem of *Floy* tags was subject to fatigue at the site of attachment to the numbered tag. Sixty-eight percent of the 1983 tags recovered in 1984 had lost the numbered portion of the tag but had retained the anchor and stem of the tag. In these cases, the scar caused by tagging was easier to spot than the protruding monifilament but trained observers had little difficulty in detecting either. Without numbered tags, individuals could not be identified or tagging date determined on recapture. The *Floy* tags also left noticeable scars on trout which may have caused undetected mortalities among tagged fish. The

Table 8. Geometric mean regressions of channel preferences by ascending trout during 1984 ($\log_e$ number of trout in channels).

Channels	Slope	Confidence Limits		Intercept	Confidence Limits		r^2
1 & 2	1.20	0.95	1.45	0.55	-0.05	1.04	0.33
1 & 3	1.00	0.79	1.21	-0.18	-0.60	0.23	0.31
3 & 2	1.20	0.94	1.46	0.77	0.28	1.26	0.24

Figure 8. Type, attachment method and location of tags used to tag Sutton River brook trout.


'Floy' double anchor tag
Tied tag

second tagging technique, that of tying the tags on with needle and monifilament, was used almost exclusively during 1984. This method resulted in longer handling times but no noticeable scarring.

Too few trout were recaptured (less than 2% of 1983 tagged trout) to estimate the number of individuals, the spawning frequency or the age specific mortality rates in the Sutton River population (Table 9). Recaptured trout comprised only 0.5% of the 1984 catch. However, fishermen and natives did report catching tagged trout along the length of the Sutton River and throughout the season during both 1983 and 1984 (Table 10). Tagged trout were also recovered from other rivers in the Hudson Bay watershed. Tagged trout were recaptured by natives in Burnpoint Creek (25 km W), Wachi Creek (55 km W), and perhaps the Winisk (90 km W), and Attawapiskat Rivers (100 km E, 250 km S). Unfortunately, numbers were not recorded and the tags were either not returned to the M.N.R. or were lost in transit. An M.N.R. crew tagging polar bears (*Ursus maritimus*) on the Brant River (50 km E), caught a mature male trout tagged with a *Floy* tag during August 1984. As fishing pressure increases in the Hudson Bay Lowlands during the next few years, it is expected that additional tags will be recovered.

Table 9. Number of brook trout tagged and recaptured during the study.

Year	No. Tagged	1983 Recaptures	1984 Recaptures	Total Recaptures
1983	964	17	---	17
1984	2093	22	15	37
Total	3057	39	15	54

Table 10. Information on tag recoveries.

Tag Year	Recovery Year	Tag Date (d.m)	Recovery Date (d.m)	No. of Days	Distance Upstream[1] (km)	Tag No.[2]
1983	1983	23.07	15.08	22	45	10509
		23.08	23.08	0	2	11065
		14.08	23.08	9	2	11029
		20.08	23.08	3	2	11197
		26.07	27.08	32	40	10767
		23.07	27.08	35	4	10509
		13.08	13.08	0	2	11034
		24.07	30.08	37	14	10578
		01.08	07.09	37	-	10857
		20.08	12.09	23	2	11221
		23.07	14.09	52	8	10573
		09.09	15.09	6	8	11414
		13.08	16.09	34	2	11036
		13.08	16.09	34	2	11035
		22.08	17.09	26	8	11238
		15.08	19.09	35	8	11148
		14.08	12.09	29	8	11122
	1984	09.08	28.05	293	1	10974
		26.07	04.06	312	W	10819
		14.08	07.06	297	W	11137
			03.07		W	
			03.07		W	
			21.07		W	
			24.07		W	
			24.07		W	
			24.07		W	
			25.07		W	
			25.07		W	
			26.07		W	
			28.07		W	
			28.07		W	
			28.07		W	
		19.08	29.07	344	W	11207
			30.07		W	
		01.09	01.08	335	W	11291
			07.08		W	
			01.09		W	
		20.08	09.09	385	W	11227
		25.07	15.09	417	2	10730

Table 10. con't... .

Tag Year	Recovery Year	Tag Date (d.m)	Recovery Date (d.m)	No. of Days	Distance Upstream[1] (km)	Tag No.[2]
1984	1984		06.07		W	
		04.07	10.07	6	-	12726
			25.07		W	
			26.07		W	
		03.08	07.08	4	4	14206
		20.07	09.08	20	55	13225
		10.08	11.08	1	0	14392
		06.08	15.08	7	-	14351
			22.08		6	
		24.07	26.08	33	6	13826
		20.07	06.09	48	70	13250
		02.09	10.09	7	6	14639
		02.09	12.09	10	6	14606
		11.08	14.09	34	6	14418
		11.09	17.09	6	8	14970

---

[1] W - captured at weir either one year later or while swimming upstream after being tagged swimming downstream. Tagged trout recovered swimming downstream after being tagged swimming upstream within the previous 30 days were not considered to be recaptures.

[2] No tag number indicates that there was either a tag scar or part of a tag remaining but the numbered portion had been lost (see text). Tag numbers were required to determine tagging date and number of days at large.

3.2 e) Marks and parasites.

Several trout caught at the weir (<1%) bore scars or other marks that were attributed to encounters with either piscivorous birds or marine mammals. Scars attributed to birds were sets of paired punctures (and slashes) that resembled talon marks. Scars attributed to marine mammals were rows of conical impressions and rakings, usually on the ventral caudal peduncle. Although talon marks were more numerous than teeth marks, neither was common.

The most numerous scars found on the trout were round wounds approximately 2-3 cm in diameter that resembled lamprey scars. Scarred trout were not restricted to any one size or age class (Fig. 9). Both fresh and healed scars were observed, although fresh scars were observed only on angled trout caught above the weir. A third of the scarred trout were sexed; 27 percent were female and 73 percent were male. Forty percent of the trout that had been attacked had more than one wound; one individual had been attacked 10 times (Fig. 10).

The majority of brook trout were internally parasitized by tapeworm. Tapeworms were not examined to determine if they were of marine or freshwater origin (probably *Proteocephalus parallacticus* and/or *Eubothrium salvelini*). Although intestinal loading was often heavy, this parasite did not seem to affect the condition of the trout adversely.

Figure 9. Fork length distribution of Sutton River brook trout that had been attacked by parasitic lampreys.

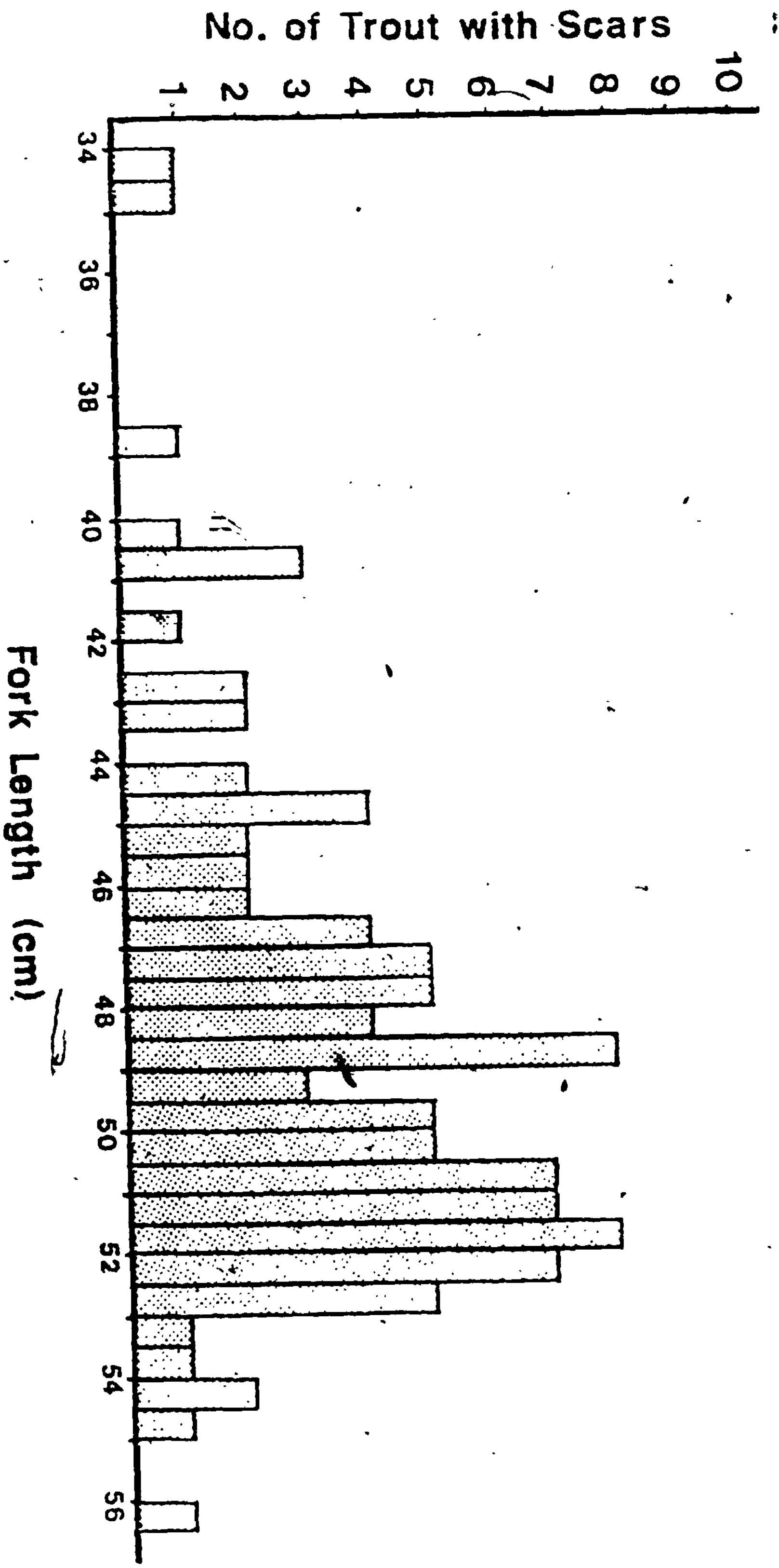
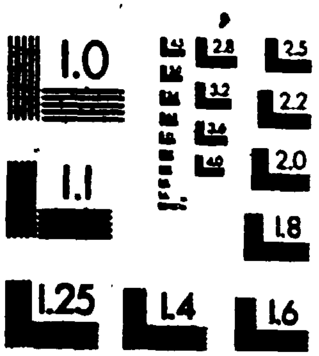
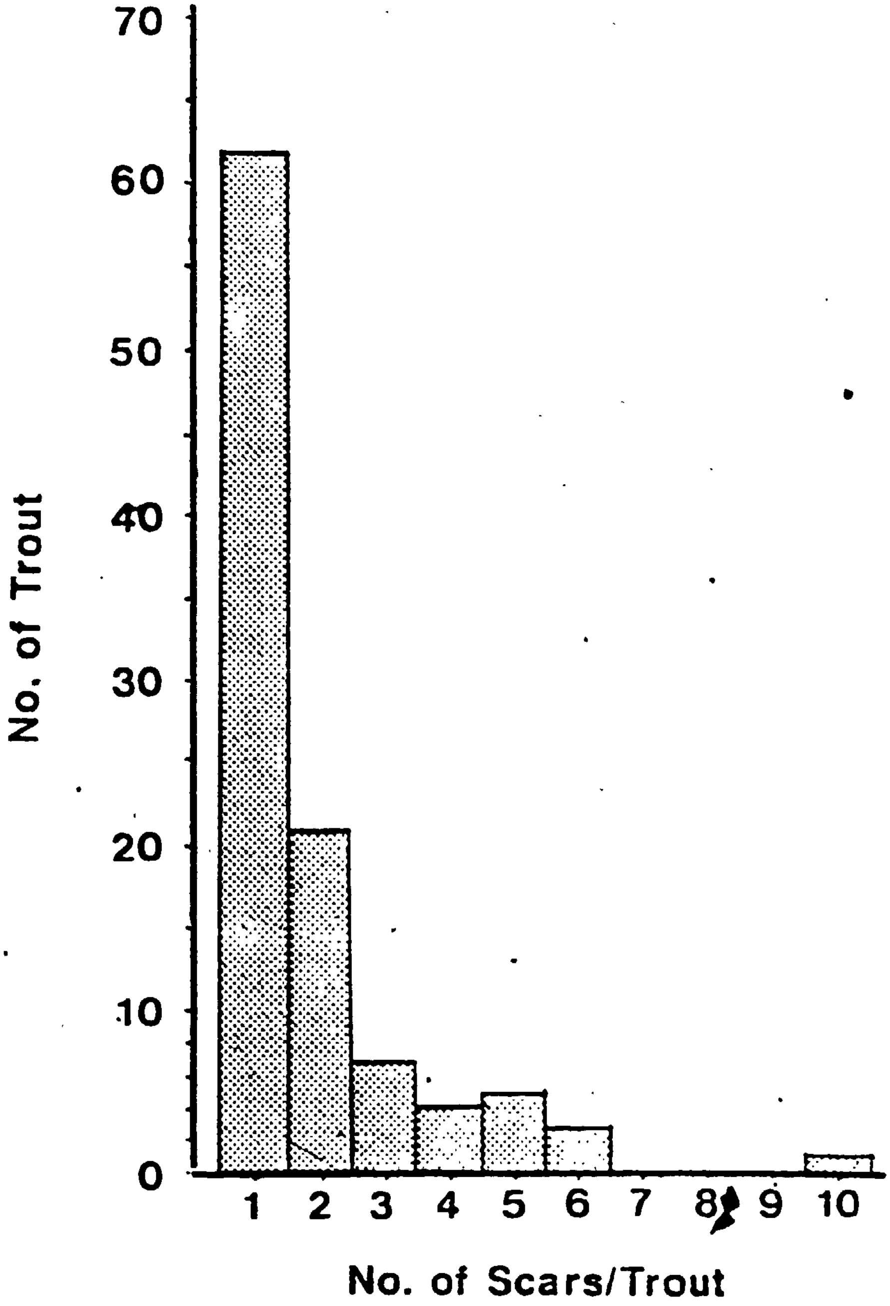

No. of Trout with Scars
1
2
3
4
5
6
7
8
9
10
34
36
38
40
42
44
46
48
50
52
54
56
Fork Length (cm)

Figure 10. The frequency of multiple lamprey scars per brook trout.

2

MICROCOPY RESOLUTION TEST CHART
NBS 1010a
ANSI and ISO TEST CHART No. 2





No. of Trout
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
No. of Scars/Trout

3.3 Ageing.

3.3 a) Comparison of methods.

Scale determined ages consistently under-estimated otolith determined ages (Table 11). In contrast, fin ray determined ages were similar to otolith determined ages (Table 12). Fin ray determined age was also a better predictor of otolith determined age than scale determined age was (Table 13). However, fin ray determined age was significantly different (95% confidence interval of the slope does not encompass 1.0) from otolith determined age (Table 13). Otolith determined ages were readily discernible until age 8+; otoliths indicating a greater age than 8+ were read as +/- one year (verified by Dr. J. Casselman, M.N.R.).

3.3 b) Length and age.

The Peterson method of length-frequency histograms indicated that brook trout growth rate approximated 10 cm per year (or more precisely 3.3 cm/month for each of the summer months) until the trout reached 5+ years (Fig. 11). Length frequency programs (e.g., ELEFAN, LENFRE) were used to separate age classes. As with the frequency analysis programs used for the run analysis, these methods proved unsatisfactory. In addition to problems caused by non-Gaussian distributions and outliers, the results from these computer models were neither stable nor reproducible

Table 11. A comparison of ages as determined from 298 trout that were aged by both scales and otoliths.

	Scale Age.								
Otolith Age	1	2	3	4	5	6	7	8	9
1									
2		10	2						
3		4	57	14	2				
4			26	29	3				
5			12	36	10	3			
6			3	29	10				
7			1	13	5				
8				2	9				
9			1	1	1				
10				1	6	2			
11				2	1				
12				1	1				
13									
14									
15					1				

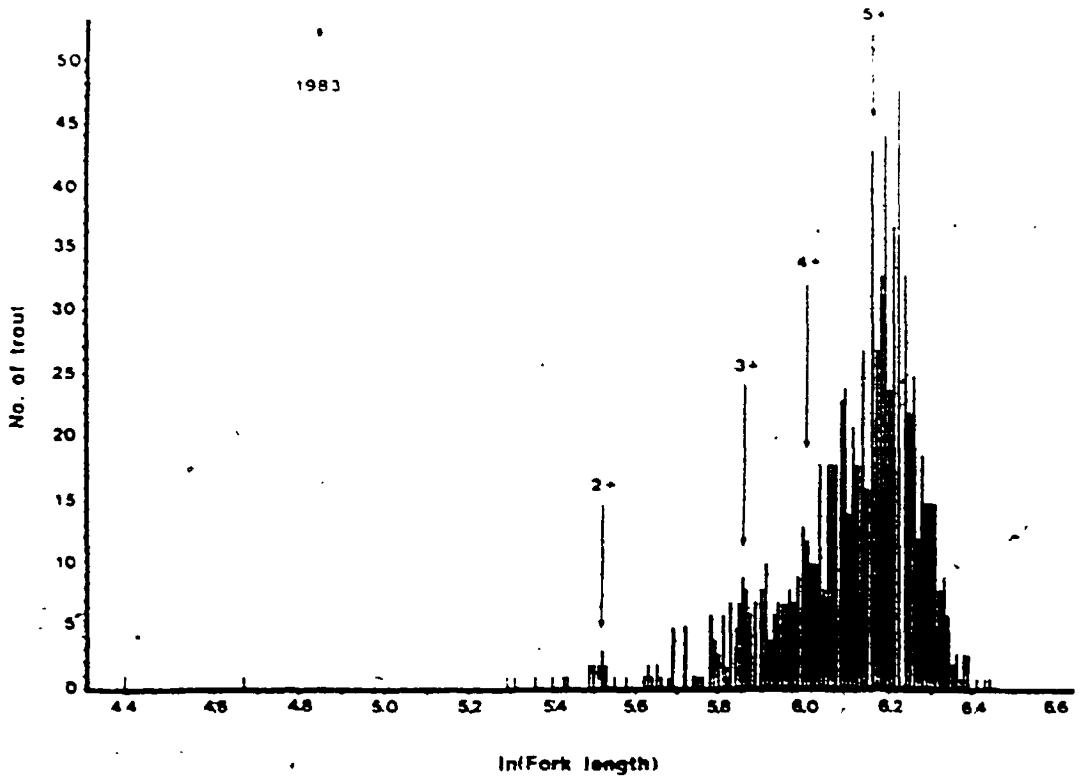
Table 12. A comparison of ages as determined from 295 trout that were aged by both fin ray sections and otoliths.

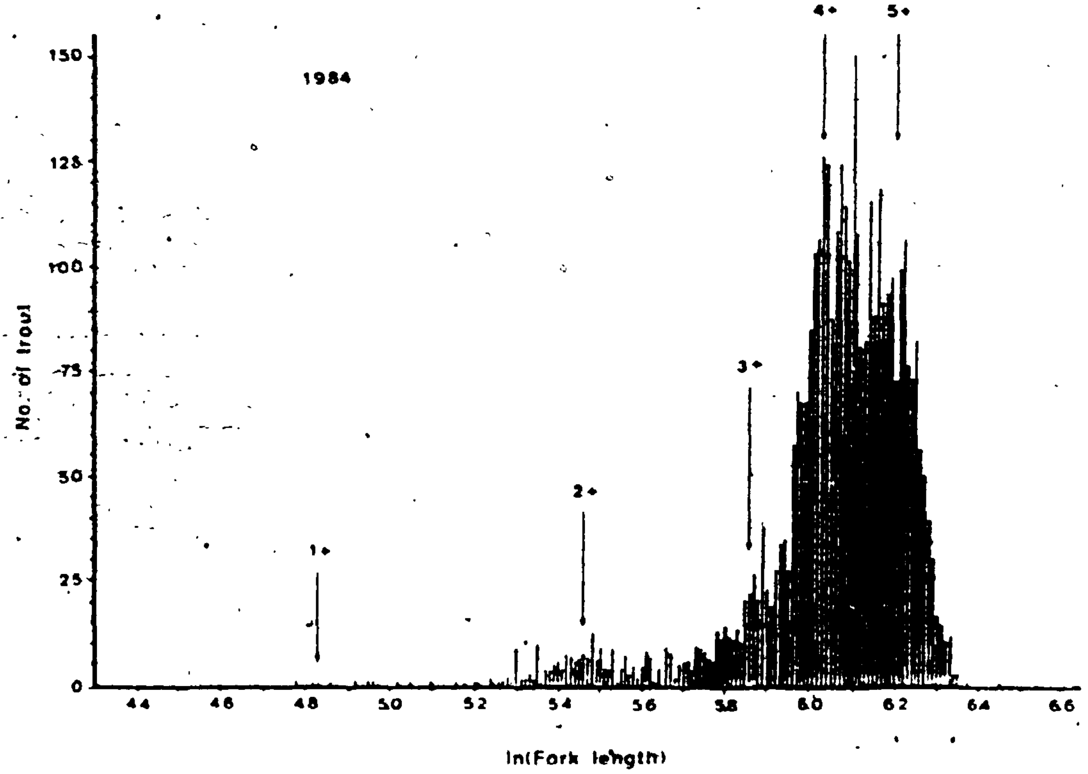
	Fin Ray Age.												
Otolith Age	1	2	3	4	5	6	7	8	9	10	11	12	13
1													
2		11	1										
3		9	65	7									
4			13	43	6	2							
5				16	31	21	1						
6				2	14	35	2						
7					3	8	8						
8							3	4	3	1			
9								2	2				
10								2	2	3	1		
11									1	1			
12									1		1		
13												1	
14													
15												1	

Table 13. A comparison by geometric regression, of scale and fin ray determined age with age as determined from otoliths.

Structure	GM Equation	95 % Confidence Limits Slope	 Intercept	r^2
Scales	Y= 1.77 + 0.41	0.39 - 0.43	1.66 - 1.89	0.80
Fin Rays	Y= 0.08 + 0.96	0.94 - 0.98	-0.02 - 0.19	0.96.

Figure 11. Length frequency distributions used to age trout by the Peterson method. Too few small trout were caught at the weir to determine modal lengths for 1+ during 1983.


1983
No. of trout
50
45
40
35
30
25
20
15
10
5
0
2+
3+
4+
5+
4.4
4.6
4.8
5.0
5.2
5.4
5.6
5.8
6.0
6.2
6.4
6.6
ln(Fork length)


1984
No. of trout
150
125
100
75
50
25
0
1+
2+
3+
4+
5+
4.4
4.6
4.8
5.0
5.2
5.4
5.6
5.8
6.0
6.2
6.4
6.6
ln(Fork length)

with respect to interval width. Attempts to determine optimal interval width for analysis of length frequency data proved to be extremely tedious and time-consuming (hence expensive) to perform. Since these methods failed to distinguish stable and reproducible modals, they were abandoned and the results are not reported.

A similar length at age relationship was determined for fish aged by counting annuli on scales as by the Peterson method. However, there was considerable variation in these estimates and results after 5+ years were not distinct (Fig. 12). Sectioned pectoral rays provided less variable and conservative estimates of the length age relationship (Fig. 12). Sagittal otoliths, after cutting and burning, provided comparable estimates to those of pectoral fin rays (Fig. 12). An F-max test for homogeneity of variance described the variance of the length on age regression for scale derived data (log-log) as significantly different ($p<<0.001$) from that derived from fin rays or otoliths. Variances of fin ray and otolith derived data (log log) were homogeneous (Y on X, $p>0.50$; X on Y, $p>0.20$). Analysis of covariance results indicated that otolith derived data were a more conservative estimate of the length age relationship than fin ray derived data (slopes, $p=0.07$; intercepts $p=0.05$). Analysis of covariance on the X on Y relationship revealed a significant difference in intercepts ($p=0.02$).

Figure 12. a) Growth curve for Sutton River brook trout as determined by scales (solid diamonds), fin ray sections (open circles) and otoliths (solid circles). Mean and 95% confidence limits reported. Dotted line is the continuation of the curve established by age classes 1+ through 4+. The difference between this curve and the observed may be the cost of reproduction.

a)

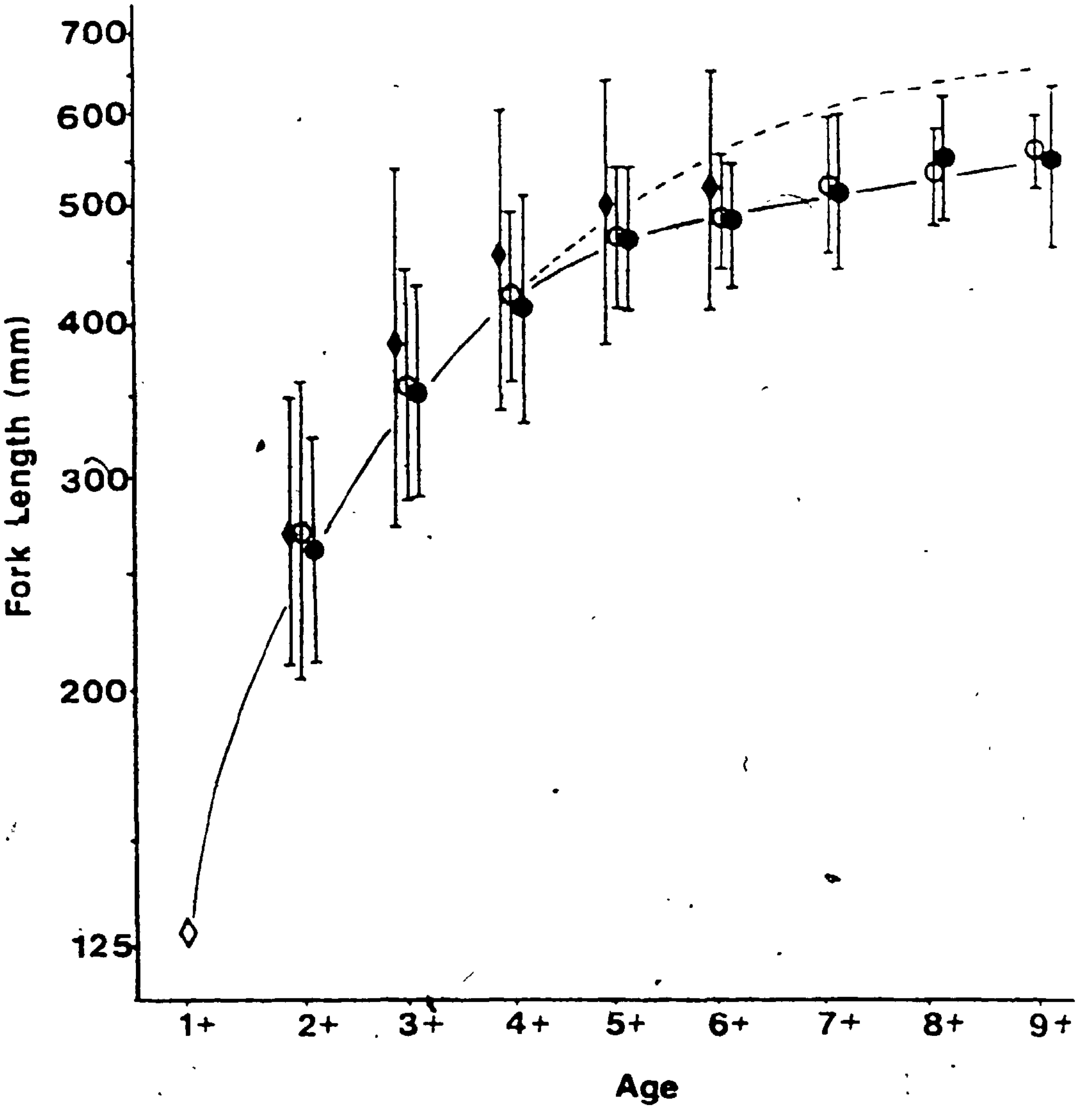
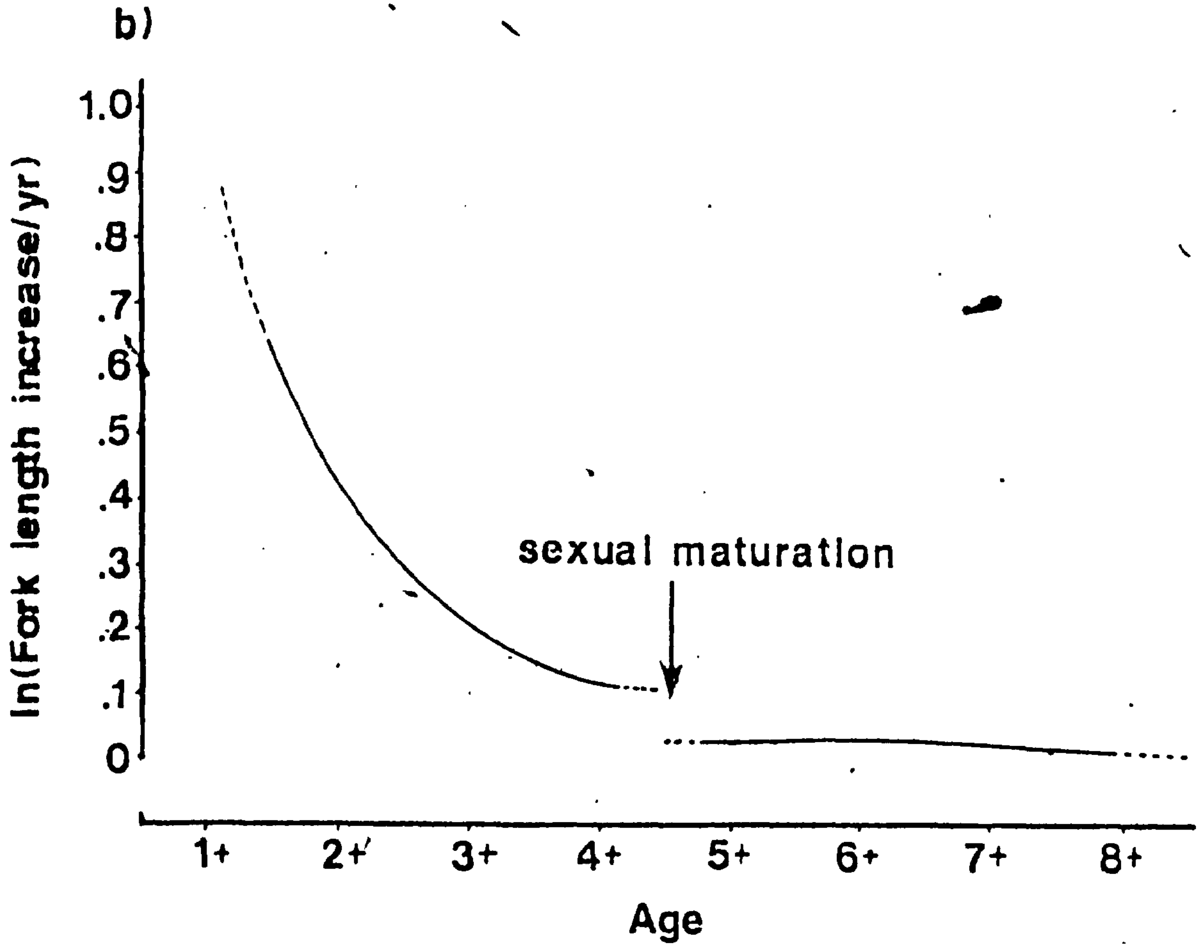


Figure 12. b) The age specific growth increment derived from the growth curve is regressed against otolith age to display the discontinuous nature of the growth curve at the age of maturation.


b)
ln(Fork length increase/yr)
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
sexual maturation
1+
2+
3+
4+
5+
6+
7+
8+
Age

3.3 c) Validation of length at age estimates.

Validation of length at age estimates from tag returns was only partially successful due to the low number of returns. Twenty-three tagged trout were recaptured one or more years after tagging; initial and final fork lengths were available for only two of these fish (tagged fish # 11291 & # 10492). The fish tagged as # 11291 was tagged at a fork length of 331 mm (<1% below the mean ln fork length of otolith aged 3+ trout) and recaptured the following season at a fork length of 385 mm (<1% below the mean ln fork length of otolith aged 4+ trout). The other tagged trout (# 10492), tagged at a fork length of 463 mm (<1% below the mean ln fork length of otolith aged 5+ trout) was recaptured by an angler after two years at a total length of 519 mm (equivalent fork length: 505 mm; equal to the mean ln fork length of otolith aged 7+ trout).

Since no method of directly validating the age length relationship (i.e., fish of known age or tetra-cycline injection experiments) was available, the most conservative estimate (otolith derived data), validated indirectly by the above methods, was chosen for use in the rest of this study (Table 14). Otolith derived age data were also used for the comparison with other studies (Fig. 13).

Table 14. Fork length ranges used to age trout. Lengths greater than 53.3 cm (7+ upper limit) were grouped and assigned the age of 8+.

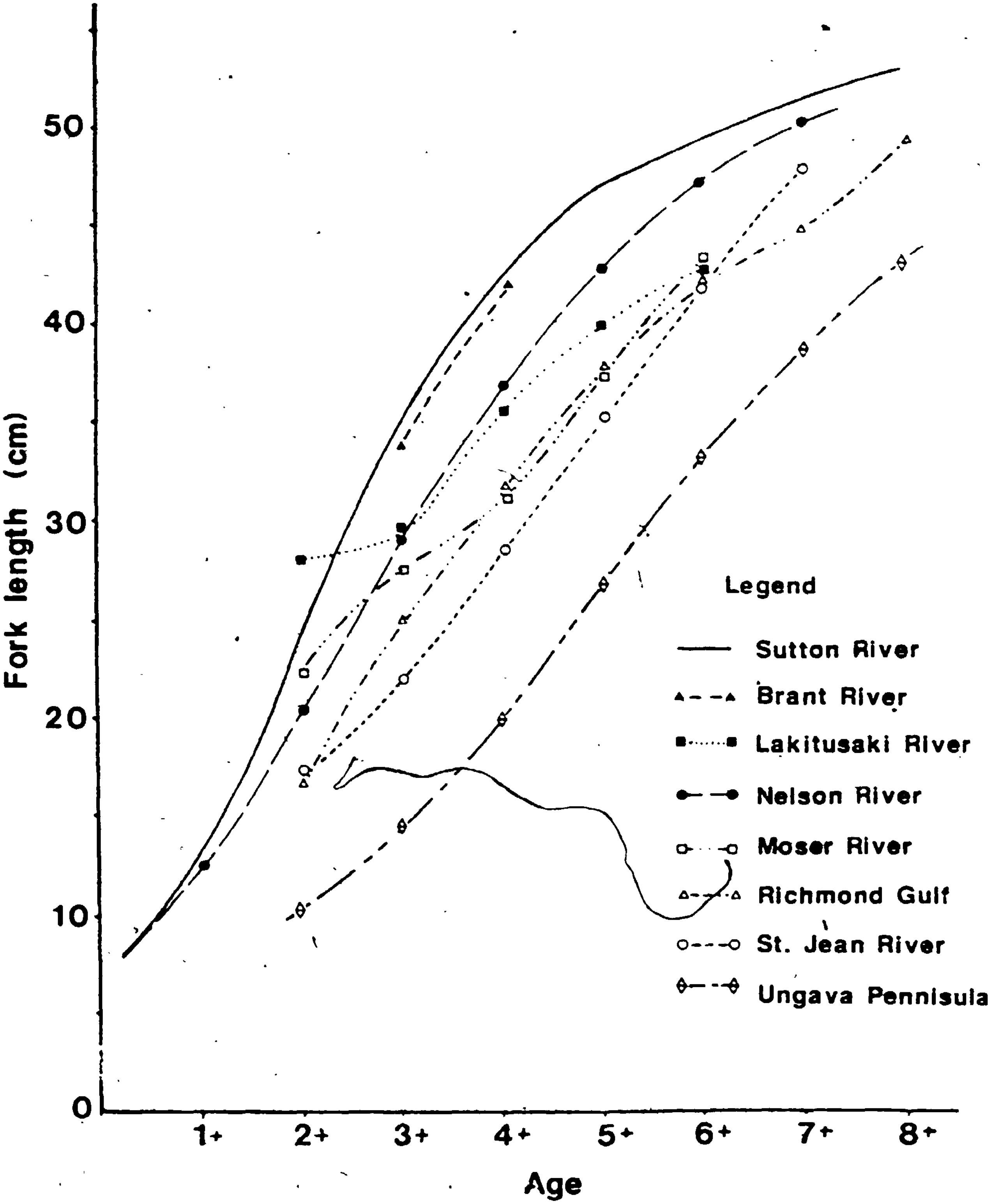
Age Class	Mean Fork Length from aged trout. (cm)	Confidence limits (cm)	N	Assigned length range (cm)
<u>June</u>				
3+	31.9	29.1 - 35.0	5	
4+	30.4	-----	2	
5+	45.4	-----	2	
<u>July</u>				
2+	24.8	-----	1	< 30.9
3+	32.6	29.8 - 35.6	14	30.9 - 38.5
4+	43.3	41.6 - 45.1	24	41.6 - 45.9
5+	47.4	46.5 - 48.3	49	46.0 - 48.3
6+	48.6	47.9 - 49.5	43	48.4 - 49.4
7+	51.0	49.2 - 52.8	19	49.5 - 53.2
8+	54.9	52.9 - 57.0	12	> 53.3
9+	53.7	47.5 - 60.8	4	
10+	54.0	51.2 - 57.0	7	
11+	53.7	49.6 - 58.2	4	
12+	56.0	53.0 - 59.2	3	
15+	56.5	-----	1	

Table 14. con't...

Age Class	Mean Fork Length from aged trout. (cm)	Confidence limits (cm)	N	Assigned length range (cm)
<u>August</u>				
2+	25.9	24.2 - 27.7	7	23.1 - 31.6
3+	35.0	34.0 - 36.2	33	31.7 - 37.9
4+	40.0	38.8 - 41.3	23	38.0 - 43.1
5+	46.7	44.5 - 49.0	9	43.2 - 48.5
6+	47.0	42.5 - 52.0	4	48.6 - 49.3
7+	----	-----	-	49.4 - 53.2[1]
8+	----	-----	-	> 53.2[1]
10+	53.8	-----	2	
<u>September</u>				
2+	26.7	20.2 - 35.4	4	20.2 - 35.6
3+	36.6	35.7 - 37.4	29	35.7 - 38.3
4+	41.0	39.3 - 42.8	13	38.4 - 42.9
5+	45.2	43.0 - 47.6	11	43.0 - 45.1
6+	46.6	42.8 - 50.7	4	45.2 - 50.7
7+	46.8	-----	1	50.8 - 53.2[1]
8+	----	-----	-	> 53.3[1]

[1] Limits derived from July, 1983 data.

Figure 13. A comparison of the length-at-age relationships for anadromous populations reveals that the Sutton River brook trout grew quicker than brook trout at other localities. Populations from the southwest Hudson Bay coast are represented with solid symbols.


Fork length (cm)
50
40
30
20
10
0
1+
2+
3+
4+
5+
6+
7+
8+
Age
Legend
Sutton River
Brant River
Lakitusaki River
Nelson River
Moser River
Richmond Gulf
St. Jean River
Ungava Pennisula

3.3 d) Age composition of runs.

Using the above age length relationship, the age composition of each of the runs was calculated. Early runs were comprised of all age classes moving up and down the river. The major run of July in both years was dominated by trout 4+ or older. In later runs, older fish (>5+ yr) comprised an increasingly smaller percentage (Fig. 14).

Mean fork length of aged trout decreased during the summer indicating the largest trout of an age class ascended the river first (Table 15).

Figure 14. Age composition of upstream runs during 1983 and 1984. Trout were aged by fork length. Mature trout (4+ and older) are represented by shaded bars. The number of trout measured in each run appears at the top of each histogram.

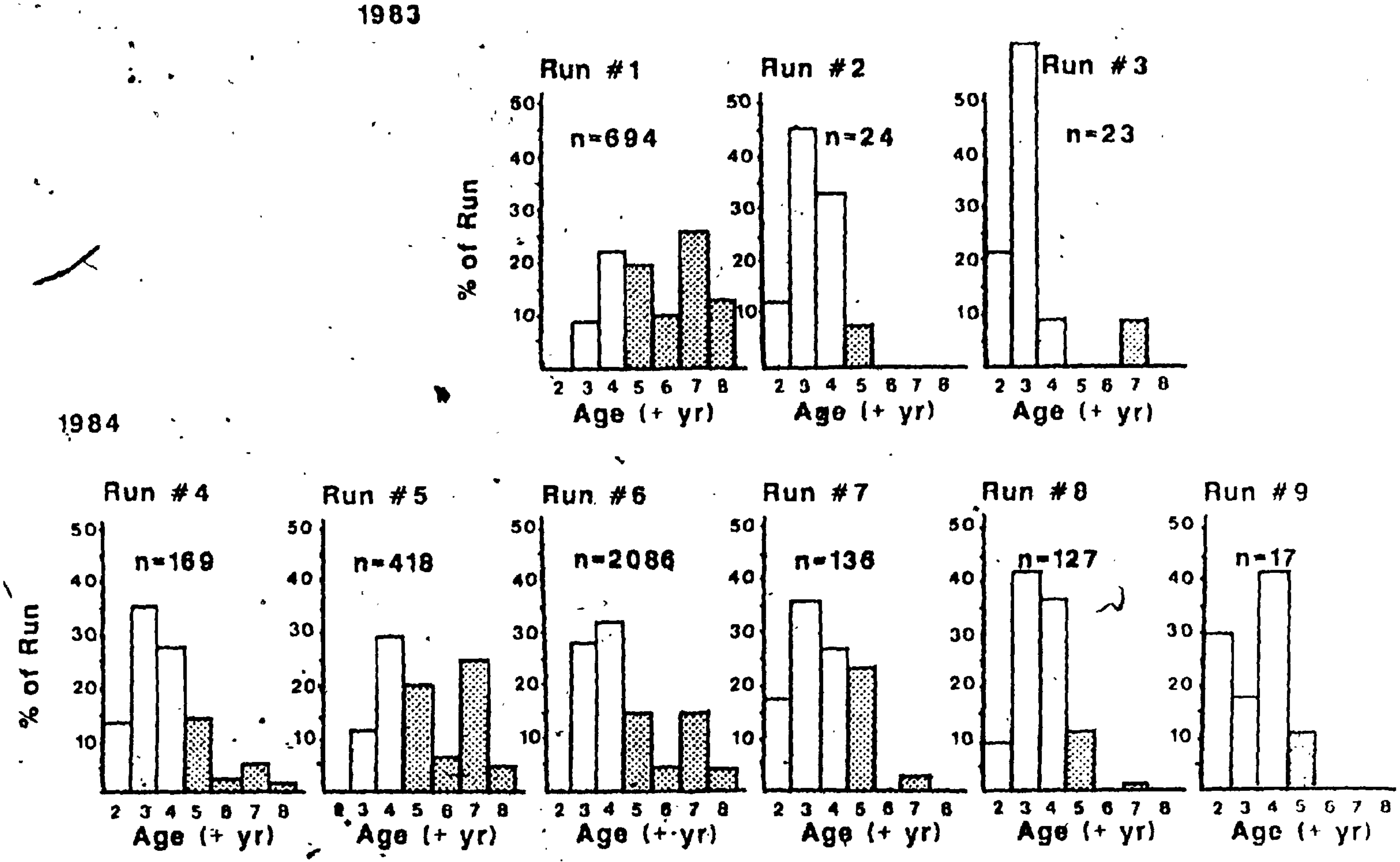

1983
Run #1
n=694
Run #2
n=24
Run #3
n=23
1984
Run #4
n=169
Run #5
n=418
Run #6
n=2086
Run #7
n=136
Run #8
n=127
Run #9
n=17
% of Run
50
40
30
20
10
2 3 4 5 6 7 8
Age (+ yr)

Table 15. Mean fork lengths of aged trout caught at the weir during 1983. The number of trout appears in brackets.

Age Class	July (cm)	August (cm)	September (cm)
2+	31.9 (5)[1]	26.5 (4)	24.5 (3)
3+	35.3 (8)	34.6 (17)	36.6 (29)[1]
4+	43.9 (23)	40.8 (16)	41.0 (13)[1]
5+	47.5 (48)	46.3 (8)	45.3 (11)[1]
6+	48.9 (42)	47.0 (2)	46.6 (4)[1]
7+	51.0 (19)	------	------
8+	54.9 (12)	------	------

[1] Trout caught by angling.

3.4 Reproduction.

3.4 a) Sex ratios.

Dead trout were examined to determine sex and maturity stage. Trout were sexed as either male, female or unknown (usually too young to sex accurately). Attempts to sex live trout using the presence of a kype were not successful as both females and males developed kypes.

Females dominated July runs (female:male ratios ranged from 1.07 to 1.36) during both years (Fig. 15). Males dominated the other runs (female:male ratio ranged from 0.67 to 0.86) with the exception of Run #2, during 1983 (female:male = 2.5, n=23). Trout too young to sex (unknowns) were not common at any time.

The segregation of sexes was also evident along the axis of the river. August, 1985 sampling (by angling) of the entire length of the river indicated that the upper reaches were occupied by females, the lower reaches by males and the river mouth (including the Base Camp area) by trout too young to sex (Fig. 16). Furthermore, females were noticeably spaced out over gravel beds although spawning did not occur for two to four weeks. On any one gravel bar trout were ordered by size along the river axis with the largest females furthest upstream, and hence most likely to be angled. Although it was observed that spacing between

Figure 15. Sex composition for upstream runs of brook trout during 1983 and 1984. The ratio of females to males and the number of trout sexed in each run appears at the top of each histogram. I - immature (sex unknown), M - male, F- female.

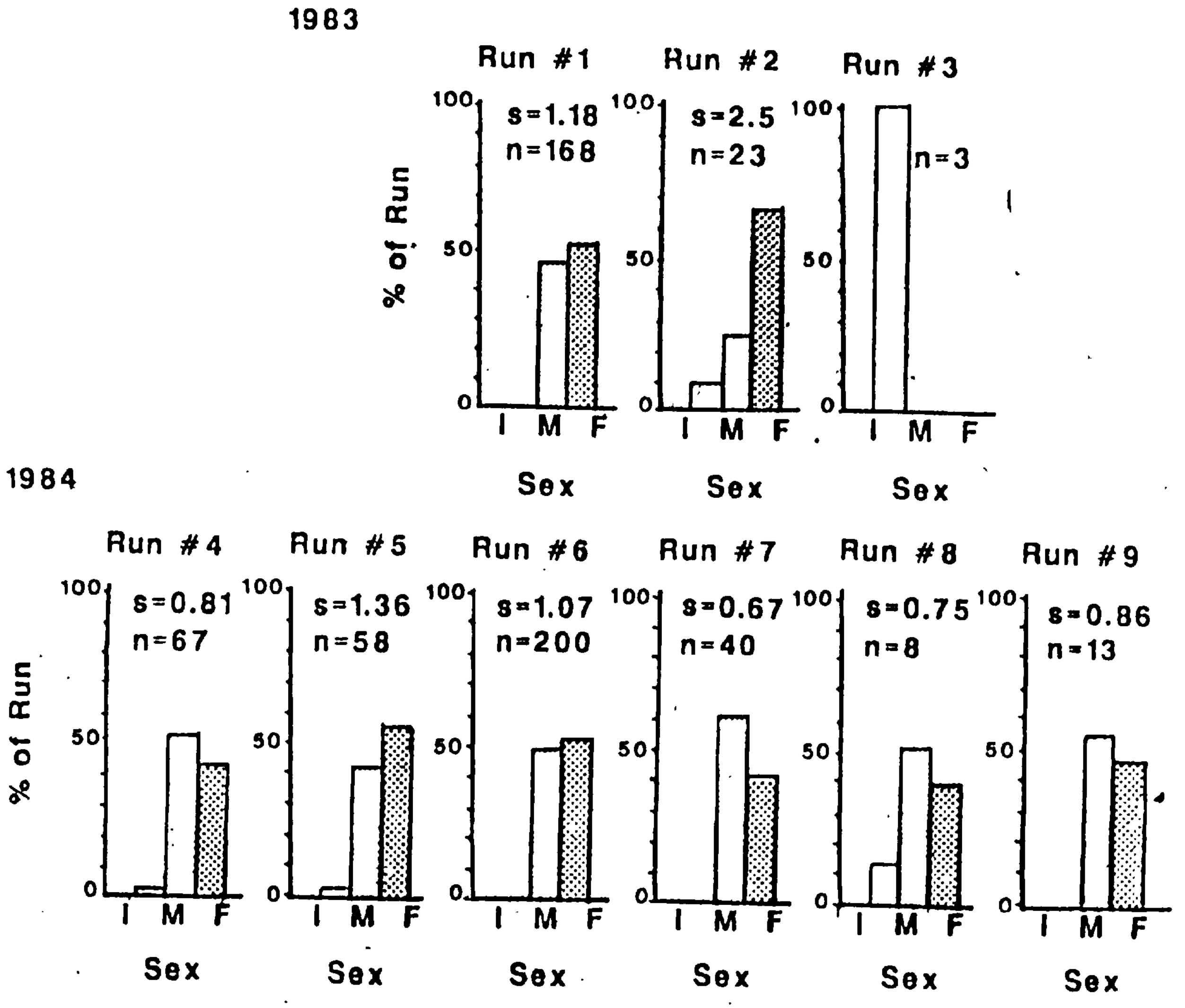
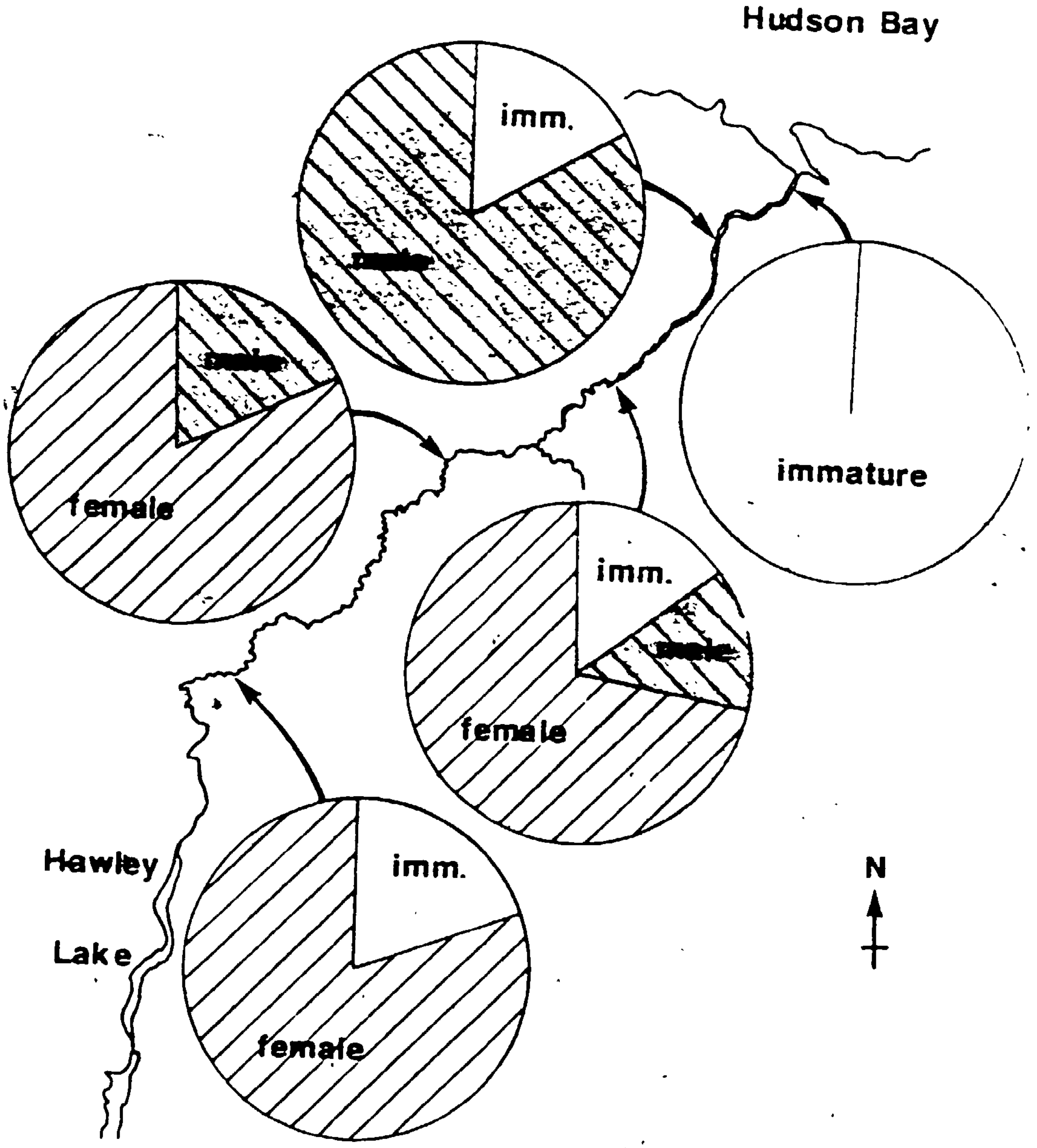

1983
Run #1
s=1.18
n=168
Run #2
s=2.5
n=23
Run #3
n=3
% of Run
100
50
0
I M F
Sex
1984
Run #4
s=0.81
n=67
Run #5
s=1.36
n=58
Run #6
s=1.07
n=200
Run #7
s=0.67
n=40
Run #8
s=0.75
n=8
Run #9
s=0.86
n=13

Figure 16. Sex ratios of brook trout encountered along the length of the Sutton River, August 1985. The preponderance of immature fish near the mouth of the river resulted in a significant ($p<0.002$) reduction of mean weight there. There were no significant differences in mean weights or lengths of males and/or females at any site along the river.


Hudson Bay
imm.
male
male
female
imm.
male
female
immature
imm.
female
Hawley
Lake
N

females differed with female size, no measurements were taken. It was estimated that females were separated by approximately 2.5 m along the axis of the river and 1.5 m laterally (for 22 trout at three sites). Few behavioural interactions were observed between neighbouring females. Males generally inhabited quicker flowing stretches of the river where observation was difficult.

3.4 b) Age of first reproduction.

The age of first reproduction was estimated from the maturation stages of otolith aged females. The age of first reproduction for 50% of the population was 4+. The few 3+ that were mature were significantly larger than the rest of their age class. Those 4+ that were not mature were significantly smaller than the rest of their age class (Table 16). All females of age 5+ or greater had entered the river during the July runs. Maturing fish ascending the river in August and September were age 3+ or 4+ (Table 17).

Sutton River brook trout matured at a larger size than brook trout from other anadromous populations. However, brook trout from many populations matured at the same age as those of Sutton River. There was no correlation between age and size at maturation. Neither was age nor length at maturation correlated with age or length at smoltification of anadromous brook trout populations (Table 18).

Table 16. Percent mature and mean fork length of females of known age (aged by otoliths).

Age Class	n	Per cent		Mean size	
		Mature	Immature	Mature	Immature
0	-	0	100	----	----
1+	-	0	100	----	----
2+	3	0	100	----	25.6
3+	17	23	77	38.0	32.6[1]
4+	17	77	23	42.7	39.3[2]
5+	21	100	0	46.0	----
6+	25	96	4	48.4	46.9
>6+	31	100	0	52.3	----

N.B. Immature gonads made sex determination for age classes one and two difficult, hence lengths and numbers of 'females only' are not available.

[1] Significant difference in mean size ($t_{15}=3.03$, $p<0.01$).

[2] Significant difference in mean size ($t_{15}=3.71$, $p<0.01$).

Table 17. The ratio of immature females (stages 2 and 3) to mature females (stages 4 through 7) in upstream runs for 1983 and 1984.

Age Class	Peak Date of Run								
	July				August			September	
	3	16	21	30	13	16	31	2	10
Year	84	84	83	84	83	84	83	84	84
2+	7:0	0:0	0:0	0:0	0:0	1:0	0:0	0:0	3:0
3+	9:0	1:0	3:5	16:0	8:0	5:1	0:0	0:0	0:0
4+	4:0	5:0	0:19	7:17	2:2	1:5	0:0	1:1	0:2
5+	0:0	11:0	1:19	4:15	0:0	0:3	0:0	0:1	0:0
6+	0:0	5:0	0:8	1:8	0:0	0:0	0:0	0:0	0:0
7+	2:0	6:0	0:18	5:10	0:0	0:0	0:0	0:0	0:0
8+	0:0	2:0	0:15	1:6	0:0	0:0	0:0	0:0	0:0

N.B. Many of the females classified as maturity stage 3 may be early caught mature fish (stage 4). Only one trout identified as definitely immature (stage 2) exceeded 38 cm (4+); this fish was heavily scarred from mammalian teeth.

3.4 c) Spawning.

Maturing females ascended the river during July runs. Few females ascended during August or September; those females that did were at an advanced stage of maturity (Fig. 17). Females that were either 'ripe and runny' or spent were not caught by angling until the first week of September, 1983 and 1984. All mature females caught after the second week of September, 1983 and 1984, were spent (Fig. 18). Hence, spawning was synchronous within the river during a 14 day period.

3.4 d) Fecundity.

Thirty ovaries of mature females were collected during 1985 to determine the fecundity fork length regression of the Sutton River population. Regressing egg number of paired ovaries revealed two outliers that were removed from subsequent analysis (Fig. 19). An egg number on fork length geometric regression was significant ($r^2=0.39$, $p<0.02$);

$$\ln(\text{Egg No}) = 1.90 \ln(\text{Fork Len}) - 3.83$$

The fork length of females ranged from 36 cm to 48 cm; the egg count from 1714 to 2606 eggs.

The effect of growth rate on initial and potential lifetime fecundity was modelled using the observed length specific fecundity and growth rate (Fig.20) relationships. A second data set was generated by reducing the instantaneous

Figure 17. Percent of females sampled that were determined mature (heavy shading) by dissection and examination of the gonads. Early-run mature females may not have been identified as such since the gonads did not showed signs of enlargening for the current year's reproduction till mid-July.

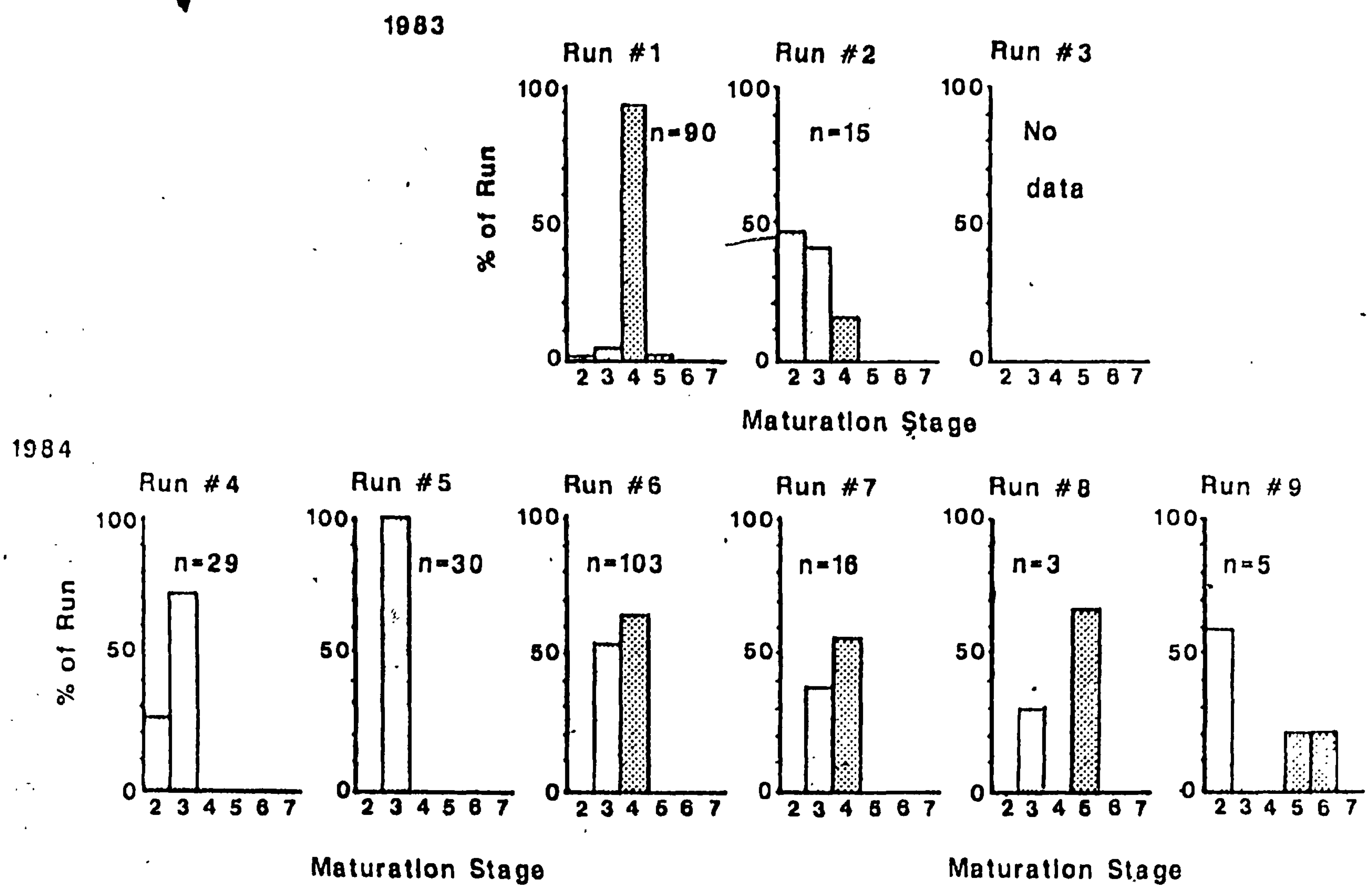

1983
Run #1
n=90
Run #2
n=15
Run #3
No
data
% of Run
100
50
0
2 3 4 5 6 7
Maturation Stage
1984
Run #4
n=29
Run #5
n=30
Run #6
n=103
Run #7
n=16
Run #8
n=3
Run #9
n=5
% of Run
100
50
0
2 3 4 5 6 7
Maturation Stage
Maturation Stage

Table 18. Age and size (mm) of smoltification and maturation for anadromous brook trout populations.

Location	Smoltification		Maturation		Source.
	Age	Size	Age	Size	
Sutton R. Ont.	0+	80	4+	427	this study.
Nelson-Hayes R. Man.	0+	68	4+	377	Gaboury; 1978.
Richmond Gulf, Que.	3+	248	6+	410	Dutil & Power, 1980.
Newfoundland	2+	<136	4+	>196	Scott & Crossman, 1964.
St. Jean R. Que.	2+	168	4+	277	Castonguay et al. 1982.
Ellerslie Bk. P.E.I.	1+,2+	120	2+	170	Smith & Saunders, 1958.
Moser R., N.S.	3+	170	3+	240	Wilder, 1952.
Hatchery	0+	110	1+	330	Sutterlin et al., 1976.

Figure 18. Percent of females, by week, that were 'ripe and runny' or 'spent, during late August and early September, 1983 and 1984. Spawning occurred at a similar time both years. Water temperatures appear above the histograms. Malfunction of the continuous recording thermometer during 1984 meant that temperature ranges only were available for September, 1984.

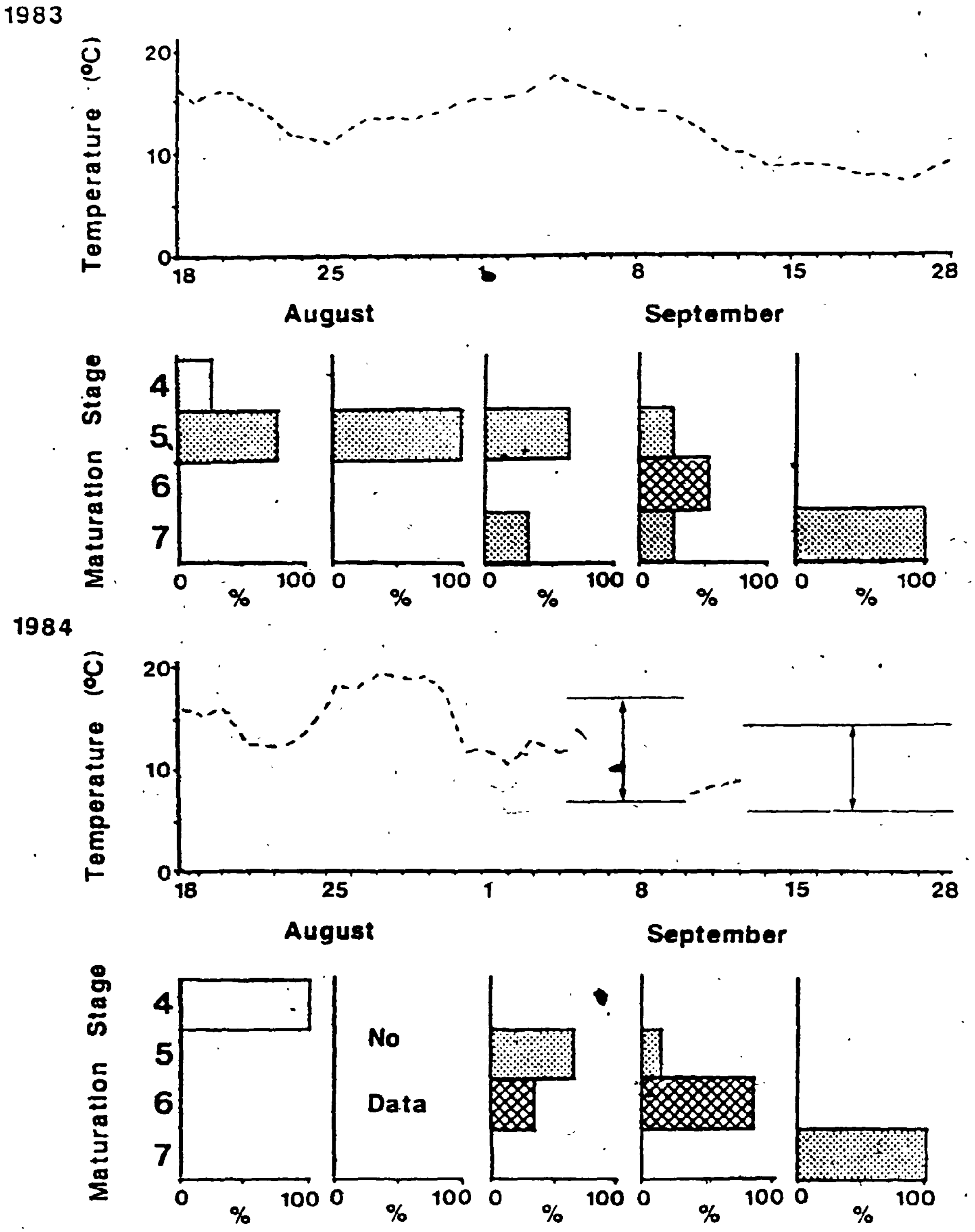

1983
Temperature (°C)
20
10
0
18
25
1
8
15
28
August
September
Maturation Stage
4
5
6
7
0
%
100
1984
Temperature (°C)
20
10
0
18
25
1
8
15
28
August
September
Maturation Stage
4
5
6
7
No
Data
0
%
100

Figure 19. Egg counts per ovary from 14 trout. Geometric regressions were significant (p<0.01) with two outliers (open circles) included (dashed line) or excluded (solid line).

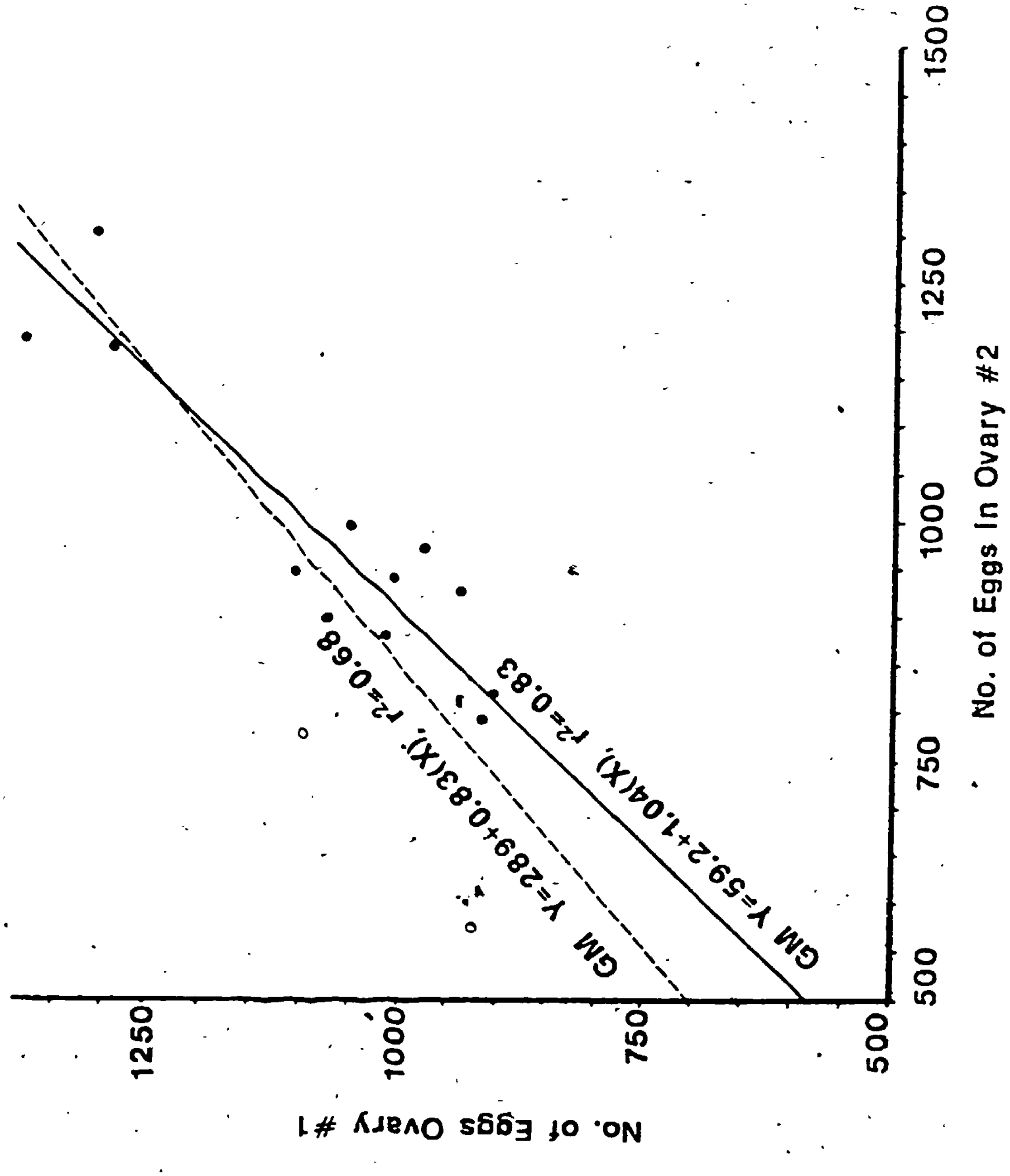
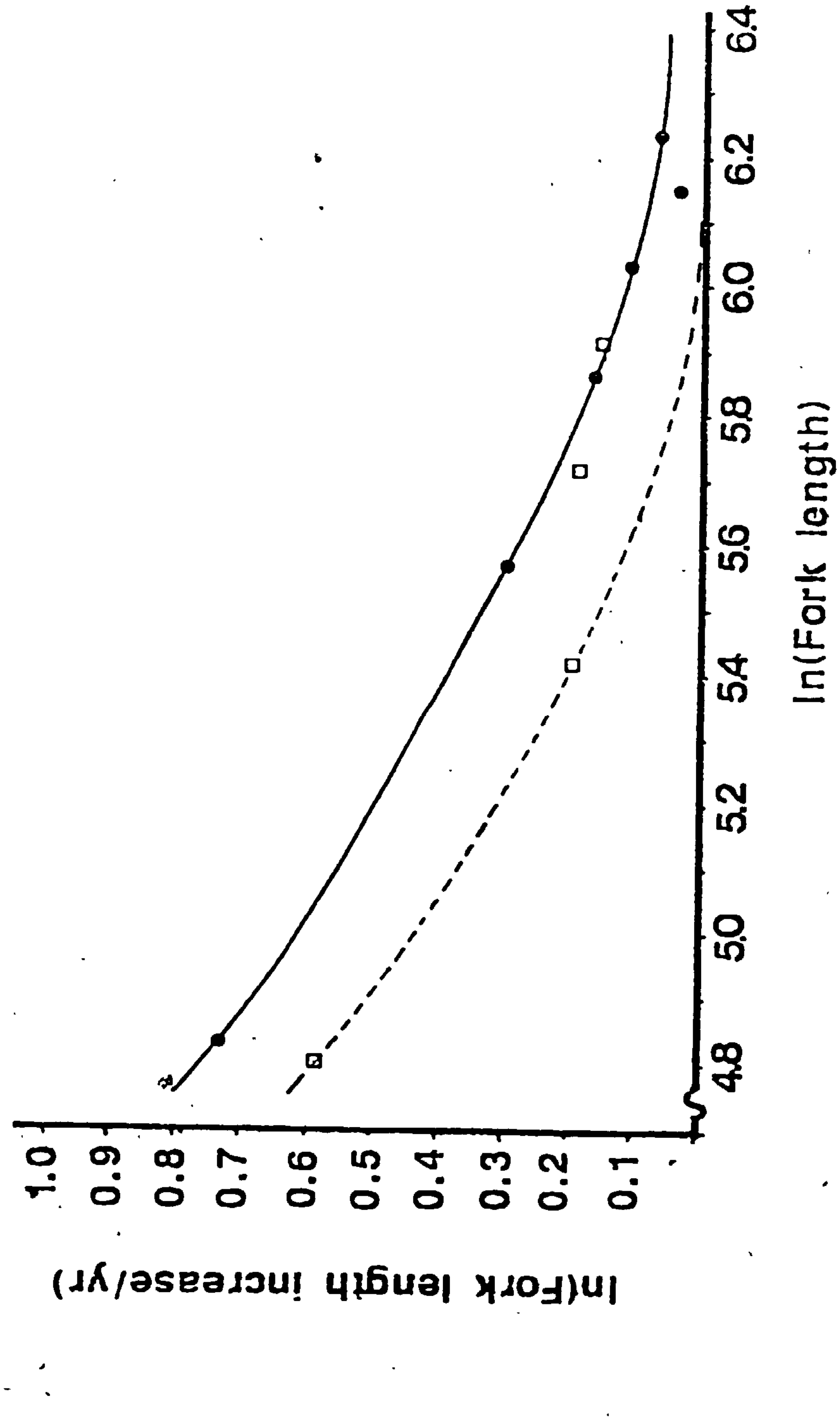

GM Y=59.2+1.04(X), r²=0.83
GM Y=289+0.83(X), r²=0.68
No. of Eggs In Ovary #2
500
750
1000
1250
1500
No. of Eggs Ovary #1
500
750
1000
1250

Figure 20. Length-specific annual length increment increase of the Sutton River brook trout (solid circles). Dashed line is the increment increase for a population with a 20% reduction of growth rate. The latter models the anadromous Moser River brook trout population (open squares).


ln(Fork length increase/yr)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
4.8
5.0
5.2
5.4
5.6
5.8
6.0
6.2
6.4
ln(Fork length)

growth rate by 20% at each length. This corresponded to the growth rate reported for the anadromous Moser River brook trout population (Wilder, 1952).

The effect of post-reproductive growth rate on lifetime fecundity was modelled by imposing a cost of reproduction as measured as a percent of the year's growth on the previous data sets (e.g., curtailment to 5% of a year's growth is equal to a 95% cost of reproduction). These calculations were then repeated for differing ages at maturation (Fig. 21). Initial and subsequent fecundities were summed and graphed as potential lifetime fecundity (Fig 22).

Figure 21. Relationship of age specific fecundity, with varying reproductive costs imposed, and age for a female brook trout with growth similar to that of the Sutton River population (triangles: open 80%, closed 85%, circles: open 90%, closed 95%). Also included (solid squares) is the age specific fecundity, with no reproductive cost imposed, realized by a female that grew at 80% of the rate of that the Sutton River population (e.g., Maritime population; Wilder, 1952).

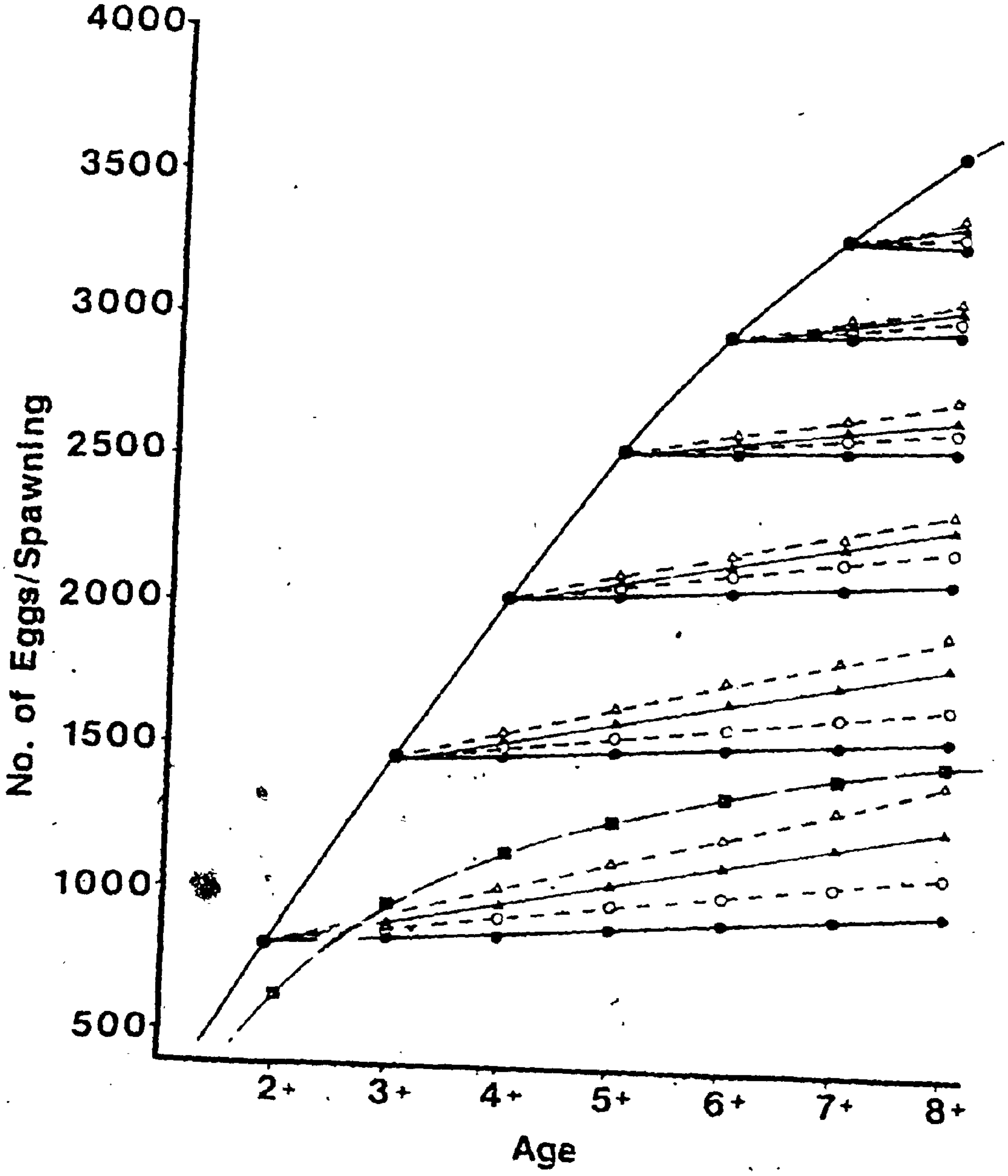
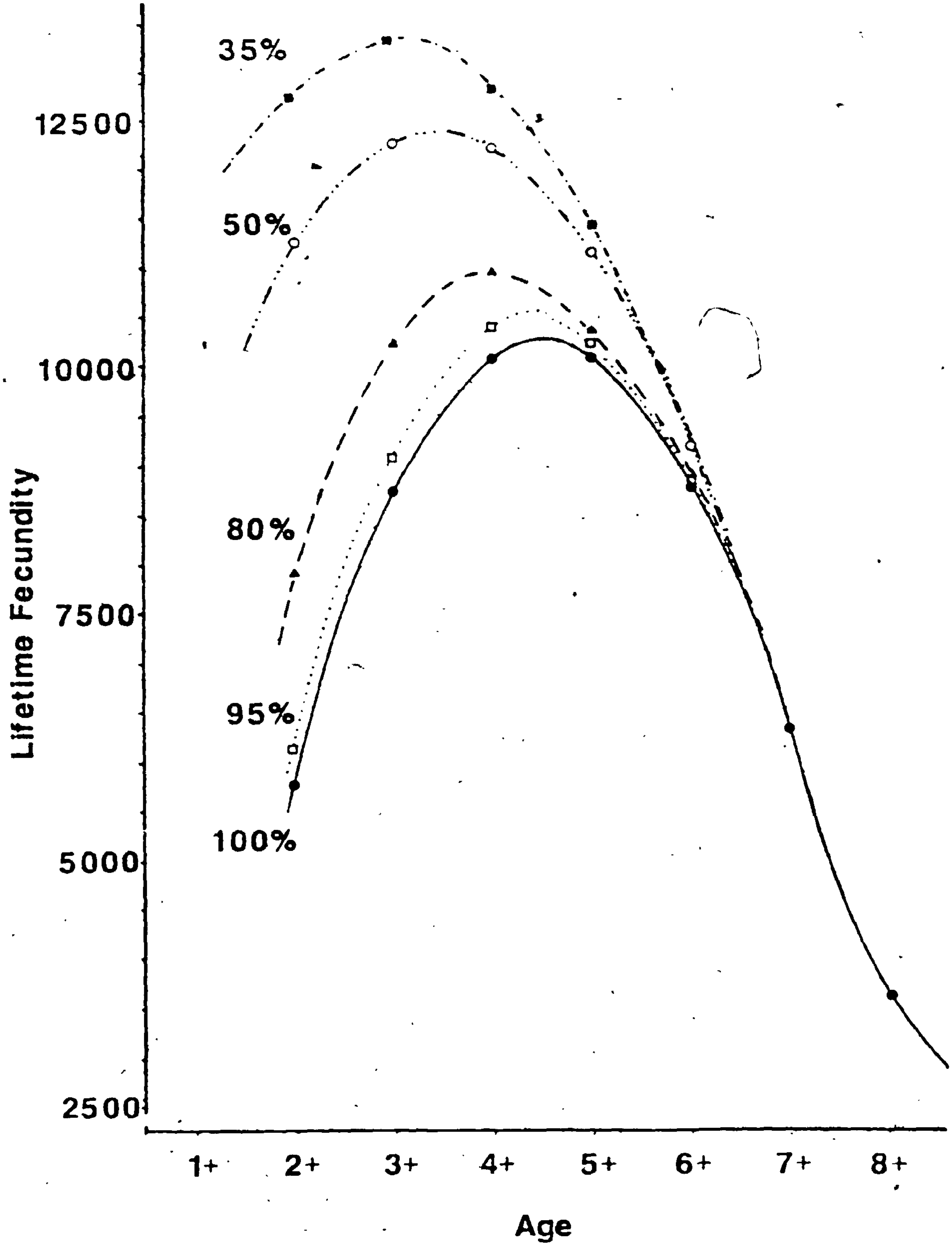
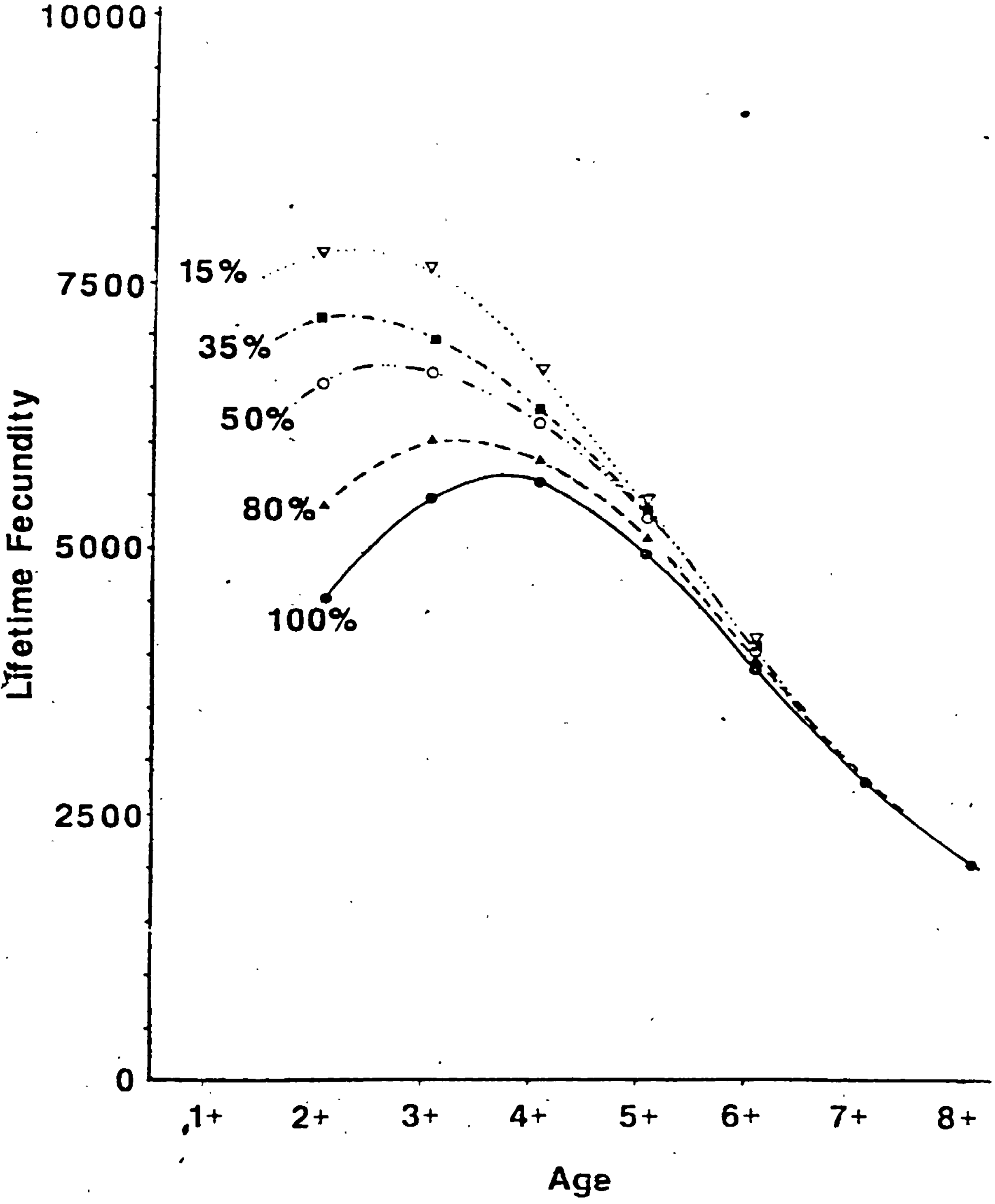

4000
3500
3000
2500
2000
1500
1000
500
No. of Eggs/Spawning
2+
3+
4+
5+
6+
7+
8+
Age

Figure 22. Effect of varying pre-reproductive and post-reproductive growth rates on potential life time fecundity at different ages of maturation. Optimal maturation age was sensitive to growth occurring before and after maturation. A reduction in pre-reproductive growth rate shifted the optimal maturation age towards the left; a reduction in post-reproductive growth rate (i.e., increased cost of reproduction, ranging from 15% to 100% of the year's potential growth) shifted the optimal maturation age towards the right. a) Sutton River model, b) Moser River model.

a) Sutton River model





b) Moser River model

3.5 Parr.

Sutton River brook trout parr exhibited rapid increase in length during the short summers. During the 45 day period that parr were caught, they increased their length by 61% (Fig. 23). Parr were not evident in the river before mid-June or after late August.

Sutton River brook trout parr reach sizes during their first summer that surpass lengths attained by parr of many southern populations (Table 19). The difference in growth rate is further accentuated when hatching date is taken into account. Southern populations hatch earlier and hence have a longer time to grow than northern populations. Furthermore, Sutton River parr lengths were determined from samples captured on a single day each month. In July and August the sampling date was before the middle of the month, hence the range is conservative.

Mean instantaneous growth rates were calculated for Sutton River parr by converting total lengths into weights using the equation:

$$\text{Log}(W) = -5.257 + 3.154\ \text{Log}(L)$$

(from Cooper, 1961)

The weight gain/day was then calculated and divided by the average weight for the time period to attain the mean instantaneous growth rate with units of %weight·day^{-1} (Table 20). Since the mean instantaneous growth rate is a weight

Figure 23. Growth of parr in the Sutton River during 1984. Mean and 95% confidence limits are shown. Sample size (n) also appears on the graph.

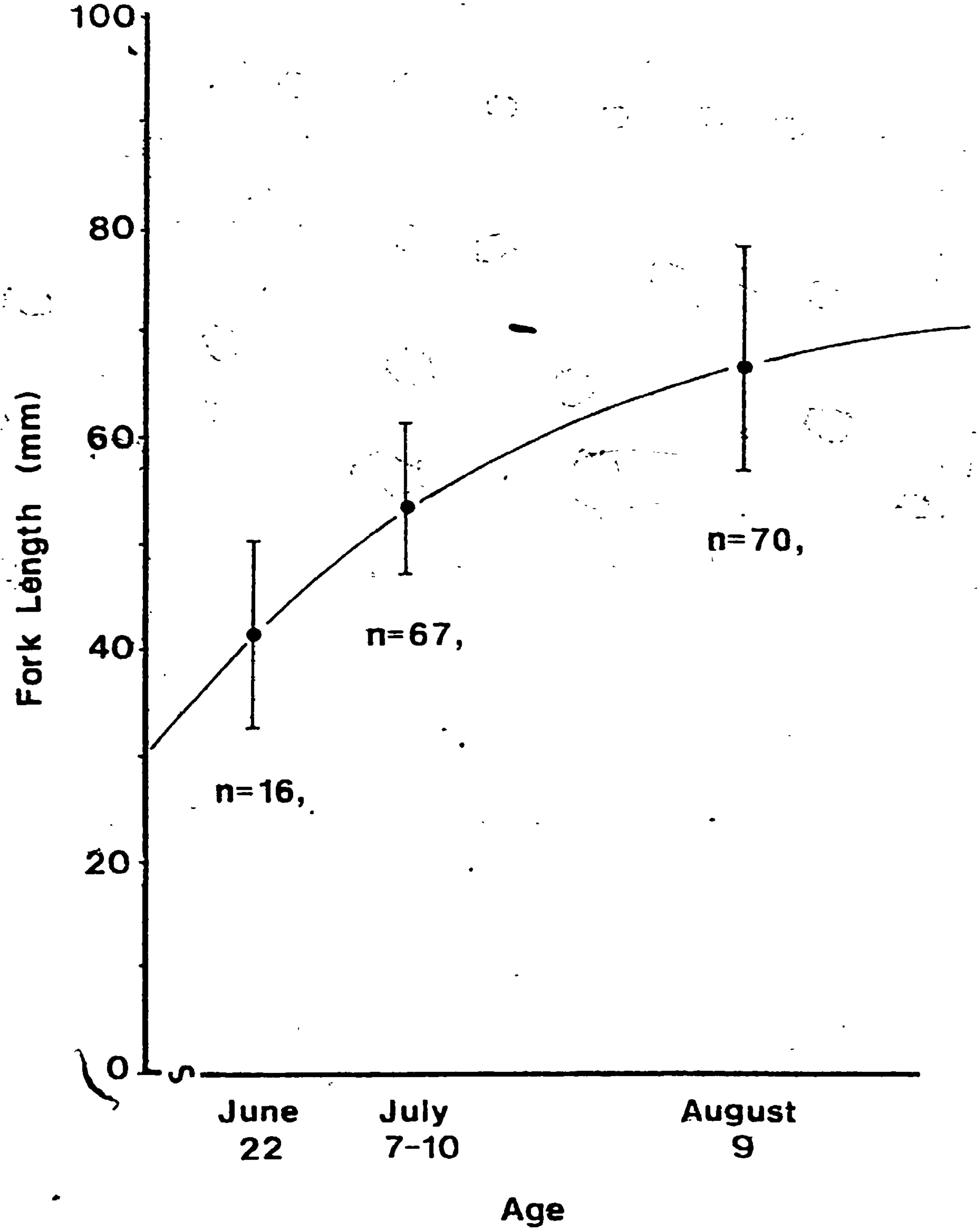

100
80
60
40
20
0
Fork Length (mm)
n=16,
n=67,
n=70,
June
22
July
7-10
August
9
Age

Table 19. Range of total lengths of 0+ age parr in some North American populations. Measurements are of total length (mm) and sample size where available appears in brackets after the range.

Location	Month		
	June	July	August
Sutton River	36-50 (16)	46-64 (67)	57-82 (70)
Nelson-Hayes R.[1]	19-27	22-44	43-74
S. Ontario	36-46 (21)	28-69 (13)	33-58 (85)
Nova Scotia			56-61 (45)
New York	53-58	33-61	56-71 (76)
Michigan	30-94 (42)	36-102 (240)	
Wyoming		20-33 (152)	43-104 (244)
Indiana		64-127	43-122 (3149)
California			33-43 (261)
Hatcheries	30-102 (409)	41-127	71-135

data summarized from Carlander (1969).

[1] from Gaboury (1978)

N.B. Sutton River data underestimates size ranges for July and August as samples were collected during the first week of each month.

dependent variable, it was regressed against mean weight to determine the slope (b=-1.67).

Instantaneous growth rate factors ($I.G.R._{fac}$) were calculated by dividing the mean instantaneous growth rate ($I.G.R._{obs}$) by the maximum instantaneous growth rate ($I.G.R._{max}$) as given by Brett (1979). Calculation of instantaneous growth rate factors for river dwelling parr for June through August were straight forward as lengths and weights of parr were available. Lengths and weights of river dwelling parr were estimated for September by extrapolating the parr growth curve (Fig. 23). However, lengths and weights of marine parr, as well as their growth rate were unknown; attempts to capture parr in the Sutton River estuary or nearshore Hudson Bay during late summer had failed. Hence, it was necessary to assume that the length of 1+ fish in spring was similar to that of the 1+ fish during the preceding October and that the weight of October fish was in the same proportion to length as it was during July and August before instantaneous growth rates could be calculated (Table 20).

Brook trout parr dominated (43%) seine hauls upstream of the Base Camp (Table 21). One thousand seventeen parr were seined and fin-clipped from seven areas above the Base Camp between July 16, and August 13, 1984. Brook trout parr were observed to migrate downstream through the weir during August 1983 and 1984. Parr drifted passively, facing into

Table 20. Calculation of habitat suitability of Sutton River and Hudson Bay for young trout as measured by an adjusted instantaneous growth rate factor (I.G.R._{fac}). Instantaneous growth rates (I.G.R.) expressed as percent weight gain day^{-1}/ avg. weight. I.G.R._{max} were calculated from Brett (1979). Total lengths (TL) expressed in mm, weights in g.

	River			Bay
Parameter	June-July	July-Aug.	Aug.-Sept	Aug.-Oct.
No. of Days	14	30	30	60
Initial TL	42.4	56.6	70.7	70.7
Final TL	56.6	70.7	75.0	124[1]
Initial Wt.	0.75	1.87	3.77	3.77
Final Wt.	1.87	3.77	4.54	22.2
Avg. Wt.	1.31	2.82	4.16	12.98
Wt. Diff.	1.12	1.90	0.77	18.4
Wt. Gain/Day	0.08	0.06	0.26	0.31
I.G.R._{obs}	6.1	2.1	0.6	2.4
I.G.R._{max}	5.3	4.1	3.2	2.1
I.G.R._{fac}	1.15	0.51	0.19[2]	1.14[3]

1. Length of smallest 1+ trout caught in June, 1984.
2. h_1
3. h_2M

Table 21. Composition by family (except brook trout), of seine hauls from seven areas above the Base Camp, July 16 - Aug. 14, 1984.

#	Brook Trout	Cyprinid	Gaster-osteids	Cottids	Catostomid	Percid
1.	73	4	4	2	71	11
2.	200	154	22	5	38	118
3.	195	86	25	47	42	64
4.	136	88	73	56	46	133
5	51	20	0	1	6	3
6	205	52	27	22	28	59
7.	157	12	0	5	22	5
	1017	416	151	138	253	393

the current, until they met an obstruction such as the weir. The parr remained 20 to 200 cm away from the weir following it down and across current for varying distances before they turned quickly and darted downstream through the weir. Parr resumed their upstream facing passive drift about 1 m downstream of the weir. The parr usually occurred in poorly defined aggregations numbering from a half dozen to several hundred; movement was not synchronized. Dense aquatic macrophyte stands and shallow water (0 to 20 cm) made seining downstream of the weir extremely difficult between August 15, and September 4, 1984. Water temperatures were high and variable. Few parr (149) were recovered downstream of the weir; none was fin clipped.

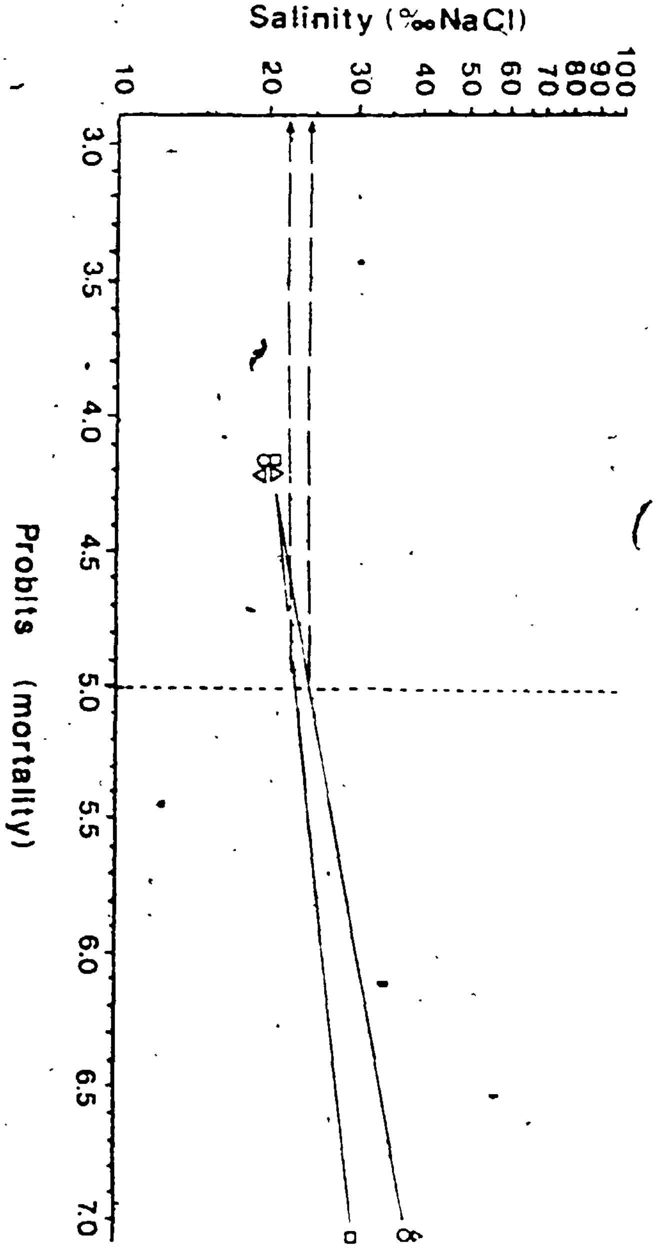
3.6 Bioassay.

Ninety parr were maintained without mortality in 45 l pails of aerated river water for three days before testing in each of four trials. Assays consisted of a control (0°/oo NaCl) and two to four experimental (saline) solutions ranging from 10 to 40°/oo NaCl (Table 22). There was no difference in the fork length of parr within assays. No mortalities occurred in controls (0°/oo NaCl) or in isosmotic (10°/oo NaCl) salinities even when maintained beyond 132 hr. All four assays were consistent with a 96 hr LC50 of 21°/oo NaCl (Fig. 24). This did not change with size although parr grew significantly between July 10 and August 9 (Fig. 23).

Table 22. Test solution concentrations used in bioassays of parr tolerance to NaCl.

Trial No.	Date	Salinity of solutions (‰ NaCl)				
		1	2	3	4	5
1.	July 10	0	9	21	39	
2.	July 10	0	10	21	40	
3.	Aug. 9	0	10	20	30	40
4.	Aug. 9	0	10	20		

Figure 24. Probit graph of 96 hr survivorship on ln salt concentration for salinity bioasssays. The calculated LC_{50} ranged from 22 to 25 °/oo NaCl. Trial 1 - triangle, Trial 2 - circle, Trial 3 - square, trial four - inverted triangle.


Salinity (‰NaCl)
10
20
30
40
50
60
70
80
90
100
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
Probits (mortality)

3.7 Length and Weight Analysis.

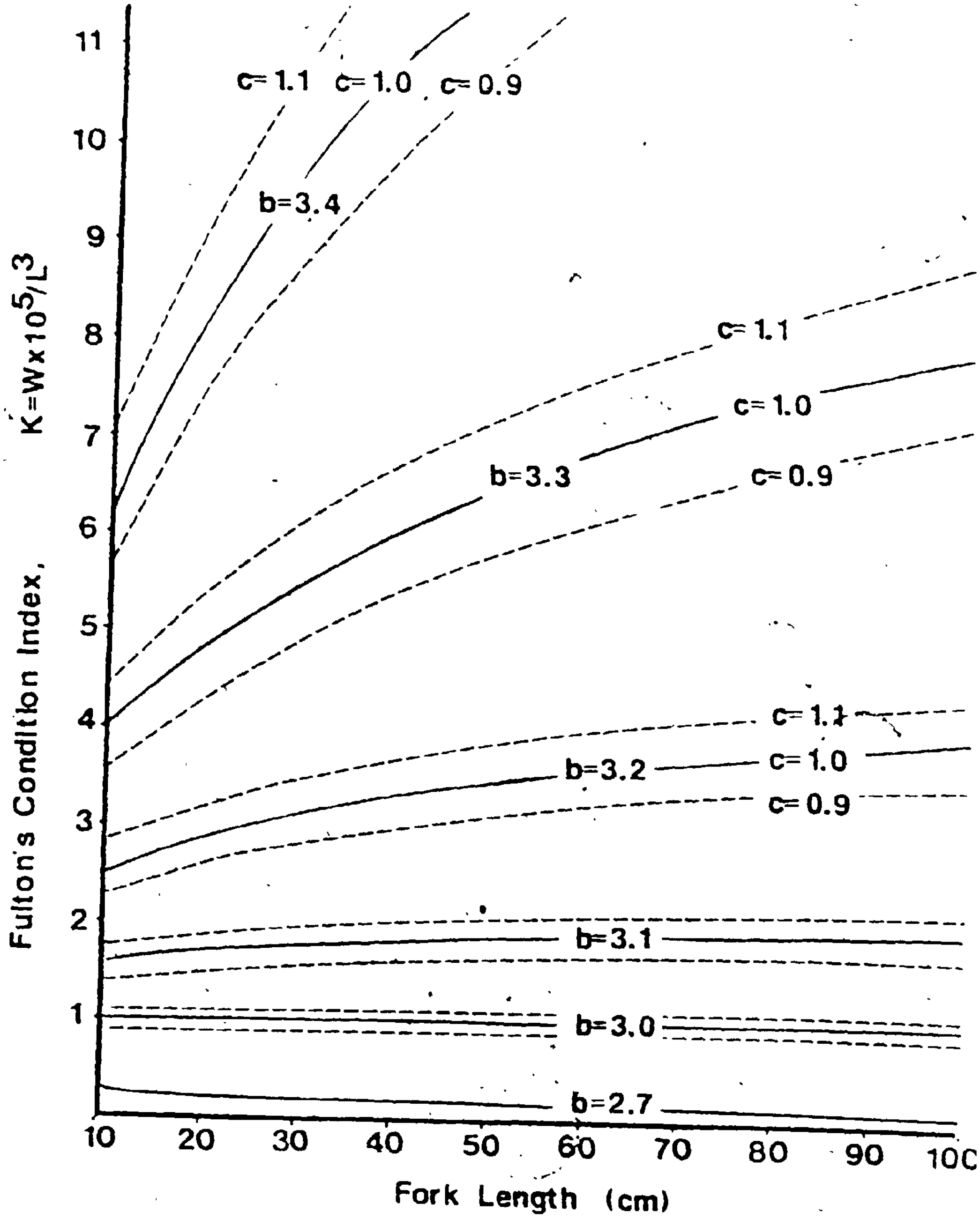
Condition indices have been used to compare the weight length relationship of fish. The most commonly used index or factor is that of Fulton (Ricker, 1975). Fulton's condition factor,

$$K = W * 10^{5} / L^{3}$$

is equal to unity when growth without shape change occurs. Changes in K are not linear; if the fish becomes leaner with length, K approaches zero; if the fish fattens with length, K approaches infinity. Fulton's factor is also sensitive to changes in both the slope and intercept of the weight on length regression, as K is the product of e^{a} and $L^{(b-3)}$ (the variation associated with the deviation of 'b' from 3.0). As 'b' deviates from 3.0 the length of the fish becomes increasingly important (Fig. 25). Log transformations do little to stabilize K. Hence condition indices were abandoned in favour of geometric regressions.

Weight on length geometric regression for the complete sample suggested allometric growth ($W = -11.86\ L^{3.047}$). A between year comparison if not prevented by non-homogeneous variances ($F\ max_{2,812,\ 414} = 1.59$; $p<<0.001$), would have indicated minor (1983: $b=3.17$; 1984: $b=3.07$) but significant differences between slopes (slopes: $t_{577}=3.83$; $p<<0.001$).

Figure 25. Dependence of Fulton's condition factor (K) on the length of the individual and the slope (b) of the weight on length regression. The slope was varied from 2.7 to 3.4 in this simulation, and the intercept (C) was fixed at 0.9, 1.0 and 1.1 for each slope (varying the intercept had a decreasing effect as the slope decreased and hence, is not shown for slopes below 3.0). The value of the slope normally varies from 2.78 to 3.21 for brook trout (Carlander, 1969) and in this study varied from 2.62 to 4.73.


Fulton's Condition Index, K=W×10^5/L^3
Fork Length (cm)
11
10
9
8
7
6
5
4
3
2
1
10
20
30
40
50
60
70
80
90
100
c=1.1
c=1.0
c=0.9
b=3.4
b=3.3
b=3.2
b=3.1
b=3.0
b=2.7

Weight on length regressions were calculated for each age class of otolith aged trout regardless of sex (Table 23). Young trout (3+ and 4+) added weight significantly faster than length, while trout in their sixth year (5+) added length significantly faster than weight. Older mature trout (6+ and greater) approximated the isometric condition (Fig. 26). Weight on length regressions for each of the 3+ through to 5+ age classes were significantly different by ANCOVA (Slopes: $F_{2,124}=23.98$, $p<<0.001$). There was a significant ($0.01<p<0.05$) inverse relationship between slope and age/length.

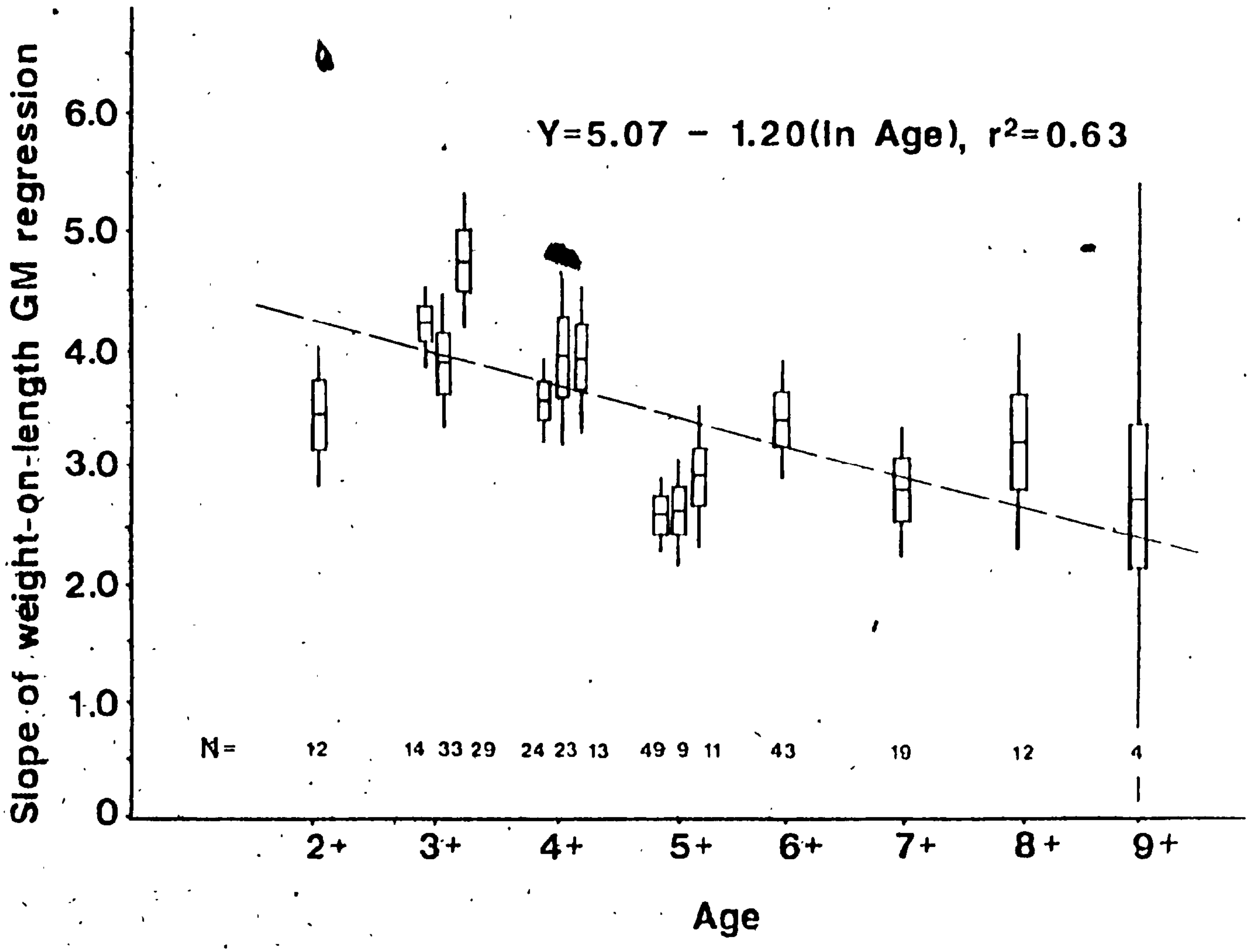
Table 23. Weight on length geometric regressions for otolith aged trout caught at the weir ($W = \ln(\text{weight})$, $L = \ln$ (fork length).

Age	Regression Equation	95% Confidence Limits				N	r^2
		Slope		Intercept			
July							
3+	$W = 4.18\,L - 18.4$	3.81	4.54	-20.3	-16.1	14	0.98
4+	$W = 3.54\,L - 14.5$	3.19	3.91	-16.7	-12.4	24	0.95
5+	$W = 2.58\,L - 8.68$	2.25	2.92	-10.7	-6.62	49	0.81
August							
3+	$W = 3.86\,L - 16.3$	3.30	4.42	-19.6	-13.1	33	0.84
4+	$W = 3.93\,L - 16.8$	3.20	4.66	-21.2	-12.4	23	0.83
5+	$W = 2.62\,L - 8.84$	2.11	3.12	-12.0	-5.72	9	0.95
September							
3+	$W = 4.73\,L - 21.6$	4.17	5.28	-24.9	-18.3	29	0.91
4+	$W = 3.88\,L - 16.6$	3.27	4.49	-20.3	-13.0	13	0.94
5+	$W = 2.92\,L - 10.8$	2.33	3.51	-14.5	-7.24	11	0.93

N.B. Significant differences existed between the slopes of 3+, 4+ & 5+ age classes for July and September. Variance was not homogeneous for August comparisons.

Significant differences existed between intercepts of 3+ age classes for July, August and September; 4+ age classes for July and September and 5+ age classes for July, August and September.

Figure 26. Reduction of the weight-on-length regression slopes with age. Mean slope with 95% confidence limits, shown for 3+ to 5+ age classes for each of July, August and September, 1984; months were grouped for 6+ to 9+ age classes.


Y=5.07 - 1.20(ln Age), r²=0.63
Slope of weight-on-length GM regression
6.0
5.0
4.0
3.0
2.0
1.0
0
N=
12
14 33 29
24 23 13
49 9 11
43
19
12
4
2+
3+
4+
5+
6+
7+
8+
9+
Age

migrations were advanced, possibly by as much as three to four weeks during 1984 (G. Kolonoski, pers. comm.). Hence, brook trout must use cues other than temperature or flow rates to signal the initiation of their return migration to the river.

Celestial cues, particularly photoperiod, are a likely alternative. Photoperiod has been shown to be a 'directive factor' (Brett, 1979) or 'releasing mechanism' (Baerends, 1971) for migratory and reproductive events, physiologically and behaviourally, for brook trout and other salmonids (R.L. Saunders and co-workers). At northerly latitudes changes in photoperiod length are more pronounced than at temperate latitudes thereby allowing greater precision in the determination of celestial time or in the timing of yearly events than is possible at temperate latitudes. Photoperiod would be a likely cue that brook trout use to time their return migrations into the Sutton River.

Considerable effort was exerted in tagging ascending trout so that the population size could be estimated, the spawning frequency and migration routes determined, and ageing and length at age estimates verified. Few recaptures/returns and a faulty tag design that failed to retain numbered portions of the tag negated most of this work. In addition, manpower difficulties prevented increasing the recapture effort upstream of the camp. However, it is unlikely that with increased effort the determination of acclimation temperature. Houston (1982) reported that the effect of diurnally fluctuating temperature was an increase in the thermal resilience of the fish (an increase of the realized acclimation temperature). The amplitude of the increase observed in the realized acclimation temperature was not predictable. An increase of 4°C was observed in the realized acclimation temperature of cutthroat trout (*Salmo clarki*) that experienced a +/-5°C fluctuation (Heath, 1963), but rainbow trout (*S. gairdneri*) whose ambient temperature fluctuated +/-7° and +/-4°C increased their realized acclimation temperatures only by 2.4° and 1°C respectively (Threader and Houston, 1982). However, it is not known what effect of variable (such as observed in the Sutton River), as opposed to regular, fluctuations has on the LT$_{50}$(°C) of brook trout or other fish. It is assumed that the response of charrs (*Salvelinus*) would be similar to that of trout (*Salmo*) and that variable fluctuation would not negate the effect of constant fluctuations on the thermal resilience of fish. Hence, the river temperatures observed at Base Camp may not be considered lethal to adult brook trout and the reason for anadromy of the Sutton River brook trout is other than lethal summer river temperatures.

Fish are less tolerant of high temperature than they are of low temperature. As temperature increases above the optimum, digestion rates, metabolic demands, maintenance ration, and excretion rates increase, food consumption is reduced, and conversion efficiencies decline precipitously (Brett, 1979). Brook trout held at a constant temperature of 6°C below their optimum temperature outgrew trout held 2°C above their optimum temperature (McCormick et al., 1972). Likewise, brook trout held at 2°C have a higher mean instantaneous growth rate than those held at 22°C (by extrapolation; McCormick et al., 1972). Declining ration quality or quantity necessitates preference for water that may be much below optimum temperature rather than for water that may be slightly elevated above optimum temperature. Furthermore, McCormick et al. (1972) reported that there was a net biomass loss, due to mortality, from populations of brook trout held at temperatures greater than 19°C. Hence temperature, when coupled with poor ration quality or quantity, may force the Sutton River brook trout to be anadromous during the summer months. Furthermore, if diurnally fluctuating temperatures affect the final preferred temperature as they do acclimation temperatures, the realized temperature of the river may exceed that of the observed and amplify the preceding effects.

4.2 Weir Data.

Incomplete blockage of the river during 1983 and low water levels that prevented fish from ascending the river during August 1984 hindered the comparison of the fishing ability of the weir during 1983 and 1984. The small numbers of tag recaptures during both 1983 and 1984 (and subsequent years) prevented estimation of year class strength and thereby further compounded the difficulty of estimating the weir's fishing ability.

Calculation of catch per unit effort (C.U.E.) estimates indicated that the weir captured 10% more trout per unit effort (the number of meters of weir x the number of hours operational) in 1984 than 1983 (1.8×10^6 m·hr, 3922 trout; 7.1×10^5 m·hr, 1381 trout respectively). When adjusted to similar operation times (July 17 to September 11), 1.7 times the 1983 effort produced 2.3 times the trout during 1984. The increased C.U.E. during 1984 may have been the result of low water levels which prevented trout that normally ascended the smaller Hudson Bay tributaries from doing so and instead forced them to ascend the deeper channelled rivers such as the Sutton River.

Low water levels and in particular low flow rates during 1984 also resulted in trout jumping over the weir at night and thus eluding enumeration. Jumping was not observed during 1983 although water levels were often within 20 cm of the top of the weir. Low flow rates during 1984 may have reduced the 'leading effect' of the weir, and hence the effectiveness (attractiveness) of the traps. Faced with this apparently 'unpassable' barrier trout may have elected to jump over the weir.

Peak dates of runs occurred at similar times of the year during 1983 and 1984 even though river and bay conditions differed substantially between the years. The precision of the timing of the runs between years indicates that brook trout may not use river or bay conditions as a cue for migration. Runs number 7 and 8 during 1984 peaked one year (+/- 1%) after runs number 2 and 3. Run number 6 peaked 10 days earlier in 1984 than did run number 1 in 1983. However it was difficult to assign a peak date to Run 1 due to the peculiarities of weir operation during 1983. The greatest number of trout to ascend the river in one day during 1983 occurred five days after the assigned peak date; the next night the weir was damaged by flood waters. The weir was not operational during July 27 - July 31, 1983, which corresponded to the period of the greatest migration during 1984, so the peak date of Run number 1 may be inaccurate and premature by 9 days. River temperature and water level patterns were not similar for the two years and circumstantial evidence (i.e., ice persistence and bear migrations) suggest that water temperatures were warmer in the bay during 1984 than 1983. Both ice melting and bear migrations were advanced, possibly by as much as three to four weeks during 1984 (G. Kolonoski, pers. comm.). Hence, brook trout must use cues other than temperature or flow rates to signal the initiation of their return migration to the river.

Celestial cues, particularly photoperiod, are a likely alternative. Photoperiod has been shown to be a 'directive factor' (Brett, 1979) or 'releasing mechanism' (Baerends, 1971) for migratory and reproductive events, physiologically and behaviourally, for brook trout and other salmonids (R.L. Saunders and co-workers). At northerly latitudes changes in photoperiod length are more pronounced than at temperate latitudes thereby allowing greater precision in the determination of celestial time or in the timing of yearly events than is possible at temperate latitudes. Photoperiod would be a likely cue that brook trout use to time their return migrations into the Sutton River.

Considerable effort was exerted in tagging ascending trout so that the population size could be estimated, the spawning frequency and migration routes determined, and ageing and length at age estimates verified. Few recaptures/returns and a faulty tag design that failed to retain numbered portions of the tag negated most of this work. In addition, manpower difficulties prevented increasing the recapture effort upstream of the camp. However, it is unlikely that with increased effort the recapture rate of previous year's tags would have increased by more than a few percent as recapture rates at the weir were also low throughout the summer of 1984.

Among the plausible explanations for low recapture rates are the following:

i) Loss of tags,

ii) Incomplete detection of tags,

iii) Trap shyness,

iv) Lack of annual fidelity to the Sutton River (including alternate year spawning, semelparity, and straying),

v) Winter or marine dieoffs (undifferentiated mortality), and

vi) Differential (tagging) mortality.

Double anchor *Floy* tags described by Thorson (1967) and Dell (1968) were used during 1984. When properly placed (i.e., anchors engaged with the interneurals), tag loss is minimal for brook trout 15 cm or greater in length (Carline and Brynildson, 1972). Proper placement of anchors was verified in this study by killing and dissecting arbitrarily chosen tagged trout.

In response to poor tag recovery rate and tag breakage, the tagging method was changed to a conservative but time consuming method of needle and line. This method left less of a scar but numbered portions of the tags were retained by the fish and the tags were more visible to fishermen. Nevertheless, tag recoveries did not alter appreciably indicating that neither the tagging method nor tag loss was the likely cause of low tag recovery rates.

Incomplete tag detection was not a problem in this study. Intact *Floy* tags and tied tags were apparent to fishermen who were unaware that trout were tagged and to trained observers. Many trout tagged with *Floy* tags and especially those that had lost the numbered portion, developed ulcers or scars similar to that described by Keller (1971). This attracted attention to the tagged area, increasing the likelihood of tag detection. Furthermore, all handled fish were scrutinized for scars or wounds arising from tagging, lamprey attacks or other causes, decreasing the likelihood that any tag or tagging scar went undetected.

There was no evidence to indicate that tagged trout avoided traps more effectively than untagged trout. It is unlikely that brook trout would learn to avoid weir traps and attempt to jump the weir after only one encounter with a trap in the previous year. However, if this were the case, these 1983 tagged fish which would be equally as vulnerable to angling as untagged fish, should have formed a greater percentage of the 1984 angled catch than they did of the 1984 weir catch. Only one trout tagged in 1983 was angled during 1984 when the weir was operating. Hence, trap shyness is not an explanation of the low tag recovery rate.

Trout may not return annually to the Sutton river because they spawn in alternate years, or because they are semelparous. Straying between tributaries of Hudson Bay would also decrease the number of trout returning to any one tributary each year.

The first documentation that wild brook trout may not spawn regularly was by Vladykov (1956). He reported finding that "Among adult trout collected in Lake Grelon in fall of 1952, which were in immature condition, some females still retained odd large ova in the abdominal cavity, left over from the 1951 season." (p. 825). It was Vladykov's opinion that this was the result of inadequate diet and not of infection by the cestode *Diphyllobothrium* which causes sterility. Similarly, resource limitation was inferred by Power (1980) as an explanation of irregular reproduction by northern anadromous female brook trout of the Ungava Peninsula. There, individual females bred during two out of every three years, or, only during alternate years (males spawned annually). Coupled with resource limitation were short northern summer seasons that aggravated the situation by limiting the period during which brook trout were active.

Sutton River brook trout do not exhibit the symptoms of resource limitation. This population has one of the fastest growth rates to appear in the literature and the fish attain large sizes. Therefore, the population is an unlikely candidate for irregular spawning.

Recovery of trout tagged in previous years was too infrequent to confirm that alternate year spawning does not occur in Sutton River. However 30% of the 1984 recaptures that had been tagged during 1983 were killed and dissected; mature females accounted for 57% of these trout. Since it was impossible to confirm that these fish spawned in the previous year, it can only be stated that all of these females ascended the river during 1983 at sizes that equalled or exceeded the 50% size of maturity. Unfortunately, only one 1983 tag was returned during 1985 (of which the sex was not determined) preventing any further enlightenment.

Semelparity is also not a likely explanation for low tag returns. Semelparity has not been reported for brook trout or any other member of the genus *Salvelinus*. The presence of many age classes after the age of 50% maturity and the absence of old immature females discount the existence of such a strategy in this population. Furthermore, recovery of autumn spawned fish in March, and females with atretic eggs in June, also indicates that this population like other brook trout populations is iteroparous.

"Surprisingly little work has been done on the homing ability of brook trout (*Salvelinus fontinalis*)." (O'Connor and Power, 1973). The first mention of brook trout displaying a homing tendency appeared in a "Manual of fish culture" (1900, p. 83; from Vladykov, 1942). Early transplant studies of spawning brook trout confirmed that between 7% and 11 % of transplanted trout return to the 'exact' location at which they were caught within 48 hrs (Vladykov, 1942). Tagging of anadromous Moser River brook trout revealed that the return rate for homing brook trout was greater than that reported for spawning fish by Vladykov but it also confirmed that straying does occur (White, 1940;1941). Later studies reported that 99% of migratory brook trout chose correctly between two creeks 500 m apart one year after tagging (O'Connor and Power, 1973).

Smith and Saunders (1958) concluded that the potential for straying of anadromous trout was limited due to the "... strong tendency to stay in the home estuary after running to salt water..." (within 5 km of the river mouth). Richmond Gulf (east coast of Hudson Bay) studies showed that without exception the anadromous brook trout did not stray more than 5 km from the river mouth (Dutil and Power, 1980).

This contrasts with the tagging results of the present study. Eight percent of the tags returned originated from Hudson Bay tributaries other than the Sutton River, indicating that there is movement of brook trout along the inshore waters. It is possible that the lower salinities of the southwest coast inshore waters and the lack of well defined estuaries along this coast result in the trout treating this section of Hudson Bay as one large estuary. Furthermore, the extensive tidal mud flats (often exceeding

8 km in width) may contribute to this phenomenon and the associated tidal currents may passively transport trout considerable distances.

An additional explanation for straying of brook trout was offered by Weir (pers. comm.). While engaged in trout studies along Ontario's James Bay coast, Weir hypothesized that inter-river movement was an important aspect of the life history of trout from the small tributaries of that region. Weir's preliminary studies indicated that anadromous trout that left their natal streams with the spring floods were unable to reascend the streams in late summer if water levels were reduced. Faced with such an option, these 'stranded' trout would ascend and reproduce in nearby rivers with deeper channels. This would account for trout tagged in one river system being recaptured in a nearby watershed. The similar topography and climate of the two areas (James Bay and Hudson Bay coastal plains) may mean that the same mechanism is responsible for the recovery in other river systems of trout tagged in Sutton River. Nevertheless, inter-river movement and straying does not explain the loss of 98% of the tags.

There was no evidence from non-tagging sources that a large winter kill or marine kill occurred during 1983-1984. The presence of numerous mature brook trout during 1984 supports the conclusion that there had not been a large mortality. Sportsmen did not notice any decline in C.U.E.

that would have accompanied a dieoff, and there were no reports of numerous dead fish in the river.

The most likely explanation of the low number of tag returns is differential mortality (mortality due to tagging). However, studies using *Floy* tags indicate that mortality due to tagging is generally less than 2% (Rawston, 1973). Endocrinological studies I conducted with Sutton River brook trout during 1984 and 1985 revealed a possible mechanism that may have elevated the mortality rate of tagged fish.

It was found that trout that had migrated into fresh water from Hudson Bay were unable to coagulate their blood (see Appendix II). Fish injured as they entered or ascended the river bled to death. Tags in place during this time undoubtedly were a potential cause of bleeding, either from the tagging procedure or from being a continual irritant until sufficient scar tissue could form around the tag. Snagging of the tag at any time in nets, traps, or debris also stimulated bleeding. Bleeding from tag wounds was usually minor and therefore dismissed as unimportant during the first two years of study. In hindsight, it is clear that tagging caused the death of many fish. These trout would have continued their ascent for several days (perhaps ascending the full length of the river) bleeding slowly and gradually becoming weaker. Once the trout left the lower stretches of Sutton River, they or their corpses were never seen or recovered again. This would have greatly diminished the number of live tagged trout. Furthermore, survivors may have been so stressed by blood loss that they were no longer representative of the population.

Anglers during July to September often caught and released up to 100 trout per day per person; this also contributed to many mortalities as indicated by the numerous dead trout that floated downstream for five to seven days after the anglers left the area. Lack of coagulation, together with prolonged and rough handling, are thought to be responsible for the numerous mortalities attributed to anglers (Steele, 1985; unpublished report to M.N.R.).

Trout entered the weir only during the night, usually after midnight. Smith and Saunders (1958) found the greatest movement in Ellerslie Brook (P.E.I.) also to have occurred at night, usually between 18:00 and 22:00 hr. Sutton River trout movements were later than those of P.E.I. populations, probably due to the higher latitude and hence later and longer summer twilights. Trout were not observed in the delta during daylight hours even though high tides often occurred then (two tides a day, 23:05 hr cycle). All major activity including movement and jumping of the weir was nocturnal. This may have been in response to either high (potentially lethal) daytime temperatures in the shallow water of the delta region or the presence of numerous visually-oriented avian predators (e.g., ospreys, bald eagles, golden eagles). Several trout bore scars from unsuccessful predation attempts by birds, indicating that these birds may be a serious threat to the fish. The shallow waters of the delta region provided little protection from aerial attackers. In general, little cover was available to the fish in much of the lower river due to it's shallow nature and pristine clarity hence the trout would be at risk for much of the time that they were in the river.

Few trout bore scars from encounters with whales or seals. The low frequency of scarring from marine mammals may indicate either fewer encounters with them than with avian piscivores or that trout had less chance of surviving an encounter with a marine mammal.

Lamprey attacks were the most frequent cause of brook trout scarring. The lamprey implicated in the attacks was the parasitic silver lamprey, *Ichthyomyzon unicuspis*. Since no lampreys were recovered, identification of the species was based upon scar diameter and likely distribution (Hubbs and Potter, 1971; Scott and Crossman, 1973). Although lampreys were previously unreported from Hudson Bay, the silver lamprey has been recovered from the Nelson River system in Manitoba. From this point of entry into the Hudson Bay watershed, the species could colonize Hudson Bay tributaries both north and south of the Nelson-Hayes River system. The expansion of this species range has probably been slowed by its intolerance of salt water (Scott and

Crossman, 1973). This avoidance of salt water may also prevent the lamprey from following the trout into brackish water to parasitize them there (Hubbs and Potter, 1971). Moreover, it explains the presence of fresh scars only on the trout angled above the weir. Lamprey parasitism for the Sutton River brook trout is strictly a freshwater danger.

Parasitism by silver lamprey does not seem to be lethal in all cases to brook trout but does predispose a trout to further parasitism as 40% of parasitized trout had multiple scars. Whether this is due to the trout being so weakened by the initial attack that they were unable to ward off future attacks or that these trout frequent different habitats than the general population is not known. Likewise, no reason is suggested for the sexual bias (three times as many males attacked as females) observed in parasitized trout. The presence of this parasitic lamprey in the Sutton River is of grave concern because if it becomes abundant there is the potential for it to deplete the trout population by attacking fish when the blood can not be coagulated.

4.3 Ageing and Growth.

Scales have long been the most popular method of ageing temperate fishes including brook trout. Cooper (1951) showed that scales provided both accurate and precise estimates of age for brook trout less than five years old. However, scales may yield erroneous results if growth rate is slow. Alvard (1954) was unable to obtain reliable age estimates from trout scales if the growth rate of the trout was less than 2 cm/yr and Vladykov (1956) found age determination by scales unsatisfactory for slow growing and possibly stunted brook trout from Quebec lakes.

A problem in determining age from scales of fishes that is restricted to individuals from northern or cold reared populations is the absence of first annulus. Jensen and Johnsen (1982) reported that parr from the members of the genus *Salmo* fail to develop the initial annulus when held in cold environments. This results in the under-estimation of the true age by one year for all age classes. Members of the genus *Salvelinus* react similarly, necessitating validation of ageing in cold reared populations. Length frequency distribution analysis is commonly used for this purpose and together the two methods provide accurate age determinations (Lee, 1969; Coleman, 1970; Saunders and Power, 1970; Hazel, 1976; O'Connor and Power, 1976).

Neither of these factors was responsible for the variability observed in the scale determined ages for the Sutton River brook trout, as these fish grew quickly (from length frequency distributions), were not maintained in cold water for their first summer and the discrepancy between scale-determined and otolith-determined ages increased with age.

Dutil and Power (1977) reported that scale-determined ages may not be accurate for the anadromous trout populations of northern Quebec. They observed that 33 of 74 scale determinations underestimated the otolith determined age of anadromous Richmond Gulf brook trout by a mean of 1.5 yrs. The variability associated with the scale determined ages observed for the Sutton River brook trout was similar to that reported by Dutil and Power (1977). In the present study of 298 scale-otolith comparisons, 167 scale determinations underestimated otolith determined age by a mean of 2.1 yrs. Underestimation increased in frequency and magnitude with otolith determined age, therefore the greater mean number of years underestimated may have been influenced by the inclusion of older fish in the Sutton River sample.

Gaboury (1978) in a study of 38 possibly anadromous brook trout found that scales estimated fin ray determined and otolith determined age differently. Forty-eight percent of scales either underestimated (15%) or overestimated (33%) fin ray determined age and 42% of scales underestimated otolith determined age. Nevertheless, Gaboury concluded that scales were valid for ageing Nelson-Hayes River brook trout as the Chi-squared statistic for a comparison of ages derived by the three methods (scales, fin rays and otoliths) for a subsample of 22 of the fish was not significant at the 95% level. Wide confidence limits on the geometric mean regressions (fin ray - scale comparison, slope: 0.89 +/-0.25 intercept: 0.68 +/-1.17; otolith - scale comparison, slope: 1.01 +/-0.19, intercept: -0.50 +/-1.01) also indicate no significant difference between the methods. However, an increase in sample size and inclusion of older age groups in the sample might have indicated otherwise.

In contrast, Frost (1973) found little discrepancy between scale determined ages and otolith determined ages (10% of scales underestimated the otolith age by one year or less) for the non-anadromous Windermere Lake charr (S. *willughbii = alpinus*?). Frost attributed the observed differences to erosion (=resorption) of the anterior edge of the scale during the spawning period and to the slow growth rate of these fish (2.3 - 3.1 mm/yr).

Scale resorption is often responsible for difficulty in determining scale age and underestimating true age (Liew, 1974; Linfield, 1974; William & Bedford, 1974; Dutil & Power, 1976; Hecht, 1980). Resorption of scale margins during spawning (or other stressful times) is common in many fishes; it probably was first observed in Atlantic salmon and searun trout or char by Crighton in 1935 (Simkiss, 1974). Resorption may be severe enough to reduce the scales "so that only the centers remain in the scale pockets" (Bilton and Jenkinson, 1968). The amount of resorption is dependent on the stress the fish is subjected to and the availability of calcium to the fish. Any change in the availability of calcium affects the deposition rate of $CaCO_3$ on the scales and hard structures (e.g., otoliths, fin rays, vertebrae) of the fish (Williams and Bedford, 1974). Resorption occurs from the scales, but not the hard structures, when Ca^{++} debts occur internally (i.e., during spawning, heat or other stress). Calcium and phosphorus are relatively stable in teleost bone and otolith; they are not available for resorption (Simkiss, 1974; Rodgers, 1984). This makes these 'hard' structures reliable for ageing (Linfield, 1974).

Too few scale-otolith comparisons (Frost, 1973; Dutil and Power, 1976; Gaboury, 1978; and this study) have been reported to conclude that scale resorption is more severe in anadromous species than non-anadromous species, but severe scale resorption should be suspected in anadromous species as calcium availability fluctuates with environmental osmolarity. In fresh water, Ca^{++} must be actively sequestered by trout; in salt water, Ca^{++} is actively excreted by trout. A trout entering salt water must cease sequestering calcium and start excreting it. A temporary calcium surplus may occur as evidenced by the strongly opaque 'sea check' that is deposited on the scales with this transition. As fish change from salt to fresh water, the Ca^{++} pump must be reversed and a temporary calcium debt may occur (physiological demands also increase at this time as calcium is implicated in freshwater osmoregulation), resorption of calcium carbonate from the scales would be expected, resulting in erroneous scale determined ages. Further support for this speculation comes from Simkiss's (1974) observation that "if the fish is held at the river mouth [intermediate salinities?] before spawning, resorption may be very pronounced...".

Osmoregulation-triggered resorption may explain the differences in the comparisons of scale-determined and otolith-determined ages between freshwater charr (Frost, 1973) and anadromous charr (Dutil and Power, 1976; this study). This may also explain why, given sufficient growth rates, freshwater brook trout scales are considered reliable for ageing (Cooper, 1951) and anadromous brook trout scales are not (Dutil & Power, 1976; 1980; Castonguay et al., 1982; this study).

Fin rays are seldom used as ageing structures for brook trout yet fin rays, and in particular the first pectoral ray/spine, are the preferred structure for age determination for many fishes including catfish, sturgeon, and suckers (Jearld, 1983). Pectoral rays were assessed as an ageing structure for brook trout as they are easy to remove, do not require killing the fish and as (semi-) hard structures should retain the reliability typical of otoliths and vertebrae. A potential problem with fin rays is that the first annulus may be missed if the ray is not removed close enough to the articulation.

In this study, fin ray determined ages significantly under-estimated otolith determined ages, although the discrepancy was minor. Only 4% of age estimates determined from fin rays differed from otolith determined age by more than one year (1% over-estimated, 3% under-estimated). Hence, if it was not for the problems associated with blood clotting in this population, pectoral fin rays would have provided a quick non-lethal method of determining ages of these fish.

The Peterson method of length frequency distribution provided results that were in agreement with scale reading for the first 5 age classes. The short spawning season of the brook trout and a favourable growth rate undoubtedly aided in separating the modals (Tesch, 1971; Ricker, 1975). Furthermore, length at age observations from two trout recaptured at one and two years after tagging agreed with that predicted from otolith age determinations, indicating that the otolith ages are either correct or if tagging retarded growth, conservative.

Growth retardation has been reported following tagging for several species. *Monel* jaw tags are known to retard growth in brook trout (Smith, 1957) and lake trout (DeRoche, 1963) but little work has been done with *Floy* tags. *Floy* tags have been reported to curtail growth in bullheads (*Ictalurus nebulosus*) particularly if the fish are tagged in spring (Gunn et al., 1979). The single study of the effect of tagging brook trout with *Floy* tags indicated that "the *Floy FD-67* anchor tag initially retarded growth of domesticated brook trout but had little effect thereafter" (Carline & Brynildson, 1972). The results of the current study also suggests that growth retardation due to tagging may be minor (assuming correct ageing), but if retardation does occur then the growth rates of untagged fish would be even greater than they are assumed to be in this study.

Anadromous brook trout generally have greater growth rates than brook trout that remain resident in fresh water (Wilder, 1952; Carlander, 1969; Gaboury, 1978; Power, 1980; Dutil and Power, 1980; Castonguay et al., 1982). Dutil and Power (1980) reported as much as a 2.3 fold increase in growth rate of northern brook trout associated with their entry into brackish water. Although the advantages of marine (brackish) life are usually thought to be related to ration (a combination of prey abundance and prey quality), other factors may also be important (e.g., temperature regimes and/or osmotic induced growth hormone secretion; see Appendix I). Due to the difficulties in capturing brook trout while they are in marine waters, little study has been devoted to this aspect of their life history other than the cursory examination of incidentally caught specimens. Since attempts in the present study to recover brook trout from Hudson Bay were unsuccessful due to logistical problems (i.e., wind, ice, and bears), this phase of the life history remains a mystery.

The extreme growth rate that characterizes anadromous populations is not evident during the parr stages. Sutton River parr are fast growing (Fig. 23), but like other parr that will later be anadromous, do not grow faster than parr of some northern United States populations (Carlander, 1969; Fig. 13, Power, 1980). In northern anadromous populations, the parr often grow slower due to either harsh conditions or short growing seasons (Dutil and Power, 1980). The difference in the growth rate between anadromous and resident populations does not become apparent till the brook trout 'smoltify', usually at age 2+ or 3+ (White, 1941; Wilder, 1952 ; Carlander, 1969; Gaboury, 1978; Power, 1980; Dutil and Power, 1980; Castonguay et al., 1982). However, Sutton River brook trout run to sea at 0+ and the growth advantage is apparent by 1+. This allows Sutton River trout to prolong the period of 'depensatory growth' (Ricker, 1975) and compensatory growth does not occur till the third summer (2+). Compensatory growth occurs during the first summer for most brook trout populations for which Carlander (1969) gives information.

Sutton River brook trout continue rapidly growing after the inflexion at rates that exceed those of other anadromous populations (Wilder, 1952; Carlander, 1969; Scott and Crossman, 1973; Coleman, 1970 and Dutil, 1976 from Power, 1980; Power, 1980; Dutil and Power, 1980; Castonguay et al. 1982). Only the anadromous populations of the south-west coast of Hudson Bay in rivers immediately to the east (Brant River, Wypkema, 1975) and to the west (Nelson-Hayes Rivers, Doan, 1946; Gaboury, 1978) of Sutton River approximate these growth rates. Although superior growth rates have been reported for non-anadromous trout from hatcheries (Carlander, 1969), and in some cases from the first generation of introductions into newly reclaimed ponds (Rawston, 1941; Power, 1980), the growth rate of the Sutton River brook trout remains a record for natural populations (Fig. 13).

The extreme growth rate that characterizes the south-west Hudson Bay coast anadromous brook trout (Sutton, Nelson-Hayes and Brant rivers) continues in Sutton River brook trout until sexual maturity. During the summer of the fifth (4+) year the fish's resources are channelled into reproduction: an abrupt decrease in growth and instantaneous growth rate occurs. The reduction in growth may be a result of reallocation of energy stores to the gonads or is, more likely, a result of the change in behaviour that returns mature trout to the rivers during July instead of at the end of the season. Since there was no evidence from angled trout (either mature or immature - parr excepted) to suggest that trout continue to grow in the river, growth is assumed to occur mainly in the marine (brackish) environment. Therefore early return from the marine waters of Hudson Bay would certainly account for the diminished growth rate. Once mature, the trout do not regain their previous growth rates since they continue to allocate the available resources to reproduction, returning to the rivers in July each year. The limit of growth accompanying reproduction for these trout was approximately 5% of the length per year or less, and the instantaneous growth rate was 1% or less.

4.4 Reproduction.

Mature brook trout ascended the river in July yet they did not spawn till the second week of September (Fig. 18). The reason that mature trout forego two months of sea growth to ascend the river in July, although they do not spawn till September, is speculative. Lake whitefish, another anadromous autumn spawner of the Sutton River also ascend Hudson Bay rivers several months previous to spawning indicating that the advantages of early migration are not restricted to brook trout. Morin et al., (1981) observed a similar phenomenon in the anadromous coregonids of James Bay. In a comparison of the life history variation of anadromous cisco (*Coregonus artedi*) and lake whitefish (*C. clupeaformis*) that inhabit the tributaries of eastern James Bay no significance was attached to this early migration undertaken by both species (Morin et al., 1982). Bernatchez and Dodson (1985) speculated that coregonids ascend northern rivers and in particular the Eastmain River of the James Bay region, while the rivers are 'warm' (12°C) to prevent cold temperature fatigue on their migration. Bernatchez and Dodson were able to demonstrate, using immature non-anadromous southern Ontario lake whitefish, that these fish had reduced stamina at low temperatures. They concluded that there would be excessive mortalities due to cold temperature fatiguing in wild northern anadromous populations if the mature fish tried to migrate later. This remains to be documented. Furthermore, Bernatchez and Dodson failed to explain why the runs are so early in the summer and do not occur at a later date but while the rivers are still warm. Contradicting their conclusions are the existence of ascending runs of immature fish that do occur during cold water conditions (Morin et al., 1981; this study) and early runs of mature fish that persist on rivers that are less challenging than the Eastmain River.

An alternate hypothesis to that of Bernatchez and Dodson is that these salmonids move into the warm waters of the rivers to allow their gonads to mature or develop. Cold temperatures are known to suppress or even prevent maturation of gonads in salmonids. Leitritz (1960 from Goryczko, 1972a) found that temperatures below 1.3°C indefinitely suspended maturation of the ovaries of chinook salmon (*O. nerka*). Goryczko (1972a, 1972b) reported the prevention and/or suspension of gonadal maturation of male and female rainbow trout at temperatures of 5°C or less regardless of the individual's previous experience. Hence, it is conceivable that the salmonids of James and Hudson Bays must migrate to warmer water before spawning to allow their gonads to develop or risk losing a chance to reproduce that year. The date of this early migration would be dependent on the temperatures of the salt water and the river water; little variance in date would be expected between rivers since the Bay would be common to all stocks.

Larger and older trout ascended the river during July, smaller and younger trout ascended the river in August or September (Fig. 7; Fig. 14; Table 17). This results in larger fish being more common upstream than by the weir (Fig. 16). It is not known if larger fish with a proportionally greater gondal amount require longer (more degree-days) to mature their gonads or if they enter the rivers earlier due to experience from past years.

This size segregation may also have occurred if smaller fish remained in marine water longer in an attempt to increase their size/reserves to that approximating the larger fish. Support for this speculation includes the observation that late run mature fish were younger than peak run fish (Fig. 14; Table 17) and the average length of trout in runs decreased during August and September (Fig. 7). Late run fish were also leaner (Fig. 26).

There was also a segregation as to sex in the runs; females dominated July runs and males dominated August and September runs during 1984 (Fig. 15). Too few trout were sexed during August and September of 1983 to determine if the trend persisted between years. The reason for this segregation may be a result of females requiring longer than males to mature/develop their gonads, but this remains to be documented. Female domination of earlier runs also results in females being common upstream and males downstream during August (Fig. 16).

The run of mature brook trout was accompanied by numerous immature brook trout (3+ fish that would spawn during the following season). The reason that these immature individuals ascend the river at this time is obscure (Huntsman, 1938; White, 1940; Castonguay et al. 1982). Although it is likely that a few immature individuals may be entrained by schools of migrating mature trout that will ascend the rivers this does not account for the existence of the runs of immature fish during August. Furthermore these immature fish did not continue their growth in fresh water during the summer (Table 15). Examination of the stomach contents of angler caught trout during July and August revealed that stomachs were generally empty or contained a single food item of little consequence (e.g., stonefly larvae, caddis fly larvae or terrestrial insect). Not till September did trout stomachs (60%) contain small rodents and scavenged trout eggs. Until further study is devoted to the marine residence of the brook trout the reason for the early migration into fresh water of immature trout will remain a mystery.

There have been numerous attempts to correlate various aspects of the life history of fishes with the age at which they mature (Stearns, 1976). Juvenile growth rates, often disguised as 'age of smoltification , have been correlated with the age of maturation for Atlantic salmon. The inverse ratio hypothesis (Hutton, 1937) correlated slow growing parr that smoltified at a late age with early return as mature adults. Faster growing parr which smoltified earlier spent more time at sea (Naevdal, 1978, 1983; Bailey and Saunders, 1984; Chadwick et al., 1986; Ritter et al. 1986). However many contradictory studies exist (Ricker, 1972; Saunders, 1981; Thorpe and Mitchell, 1981; Bielak and Power, 1986), making it doubtful that a cause-effect relationship actually exists (Gardner, 1976; Power, 1986). Conversely, the conflicting results may indicate that such a relationship is weak and regional differentes may override any general trend.

The brook trout literature is similar to that for the Atlantic salmon in that no persistent correlation is obvious between parr growth rate (smoltification age) and maturation age (Table 18). The results from the Sutton River population partially support the hypothesis in that Sutton River brook trout parr had a rapid growth rate and a delayed maturation but the hypothesis is also refuted by reports of populations with slower growing parr maturing even later (Dutil and Power, 1980).

Sub-adult (sea) growth rates have also been correlated with maturation age (Schaffer and Elson, 1975). This was an extension of fecundity being proportional to body size, and the rate of growth being diminishable by reproduction. This results in an animal that reproduces for the first time in the current year being less fecund next season than if it delayed maturation by one year (Bell, 1976).

Since mortality rates could not be estimated for the Sutton River population due to the lack of tag recoveries, and age specific mortality rates (or survivorship) are not widely reported for anadromous brook trout populations, many of the hypotheses correlating initial maturation age with various mortality ratios could not be tested. However, data derived from the Sutton River population as well as the literature did allow the effects of growth rate and reproductive cost in the absence of mortality to be examined. These are both important determinants of fecundity (Gadgil and Bossert, 1970; Caswell et al., 1984).

Modelling of the brook trout populations of Sutton River and the Moser River, N.S. (Wilder, 1952) demonstrated that initial fecundity is sensitive to changes in pre-reproductive growth rates (Fig. 21). The approximately 20% reduction in the growth rate (e.g., Moser River population) reduced the initial fecundity at all ages to values less than that observed for fish that matured initially at 3+ years under a faster growth schedule (e.g., Sutton River). The optimal age for initial maturation as determined by lifetime fecundity was also sensitive to growth rate as the

20% reduction in growth rate resulted in advancing maturation by one year (Fig. 22). Hence, increased pre-reproductive growth rates favoured the postponement of maturation. This supports Schaffer and Elson's (1975) prediction of accelerated sea growth favouring maturation at older ages.

The advancement of maturation could also be induced by manipulating the post-breeding growth rate. This was accomplished by imposing a cost of reproduction as measured in the percent of the reproductive year's growth that would have occurred if reproduction had not occurred. Increased costs of reproduction favoured the postponement of maturation to the limit determined by pre-reproductive growth rates (Fig. 22). This was synonymous with Schaffer and Elson's (1975) prediction that increased migration costs would result in delayed maturation as migration costs are one of the costs of reproduction for anadromous salmonids. For the Sutton River brook trout that have both a high pre-reproductive growth rate and an increased cost of reproduction due to migration and foregoing marine feeding in July and August, it is expected that maturation would be delayed if lifetime fecundity was to be maximized. In fact, the observed maturation age is as predicted with a high cost of reproduction.

years may have been a sampling artifact as age distributions varied slightly between years).

The effect of gonadal maturation on the weight on length regression is not clear, as there were significant (p<<0.01) departures from variance heterogeneity in the Sutton River data for both years. Non-heterogeneous variances of weight on length regressions also prevented testing whether mature trout gained weight due to feeding in fresh water or if these trout were limited to the somatic reserves with which they ascend the river. Lack of evidence of extensive feeding while the trout are in the river during the summer and the extremely poor condition that spent trout are in during the winter suggest the latter may be true. Non-heterogenous variances of weight on length regressions also existed between early run and late run trout preventing testing if early run trout ascended with proportionally greater reserves than late run trout. Further confounding the two latter comparisons were differences in length (mature and early run trout were longer than immature and late run trout respectively) and the decreasing slope of the weight on length regression with length/age (Fig..26).

In fact, there has been little interest in the change of shape with age in fishes. Carlander (1969) states that "... the slope will usually be above 3.0 because most fish become plumper as they grow", as fry and fingerlings are usually quite slender. This was opposite to the trend of the

Since greater pre-reproductive growth rates led to greater optimal ages of maturation, and minimal reproductive costs would fix the optimal age at age 0+, pre-reproductive growth rate necessarily determined the magnitude of the effect of reproductive costs. This suggests that accelerated pre-reproductive growth would destabilize the maturation age aspect of the life history. The consequences of this destabilization would include rapid shifts in the life history variables of quickly growing populations that adjusted post-breeding growth rates according to exploitation or other causes.

4.5 Parr.

Sutton River brook trout parr reach lengths by mid-August that exceed those of parr from southern Ontario populations and are comparable to the lengths attained by parr from northern United States populations (Table 19). However, the Sutton River population has a shorter growing season than these other populations, indicating that the growth rate of the Sutton River parr may be greater than that of parr in the other populations. Never-the-less, the growth rate of the Sutton River parr does not exceed that observed for parr from Wisconsin (Power, 1980) and Wyoming trout populations, or that obtained in hatchery reared populations (Carlander, 1969).

Mean instantaneous growth rates are weight dependent, decreasing with size at a constant rate. Brett (1979) calculated the slope of the mean instantaneous growth rate-weight regression to be -0.41 for salmonids ~~and~~ slopes for brook trout ranged from -0.33 to -0.47 (Haskell, 1959; Cooper, 1961; respectively). The slope of the mean instantaneous growth rate on weight regression for the Sutton River parr exceeded this value four-fold indicating that the observed decrease in the mean instantaneous growth rate during August was due to other variables than an increase of weight (e.g., temperature, ration). Although July and August parr inhabited similar stretches of the river, the parr were subjected to different conditions. River waters were warmer and water levels were lower during August for both years.

The difference between the observed and previously reported slopes of the mean instantaneous growth rate-weight regression may be due to the inability of larger parr to enter water of an optimum temperature. Parr are known to be less tolerant of high temperatures than adults are. Swim-up alevins have a 7 day LC_{50} (°C) of 24.5°C (McCormick et al. 1972) and younger stages are more sensitive. Sutton River temperatures often exceed these temperatures, as previously documented. Hence, parr must be able to seek refuge in cooler waters than present in the main flow of the river.

G. Power and co-workers observed that Arctic charr parr of the Ungava peninsula are more numerous in shallow waters during crepuscular hours than during the day. The same was observed in this study for brook trout parr in the Sutton River. Power determined that parr hide in the intersititial spaces of the riverbed gravel and cobble during the daylight hours. Power hypothesized that this was a predator avoidance behaviour (pers. com.) although there is a low density of aquatic sight-oriented predators in both the Ungava and Lowland systems (Table 21). An alternate explanation is that parr 'thermoregulate' by this behaviour, moving deeper into the cooler riverbed water to escape stressful daytime high temperatures. As such, parr would shuttle back and forth between the river and riverbed to remain in the optimal temperature range. The rapid freshwater growth rates of the parr support this hypothesis in part but further experimentation including riverbed water temperature records and activity budgets of the parr must be performed to verify this. Parr may remain in such a system until either the intersititial waters warm to correspond with river temperatures as summer progresses or the parr grow to a size where they are no longer able to penetrate deep enough in the riverbed to obtain the cooling benefit of the intersititial waters.

Regardless of the cause of the August decline in growth rate, little advantage is obtained by larger parr if they remain in the river past mid-August. Extrapolation of the fork length on age regression (Fig. 23) suggests that growth declines to zero by late August for river dwelling parr. With such a low 'habitat suitability of the river' (h_1) the 'expectation from migration' (E) to other habitats (h_2) does not have to be great for an advantage to be gained by migration ($h_1/E < 1$; Baker, 1978).

Salinity challenges during July and August revealed that at the length and ages tested, parr were tolerant of brackish waters. All parr tested (of which some had been involved in a passive downstream migration before capture) had a similar 96 hr LC_{50}(‰) of approximately 21 ‰ NaCl (Fig. 24). This is similar to that reported by

Sutterlin et al. (1976) for Maritime brook trout parr. Coastal waters of Hudson Bay influenced by rivers or direct runoff had summer salinities of 5 - 11 °/oo (person. obs.), while Bay water 50 km offshore had salinities of 24°/oo (Barber, 1968; Anderson and Roff, 1980; Prinsenberg, 1982a). Hence, during both July and August parr had access to an estimated 30 km wide strip of coastal waters that did not exceed their 96 hr LC_{50}. Since mature trout were not tested the final acquired salinity tolerance of these trout is not known. Nor is it known to what extent mature trout penetrate offshore waters.

Attempts to capture parr in the Sutton River estuary or nearshore Hudson Bay failed, preventing a direct assessment of the 'habitat suitability of Hudson Bay' (h_2) or even confirmation that parr occupied marine habitats. Hence, the cost/benefit of migrating to Hudson Bay together with the suitability of Hudson Bay as a habitat (h_2M) was estimated indirectly. Instantaneous growth rate factors (Table 20) were adopted as a measure of habitat suitability. Thus it can be shown that late summer migration to the marine environment conferred greater instantaneous growth rate factors on young trout than if they remained in the river ($h_2M > h_1$; Table 20). Not included in these calculations were different mortality rates between the two habitats or other components of Baker's (1978) 'action-dependent potential reproductive success' (S) that may alter the expectation from migration (E).

4.6 Suitability of Hudson Bay as a habitat for brook trout.

Does Hudson Bay have a sufficient forage base that is accessible to brook trout to support the observed growth rate?

> Is Hudson Bay a barren sea which does present suitable conditions for the development of a fishery of any magnitude? Do the cold waters of this vast and most striking inland sea contain no fish? Is it true that the body fluids of most fish will freeze in cold waters of Hudson Bay and will such a temperature kill most fishes? Yes, all this is true, as far as warm water forms are concerned, but there are many arctic and subarctic forms which will thrive, feed and breed only under these specific conditions and which will die and perish in a different environment. (Bajkov, 1975).

The productivity of Hudson Bay has been a source of speculation since Henry Hudson sailed into the inland sea in 1610. The general consensus of the pre-W.W.II literature was that Hudson Bay was a desert sea (Bajkov, 1975). A flurry of military and civilian activity in the north during the post W.W.II era focussed attention on the Bay again (Barber, 1968). Overflights and oceangraphic cruises during 1955, 1961, 1962 and 1975 ascertained that Hudson Bay, although oligotrophic as a whole, was not a desert sea. These explorations also indicated that the south-west coast, from Churchill to Cape Henrietta Maria, was atypical of the rest of the Bay. Information on this area is scant as persistent ice excluded all of the oceangraphic cruises (although in 1975 the C.C.G.S. Narwhal penetrated to within 75 km of the coast of the Sutton River area).

What has been ascertained is that the general counter-clockwise surface currents that exist in Hudson Bay (Hachey, 1931, 1935, in Bajkov, 1975; Barber, 19687; Pett & Roff, 1982; Prinsenberg, 1982a) pass from west to east in this area. A similar current that exists at depth (Pett & Roff, 1982) is interrupted north of Winisk by the Central Hudson Bay Shoal that protrudes 150 m from the sea-bed and the cold (−1.7°C) marine (32°/oo NaCl) deepwaters are forced to the surface and towards shore. These cold marine waters confine the freshwater runoff entering the Bay in this area (one third of the total Hudson Bay freshwater input) to the inshore coastal area and create the steep salinity gradients that have been found between the inshore and offshore water masses (Prinsenberg, 1977; Anderson & Roff, 1980). The salinity of the inshore water mass probably fluctuates with climate and season. Prinsenberg (1982b) found that salinities of James Bay (east of Cape Henrietta Marie) fluctuated from 23°/oo during the summer to 31°/oo during the winter when freshwater runoff input to James Bay was at a annual minimum. A similar phenomenon probably occurs along the south-west coast of Hudson Bay where freshwater runoff inputs are equally important in maintaining salinity gradients. The severe winters of the Sutton River site might reduce fresh water inputs during the winter to the extent that marine waters (32°/oo) likely butt the shore during winter.

Prevailing summer winds pile drift and pack ice against the shore, limiting temperatures of the inshore water (Anderson & Roff, 1980). Carbon-nitrogen ratios, live seston percentages, biocarbon:particulate organic carbon ratios, biocarbon chlorophyll a ratios and individual biomass variables indicated that the inshore area has a low biomass possibly stemming from the intrusion of the offshore waters (Anderson & Roff, 1980; Anderson et al., 1981). As of yet there are no published estimates of primary productivity for the inshore or offshore area but from the biomass data "...it appears that during the summer months Hudson Bay (as a whole) is an oligotrophic body of water of low productivity ..." (Anderson & Roff, 1980).

Densities and distributions of potential forage fish for anadromous brook trout in Hudson Bay have not been ascertained. It is thought that three genera of potential forage fish are numerous in the Bay: sand lance (*Ammodytes*), eelblennies (*Lumpenus*) and capelin (*Mallotus villosus*) (Barber 1968). It is known that anadromous brook trout do utilize these fishes as food. Dutil and Power (1980) reported that capelin and sand lance constitute the major stomach contents (71% and 7% resp.) of anadromous brook trout of the Richmond Gulf region (east Hudson Bay) and Department of Fisheries workers have found sand lance, eelblennies and capelin in stomachs of trout captured in James Bay during the summer.

These fishes would be most vulnerable to brook trout when they invade the inshore waters during spring and summer for spawning. Sand lance spawn in the shallow waters during late spring, eelblennies spawn in mid-depth inshore waters during late spring and early summer, and capelin invade the deeper inshore waters (<50 m) to spawn during early and mid summer (Leim and Scott, 1966). Spring concentrations of the piscivorous beluga whale off the Winisk - Brant River area indicate that small fish are found in large numbers in this area of Hudson Bay. Hence it was no surprise to find capelin in the stomachs of Sutton River trout entering the river from the Bay during July and August. It is these three marine fish that might provide the Hudson Bay lowland brook trout with the forage base needed to sustain the observed growth rates.

4.7 Weight on length relationships.

Condition indices have been used to compare the weight-length relationship of fish from different age classes and/or populations with little regard to the length of the fish being compared. In fact, condition indices are sometimes thought of as a method of standardizing length so weight comparisons may be made. However, the relationship between shape (slope of the regression) and the condition index is not linear over length (Fig. 25).

Since condition indices may fail to discriminate between i) fish that may be of a different shape to start with and do not change shape as they grow, and ii) fish that do change shape as they grow, their use is restricted. Furthermore, the requirement that fish being compared should be of the same length (except in the special case where b=3.0 and r=1.00) encourages the substitution of geometric mean regressions in place of condition indices. Regressions also have the advantage of being statistical entities that may be compared (ANCOVA) with estimatable confidence limits (see Ricker (1973) for G.M. regression methods).

Although most fish usually have weight on length regression slopes approximating 3.0, regression slopes of *Salvelinus* typically exceed 3.0. Carlander (1969) provides weight on length regressions for 22 sets of data, with slopes ranging in value from 2.78 (Age II, Baldwin Pond, Que.) to 3.21 (anadromous, Moser River, N.S.). The mean slope from these data sets was 3.05 (std. dev. 0.12). Anadromous trout are typically heavier at length than resident trout due to the richer environment the former inhabit (e.g., Moser River, N.S.: anadromous, b=3.21; resident, 2.85; p<0.01; Wilder, 1952). However Gaboury (1978) reports the opposite for trout of the Nelson -Hayes River tributaries. His anadromous trout had slopes of 3.01 and young-biased resident trout had slopes of 3.43, both of which he considered approximated the idealistic 3.0' Doan (1946) reported average weights and lengths from the same tributaries 30 years prior to Gaboury from which it was possible to calculate weight on length regressions. Slopes derived from Doan's data ranged from 2.84 to 3.85 (3.55, 3.05, 3.85, 3.43, 3.45, 2.84, 3.13, 2.85); but it is not known which of these fish were anadromous. The slopes of the geometric mean regressions were only slightly higher (+0.01 to +0.02). Dutil and Power (1980) also reported average weights and lengths from which it was possible to calculate a weight on length regression. Anadromous Richmond Gulf brook trout were characterized by slopes of 3.36 (G.M., v=3.40). This is consistent with anadromous fish being heavier at length than freshwater populations (Carlander, 1969). Slopes of the weight on length regression for Sutton River brook trout during both years were also greater (combined, b=3.10, G.M., v=3.20) than slopes of freshwater populations. (Minor but significant differences between years may have been a sampling artifact as age distributions varied slightly between years).

The effect of gonadal maturation on the weight on length regression is not clear, as there were significant (p<<0.01) departures from variance heterogeneity in the Sutton River data for both years. Non-heterogeneous variances of weight on length regressions also prevented testing whether mature trout gained weight due to feeding in fresh water or if these trout were limited to the somatic reserves with which they ascend the river. Lack of evidence of extensive feeding while the trout are in the river during the summer and the extremely poor condition that spent trout are in during the winter suggest the latter may be true. Non-heterogenous variances of weight on length regressions also existed between early run and late run trout preventing testing if early run trout ascended with proportionally greater reserves than late run trout. Further confounding the two latter comparisons were differences in length (mature and early run trout were longer than immature and late run trout respectively) and the decreasing slope of the weight on length regression with length/age (Fig..26).

In fact, there has been little interest in the change of shape with age in fishes. Carlander (1969) states that "... the slope will usually be above 3.0 because most fish become plumper as they grow", as fry and fingerlings are usually quite slender. This was opposite to the trend of the

Sutton River brook trout. Fish greater than 3+ gained weight less quickly with age (Table 23). This was most noticeable during July for 3+, 4+, and 5+ before maturation of gonads increased variance. It is speculated that the decrease of the weight on length regression slope was the result of the prolonged secretion of GH by these fish and was not mediated by diet or mortality (see Appendix I).

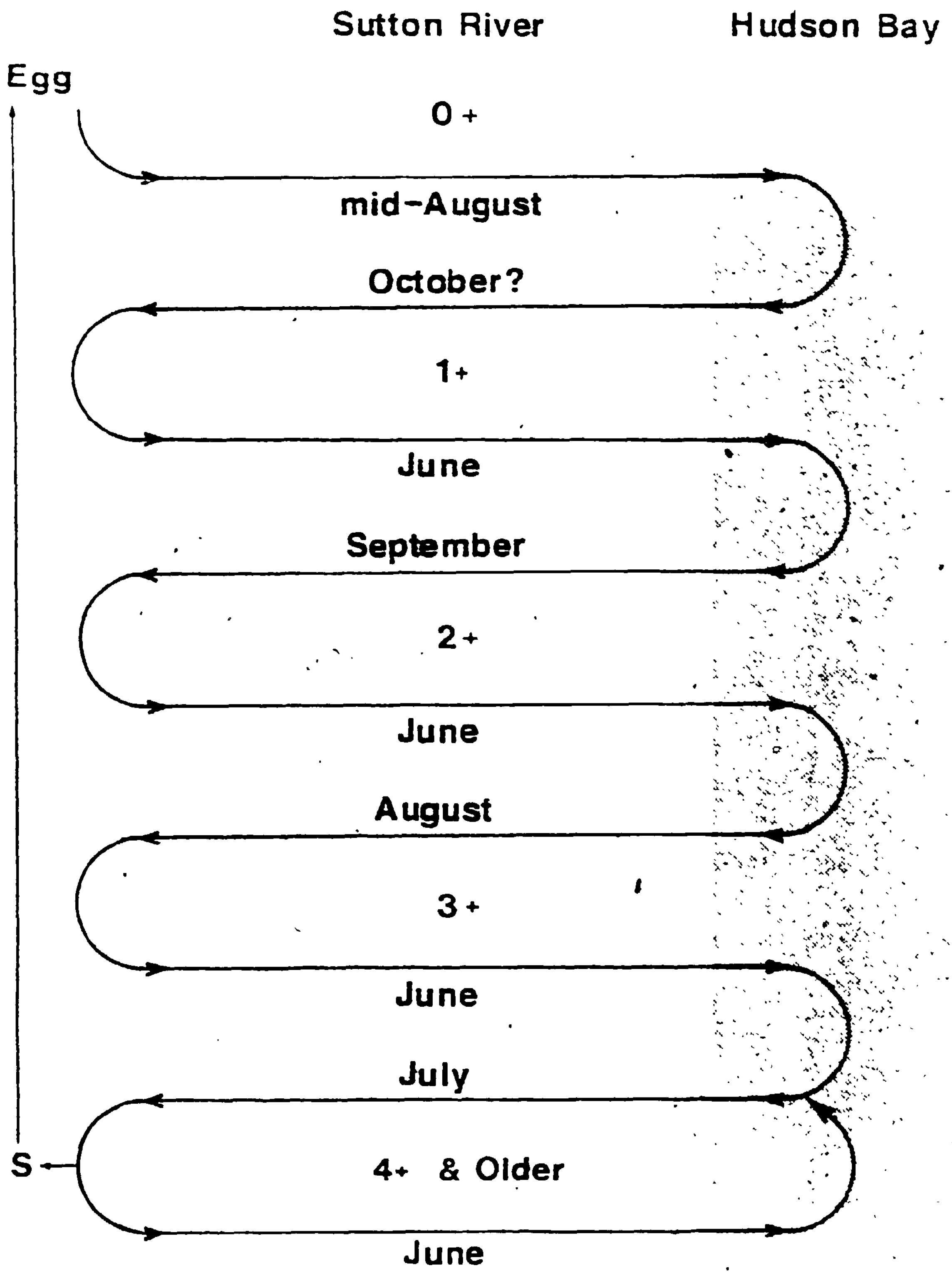
5. SUMMARY AND CONCLUSIONS.

5.1 Summary of Sutton River brook trout life history.

Eggs are laid in gravel redds during the first and second weeks of September when water temperatures are between 5° and 15 °C. Low temperatures (0°C) from late September to mid-May slow development of the eggs; hatching occurs in late spring. Parr are not common in the water column until mid-June. During the first summer parr grow rapidly. The parr are crepuscular and hide in the cooler interstitial water of the gravel river bed during the day, possibly behaviourally thermoregulating. By mid-August, they have reached 80 mm and start passively migrating downstream to the inshore waters of Hudson Bay. Parr are not seen again that year; presumably they re-enter the river under the ice in October or November and spend the winter amongst the gravel of the riverbed. During the winter the temperature of Hudson Bay drops below the species' lower lethal temperature (0°C) of forcing all ages of brook trout to seek refuge in the warmer (0°C) waters of the rivers.

After ice-out in the spring, all ages of trout with the exception of the young-of-the-year, migrate downstream (Fig. 27). The trout gorge on spawning marine fishes during the spring and summer and display phenomenal growth. Two and three year olds (1+ and 2+) return to the river during late September and perhaps October or November. Four year olds

Figure 27. Diagram depicting the life history of the anadromous Sutton River brook trout. S denotes spawning.


Sutton River
Hudson Bay
Egg
0 +
mid-August
October?
1+
June
September
2+
June
August
3+
June
July
S
4+ & Older
June

(3+) return during August and September ultimately to escape the Bay winter temperatures. It is unknown why they return so early. Five year olds (4+) and other older trout that spawn in September return to the river in July (and the first week of August), possibly to allow their gonads sufficient time to develop or mature in the warmer fresh water (cold temperatures typical of the Bay may inhibit gonad maturation).

Trout reproduce annually after reaching 4+ years (oldest reproductively active fish aged was 15+) leaving the river in May or June, returning in July and spawning in September (Fig. 27). Except during the fall when trout gorge on small mammals and scavenged trout eggs, little feeding is done in the river due to its oligotrophic nature. The rapid growth that makes it advantageous to delay maturation till 4+ occurs entirely in the marine environment.

5.2 Conclusions.

The life history of the Sutton River brook trout population is that of a fast-growing unexploited population that is not dominated by the effects of its northerly latitude. Although the Sutton River population is unusual in that much of its habitat has only recently emerged from glaciation, hence may be considered a recent descendent of the original stocks of brook trout that followed the glaciers north (McGlade, 1981), its life history is reminiscent of the life histories of the unexploited populations that were reported for North American east coast populations during the 1800's by European settlers (Power, 1980). These southerly populations, after being subjected to extensive exploitation and habitat degradation for approximately two centuries now exhibit very different life histories. In many of the northern United States and southern Canadian populations females mature at 1+ providing the majority of the reproductive effort (Hunt, 1966, 1969, 1974). Mature trout are usually removed from these exploited populations by 3+; few, if any, live beyond 5+). Undoubtedly, these populations represent one extreme of the plastfcity that the species is known for and populations like the Sutton River represent the other extreme. Nordeng (1983) was able to demonstrate that in Arctic charr, which displays a similar degree of variability in life history, much of the plasticity is inherent in the genetic constituent of each population. This is undoubtedly true for its sibling species the brook trout as well.

The Sutton River brook trout, like other coastal populations of trout, are anadromous; there was no indication of a non-anadromous portion of the population. Migrations occurred at similar times each year despite widely differing environmental conditions. This suggests that the brook trout may use celestial or other non-environmental cues to time their migrations. During migrations, trout strayed considerable distances and made use of other rivers than the Sutton for over-wintering and/or spawning. All movements associated with migrations while in freshwater occurred at night, possibly as a response to the presence of many avian predators. Trout travelled the full length of the Sutton River although spawning was more concentrated in the general vicinity of its confluence with the Aquatuk River than elsewhere.

Length-frequency graphs (i.e., Peterson method) and scales were of limited use for ageing trout. Scales were neither reliable nor accurate for ageing because of Ca^{++} resorption that was further aggravated by the anadromous habits of the trout. Otoliths and fin ray sections were both reliable and accurate as ageing structures, although the collection resulted in killing the specimen (otoliths due to their internal location and fin rays due to lack of blood coagulation). Trout ranged in age from 0+ to 15+ with the majority between ages 4+ and 8+.

Contrary to predictions, Sutton River brook trout grew rapidly. This growth was entirely the result of marine feeding, indicating that there was an abundance of forage fish available to the trout in Hudson Bay. Hence Hudson Bay could not be considered 'a desert sea' as earlier literature reported.

Except for the parr which grew rapidly and migrated towards saline water during their first summer (age 0+), trout did not grow while resident in the river. This was due to high temperatures and a scarcity of suitable forage.

Rapid pre-reproductive growth reversed predictions of delayed physiological capability to spawn and early maturation thereafter and instead contributed to the early attainment of the physiological capability to spawn and delayed maturation thereafter. The trout typically spent three additional seasons migrating to the Bay after reaching 140 mm in length before spawning for the first time. When they did mature they were large (43 cm) rather than small as predicted with a low growth rate.

As predicted reproduction was costly, but for different reasons than theorized. Cold marine temperatures forced mature trout to seek the warmer waters of rivers to allow their gonads to develop and/or mature. Therefore these trout had to forego the summer of marine feeding that was responsible for their phenomenal pre-reproductive growth rates and exist on somatic stores accumulated before they entered the river. Further contributing to reproductive costs were river temperatures that exceeded the trout's optimal temperature and a scarcity of prey in the river. Hence there was little somatic growth once these trout attained maturity.

Contrary to initial predictions, there was no evidence that these trout 'missed' years once maturation was attained. Experienced spawners returned early each year, structuring the runs by size (largest fish first).

Increased number of seasons spent in the saline waters of the Bay was correlated with a decrease in the slope of the weight on length regression. A sustained GH produttion while in the Bay was implicated as the probable cause. Excessive GH production also resulted in a torpedo like shape and excessive mucus production that characterized these fish. The slope of the weight on length regression stabilized with maturation as mature fish spent less time in the Bay.

The blood of Sutton River brook trout did not coagulate during the first few weeks of entry to fresh water. This resulted in numerous mortalities due to tagging and angling.

Trout bearing scars of wounds inflicted by several sources (e.g., predators, anglers, and lampreys) indicate that this condition was not permanent. Unfortunately, the greatest angling pressure is exerted on the population during the period that the blood does not coagulate. Furthermore, the arrival of a parasitic lamprey on this coastline may have disastrous results for this population that has only recently been discovered by sport fishermen.

This thesis has culminated with the Provincial government of Ontario petitioning the Federal government of Canada for an immediate change in the laws that regulate and protect the Hudson Bay Lowland brook trout fishery.

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APPENDICES.

Appendix I.

Intermediate salinities stimulate growth in a northern population of the anadromous salmonid, *Salvelinus fontinalis*.

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ABSTRACT

Steele, P.O. and Steele, A.M., 1986. Intermediate salinities stimulate growth in a northern population of the anadromous salmonid, <u>Salvelinus</u> <u>fontinalis</u>. Aquaculture,

A study of an anadromous population of brook trout, <u>Salvelinus</u> <u>fontinalis</u>, in the Hudson Bay Lowlands of Ontario, indicates that these trout exhibit dramatic growth rates (3.3 cm/month) when inhabiting the cold (-1° to +5°C) isosmotic waters of Hudson Bay during the summer months. Physiological and morphological evidence (mucous cell activity, skin colouration, elongated shape) suggests that the high growth rates may be due to elevated levels of growth hormone (GH). Radioimmunoassays confirmed that trout entering the Sutton River had elevated concentrations of GH. In some fish these concentrations were an order of magnitude higher than those of individuals resident in the river for three or more days.

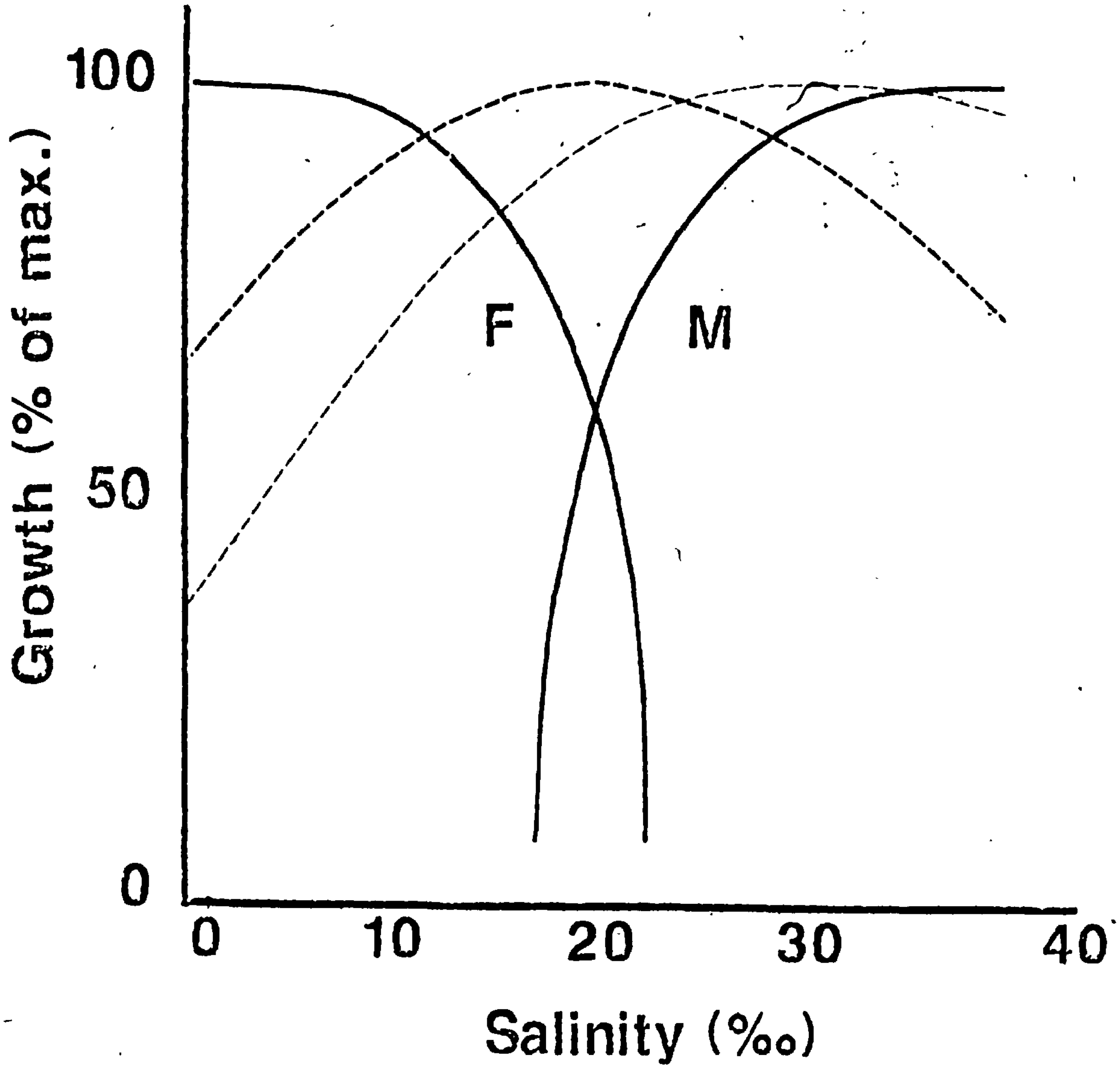
We hypothesize that transient increases of hormones such as GH that accompany the transition to sea water, particularly during smoltification, may be prolonged by maintaining the fish at isosmotic salinities.

INTRODUCTION

Increasing salinities are detrimental for most freshwater fishes as are decreasing salinities for marine fishes. Anadromous fishes display a different response to changes in salinity than do non-anadromous fishes. Maximum growth rates are achieved at intermediate salinities by many anadromous species (Fig. 1). Rainbow trout (Salmo gairdneri) have an optimal salinity range of 15-28°/₀₀ where food consumption is highest (and, therefore, where growth rate may be expected to be greatest; MacLeod, 1977). Pre-smolt Oncorhynchus kisutch experience up to a six-fold increase in growth rate, and a two-fold increase in food intake and food conversion efficiency when held at intermediate (5 to 10 °/₀₀ NaCl) rather than extreme (0 or 20°/₀₀ NaCl) salinities (Otto, 1971). Reduced osmoregulatory costs may explain this increase in growth rate (Payne, 1979; Moyle and Cech, 1982; p. 72, 102). This is supported by Rao's (1968) observation of reduced oxygen consumption at 7.5°/₀₀ NaCL for Salmo gairdneri. However, the absence of reports of growth increases of similar magnitude for euryhaline fish (maximum increase reported does not exceed 10°/₀; Payne, 1979) suggest other factors may be responsible.

In 1983 and 1984 we observed growth rates in an anadromous salmonid that exceeded previous reports (cf., Carlander, 1969; Power, 1980). Brook trout (Salvelinus

Figure 1. Effect of salinity on growth of various fishes expressed as a percentage of the maximum rate determined for each species (adapted from Brett, 1979). Solid lines, stenohaline fishes, freshwater (F) and marine (M); light dashed line, euryhaline fish; heavy dashed line, anadromous fish.


100
50
0
Growth (% of max.)
0
10
20
30
40
Salinity (‰)
F
M

fontinalis) that migrated into the cold waters of Hudson Bay for three summer months grew an average of 10 cm (Steele, 1986). These fish, on returning to fresh water during August were characterized by copious quantities of mucous, a silvery colouration, and a torpedo-like shape. Slopes of logarithimic weight-on-length regressions were significantly lower (ANCOVA; $p<0.01$) in consecutive age classes until the age of first reproduction. These trout became thinner with age, instead of fattening as is usual for salmonids. This circumstantial evidence led us to suspect that prolonged stimulation of growth hormone production was occurring in these fish.

The Sutton River anadromous brook trout population differs from many anadromous trout populations in that it does not have access to full strength (35°/oo NaCl) sea water. Surface salinities of Hudson Bay, in the vicinity of Sutton River, vary from 6 to 15°/oo NaCl. Temperature of the surface waters varies from -1° to +5°C. Marine ice is present until August most years and strong winds prevent thermal stratification. Yet, Sutton River trout demonstrate dramatic growth while in these waters.

METHOD

Sutton River, one of the major watersheds of the Hudson Bay Lowlands, originates at Hawley Lake (54°30'N, 84°40'W) and flows north to Hudson Bay (55°15'N, 83°45'W). The river is considered by anglers to be one of the best trophy brook trout rivers of North America.

The length of time anadromous Sutton River trout have been in fresh water is a function of the distance they have migrated upstream during late summer (Steele, 1986). By sampling at different distances upstream from Hudson Bay, different freshwater residency times may be approximated.

The first site sampled, a 1 m deep pool at the junction of Hudson Bay and Sutton River, was only accessible to trout at high tide. Salinities varied from 0 to 6°/₀₀. Trout were caught as they entered the pool with the incoming tide. Hence, trout captured at Site 1 had been in fresh water for less than six hours. Site 2, separated from Site 1 by an extensive delta system (1 to 20 cm deep), was 3.7 km upstream from Hudson Bay. Site 2 was at the first available refuge for the trout after traversing the delta. Trout moved through the delta only under the cover of darkness. We estimated that trout captured at this site had been in fresh water for 6 to 12 hours. The third site, located 40 km upstream of the first two sites, supported few if any resident trout. Therefore, the trout angled at this site were probably migratory fish that had been in the river for a minimum of three days. Logistical problems (ice, wind and polar bears) prevented sampling trout in the saline waters (6 to 15°/oo) of Hudson Bay.

Trout were collected by angling from Sites 1 through 3 between 09:00 and 11:00 EST on August 5, 7 and 8, 1984 respectively. Ten ml blood samples were extracted by caudal peduncle puncture after fish were immobilized by cranial concussion. Samples were placed on dry ice and transported to Western BioAnalytic's Vancouver laboratory. There, plasma growth hormone (GH) values were determined by double antibody radioimmunoassay (Wagner, 1984).

Descriptive statistics and analysis of variance (ANOVA) were calculated on log-transformed data, because the original values were positively skewed.

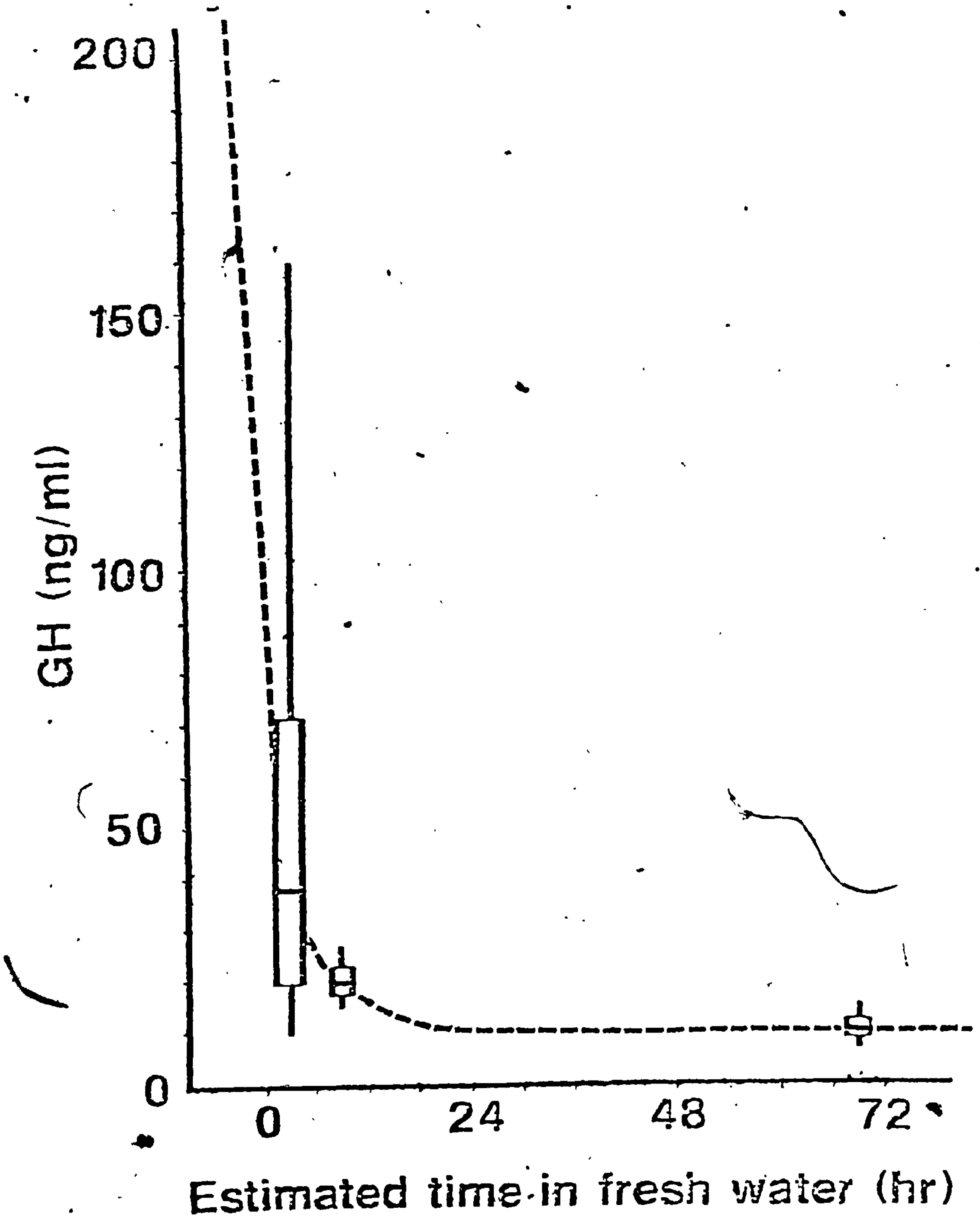
RESULTS

GH levels were obtained for a total of 37 anadromous brook trout from the three locations (Table 1). Extreme values ranging from 4 to 750 ng/ml were found only at the fresh and salt water interface (Site 1). Mean GH concentrations decreased with increased distance upstream, which we believe to be highly correlated with freshwater residency time (Fig. 2). The higher variability of GH values at Site 1 (coefficient of variation at Sites 1 through 3; 56°/₀, 18°/₀, and 22°/₀ respectively) tended to mask the overall decrease of GH values with the time spent in fresh water (ANOVA, F=3.092, P=0.057). The second fish sampled at Site 3 was excluded from the analysis as it was atypical of fish sampled at that site.

Growth hormone values of brook trout captured at three different sites in the Sutton River, Ontario.

Sample No.	GH (ng/ml)	Fork Length (cm)	Weight (kg)	Sex
Site 1				
1.	26.	37.5	0.58	F
2.	11.	40.1	0.80	M
3.	5.	37.5	0.62	F
4.	45.	34.0	0.39	U
5.	450.	39.6	0.67	M
6.	600.	37.9	0.60	F
7.	8.	35.3	0.50	F
8.	13.	50.7	1.37	F
9.	4.	40.3	0.73	M
10.	750.	--	—	U
Site 2				
1.	18.	49.1	1.23	F
2.	9.	38.0	0.58	F
3.	16.	44.0	1.00	F
4.	62.	44.9	1.02	F
5.	22.	49.5	1.27	F
6.	12.	41.9	0.83	M
7.	35.	41.4	0.85	F
8.	29.	48.0	1.28	F
9.	15.	49.9	1.57	M
10.	10.	51.1	1.61	F
11.	14.	36.1	0.49	F
12.	13.	43.9	0.95	F
13.	29.	46.4	1.10	M
14.	27.	41.4	0.77	F
15.	19.	48.6	1.33	F
16.	19.	33.7	0.39	M
17.	62.	44.5	1.04	M
Site 3				
1.	7.	25.2	0.21	M
2.	83.	40.9	0.89	F
3.	13.	51.0	1.60	M
4.	8.	48.8	1.32	F
5.	6.	50.0	1.59	M
6.	5.	49.3	1.49	M
7.	23.	40.3	0.77	M
8.	11.	39.0	0.73	F
9.	8.	48.7	1.43	M
10.	22.	43.6	0.93	F

Figure 2. Plasma GH concentrations of anadromous brook trout migrating into fresh water. Shown is the mean, with one standard error (vertical rectangle), and 95% confidence interval (vertical line) for log transformed data.


GH (ng/ml)
200
150
100
50
0
0
24
48
72
Estimated time in fresh water (hr)

DISCUSSION

Elevated values of GH in fish leaving Hudson Bay were consistent with the hypothesis of prolonged elevation of growth hormone levels while resident in an isosmotic environment. The GH values for fish leaving Hudson Bay were an order of magnitude greater than those of fish that remained in fresh water for three days or more. On entry into fresh water, rapid modification of GH levels occurred. Low GH values in some fish at Site 1 reflected the ability of the endocrine system to respond rapidly to environmental change. Less severe reductions of GH levels accompanied longer freshwater residency times (Sites 2 and 3) as trout acclimated to the fresh water and moved upstream.

The function of growth hormone in teleosts is not well understood. GH is implicated in protein (Enomoto, 1964; Higgs et al., 1975, 1976) and fatty acid mobilization (Higgs et al., 1975, 1976, 1977; McKeown et al., 1976; Markert et al., 1977), diabetogenisis (Leatherland et al., 1974; McKeown et al., 1975), and certain metabolic changes that accompany exercise in salmonids (McKeown and Van Overbeeke, 1972; McKeown et al., 1975).

GH is also implicated in osmoregulation since GH injections cause enhanced seawater survival. Smith (1956) found that injections of mammalian GH increased the salinity tolerance of brown trout (Salmo trutta). Smith suggested that the mechanism may have been a GH-mediated increase of metabolic rate. Komourdjan et al. (1976) reported that porcine GH-injected Atlantic salmon (S. salar) parr were tolerant of sea water while controls were not. GH-injected parr also grew faster, both in length and weight than controls, but condition factors of the GH- injected parr decreased considerably while those of the controls increased. Increases in growth rates (two to six times) and lower condition factors were also observed in young coho salmon (O. kisutch) injected with bovine GH (Higgs et al., 1976). Bovine GH and Tilapia GH injections caused increased salinity tolerance, as measured by reduced plasma sodium concentrations in sockeye salmon (O. nerka) that had been transferred into sea water (Clarke et al., 1977).

In addition, increased GH values have been observed in juvenile O. kisutch exposed to sea water (Sweeting et al., 1985). GH values increased within 12 hours of transferring the fish into sea water and remained elevated for the duration of the experiment (24 hrs).

To date, normal GH levels for mature salmonids, whether in fresh or saline water, are not known. Nor has monitoring of GH levels in juvenile salmonids in saline water been extended beyond 24 hrs. Hence the role of intermediate salinities as opposed to normal (marine) salinities in sustaining GH is speculative. However, it is known from observation that Sutton River brook trout experience enhanced growth rates at intermediate salinities.

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Appendix II.

Inhibition of blood coagulation in cold-adapted anadromous brook trout, *Salvelinus fontinalis*.

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Abstract

Blood coagulation in teleosts normally occurs rapidly. Low temperatures (<0°C) inhibit coagulation but the mechanisms responsible remain unknown.

In cold-adapted anadromous brook trout, (*Salvelinus fontinalis*), coagulation was completely inhibited during return migration into Sutton River from Hudson Bay. This inhibition was unaffected by river water temperature or gonadal maturity.

At present, we have not determined how blood coagulation is inhibited. One possible mechanism under investigation involves the dual action of proteolytic enzymes, such as plasmin, that may simultaneously degrade both plasma fibrinogen, and excessive amounts of growth hormone characterizing this population.

Introduction

Teleost blood coagulates faster than mammalian blood (Komatsu et al., 1970). Mean clotting time for freshwater fishes ranges from 10.8 sec in goldfish (Carassius auratus) to 41.3 sec in smallmouth buffalo (Ictiobus bubalus), (Smith et al., 1952). Srivastava (1969) reported mean clotting times for four freshwater fishes, of which two (Heterpneustes fossilis and Clarias batrachus) were air-breathers. Although they differed significantly, coagulation occurred within 30 sec.

Marine teleost blood also clots quickly (Doolittle and Surgenor, 1962). Komatsu et al. (1970) compared clotting times for marine and freshwater fishes and two mammals (man and rabbit). At temperatures below denaturation, teleost blood clotted significantly faster than either mammal.

Coagulation in teleosts is prolonged by external and internal factors, e.g., temperature (Komatsu et al., 1970), stress (Casillas & Smith, 1977; Woodward et al., 1979), plasma salinity (Holst, 1975), and disease (Lester & Budd, 1978; Schumacher et al., 1956). Komatsu et al. (1970) reported extended clotting times (100 sec) when blood from the Antarctic fish Trematomus borchgrevinki and hatchery-reared trout (Salmo gairdneri) was subjected to low temperatures (-2°C). In contrast, blood from carp (Cyprinus *carpio*) and western sucker (*Catostomus occidentalis*) ceased to form clots at low temperatures.

Prolonged plasma clotting times occurred when plasma salinity was increased for freshwater fish or decreased for marine fishes. Complete inhibition occurred in goldfish plasma at salinities greater than 15 °/₀₀ NaCl. Salinities less than 2.5 °/₀₀ inhibited coagulation in *Helotes sexlineatus* and *Cnidoglanis macrocephala* (Holst, 1975).

Complete inhibition of coagulation has also been reported in spent salmon. Katz and Southwood (1950) reported that blood of spent salmon (*Oncorhynchus kisutch*) required from 2.3 to more than 13 min to clot, whereas, clots formed in blood from healthy salmon in less than 10 sec. Hougie et al. (1971) found a lack of clottable fibrinogen and reduced levels of prothrombin and Factor V in blood of spent salmon. Hougie (1971) verified these observations and reported that the plasma was hemolysed and the hematocrits markedly reduced.

Incoagulablity of iteroparous salmonid blood is unreported. Concurrent with work on growth hormone (GH) levels of returning anadromous brook trout, (*Salvelinus fontinalis*), we determined that such a condition prevails in the Sutton River population.

Methods

Sutton River, one of the major watersheds of the Hudson Bay Lowlands, originates at Hawley Lake (54° 30′ N, 84° 40′ W), and flows north to Hudson Bay (55° 15′ N, 83° 45′ W). It is considered by anglers to one of the highest quality trophy brook trout rivers in North America.

Eleven brook trout were removed from weir traps capturing upstream-moving fish near the mouth of the Sutton River on August 4, 1984. Seven to fifteen ml of blood were obtained from the caudal vessel of these fish. Varied attempts were made to promote coagulation in these initial blood samples.

To determine if the initial results were a sampling artifact, an undetermined number of angled trout were placed in holding cages overnight. Fish bleeding from injuries caused by hooking were placed in one cage, non-bleeding fish in another. Live fish were counted and released next morning. Dead fish were dissected.

During the next four days, three additional sites were sampled by angling. The first site, sampled August 5, was at the junction of Hudson Bay and Sutton River. This site with salinities varying from zero to six °/oo, was only accessible to trout at high tide. Trout captured here had been in fresh water for less than six hours. Site two, sampled on August 7 was separated from site one by an extensive, shallow delta system (1 to 20 cm deep). This site was immediately below a fish weir 3.7 km upstream from Hudson Bay. Trout captured at this site had been in fresh water for six to twelve hours. A third site sampled during 1984, was located 40 km upstream from the seconod site, and supported few resident trout. Generally, trout angled at this site were migratory individuals that had been in the river for a minimum of three days. Logistical problems (ice and wind) and the potential polar bear hazard prevented sampling of trout from saline waters (six to fifteen $^0/_{00}$ NaCl) in Hudson Bay.

Ten ml blood samples were extracted by caudal peduncle puncture from angled trout immobilized by cranial concussion. Samples were examined for 10 min for evidence of coagulation prior to disposal.

In 1985, samples were collected along the entire length of Sutton River during a nine day period (August 31 - September 7). Trout were angled throughout the day. Fish were immobilized by cranial concussion and ten ml blood samples were withdrawn from the caudal vessel. Fish were killed, measured, weighed, sexed and state of sexual maturity categorized. Two heparinized microhematocrit tubes were filled with blood from each sample. Four and one half ml of blood from each sample was mixed with buffered sodium citrate solution in silicone-treated tubes and placed on ice. The remaining blood was examined for signs of clotting for 30 min. The microhematocrit tubes were hand centrifuged until no further reduction in the hematocrit was apparent. The blood samples in sodium citrate were centrifuged electrically in the laboratory to permit removal of the plasma layer which was subsequently stored in ultracold. Control samples, taken from fish raised commercially (Van Aquaculture Inc.) in southern Ontario were processed similarly.

Results

Initial samples from August, 1984, revealed no clotting. Gentle agitation, aeration, cooling, or heating did not induce coagulation. After three days without any indication of clotting, the samples were discarded.

Cage experiments indicated that the lack of blood coagulation was not a sampling artifact. Bleeding fish either died or were severely stressed by morning. Non-bleeders displayed no ill effects. Dissection revealed little or no blood in carcasses of the dead fish.

Twelve fish were captured at site one. Of these one blood sample displayed limited signs of clotting. Of 19 samples taken at site two, none coagulated. At site three, we obtained twelve samples, all incoagulable (one trout captured at site three contained less than one ml of blood). Samples included mature and immature, male and female specimens.

During 1985, 41 brook trout were sampled along the length of the river. Sampling locations ranged from near site two to within several km from the source. No clotting was observed in any of the samples. Again, samples included mature and immature, male and female specimens.

Hematocrit values ranged from 23 to 85. Males had significantly higher hematocrits than females; immature fish were intermediate (Table 1).

Laboratory results indicated elevated plasma calcium and tri-glyceride concentrations. Neither of which is known to inhibit coagulation at observed concentrations. In fact, plasma calcium is required for blood coagulation and tri-glycerides have been reported as anti-fibrinolytic agents in mammalian studies. However, we suspect that elevated tri-glyceride concentrations act as blood antifreeze enabling survival in cold (<0°C) marine waters of Hudson Bay.

Table 1. Mean hematocrits of Sutton River brook trout sampled during 1985.

Sex	Hematocrit (mean)	N	Hematocrit (range)	Confidence limits
Mature Male	63.5	10	38.5 - 82.0	52.2 - 74.7
Mature Female	42.7	19	23.0 - 62.0	37.2 - 48.3
Immature (unsexed)	55.6	11	39.0 - 84.0	45.4 - 65.8

Conclusions

1. Cold-water adapted anadromous brook trout have incoagulable blood upon return from Hudson Bay.

2. Residency in fresh water did not reduce this tendency.

3. All fish, irrespective of sex or state of maturity, exhibited no blood coagulative ability.

4. Males had higher hematocrits than females, whereas immatures were intermediate.

5. Investigations into the cause of this phenomenon continue. We suspect that the proteolytic enzyme, plasmin, may be implicated. Plasmin degrades fibrinogen, growth hormone, and ATCH (Merskey et al., 1959). We speculate that a rapid decline in GH observed when trout re-enter fresh water is affected by plasmin, or a similar fibrinolytic agent.

6. Establishment of normal values for components involved in blood coagulation would permit disease diagnosis, development of screening tests as general health indicators, and aid in the determination of fish sensitivity to environmental stresses (i.e., pollutants).

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1. Background Information.

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2. Publications.

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Steele, P. and A. M. Steele. 1986. Intermediate salinities stimulate growth in a wild population of the anadromous salmonid, *Salvelinus fontinalis*. submitted to CJFAS.

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Dickman, M., J. Smol and P. Steele. 1980. The impact of industrial shock loading on selected biocoenoses in the lower Welland River, Ontario. Water Poll. Res. J. Can., Vol. 15:17-31.

ii) Abstracts (published)

Steele, P. and A. M. Steele. 1986. Intermediate salinities stimulate growth in a wild population of the anadromous salmonid, *Salvelinus fontinalis*. Proceedings of the Common Strategies of Anadromous and Catadromous Fishes - an International Symposium. Boston, Mass., U.S.A.

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iii) Theses

Ph.D. Thesis; "Life history strategies of a north temperate salmonid, *Salvelinus fontinalis* in Polar Bear Provincial Park, Ontario." In progress. University of Western Ontario, London, Ontario.

M.Sc. Thesis; "Water quality and fish distribution in the Welland River, Ontario. 334pp., Brock University, St. Catharines, Ontario.

B.Sc.(Hons.) Thesis; "An investigation into the behaviour postures exhibited during aggressive interactions of male x male *Hemichromis bimaculatus*". 49pp., Brock University, St. Catharines, Ontario.

iv) Miscellaneous publications.

Steele, P., P. Assam, M. Cheek, M. Dickman and M. Gulyban. 1979. "Old (2nd) Welland Canal: pollution and abatement". 83pp., St. Catharines, Ont.

Dickman, M., P. Steele, B. Benkel, S. Grant, P. Hartman and G. Waite. 1978. "Fishery recreational potential, St. Catharines vicinity, 1978". 51pp., St. Catharines, Ont.

v) Presentations and Posters.

Intermediate salinities stimulate growth in a wild population of the anadromous salmonid, *Salvelinus fontinalis*. Common Strategies of Anadromous and Catadromous Fishes - an International Symposium. Boston, Mass., U.S., 1986.

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"Gonadal neoplasms in carp-goldfish hybrids". Forty-second Annual Meeting of the American Society of Limnology and Oceanography. N.Y., N.Y. June 18-21, 1979.

"The impact of industrial shock loading on selected biocoenoses in the lower Welland River, Ontario". Can. Symp. Water Poll. Res., Toronto, Ontario., 1978.

3. Grants and Awards.

Visiting Fellowship in Canadian Government Laboratories. Department of Fisheries and Oceans, Halifax, N.S. 1986-1987.

Hudson Bay Lowland Brook Trout Research, 1982-1986.
Funding agency: Ontario Ministry of Natural Resources.
Amount: $47,000 through U.W.O., $50,000 through District.

Research on Endocrinology of Hudson Bay Lowland Brook Trout, 1984-1986.
Funding agency: Ontario Ministry of Natural Resources.
Amount: $1000 through U.W.O.

Northern Scientific Training Grant, 1984.
Funding agency: Department of Indian and Northern Affairs.
Amount: $5,790.

Northern Scientific Training Grant, 1983.
Funding agency: Department of Indian and Northern Affairs.
Amount: $600.

Clements Award, (Twice while a student at Brock Univ.).
Funding agency: Department of Fisheries and Oceans.

I have also been successful in receiving generous funding for several Canada Summer Work Programs, and the like (2 such programs in 1984, one in each of 1979 and 1978).

4. Graduate Courses.

i) University of Western Ontario.

Animal Behaviour 536 - Animal social systems, communication, bioperiodism, and cybernetics. (M.H.A. Keenleyside).

Evolution 541 - Concepts of species, polymorphism, selection and gene flow. Theories of speciation. (D. Scott).

Graduate Seminar Course: Life history theorms. (J. Millar).

Graduate Seminar Course: Physiological ecology. (D. Ankney).

Graduate Seminar Course: Advanced Biometry. (R. Green).

Graduate Seminar Course:. Population Ecology. (P. Handford).

ii) Brock University.

Advanced Limnology 562 - Productivity, indicator species assemblages, species diversity and water quality assessment methods. (M. Dickman)

Comparative Animal Physiology 521 - Organismic function, functional evolution, control of systematic activities and physiological response to environment. (A.H. Houston)

5. Teaching Assistantships.

During the period of my graduate studies at the University of Western Ontario and at Brock University I have demonstrated numerous courses. These included: graduate and undergraduate courses in limnology, undergraduate chordate structure and function, vertebrate anatomy and various first year courses.

In addition, I have assisted with numerous aquatic biology/limnology field trips.

6. Affiliations and Memberships with Scientific Societies.

I am a member of the Canadian Society of Zoologists and the American Fisheries Society. I subscribe to the Canadian Journal of Fisheries and Aquatic Sciences, Canadian Journal of Zoology, Transactions of the American Fisheries Society, North American Journal of Fisheries Management and Progressive Fish Culturist.

In 1978, I was a member of a Canada /Germany /U.S.A. expedition to the Bancroft region of Ontario to determine the feasibility of recovering uranium from lake sediments. While at Brock University I was active in several inter-university/government expeditions, in particular the eutrophication studies of Lake St. George.

I am a supporter of conservation projects in Ontario, a member of the Ontario Federation of Anglers and Hunters and Ducks Unlimited. During my field seasons of 1983 and 1984, I was active in the Ontario Breeding Bird Atlasing project.