

A STUDY ON THE BIOLOGY OF BROWN TROUT,
SALMO TRUTTA LINN. FROM FOUR DIFFERENT HABITATS
ON THE AVALON PENINSULA, NEWFOUNDLAND

CENTRE FOR NEWFOUNDLAND STUDIES

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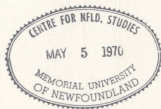
PETER K. L. LIEW

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A STUDY ON THE BIOLOGY OF BROWN TROUT,
SALMO TRUTTA LINN. FROM FOUR DIFFERENT HABITATS
ON THE AVALON PENINSULA, NEWFOUNDLAND

by

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ABSTRACT

Brown trout (Salmo trutta Linn.) were first imported into Newfoundland from Scotland in 1886 and at present are well established on the Avalon Peninsula. Some aspects of the biology of brown trout were examined in four different environments of the Avalon Peninsula: Long Pond, Topsail Pond, Western Island Pond and Windsor Lake. These waters vary in size from 16 to 1216 acres.

Scales were used to determine age and the direct proportion method was used to back-calculate length from age. Ages within these populations varied between 2 and 8 years with the 3 or 4 age-groups dominant. The combined survival rate of brown trout in the four study areas was 0.47.

There is no consistent difference in growth between males and females. The annual growth of trout was found to be dependent on habitat, size, abundance of food and the size obtained during the first year. The mean length and mean weight vary directly with these factors.

A comparison was made of the growth of Windsor Lake trout with trout from British lakes. Also, the growth of fish from the three study ponds was compared with the growth of trout from United States and British ponds and

streams. The Windsor Lake trout show faster growth than most of the British trout while the Newfoundland pond trout grow slower than those in the U.S.A., but faster than some of those from British waters.

A von Bertalanffy growth-in-length curve, $L_t = L_{\infty}(1 - e^{-K(t-t_0)})$ was fitted to age and length data; however, poor results were obtained.

The length-weight relationship was determined. The slopes (n) varied between 2.7 and 3.1. The length-weight relationships for the four study areas were significantly different at the 5% level. The regressions of body weight on body length between any two of the study areas were tested and no consistent differences were found between them. The condition factors of the four populations were also discussed.

The sex ratio is about 1:1 in the areas studied except in Windsor Lake. In Windsor Lake, the males were more abundant than females. This was probably caused by the selectivity of gill-netting and the occurrence of sexual segregation during the feeding period. Male trout mature at an earlier age and smaller size than female trout. The fecundity of Newfoundland brown trout is similar to that of fish in other areas. The fecundity increases with the age and size of the female. A linear logarithmic length-fecundity relationship was found in

Western Island Pond trout but curvilinear relationships were found in fish from Long Pond and Windsor Lake.

The spawning behaviour of brown trout was observed in an aquarium. Three hundred and ninety-one eggs were laid on gravel without being covered and some were eaten. Some of the eggs were also released without any digging and in the absence of a male.

The brown trout is an indiscriminate carnivore. The type of food eaten varies with locality and size of fish. Trichopteran and ephemeropteran larvae and nymphs, amphipods, gastropods and forage fish were found to be important food in this area. Forage fish formed the main food for fish over 35 cm.

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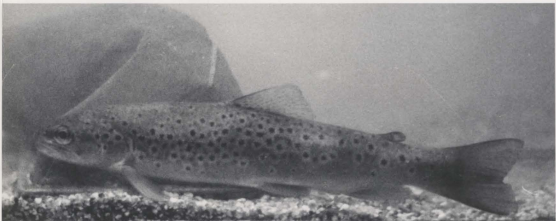
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FRONTISPIECE: THE BROWN TROUT, SALMO TRUTTA LINNAEUS.
(Age: 4+ ; Length: 27.9 cm ; Sex: female).

CHAPTER I

INTRODUCTION

1.1 General Introduction

The brown trout (Salmo trutta Linn.) of the family Salmonidae is distributed over a wide area on the continent of Europe and the British Isles, the northern tip of Africa and Northwest Asia. Through introduction it is distributed on all continents except Antarctica (MacCrimmon & Marshall, 1968).

It was first artificially introduced to Newfoundland in January of 1886 from Scotland by the Newfoundland Game Fish Protection Society for recreational purposes (Andrews, 1965). However, Wiggins (1950) regarded the introduction of brown trout into Newfoundland mainly as a result of the nostalgia of British settlers on the island.

The brown trout of Newfoundland consists of several stocks. The Lochleven trout (Salmo trutta levenensis), was imported from Scotland between 1886 and 1889 and planted in ponds in the St. John's area, the ponds draining into Topsail Brook, in Petty Harbour Ponds and South Dildo Pond, Trinity Bay. The German brown trout (S. trutta fario) was introduced in 1892 into Whiteways and Robin's Ponds, in the vicinity of Torbay and in Ocean

Pond near Whitbourne (Frost, 1940; Walters, 1954). The English brown trout (Salmo trutta) was imported into Newfoundland in 1905 or 1906 and planted in Clement's and Lee's Ponds (Frost, 1940). All these forms have been recognized as varieties of the brown trout (Salmo trutta Linn.) despite some morphological differences resulting from geographical and habitat isolation (Scott and Crossman, 1964).

After the brown trout had been introduced to Newfoundland, it became naturalized due to its adaptability and the suitable environment encountered. Besides the rivers and ponds where they were planted, anadromous populations are well established and widely distributed on the Avalon Peninsula and the north shore of Trinity Bay as well as the eastern side of the Burin Peninsula (Andrews, 1965).

It has been reported that the brown trout is displacing the native salmon in waters where they both occur in Maine (Fenderson, 1954). In Newfoundland, Andrews (1965) reported that in waters that have become populated by brown trout, the native trout (Salvelinus fontinalis Mitchill) seems less abundant to anglers, and Walters (1954) has stated that the brown trout appears to have dominated the brook trout in all rivers and streams where it now occurs. The above information seems to show that the brown trout is

replacing the native salmonids in these waters. Due to the low catchability of brown trout as well as its overabundance, it will seriously lower the productivity in terms of catchable native trout to the anglers (Fenderson, 1954). These facts have led to a re-evaluation of the wisdom of further natural spread of the brown trout in these areas.

Though the brown trout has been in Newfoundland for more than seven decades, no detailed study of it has been made. As it is an introduced species, it would seem important to gather more information on the different aspects of its biology in this area. It is hoped that this study will broaden our present knowledge of the ecology of brown trout in an introduced area. Such information is of academic importance to the ecologist as well as being of importance to the fishery biologist.

The principal aim of this study is to examine different aspects of the biology of Newfoundland brown trout such as growth, food, fecundity etc., and to compare them with the biology of brown trout in Europe, mainland America and other areas.

There have been many studies undertaken on different aspects of the biology of brown trout in Great Britain (Allen, 1938; Went and Frost, 1942; Frost and Smyly, 1952; Ball and Jones, 1960, 1961, 1962; Thomas and

Jones, 1962; Graham, 1964; Frost and Brown, 1967), New Zealand (Allen, 1951), Australia (Lake, 1957; Nicholls, 1957) and North America (McFadden and Cooper, 1962, 1964 and others) etc. These investigations are valuable in comparing the biology of brown trout taken from different localities including Newfoundland.

The productivity of a fish population is limited by the characteristics of its environment. McFadden (1962) stated that

"presumably water fertility limits primary productivity which in turn limits the productivity of the herbivores which constitute, either directly or in some cases indirectly through an additional trophic level, the food of the fish population."

In order to determine if differences in environments affect the biology of this species on the Avalon Peninsula, four sampling areas each representing a particular environment, were chosen. A total of 737 specimens were collected from these waters during the summer and fall of 1967.

1.2 Description of the Study Areas

The four selected study areas are situated on the Avalon Peninsula of Newfoundland (Fig. 1.1). Long Pond is located on the Memorial University campus; Western Island Pond is situated along Torbay Road about 13 miles from St. John's; Windsor Lake, one of the city's reservoirs, is situated off Portugal Cove Road, about 10 miles northwest

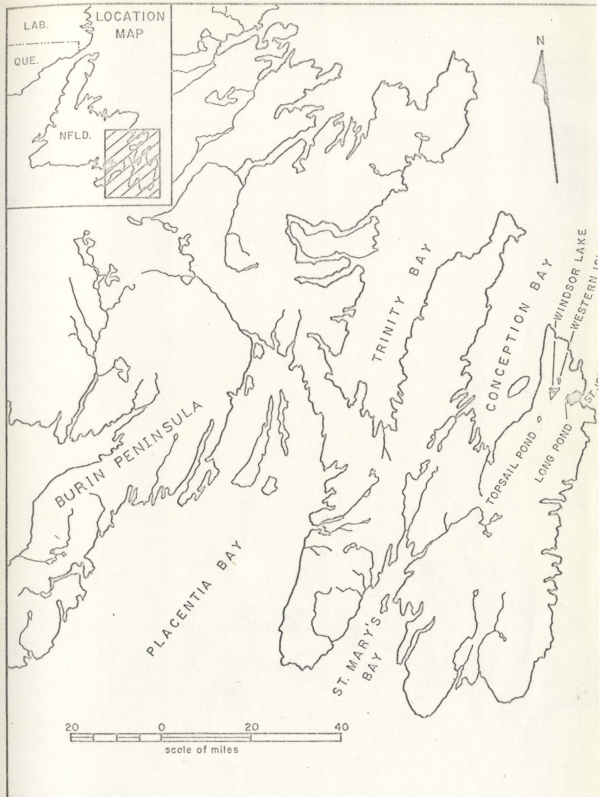


Figure 1.1 Map showing the four study areas and the distribution of brown trout in Newfoundland.

of St. John's; and Topsail Pond is a small pond situated near the Topsail Highway about 10 miles west of St. John's (Fig. 1.2). All these waters except Windsor Lake have direct drainages to the sea.

Although no bathymetric study of these waters was made, some of their physico-chemical characteristics were determined. Hydrogen ion concentration was determined by a Beckman pH meter, conductivity was determined by ^aHellige conductivity bridge, and total hardness was determined by means of a Taylor Total Hardness Set. Dissolved oxygen was determined by the Winkler's method modified by Needham and Needham (1962). The results of these measurements are summarised in Table 1.1.

TABLE 1.1 Physical & chemical characteristics
of the four study areas. Samples taken in
the summer of 1967

	Long Pond	Topsail Pond	Western Island Pond	Windsor Lake
Size (acres)	16	53	77	1216
Elevation (ft.)	177	375	372	493
pH	6.9	6.4	6.4	6.5
Dissolved Oxygen (ppm)	9.2	9.8	9.4	9.5
Total hardness (ppm)	17.9	6.4	9.5	6.9
Conductivity (micromhos)	135.2	34.2	45.0	46.0

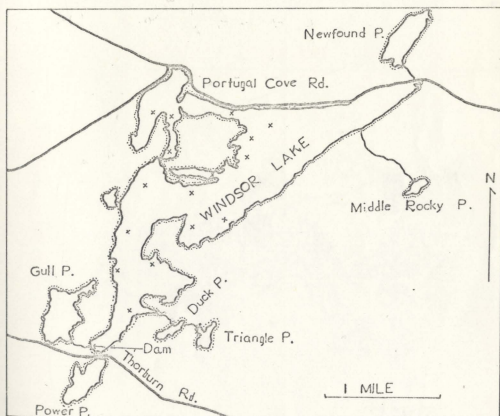
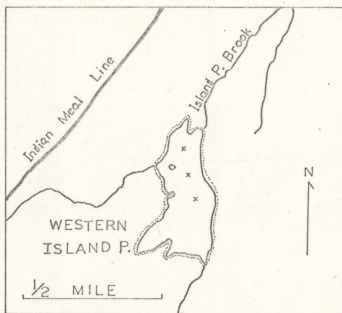


Figure 1.2 Map showing the Western Island Pond and Windsor Lake (x indicates the gill-netting sites)

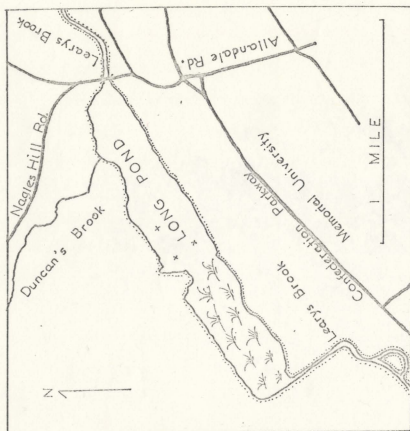
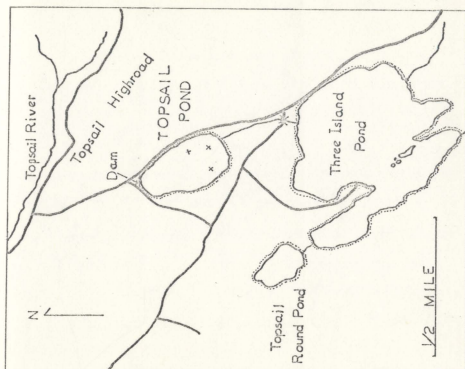


Figure 1.2 Map showing the Long Pond and Topsail Pond.
(x indicates the gill-netting sites)

Long Pond is located on the north edge of St. John's. Leary's Brook and Duncan's Brook drain into it on the west and north sides, respectively. The Rennies River carries water out of the pond on the east through Quidi Vidi Lake to the sea. Oxen Pond, Wigmore Pond, Juniper Pond, Big Pond, Middle Pond and Left Pond all drain into Long Pond through Leary's and Duncan's Brooks. The western part of the pond is occupied by dense marsh grass. Kellett (MS. 1965) reported that the bottom of Long Pond is fine silt and mud for the most part and that the shore line is composed of either cobbles or rocks 12-14 inches in diameter. The average depth is 15 feet and the deepest part, 36 feet, is in the middle of the pond. Because of the heavy drainage from the surrounding ponds, the water is fairly turbid and greenish in color.

Although eels have been reported in the pond (Andrews, 1965), none were captured by nets or eel-pots in the summer of 1967. The only species of fish other than brown trout is the ^{threespine} stickleback (Gasterosteus aculeatus).

Topsail Pond is a deep clear pond, joined by an un-named stream to Three Island Pond at the southwest end and draining into Topsail Brook by a small stream and a flume at the northeast end. The pond has a steep slope, the deepest part being about 35 feet. The bottom of the shoreline is comprised of sand and rocks which are 4-10 inches in diameter. The water is brownish in color with

very little vegetation growing in it. Brook trout and landlocked salmon occur together with brown trout in this pond.

Western Island Pond is more shallow than the other three ponds and has an abundance of aquatic vegetation, especially Spirogyra which makes the water appear greenish. There are two un-named streams draining into it on the west and northwest ends. Island Pond Brook drains its waters eastward to the sea. The middle parts of the pond are not over 10 feet deep; however, this may not represent the deepest part of the pond. The shore is rocky with rocks up to 15 inches in diameter. Both brown trout and brook trout are present.

Windsor Lake, one of the city's reservoirs, is fed by four small streams which are too shallow for trout to spawn in. The bottom is composed of sand and rock. It also has a rocky and sandy shore. Brown trout, brook trout and sticklebacks are present.

CHAPTER II

METHODS AND MATERIALS

2.1 Sampling Method

During the summer of 1967, trout were collected by using a gang of nylon gill-net composed of $1\frac{1}{2}$, 2, $2\frac{1}{2}$ and 3 inches stretched mesh in the four areas. Each net was 6 feet deep and 150 feet in length. The gang was always set with the $1\frac{1}{2}$ inch net tied to the shore and the larger meshes in sequence, running out from shore. The lead line of all nets rested on the bottom.

In most cases, the nets were set in the late afternoon and hauled in the next morning. When a single pond or lake was to be fished on consecutive days, the nets were moved to a new site in the pond or lake each morning. The specimens were brought back and examined in the laboratory.

The first Long Pond sample was taken on the 30th of May, 1967, two weeks after the ice melted. The nets were set across the pond near the inlet of the stream; three hundred and thirty-three fish were taken in this period. During October, a gang of 2 and $2\frac{1}{2}$ inch nets were set at the same site and 36 trout were obtained for fecundity analysis.

The Topsail Pond sample of 103 specimens was caught between the 8th and 16th of June. Since the pond is a summer resort, sampling was restricted to this period.

Sampling from Windsor Lake was done between the 12th and 19th of July and between the 29th of September and the 4th of October. During the fishing operation, the nets were either set from the shore towards the deep water or parallel with the shore and 88 and 55 specimens were caught respectively. The netting sites were changed daily, and most areas of the pond were covered in the hope of obtaining a representative sample.

122 fish from Western Island Pond were caught between the 16th and 18th of August.

Most of the fish caught in shallow water approximately 1 to 5 feet in depth were smaller than those caught in deeper water. Besides brown trout, speckled trout (Salvelinus fontinalis) and land-locked salmon (Salmo salar) were caught in the study areas. Most of the brook trout were caught in shallower area than the sites where the greatest number of brown trout were caught.

2.2 Measurements and Counts

All specimens except the samples from Long Pond were examined fresh. After the length, weight, and body depth and width had been measured, the specimens were

frozen for further study. These specimen were kept in a freezer at -5° C. A correction factor for shrinkage was determined and the lengths were adjusted accordingly (see 2.7).

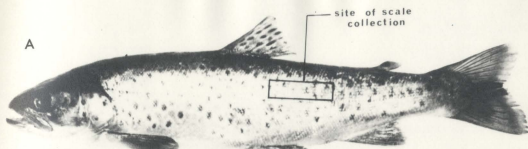
All measurements were made in the metric system. The fork length, measured from the tip of the snout to the notch of the caudal fin was recorded to the nearest centimeter. Total length was also measured for use in determining the conversion factor between fork length and total length. Body weight was measured to the nearest tenth of a gram with a spring balance.

2.3 Age Determination

Scales were used in age determination. They were taken from below the dorsal fin near the lateral line (Fig. 2.1) except when the scales in this area were missing. In such cases scales directly below the origin of dorsal fin were used. No attempt was made to study the differences in the lengths of scales from different parts of the body. The method of ageing is described in Chapter III.

2.4 Sexes and Maturity

Sex was determined by macroscopic examination of gonads. The degree of ripeness of females was based on the scale used by Vladykov (1956). No attempt was made to determine the ripeness of males. Ovaries to be used for fecundity studies were removed, weighed fresh and preserved



B

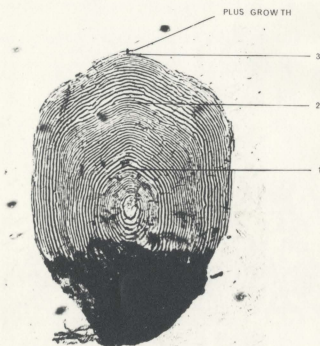


Figure 2.1 A. Brown trout showing the scale collecting site.
B. A scale from a three year old Topsail brown trout (22.3 cm),
showing scale measurements.

in 10% formalin. The method of determining the fecundity is described in Chapter IV.

2.5 Food and Feeding

The entire stomach from the lower esophagus to the pyloric sphincter was removed and preserved in 10% formalin. The contents were examined at a later date. The method for determining the stomach contents is described in Chapter V.

2.6 Sampling Error

In general investigations on the biology of a fish population, one is always faced with the problem of obtaining samples which are truly representative of the whole population. Since the gill-net is a passive fishing gear, factors such as the randomness of the fishing sites, the size of the population, movements, shape and structural peculiarities of the fish and the mesh size of the net will influence the catch in an area (Moyle, 1949; Clark, 1960).

Many investigators have found that, with the exception of fall spawning migration, brown trout seldom leave the section of the stream in which they become established (Allen, 1951; Schuck, 1945; Beyerle, 1959). Of the four study areas, all, except for Windsor Lake, are small ponds and thus the distribution of the fish is probably limited. As nets of the same size and same length were

used in these waters, it is assumed that a comparatively representative sample was obtained from each population.

In Windsor Lake, most of the area was netted in the hope of compensating for either movement or segregation of the population.

In the gill-nets the greater catches were obtained in shallow water in the medium mesh sizes with few big fish being caught in larger mesh sizes. The small number of large fish is probably due to the selectivity of the net, the low abundance of larger fish, and the fact that this species tends to feed in shallow water.

Concerning the selectivity of the net, it must be borne in mind that with regard to fish of the same age, only the faster growing, larger fish above a minimum size were gilled by the net. The undersized fish could certainly pass through and escape the net.

There is no definite answer to the question of how representative the catches of the gill-nets are. When the catches are considered on a comparative basis, we can disregard the selectivity of the gear as it is constant in all waters. It must also be assumed that movement and other behavior patterns of brown trout are similar under similar conditions if gill-net catches are to be considered as being quantitative (Moyle, 1949).

2.7 Shrinkage of Frozen Brown Trout

In order to determine the shrinkage of frozen fish samples, fifty brown trout caught in Long Pond were measured fresh, stored in the freezer and measured again after a period of two months.

A straight line relationship was established between the two measurements as follows:

$$L = 0.2205 + 1.02 L_i$$

where L and L_i are the fresh fish length and frozen fork length in centimeters respectively.

Fig. 2.2 shows the relationship between the fresh and frozen length of the 50 brown trout. The shrinkage is proportionately less at greater length, ranging from 3.46% shrinkage at 18 cm to 2.63% at 35 cm. in length.

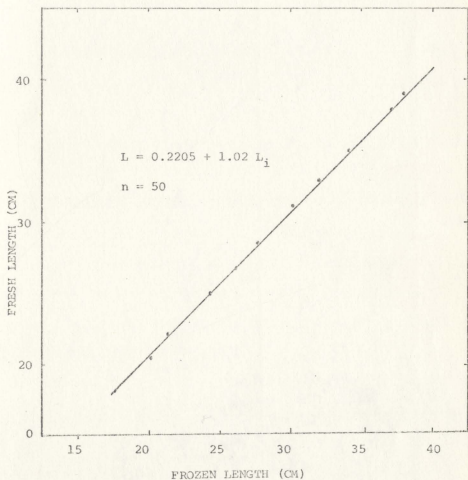


Figure 2.2 The relationship between fresh and frozen fish length of brown trout from Windsor Lake preserved in -5 C freezer.

CHAPTER III

AGE AND GROWTH

3.1. Introduction

Productivity of animal populations is currently a popular and important subject for ecological research. Knowledge of the pattern of growth of a species is essential for a clear understanding of its life-history and biology.

Growth is generally regarded as an increase in size of an organism in terms of its length or weight. Actually, growth represents a complex of processes by which material is introduced into an organism, transported throughout its system and assimilated into living material (Rounsefell and Everhart, 1953).

Carlander (1956) pointed out that fish growth rates are readily modified and very responsive to environmental factors thus making growth data valuable indicators of the general welfare of fish populations. It is the principal objective of the present study to compare the age and growth characteristics of populations of brown trout in the Avalon Peninsula, and in other areas as well.

In the study of growth in fishes many investigators have been restricted to the determination of the annual increments in length of the different age-groups

sampled from the population. Among previous studies of the growth of brown trout which include data based on length back-calculated from scales are those of Dahl (1910), Allen (1938, 1951), Swynnerton and Worthington (1939), Went and Frost (1942), Frost and Smyly (1952), Schuck (1945), Cooper (1953), Nicholls (1957), Grahams (1962), Thomas and Jones (1964), Frost and Brown (1967).

In the present study, the samples were collected in the summer and fall of 1967 from the four study areas.

3.2 Methods of Study

The material consisted of scales and data from 737 specimens obtained in 1967. The methods by which measurements were made have been referred to in Chapter II.

3.2.1 Age and Growth Determination

Three main methods of age determination have generally been adopted by fishery biologists: the length-frequency method (Peterson's method), the recovery of marked fish, and the interpretation of layers laid down in the hard parts of the fish such as scales, otoliths, vertebral bones, spines, fin rays and opercular bones etc. (Rounsefell and Everhart, 1953). Of these methods, the latter is the one most generally used for age determination.

In brown trout the scales are formed when the fish is about 3.5 cm. in length (Frost and Brown, 1967). Kipling (1962) suggests 3 stages in relation to scale formation in trout:

- (a) no scales (fish length approximately 0-3 cm.)
- (b) scales appearing and growing rapidly (fish length approximately 3-10 cm.)
- (c) scales growing as the fish grows (fish length over 10 cm.)

The number of scales is approximately constant throughout the life of ^{the} fish. Under a microprojector, the scale appears to consist of a number of concentric growth ridges or circuli. In the centre, the focus is a flat oval area without rings on its surface. During the winter months when trout usually exhibit little or no growth, the scales form narrowly spaced circuli called annuli (see Fig. 2.1 & Fig. 3). In spring and summer, fish grow at a much faster rate and the scales also grow faster and form widely spaced circuli called summer rings (Dahl, 1910; Beyerle, 1959). In Llyn Tegid, the winter rings are formed annually in September-October (Ball, 1960). The scales of fish from Long Pond were collected at the beginning of October and some scales had faint, closely arranged circuli at the edge. Since these "winter bands" were not well formed in all scales, no extra year of life was assigned to these fish. All age determinations were based on the assumption that

the number of completed bands of winter rings equalled the age of fish in completed years.

In the present study, the age of each fish was determined by examining the scales with a microprojector. This method is based on the observation that the scales grow when the fish grows and it has been validated by Dahl (1910), Lake (1957) and Kipling (1962). Although some authors like Allen (1951) considered scale reading as being subjective, Lake (1957) after checking his scale ageing data by the tagging method concluded that the results were reasonably reliable. The scales were prepared for reading and measuring by a process very similar to that described by Kipling (1962) and Frost and Brown (1967).

Scales from each specimen were taken from below the dorsal fin near the lateral line. After selection, 4 to 6 readable scales were mounted on glass slides in glycerine and water. Decisions regarding age were made after examination of at least 3 scales from each fish. All scales were aged at least twice without reference to the previous readings. In order to obviate the personal error in reading scales, the samples from Long Pond, Windsor Lake and Topsail Pond were also read by Mr. Wiseman of the Department of Fisheries, St. John's.

Scales can not only be used to determine the age but also the growth of the fish during each year of its life. Since the growth of the scale is correlated with the growth in length of the body, the amount of scale growth made at the end of each winter band can be used to calculate the length attained by the fish at the end of each winter.

Scales were measured by means of a micro-projector, at a magnification of approximately 50 times. Measurements were made from the centre of the scale to the end of each annulus and to the edge of each scale along the longest centre-posterior axis (see Fig. 2.1). The outer edge of the narrowest sclerite in each annulus was taken as the end of the year's growth. The measurements of the projected scale length were made to the nearest millimeter on a cardboard strip. Because the same magnification was always used, these measurements were used directly to calculate the size of fish by means of the direct proportion method.

3.22 Body-scale Relationship

When studying the growth characteristics of a species, it is often desirable to determine the length attained by fish at various ages. To do this it is necessary to estimate the size of fish at earlier ages from measurements of scales of older fish by means of back-calculation (Schuck, 1949).

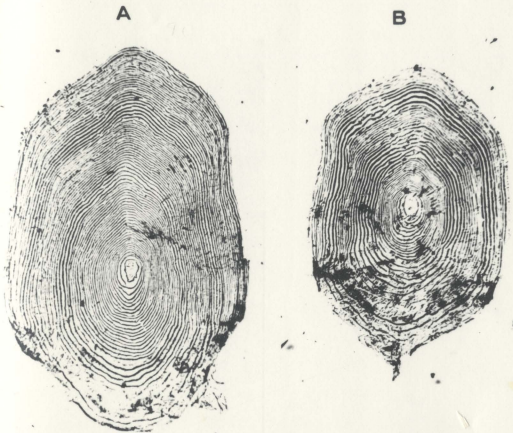


Figure 3.1 A. A scale of a 4-year old brown trout from Windsor Lake. B. A scale of a 4-year old brown trout from Topsail Pond showing two narrow growth rings presumably laid down while living in a stream.

The direct proportion method was adopted for back-calculation in the present study. Cooper (1953) concluded that back-calculation by ^{the} direct proportion method or by ^{the} direct proportion method with a correction for the body length at time of scale formation cannot be justified in growth calculations of brown trout populations. He found that the Monastyrsky logarithmic method was the most applicable to brown and brook trout populations in Pigeon River. Nevertheless, Nicholls (1957) found that the straight line relationship between fish and scale length fitted well to the brown trout populations of Tasmania. Whitney and Carlander (1957) in reviewing the methods of computing body length of fish from scale measurements mentioned that

"probably in most growth studies it is sufficiently accurate to dispense with the logarithmic transformations and to disregard the assumption that the variances of the body lengths are the same for each scale."

The fish length-projected scale length relationship was calculated from the formula suggested by Whitney and Carlander:

$$L = a + bS$$

where L is the fish length at capture, S is the projected scale length at capture, b is the slope of the regression line and a is the intercept.

In order to test if any differences existed in body-scale length between sexes, the data of Long Pond and Western Island Pond were examined. The scale diameter measurements were grouped into 5 mm intervals, and average body lengths were thus obtained for these intervals. The fitted regression lines for the body length on the scale diameter for males and females are shown separately in Fig. 3.2. In Long Pond, the regression coefficient for female is greater than that for male, but in Western Island Pond, the reverse is true.

Kipling (1962) in studying the scales of brown trout, found no significant difference between the fish length and scale length of males and females. In the present study, analysis of covariance method was used to test the differences in slopes and intercepts between the body length and scale length of each sex within each area (Table 3.1). The analysis of covariance for the sexes shows that the slopes for both areas are significantly different at the 5% significant

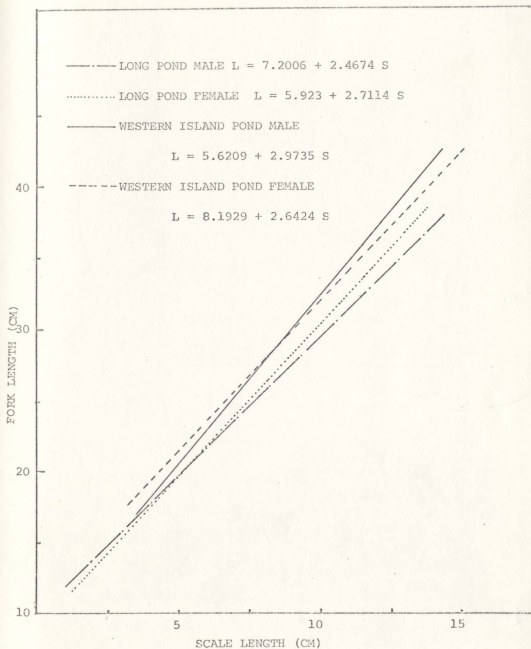


FIG. 3.2 Body-scale length relationships for both sexes of brown trout from Western Island Pond and Long Pond.

Table 3.1 Comparisons of the regressions of body length on scale diameter by analysis of covariance for the sexes of brown trout from Long Pond and Western Island Pond.

Test	Source of variation	Errors of Estimates			F
		D. F.	Sum of Squares	Mean Squares	
Between sexes, within samples		113	92.0135	0.8475	5.6549 *
Western Island	Regression coeff.	1	4.6048	4.6048	
Pond	Common Regression	114	96.6183	0.8475	0.3799
	Adjusted Means	1	0.3220	0.3220	
	Total	115	96.9403	0.8430	

At d.f. 1, 114 $F(0.05) = 3.93$;
 $F(0.01) = 6.88$.

* significant difference

Test	Source of variation	Errors of Estimates			F
		D.F.	Sum of Squares	Mean Squares	
Between sexes, Within samples		311	327.7897	1.0539	5.882 *
Long Pond	Regression Coeff.	1	6.2056	6.2056	
	Common Regression	312	333.9953	1.0704	1.9422
	Adjusted Means	1	4.1580	2.0790	
	Total	314	338.1533	1.0769	

At d.f. 1, 311, $F(0.05) = 3.86$; $F(0.01) = 6.70$

At d.f. 2, 312, $F(0.05) = 3.02$; $F(0.01) = 4.66$

* significant difference

level but not at the 1% level. No difference was found between the intercepts of the two areas.

Since the regression lines for the sexes within each area are not different at the 1% significant level, the samples of both sexes for each area are combined to facilitate computation.

Fig. 3.3 shows the regression lines of body length on scale diameter for the four study areas.

As stressed by previous workers (Hile, 1941; Carlander, 1950; Kipling, 1962; and others) the same body/scale relationship cannot be presupposed to be valid for different populations of a species. The method of analysis of covariance was applied to ascertain if there is any difference in the body-scale relationships of fish from different bodies of water. Only the means of body length based on scale length were used in the analysis. Table 3.2 shows that there is no significant difference in the slopes for the four areas but that the intercepts are significantly different at 1% level.

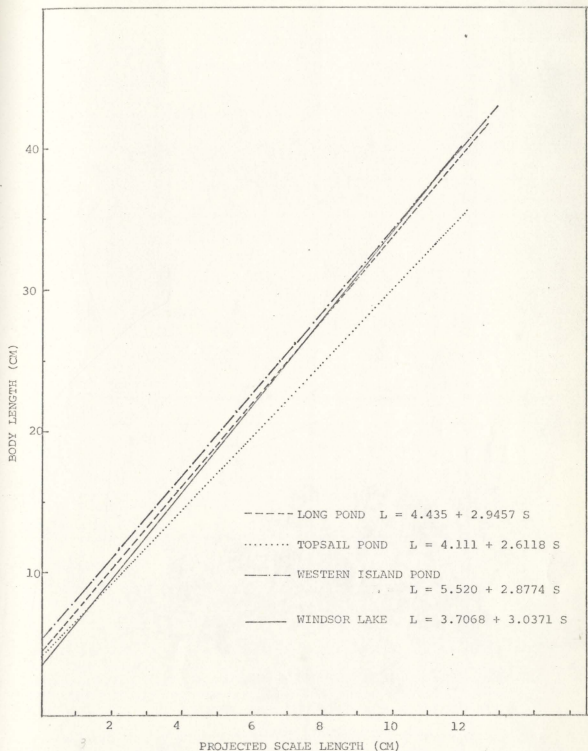


Figure 3.3 The body-scale length relationships of brown trout from the four study areas in Newfoundland.

TABLE 3.2 Comparisons of the regressions of body length on scale diameter by analysis of covariance for Long Pond, Western Island Pond, Topsail Pond and Windsor Lake

Test	Source of variation	Errors of Estimations			F
		Degree of freedom	Sum of Squares	Mean Squares	
Between Localities, Long Pond, Topsail Pond, Western Island Pond and Windsor Lake	Within samples	37	168.00	4.5405	0.1203
	Reg. Coefficients	3	1.64	0.5466	
	Common Regressions	40	169.64	4.2410	14.7292*
	Adjusted means	3	187.40	62.466	
Total		43	357.04		

At d.f. 3, 38, $F(0.05) = 2.85$, $F(0.01) = 4.34$

At d.f. 3, 40, $F(0.05) = 2.84$, $F(0.01) = 4.31$

* significant difference

Although these body-scale regression lines do not differ significantly in slopes, the difference in intercepts may induce errors in the calculated body length if we apply a single formula to the samples from all areas. Thus, samples from each area were taken into account as independent unit and the body length by age of each area were calculated separately.

It has been reported that there are different scale-length relationship for the fish smaller than 10 cm as compared with fish larger than 10 cm in length (Nicholls, 1957; Kipling, 1962; Frost and Brown, 1967). Kipling (1962) pointed out that fish under 10 cm have relatively faster growing scales than the larger ones. In the present study, very few small specimens were collected, and as none of them were smaller than 10 cm, this possible difference between small and large fish was ignored. Samples from each area were regarded as being from a population with the same scale growth rate.

The estimated body lengths were obtained for each observed scale measurement according to the formula

$$L_n = I + \frac{L_t - I}{S_t} S_n \quad \text{or} \quad \frac{L_n - I}{L_t - I} = \frac{S_n}{S_t}$$

where L_n is the length of the fish at the end of the n th year of life, I is the intercept of the body-scale relationship, L_t is the length of fish at capture, S_t is the diameter of the scale at capture, and S_n is the diameter of the scale within the n th annulus. The calculated length of fish at various ages are given for the four areas in Table 3.3.

3.23 Calculation of Mathematic Growth Curve

The von Bertalanffy growth equation (von Bertalanffy, 1938) has been widely accepted to mathematically describe the growth of a particular species. It has

Table 3.3a Calculated fork length (cm) at end of each year of life for each age group and average growth for the combined age groups of S. trutta from

Long Pond

Age group														Grand average calculated length		Incre- ment of average	
III		IV		V		VI		VII		VIII							
	M	F	M	F	M	F	M	F	M	F	M	F	M	F			
Number of fish	58	76	50	77	32	57	3	13	0	1	1	1					
1	8.8	8.5	8.3	8.5	8.5	8.8	9.0	9.1		9.1	8.8	7.9	8.7	8.5	8.7	8.5	
Calculated	2	14.1	13.0	12.5	12.7	12.9	12.9	13.1	12.9	13.0	14.5	11.0	13.4	12.6	4.7	4.1	
length at	3	18.9	17.8	17.5	17.7	18.0	18.0	18.6	18.8	19.8	19.6	16.1	18.5	18.0	5.1	5.4	
end of year	4	-	-	21.3	21.7	22.4	22.8	23.0	23.4	22.7	25.0	20.7	22.9	22.3	4.4	4.3	
	5	-	-	-	-	25.6	26.5	26.6	26.8	30.2	28.0	26.6	26.7	27.5	3.8	5.2	
	6	-	-	-	-	-	-	29.3	29.7	33.1	32.4	30.5	30.8	31.1	4.1	3.6	
	7	-	-	-	-	-	-	-	-	36.3	36.7	34.0	36.7	35.1	5.9	4.0	
	8	-	-	-	-	-	-	-	-	-	39.1	37.1	39.1	37.1	2.4	2.0	

Table 3.3b Calculated fork length (cm) at end of each year of life for
each age group and average growth for the combined age groups of S. trutta
from Topsail Pond

Age groups														Grand average calculated length		Incre- ment of average	
II		III		IV		V		VI		VII							
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
Number of fish	0	1	10	8	29	28	7	16	3	0	1	0					
Calculated length at end of year	1	-	6.0	6.5	7.0	6.7	6.3	6.1	5.8	6.1	-	7.5	-	6.6	6.3	6.6	6.3
	2	-	10.3	12.8	13.7	11.3	10.2	9.4	8.6	9.3	-	10.7	-	10.7	10.7	4.1	4.4
	3	-	-	18.8	19.1	17.2	17.3	15.6	14.8	16.8	-	19.4	-	17.1	17.6	6.4	6.9
	4	-	-	-	-	20.5	20.7	19.5	19.2	21.5	-	22.8	-	21.1	20.0	4.0	2.4
	5	-	-	-	-	-	-	21.8	21.9	24.0	-	27.1	-	24.3	21.9	3.2	1.9
	6	-	-	-	-	-	-	-	-	25.8	-	29.1	-	27.4	-	3.1	-
	7	-	-	-	-	-	-	-	-	-	-	30.0	-	30.0	-	2.6	-

Table 3.3c. Calculated fork length (cm) at end of each year of life for each age group and average growth for the combined age groups of *S. trutta* from

Western Island Pond

Age group														Grand average calculated length		Incre- ment of average	
II		III		IV		V		VI		VII							
M	F	M	F	M	F	M	F	M	F	M	F	M	F				
Number of fish	1	2	6	11	25	21	8	13	8	18	7	0					
	1	7.9 8.5	8.7 9.3	9.0 9.1	9.4 9.7	9.7 9.7	9.4 9.7	9.7 9.7	9.4 -	8.9 9.3	8.9 9.3						
Calculated	2	9.4 11.3	12.2 13.9	12.3 12.4	13.3 13.5	13.1 13.2	12.0 -	11.8 12.9	2.9 3.6								
length at	3	- -	16.2 18.6	18.4 18.6	19.2 19.9	20.7 19.6	17.7 -	17.9 19.2	6.1 6.3								
end of year	4	- -	- -	22.8 23.0	23.2 24.9	25.0 23.7	23.0 -	23.0 23.9	5.1 4.7								
	5	- -	- -	- -	27.7 28.0	28.5 27.1	26.8 -	27.2 27.6	4.2 3.7								
	6	- -	- -	- -	- -	30.5 29.7	30.1 -	30.1 29.7	2.9 2.1								
	7	- -	- -	- -	- -	- -	- -	32.6 -	32.6 -	2.5 -							

Table 3.3d. Calculated fork length (cm) at end of each year of life for
each age group and average growth for the combined age groups of S. trutta
from Windsor Lake

Age groups														Grand average calculated length		Incre- ment of average	
II		III		IV		V		VI		VII							
M	F	M	F	M	F	M	F	M	F	M	F	M	F				
Number of fish	9	5	21	17	29	17	19	10	9	0	6	1					
Calculated length at end of year	1	8.4	8.8	9.9	9.5	9.9	8.8	9.8	8.6	10.3	-	10.0	8.1	9.7	8.7	9.7	8.7
	2	14.1	15.3	17.1	16.7	16.4	14.6	17.3	13.4	17.3	-	17.5	14.4	16.6	14.9	6.9	6.2
	3	-	-	22.1	22.1	22.9	21.7	25.0	21.4	24.2	-	26.9	25.8	24.2	22.8	7.6	7.9
	4	-	-	-	-	26.4	26.2	29.2	25.8	29.5	-	32.8	33.5	29.4	28.5	5.2	5.7
	5	-	-	-	-	-	-	31.6	29.4	33.5	-	35.8	36.5	33.6	32.9	4.2	4.4
	6	-	-	-	-	-	-	-	-	35.5	-	38.2	39.4	36.8	39.4	3.2	6.5
	7	-	-	-	-	-	-	-	-	-	-	40.2	42.0	40.2	42.0	3.4	2.6

generally been claimed that the von Bertalanffy method is more satisfactory than other methods for representing growth since the equation has a physiological basis. However, whether or not this is so, it often does provide a concise empirical description of the growth curve. It is expressed as:

$$L_t = L_{\infty} (1 - e^{-K(t-t_0)})$$

where L_t is length at age t , L_{∞} is the theoretical maximum length, K is a constant determining the rate of change in length increment and t_0 is the hypothetical age at zero length.

In Newfoundland waters, von Bertalanffy growth curves have only been fitted for marine species such as cod (May et al, 1967), haddock (May, 1964), redfish (Sandeman, 1964), American plaice (Pitt, 1967) and cunner (Naidu, 1966). In^{the} present study, an attempt has been made to fit the age length data of brown trout collected from the four study areas to von Bertalanffy growth curves to verify if such growth curves describe the growth of brown trout satisfactorily.

The modified Fortran 1620 computer Program of Abramson (1965) for the von Bertalanffy growth equation was used. This program was obtained through the courtesy of K. S. Naidu who used it in his work on cunners (Tautogolabrus adspersus) (1966). The mean lengths

derived from back-calculation for each age group were used. By this computer program, the parameters, L_{∞} , K and t_0 as well as the standard deviation of the differences between the calculated and sampled lengths were obtained.

3.3 Results

3.3.1 Length Composition

The number of fish grouped in 2 cm. fork length intervals for the four areas are shown in Table 3.4. Fish from Windsor Lake and Western Island Pond appear to grow to a greater length than fish from Long Pond and Topsail Pond.

In all, except the sample from Long Pond, males were of a greater length, and age, than females. This might be due to either a higher mortality rate in females or a greater susceptibility of older males to the gill-net. Unfortunately, there are no data available to substantiate either of these possibilities. The length distribution of unsexed samples from the four areas are shown in Fig. 3.4. A clear single mode appeared in all samples although a low second peak appeared in both the Windsor Lake and Western Island Pond samples.

In Long Pond, the fish varied from 17 cm. to 39 cm. in length, with a modal length of 19 cm. The majority of the fish fall in the range 19 cm. to 29 cm. In Topsail Pond, the body-length ranged from 11 cm. to 31 cm.

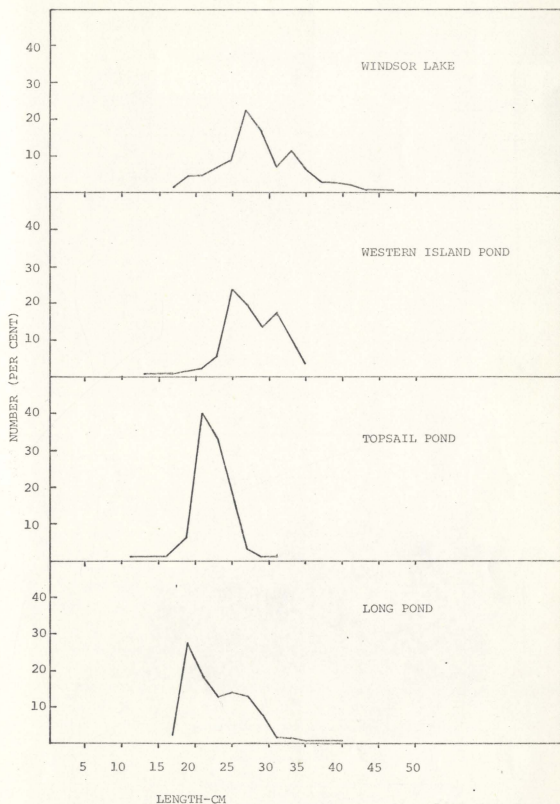


FIG. 3.4 Length composition of brown trout from the four study areas.

Table 3.4a. Length distribution of age groups of brown trout in gill-net samples from Long Pond

Length intervals (cm)	Age group												Total		
	III		IV		V		VI		VII		VIII		F	M	F & M
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F & M
16.0-17.9	5	3											5	3	8
18.0-19.9	49	38	5	9									54	47	100
20.0-21.9	18	12	26	15									44	27	71
22.0-23.9	4	4	24	11	1								29	15	44
24.0-25.9		1	20	12	8	8							28	21	49
26.0-27.9			2	3	26	15	3	1					31	19	50
28.0-29.9					16	7	4	2					20	9	29
30.0-31.9					4	1	2						6	1	7
32.0-33.9					2		2						4	0	4
34.0-35.9						1	2						2	1	3
36.0-37.9									1				1	0	1
38.0-39.9											1	1	1	1	2
Total number:	76	58	77	50	57	32	13	3	1		1	1	225	144	369
Average length:	19.5	22.7			27.6	30.4		37.0			39.1	39.0			
		19.7		22.4		26.9		30.1							

Table 3.4b Length distribution of age groups of brown trout in gill-net samples from Topsail Pond.

Length intervals (cm)	Age group												Total		
	II		III		IV		V		VI		VII		M	F	F&M
	M	F	M	F	M	F	M	F	M	F	M	F			
10.0-11.9	-	1											0	1	1
16.0-17.9			0	1									0	1	1
18.0-19.9			1	1	1	3	-	1							
20.0-21.9			7	5	12	9	3	3					24	17	41
22.0-23.9			2	1	12	11	1	6	1				16	18	34
24.0-25.9					4	5	3	4					7	9	16
26.0-27.9								2	1				1	2	3
28.0-29.9									1				1	0	1
30.0-31.9											1		1	0	1
Total															
number:	-	1	10	8	29	28	7	16	3	0	1	0	52	51	103
Average															
length:		11.8		20.5		22.2		23.3	26.8		30.9				
			21.2		22.2		22.9								

Table 3.4c. Length distribution of age groups of brown trout
in gill-net samples from Western Island Pond

Length intervals (cm)	Age group														
	II		III		IV		V		VI		VII		Total		
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F&M
12.0-13.9	-	1											0	1	1
14.0-15.9	1	-											1	0	1
16.0-17.9	1	-											1	0	1
18.0-19.9			1	1									1	1	2
20.0-21.9			1	2									1	2	3
22.0-23.9			4	2		1							4	3	7
24.0-25.9			5	1	10	12							15	13	28
26.0-27.9					9	11	2	1					11	12	23
28.0-29.9					2	1	6	4	3				11	5	16
30.0-31.9							5	3	11	2			16	5	21
32.0-33.9									4	6		3	4	9	13
34.0-35.9												4	0	4	4
Total															
number:	2	1	11	6	21	25	13	8	18	8		7	65	55	120
Average length:	16.2		23.2		26.1		29.5		31.1		33.9				
		13.9		21.7		26.1		29.7		32.4					

Table 3.4d. Length distribution of age groups of brown trout in gill-net samples from Windsor Lake

Length intervals (cm)	Age group														
	II		III		IV		V		VI		VII		Total		
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F&M
16.0-17.9		2											0	2	2
18.0-19.9	2	5											2	5	7
20.0-21.9	3	2		2									3	4	7
22.0-23.9			6	4									6	4	10
24.0-25.9			5	7		1							5	8	13
26.0-27.9			4	8	8	11	1						13	19	32
28.0-29.9			2		7	12	3						12	12	24
30.0-31.9					2	3	1	4					3	7	10
32.0-33.9						2	3	11					3	13	16
34.0-35.9							2	4		3			2	7	9
36.0-37.9								1		3			0	4	4
38.0-39.9										3		1	0	4	4
40.0-41.9												3	0	3	3
42.0-43.9											1		1	0	1
44.0-45.9												1	0	1	1
46.0-47.9												1	0	1	1
Total number:	5	9	17	21	17	29	10	20		9	1	6	50	94	144
Average length:	19.3		24.9		28.2		31.4		36.9		41.7				
		18.7		24.8		28.5		33.2			43.5				

with a mode of 21 cm. It is interesting to note that most of the fish from Topsail Pond were in the 21 cm length group and very few fish over 30 cm. were caught. If we assume that the faster growing members of each year class are more readily harvested than the slower growing ones, the heavy exploitation by anglers may reduce the members of larger fish in this area.

There are more large fish caught in Western Island Pond and Windsor Lake. Since these waters have seldom been reached by anglers, we may regard the fish populations as being unexploited, especially in Windsor Lake, where angling is prohibited. It is generally accepted that fish of an unexploited population always reached a larger size than fish from exploited populations. In Western Island Pond, the length of fish varied from 13 to 35 cm., with a mode of 25 cm., while the fish of Windsor Lake varied from 17 to 46 cm. in length, with a mode of 27 cm. The largest fish obtained measured 46 cm and was from Windsor Lake, while the smallest fish (11 cm) was from Topsail Pond.

3.32 Age Composition

The age composition of the four study areas is shown in Table 3.4. The 3+ and 4+ year classes are most abundant in these populations.

Brown (1957) stated that the usual longevity of medium-sized brown trout in captivity is 6-8 years but that this species can reach a maximum age of 18 or more years. Fig. 3.5 shows that no trout older than 8 years were found in the present study. The scarcity of older fish could be due to a high mortality in the older age groups or to the fact that older fish occur in deeper parts of the water where they are not catchable by gill-netting. McFadden et al (1962) reported that brown trout reach seven years old in Pennsylvania streams but that most are younger than 4 years of age. Cooper (1955) found that few brown trout live to be four years old in Pigeon River. Dahl (1910) showed that substantial numbers of brown trout live up to 7 years old and some reach 15 years of age. The sea-run brown trout in Newfoundland has also been found to reach 13 years of age (Williamsons, 1962).

The oldest age groups were represented in the sample from Long Pond. However, age group I was absent in these samples. These ponds undoubtedly contain individuals of age group I and their absence in the sample probably is due to the selectivity of the gill-nets and the movements of the young trout. Graham and Jones (1962) reported that most young brown trout do not descend from the nursery streams into the Llyn Tegid Lake until they are two to three years of age.

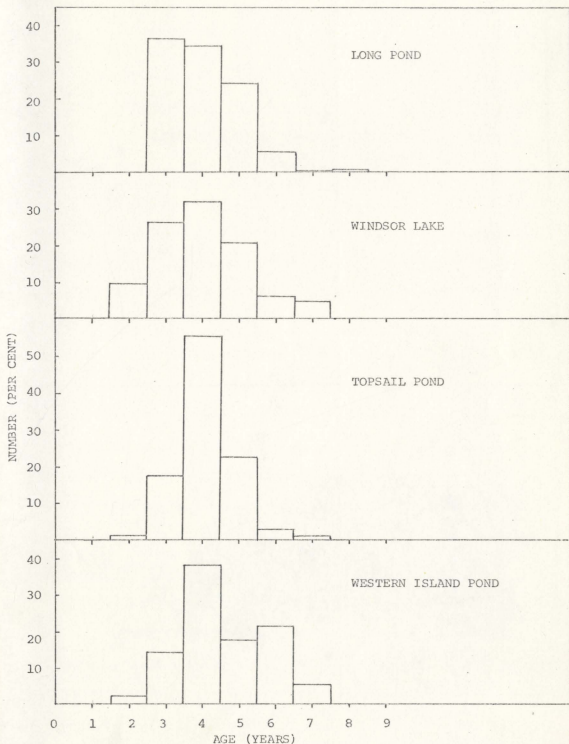


Figure 3.5 Histograms showing age distribution of brown trout from the four locations in Newfoundland, 1967.

Long Pond specimens comprised mainly 3 to 8 year old fish with a mode at three years. The 3 to 5 year old fish contributed the bulk of the catch (approximately 95%) while age-groups 6, 7 and 8 supplied the rest of the catch.

In Topsail and Western Island Ponds, where streams are available for spawning and accomodating the young, very few 2-year-old fish were present in the catches. At Topsail Pond, the modal age-group was 4 years and age groups 3, 4 and 5 comprised 95% of the catch. The 4 year old age group was most abundant in Western Island Pond sample, while the 3, 5 and 6 year old age groups were also abundant. It is noted that the 6 year old fish were more abundant than five year old in this sample. It is probably related to the abundance of 31 cm fish in the sample. The presence of a higher number of 6 year old might either indicate the abundance of this year class as a result of higher survival or as a result of gill-net selection. There is also a possibility that in brown trout certain age groups tend to be spatially segregated (McFadden et al, 1962), thus affecting the catch.

The brown trout in Windsor Lake is an unexploited population. There is no suitable spawning stream, thus the young are always in the lake. There were more 2 year old obtained in this sample than in any of the others. This may support the hypothesis that young fish tend to

remain in the streams in the other study areas. There were also more larger and older fish taken in Windsor Lake than in other areas, although there were no eight-year-old present in the sample. The 3-, 4- and 5-year-old were the major age groups as in other areas.

In general, the old fish were fewer than young in samples from the four study areas. The actual number of old fish present in these waters might determine their rare occurrence. The selectivity of the gill-netting might also influence the catchability of older fish as a result of the movement and distribution of the old fish in the water.

3.33 Survival Rate of Brown Trout

The annual total mortality and survival rate can be estimated from the abundance of successive age groups if the samples are representative and if the initial size of year classes within each area are constant (McFadden et al, 1962).

The fishing method is considered to be comparatively representative for the older trout, if not for the young trout since several mesh-sizes were used. The assumption of constant initial class size is also valid in all the areas except Western Island Pond since there is no large variation in the abundance of each year class and since the numbers of older fish decrease gradually

with increasing age (Fig. 3.5). In Western Island Pond, fish of the 1961 year class (6+) were more abundant than those of the 1962 year class (5+). This probably indicates that a variation in recruitment has taken place in this population. As McFadden et al (1962) has stated

"If recruitment had been highly variable some reversals in order of abundance of successively older age groups would be evident."

Annual survival rates of brown trout of different ages in four areas were estimated from formula 2.1 of Ricker (1958):

$$\hat{s} = \frac{N_{t+1}}{N_t}$$

where N represents the number of fish found of age t to age t+1. In most cases annual survival rate was computed from age group III to age group VI within each area except in Western Island Pond where only age groups IV and V were considered.

In view of the fact that older age classes will tend to be more scarce than younger age classes in any sample of a population, a weighted mean annual survival rate was calculated by a method described by Jackson (1939).

$$s = \frac{N_2 + N_3 + N_4 + \dots + N_r}{N_1 + N_2 + N_3 + \dots + N_{r-1}}$$

McFadden et al (1962) stated that the mean survival rates are advantageous in averaging out aberrations due to sampling error or failure to fulfill the necessary assumptions.

TABLE 3.5 Annual rates of survival of brown trout as calculated from the age composition of each population from the four areas

A R E A	A G E G R O U P				Mean
	III-IV	IV-V	V-VI	VI-VII	
Long Pond	0.94	0.70	0.18	--	0.63 (III-VI)
Topsail Pond	--	0.40	0.13	--	0.31 (IV-VI)
Windsor Lake	--	0.65	0.30	0.77	0.50 (IV-VII)
Western Island Pond	--	0.45	--	--	0.45 (IV - V)

The actual survival rates between age groups for all localities studied is shown in Table 3.5. Survival varied from area to area as well as among different-aged fish in the same water. This differs from the result obtained by McFadden et al (1962) in which survival of adult brown trout was highly variable from stream to stream, but less variable among different-aged fish in the same stream. By comparing the survival rates of age groups

IV-V from the four study areas, it is apparent that the Long Pond and Windsor Lake trout have higher survival than trout from the other two areas. In Long Pond, the high survival for age groups III and IV might demonstrate a low exploitation rate in the previous years. The sudden decline in the survival rate of V-VI year fish could be due either to high mortality or the seaward migration of the older fish. Fish in Windsor Lake have a consistently higher survival rate than fish from other areas. This rate can be used to represent the survival rate of an unexploited population in Newfoundland.

The unweighted mean annual survival for the brown trout in the four locations is 0.47. This value is in substantial agreement with those reported elsewhere. The annual survival rates for brown trout in six Pennsylvania streams were 0.358 (McFadden, 1962). Needham, Moffett and Slater (1945) calculated the average over winter survival of wild brown trout in Convict Creek, as 0.15 for all ages and Schuck (1945) found an annual survival rate of 0.361 for wild brown trout of age group V-VIII in Crystal Creek, while Nielson, Reimers and Kennedy (1957) found that the annual survival rate of brown trout from Convict Creek Lakes varied from 0.31 to 0.87. In Norwegian waters, Runnstrom (1959)

reported an average annual survival of 0.54 for all age groups from IV-VIII in Rensjo brown trout. In the Horokiwi Stream, New Zealand, Allen (1951) estimated a survival rate of 0.28 for trout less than a year old and 0.17 for older fish.

3.34 The Growth of Brown Trout

3.341 Von Bertalanffy Growth Curve

The von Bertalanffy growth curves were fitted for male, female and combined sex data of brown trout from each area. However, the data for Topsail Pond males and Windsor Lake females didn't converge in the iteration process, therefore, no growth data were obtained by this method for these males and females. This is probably due to the fact that these age-length data have a linear relationship. Owing to the absence of either male or female growth curves in some areas, only sex combined data were used in the present study.

Table 3.6 shows the parameters of von Bertalanffy growth curves for the sex combined data for various areas. The growth curves for the four areas are shown in Fig. 3.6.

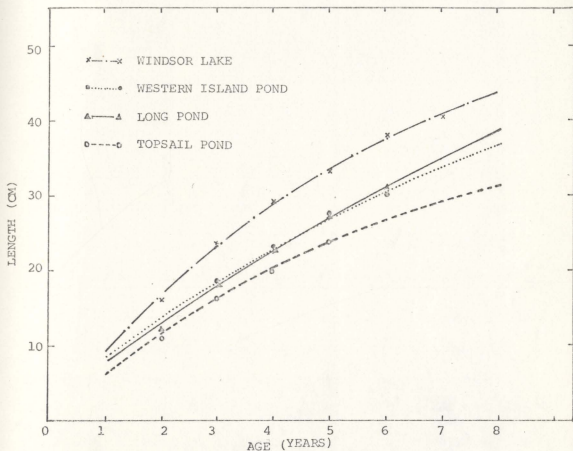


Figure 3.6. Fitted von Bertalanffy growth curves for sex-combined brown trout from the four study areas.

TABLE 3.6 Summary of values of calculated parameters, L_{∞} , K and t_0 of combined sex data from various areas (age range used to fit the equation is indicated in parentheses).

Area	L_{∞}	t_0	K
Long Pond	121.8 (1 - 6)	-0.58	0.045
Topsail Pond	42.3 (1 - 5)	0.08	0.169
Windsor Lake	59.0 (1 - 7)	0.044	0.169
Western Island Pond	69.2 (1 - 6)	-0.44	0.09

The L_{∞} values of brown trout obtained in the present study seem to differ between areas. However, the calculated values of L_{∞} are probably not realistic. Since the maximum empirical age obtained in the present study was 8 years, it was necessary to extrapolate far beyond the range of the fitted data to reach L_{∞} . Sandeman (1964) indicated that extrapolating the von Bertalanffy curve much beyond the range of the fitted data can give rise to very high standard errors if the fitted range does not extend to the asymptotic position of the curve. As this was the situation in the present study the L_{∞} values shown above are likely rather meaningless. In view of

this, there is probably no merit in comparing the L_{∞} values of this species in different study areas.

Beverton and Holt (1959) have shown for a number of species that a negative correlation exists between L_{∞} and K. This correlation is also demonstrated in the present study. The lowest K values are found in Long Pond, the smallest study area, while larger K values are found in Windsor Lake and Topsail Pond.

Windsor Lake trout showed the fastest growth, followed by fish from Western Island Pond and Long Pond, while Topsail Pond trout showed the slowest growth (Fig. 3.6). The Western Island Pond and Long Pond trout showed very similar patterns of growth. However, the Long Pond trout grew slower than Western Island Pond trout between 1 and 6 years old but grew faster than the latter after 7 years. This is probably associated with the presence of forage fish and large food organisms in Long Pond which result in faster growth of old fish.

The growth in length at age obtained by this method is very similar to the result obtained by the straight forward plot of age against back-calculated length (see next section). In view of the fact that the growth in this species in different areas is nearly linear and since some of the data as described above didn't fit the von Bertalanffy formula, it is better to express growth in the fish by the straight forward plot of age against length.

3.34b The Calculated Growth of Brown Trout

Back-calculations by using scales has been widely used by previous investigators to study the yearly growth of trout (Allen, 1938; Swynnerton and Worthington, 1939; Went and Frost, 1942; Kathrein, 1951; Cooper, 1953; Holmes, 1960; Campell, 1961; and Thomas 1964). The lengths obtained from back-calculation based on scale measurements are directly comparable regardless of the time of collection because the calculated lengths of individual fish represent increments at completed seasons of growth. Therefore, any seasonal variation in growth rate during the year is concealed. Back-calculated lengths from scales were used in the present study to compare the growth of trout from different environments.

The back-calculated lengths of both males and females are shown in Fig. 3.7. There were no distinct differences between yearly growth of male and female brown trout except in older fish. This difference may be due to the scarcity of the older specimens in the sample. In order to test if the difference between the male and female trout in different areas are significant, the specimens of age group 4 were compared. As is shown in Table 3.7, there is no significant difference between the lengths obtained by males and females. Ball and Jones (1960) also found no significant differences in growth between males and female brown trout in Llyn Tegid. Therefore, the sexes are considered together.

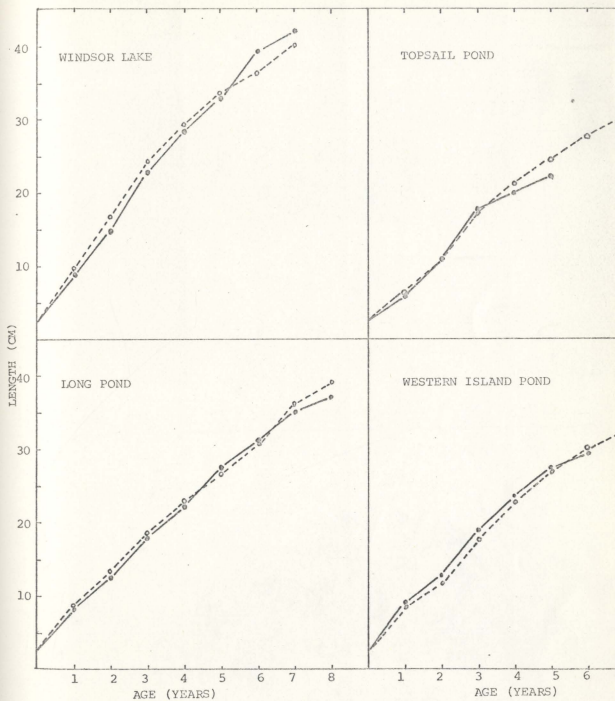


Figure 3.7 Average length at age of male and female brown trout from the four areas. (·——· female; ○-----male)

TABLE 3.7 Test between the difference in mean lengths of 4 year old male and female brown trout from four study areas

A R E A	F E M A L E			M A L E			t
	Mean length	No. of fish	Var-iance	Mean length	No. of fish	Var-iance	
Long Pond	22.5	77	8.125	22.2	50	10.33	Z=.069
Western Island Pond	26.1	21	2.03	26.06	25	1.7916	t=.576
Topsail Pond	22.2	28	2.0328	22.2	29	2.2143	t=0
Windsor Lake	28.2	17	1.9228	28.5	29	3.6884	t=.574

The mean lengths in centimeters of the trout from the four locations as calculated from scales are shown in Fig. 3.8. These growth curves were extrapolated to meet the length axis at 2.5 cm as this is the generally accepted mean length for yearling fish (0^+) (Thomas, 1964; Frost and Brown, 1967). The same figure was obtained from newly hatched fry in the laboratory during the spring of 1968.

There were striking differences between the growth curves of trout in different waters. The Windsor Lake trout showed the fastest growth rate, followed by Long Pond, Western Island and Topsail Ponds. In general, all the fish

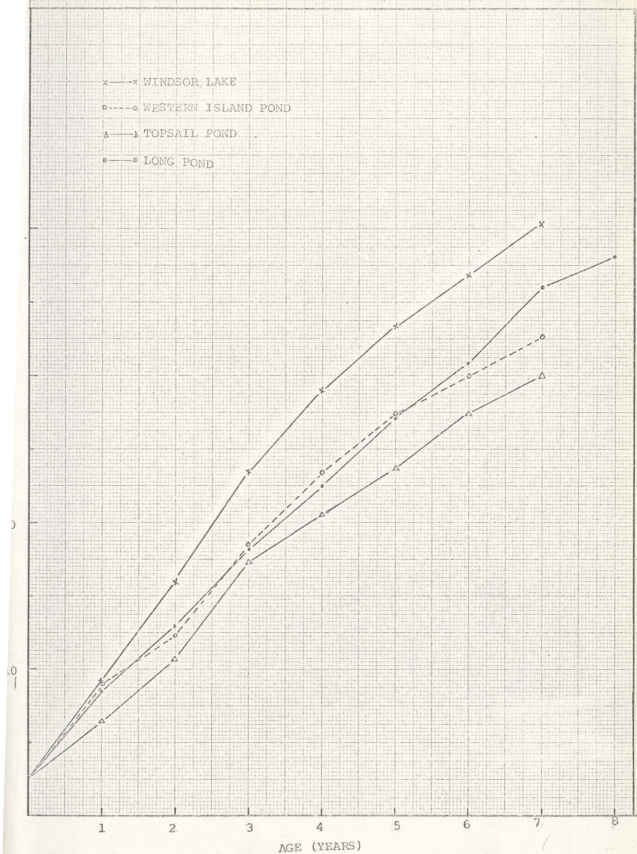


Figure 38 The annual growth in length of brown trout from the four study areas.

show the sigmoid type of growth. This means that the fish grow faster in their earlier life and slow down in their later life.

By using the method of back-calculation there is a progressive decrease in back-calculated lengths on age when calculations are made from successively older fish. This phenomenon has been named the "Lee's phenomenon". Cooper (1953) did not find Lee's phenomenon occurring in brown trout of Pigeon River, Michigan. He considered that this was probably associated with the low exploitation of the population in Pigeon River. Results similar to Cooper's were found in the present study. The calculated length of the 1st and 2nd annuli of older fish did not show any consistent lower values than those of younger fish. Inspection of the survival rate of brown trout in these areas revealed a comparatively low mortality rate. This might indicate a low exploitation of these populations which in turn could affect the absence of Lee's phenomenon in this species.

During the first year of life, the growth of pond fish is not much different from lake fish except in Topsail Pond where the length is only 6.5 cm compared to 8.5, 9.2 and 9.8 cm in Long Pond, Western Island Pond and Windsor Lake respectively. Starting from ^{the}second year, the fish in the lake exhibits much better growth than the trout in ponds. Among the pond fish, the fish of Western Island Pond and

Long Pond always exhibit a similar pattern of growth and grow faster than fish from Topsail Pond.

The trout living in ponds show a small increment in length in their first year but all show a large increment in the second year. Thereafter, the annual increment in length either decreases or varies irregularly with age. In lake brown trout, the annual length increment decreases with age. This is in contrast to Runnstrom's findings (1959) that lake brown trout exhibit a rapidly increasing annual increment in length. The difference in growth rate between the pond trout and lake trout could be caused by the fact that after trout have migrated from the streams to the ponds, they find more favourable nutritional conditions. The fish in Windsor Lake hatch in the lake and from the start have better growing condition than fish in ponds.

It has been shown by Allen (1938) that fish scales show a sudden well-marked increase in length when the fish change from stream life to lake life. However, in some waters, especially in Long Pond, not all the scales showed a marked boundary between the "stream" and "pond" life. Since Topsail Pond fish possess more scales with a sharp boundary between the "river years" and "pond years", they were used to determine if the time of migration from streams to the pond has any effect on the growth of fish (see Fig. 2.1

Table 3.8 shows the mean growth rates of fish which migrated after one and two years from the stream. The fish which migrated after one year had grown faster during their first year than the others and also show a faster growth rate than the two year migrants in the later years. This indicates the first year growth of fish as well as an earlier migration from the streams to the pond has an effect on the growth of fish in their later life. It is likely that after the fish move into the pond they attain more living space and more food, probably including, more larger food organisms than in the streams.

TABLE 3.8 Mean back-calculated length
of fish of different migrant groups of
Topsail Pond brown trout.

Age	Mean lengths (cm)	
	1 migrants	2 migrants
1	7.4	5.9
2	14.2	9.5
3	19.2	16.6
4	21.1	19.8
5	--	21.3

3.34c Growth in Windsor Lake Compared with Other Lakes

In Fig. 3.9 a calculated growth curve for Windsor Lake trout is compared with growth curves for three lakes in England and for Llyn Tegid in Wales. The curve for Windermere was taken from Allen (1938), those for Ullswater and Haweswater from Swynnerton and Worthington (1939) and data for Llyn Tegid from Ball and Jones (1960).

The Windsor Lake trout show a very striking difference in growth from other lakes in the much better growth in the first four years and the subsequent slight decrease of growth in the later years.

The British and Welsh fish (except the Windermere fish) all show a much poorer growth than Windsor lake trout. Windermere trout grow faster than other fish after the 5th year and reach a larger size at seven years.

Ball and Jones (1960) considered the slower first year growth rate of brown trout from Windermere, Ullswater and Haweswater Lakes as an artifact due to the interference of Lee's phenomenon on back-calculated lengths of fish from English and Welsh waters. Since no Lee's phenomenon has been found in the present study and no such phenomenon had been found in the literature (Allen, 1938; Cooper, 1953), this may indicate little or no occurrence of Lee's phenomenon in brown trout. If there is any slow first year growth in brown trout, it does not necessarily mean

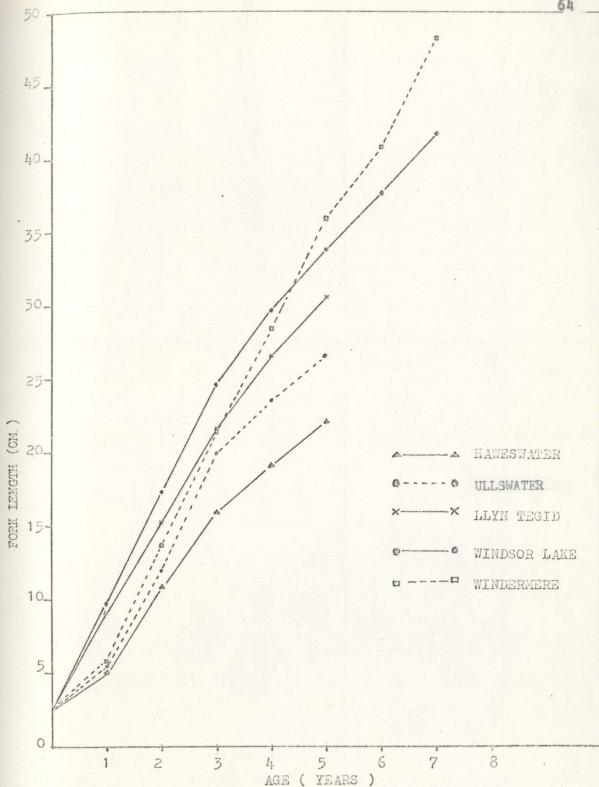


FIGURE 3.9 ANNUAL GROWTH CURVES FOR TROUT IN WINDSOR LAKE AND OTHER LAKES

that it is caused by Lee's phenomenon. There is the possibility that it results from ^{the} actual slow growth of the fish population. Therefore, it does not seem valid for Ball and Jones to conclude that the slow growth rate of brown trout in British and Welsh waters was due to Lee's phenomenon. When the length attained at the end of each year of Windsor Lake trout and Llyn Tegid trout are compared, the lengths of Windsor Lake trout show consistently faster growth than fish in Llyn Tegid. The growth pattern of Windsor Lake and Llyn Tegid trout are very similar. Since different slopes of the back-calculated curves must reflect real differences in growth rate in the second and third years (Ball and Jones, 1960), any difference between Windsor Lake and Llyn Tegid trout might indicate a difference in the actual length rather than be a reflection of the method used. Of course, this should include the difference in growth of the 1 year old. Therefore, up to age three, Windsor Lake trout grow fastest, followed by Llyn Tegid, Windermere, Ullswater and Haweswater trout.

The growth curves from Ullswater, Llyn Tegid show a reduction in growth rate after four years old. A similar reduction in growth rate also occurred in trout from Windsor Lake. In contrast, the Windermere trout showed a steady and continuous growth, at least until 5 years old. Swynnerton and Worthington (1939) regarded the difference in growth rate

between Ullswater, Haweswater and Windermere as resulting from the presence of pike in Windermere and their absence in the former two waters. However, this explanation wouldn't hold for Llyn Tegid which contains pike and shows a decline in the trout growth rate after age 3 (Ball and Jones, 1960). No pike and few predators have been found in Windsor Lake, so Gwynnerton and Worthington's explanation could be applied to the trout in Windsor Lake if one considers that there are more older trout competing for food in the lake thus reducing the growth rate in later life. Further consideration on the reduction of growth rate after the third year will be dealt with in the specific growth section.

When the mean sizes reached by 5 year old fish are compared as showed in Fig. 3.9, the fish from Windermere have the fastest growth rate, followed by Windsor Lake trout, Llyn Tegid, Ullswater and Haweswater trout.

3.34d Annual Growth in Long Pond, Western Island Pond and Topsail Pond Compared with Ponds and Streams from Other Areas.

Fig. 3.10 shows the growth curves for Long Pond, Western Island Pond and Topsail Pond, two rivers and lakes from the United States, two tarns and one river from England and Wales. The curves for Pigeon River are taken from Cooper (1953), those for Convict Creek Lakes are from Reimer et al (1955) and those for Missouri River are from Kathrein

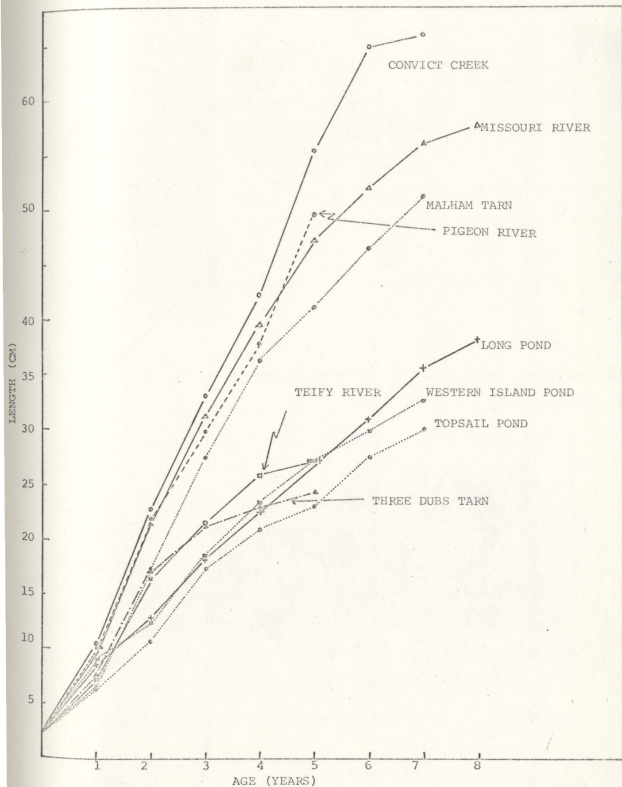


Figure 3.10 The average growth rates of brown trout in small lakes, ponds and streams.

et al (1957). The data of Three Dubs Tarn, Malham Tarn and River Teify are from Swynnerton et al (1939), Holmes (1960) and Thomas (1964) respectively. When the original data were presented as total length, the factors listed in Appendix table A based on data from Long Pond were used to convert them into fork length.

The fish from the U.S. have a much faster growth rate than those from Newfoundland and British waters. The fish from Convict Creek lakes which comprise 10 lakes ranging from 4.4 acres to 16.8 acres of surface area show the fastest growth rate and grow steadily and continuously up to 6 years old. The growth rates of fish from Missouri and Pigeon Rivers at 1- and 2-year-old are similar but slow down after the age of three years. The fish in British waters grow at more or less the same rate as the others during the first two years of life, but the growth rate of fish from Three Dubs Tarn and Teify River fall off suddenly at three year old while Malham trout exhibit a fast growth until 4-year-old.

As shown by the Fig. 3.10, the fish from ^{the} Avalon exhibit a much slower growth than their counterparts from elsewhere until 4-year-old. At five-year-old, the growth rate of Long Pond and Western Island Pond trout exceed the growth of Three Dubs Tarn trout and equal the growth of Teify River trout.

The differences between the generally faster growth of fish from the U.S. and the slower growth of fish from Newfoundland and British waters could be due to the higher productivity as well as higher water temperatures in the U.S. waters.

On the basis of fish length reached at 5-year-old, the 9 waters may be arranged in a decreasing order of growth. The Convict Creek lakes trout have the fastest growth, followed by the Pigeon River, Missouri River, Malham Tarn, Long Pond, Western Island Pond, Teify River, Three Dubs Tarn and finally the Topsail Pond.

3.35 The Specific Growth Rate

The rate of growth may be expressed as the specific growth rate, calculated from the formula:

$$G = \frac{\log_e Y_T - \log_e Y_t}{T - t} \times 100$$

Y_T is the final size (the size at time T), Y_t is the initial size (the size at time t), and $\log_e Y_T$ and $\log_e Y_t$ are the natural logarithms of the values of Y_T and Y_t ; for the first year Y_t is taken as 2.5 cm for all fish. The specific growth rates of fish in the four stations are present in Appendix Table B and shown graphically in Fig. 3.11.

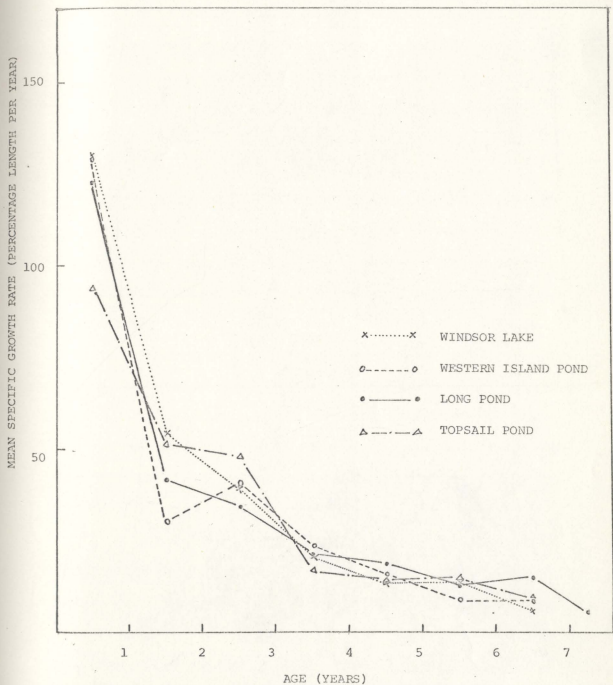


Figure 3.11. The mean specific growth rate (percentage length per year) for brown trout from Avalon Peninsula.

In general, the specific growth rate decreases as the fish grow older so that most of the fish grow at the fastest rate during the first year of life and thereafter the rates decline and become less marked as the fish grow older. In Long Pond and Windsor Lake, the decline in growth rate is very rapid at first then gradually decreases but seems to become stabilized at low levels as the fish grow. Topsail Pond trout also show a sharply decreasing rate of growth in the first year but a smaller decline between 1 and 2 years old than fish in either Long Pond or Windsor Lake. Another sharp decline, however, occurred at 3 years followed by a continuous decline. The slow down of the decreasing rate of growth rate at 1-and 2-year-old could probably be associated with the migration of young in the streams into the ponds which results in a faster growth until 3 years old when growth rate decreases.

The Western Island Pond population is different from the other populations in that at the first year of life, a more precipitous decline occurs but decrease in specific growth rate during their 2nd year of life. At ages above 3 years the growth rates of Western Island Pond fish go into a moderate decline similar to other populations and finally tend to stabilize at low levels. In pygmy whitefish (Prosopium coulteri), an exceptional increase in

the instantaneous growth rate at 2-year-old has been attributed to the attainment of some size threshold which makes available to them an unknown environmental resource (McCart, 1965). The exceptional increase in growth rate of Western Island Pond fish at 2-year-old could result from the attainment of better nutritional condition as well as living space by migrating from streams to the pond.

After the third year, the specific growth rates of trout from the four study areas are fairly similar although the fish are of varied rates as a result of the differences in growth at the first two years. The marked fall in the rate in the third year seems to be associated with the effects of the onset of maturity (Frost and Brown, 1967). The ripening of gonads reduces the amount of the nutrients available for body growth, therefore, a reduction in specific growth rate occurs in the fish.

On the basis of specific growth rate for the fourth year of life, the four locations could be arranged in the following order of decreasing growth rate: Long Pond, Western Island Pond, Topsail Pond and Windsor Lake.

3.36 Growth in weight

Table 3.9 shows the mean weights for age of all trout from the four sampling areas.

Table 3 .9. Average weights in grams of different age groups from the four study areas in Avalon Peninsula, Newfoundland. Number of fish in parentheses.

Age	Long Pond*			Topsail Pond			Western Island Pond			Windsor Lake		
	Male	Female	Mixed	Male	Female	Mixed	Male	Female	Mixed	Male	Female	Mixed
2					24.0 (1)	24.0 (1)	32 (1)	52.5 (2)	45.7 (3)	77.2 (9)	79.4 (5)	77.9 (14)
3	90.5 (54)	88.1 (69)	89.1 (123)	105.8 (10)	93.8 (8)	100.4 (18)	121.3 (6)	156.3 (11)	143.9 (17)	179.7 (21)	182.4 (17)	181.0 (38)
4	133.3 (46)	137.4 (65)	135.7 (111)	120.1 (29)	117.3 (28)	118.7 (57)	210.2 (26)	212.1 (22)	211.0 (48)	291.7 (29)	263.0 (17)	284.2 (46)
5	242.2 (28)	252.1 (55)	248.8 (83)	129.6 (7)	132.9 (16)	131.9 (23)	295.0 (7)	282.9 (13)	287.2 (20)	446.9 (20)	364.1 (10)	416.6 (30)
6	316.0 (2)	318.3 (12)	318.0 (14)	192.7 (3)	-	192.7 (3)	363.3 (8)	323.3 (17)	336.0 (25)	618.0 (9)	-	618.0 (9)
7	-	496.0 (1)	496.0 (1)	381.0 (1)	-	381.0 (1)	403.3 (7)	-	403.3 (7)	1037.3 (6)	801.0 (1)	1003.5 (7)
8	605.0 (1)	-	605.0 (1)									

* May sample only

The age-weight relationships of the four study areas are shown in Table 3.10 and Fig. 3.12. The slopes of the regression lines which might indicate the rate of growth of fish for various areas vary from 1.6777 in Western Island Pond to 2.0174 at Long Pond. The analysis of covariance for the age-weight relationships for the four study areas (Appendix, Table C) shows that these slopes are not significantly different at the 5% level. The intercepts, however, are significantly different.

Further tests on the age-weight relationships between any two study areas show the same result, except that the intercepts for Long Pond and Western Island Pond are not significantly different at the 5% level. (Appendix, Table D).

In the four study areas, the fastest growth in weight occurred in Windsor Lake. Trout from Long Pond and Western Island Pond showed a similar growth pattern, while the Topsail Pond trout exhibited the slowest growth in weight.

3.37 Length-Weight Relationship

The length-weight relationship has always been used to describe changes in the condition of fish with changes in length and to predict the weight of known length or the length of fish of known weight.

The weight of fish has been considered as a function of the length, the cube law, ($K = W/L^3$ where W is weight and

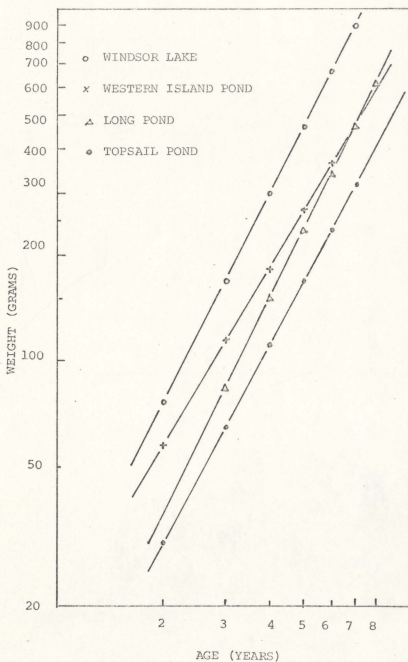


FIG.3.12 Age-weight relationships of brown trout from the four areas.

Table 3.10. Age-weight relationships for brown trout from the four study areas.

Area	Sex	Regression lines
Long Pond	male	$\log W = 0.9529 + 2.0339 \log A$
	female	$\log W = 0.7275 + 2.3442 \log A$
	mixed	$\log W = 0.9623 + 2.0174 \log A$
Topsail Pond	male	$\log W = 0.1294 + 1.3557 \log A$
	female	$\log W = 0.9207 + 1.8574 \log A$
	mixed	$\log W = 0.9168 + 1.8747 \log A$
Western Island Pond	male	$\log W = 1.0255 + 1.9958 \log A$
	female	$\log W = 1.3130 + 1.6226 \log A$
	mixed	$\log W = 1.2543 + 1.6777 \log A$
Windsor Lake	male	$\log W = 1.2851 + 1.9861 \log A$
	female	$\log W = 1.4302 + 1.6454 \log A$
	mixed	$\log W = 1.2918 + 1.9659 \log A$

L is body length), which states the weight is proportional to the cube of the length, has been used to describe the length-weight relationship of the fish.

However, body proportions of fish tend to change during growth and thus the simple cube law expression does not hold through life (Rounsefell and Everhart, 1953). A more satisfactory formula for the expression of the relationship is

$$W = a L^n$$

where W is weight, L is length, a is constant and n an exponent which always falls between 2.5 and 4.0 (Le Cren, 1951). In practice, the length-weight relationship is always calculated in logarithmic form as

$$\log W = \log a + n \log L$$

where n represents the slope of the line, and log a its intercept.

The length-weight relationships of brown trout in the four study areas were determined by arranging the fork length data into 2 cm intervals and calculating the mean weights for each of these length intervals. The line of best fit for the empirical data was computed by the regression method of least squares. The empirical length-weight data are tabulated in Table 3.11.

Table 3.12 lists the a and n for brown trout from different waters for male, female and sexes combined. The n values range from 2.7 to 3.1. These results are similar to the results obtained in British waters by Ball and Jones, 1960 (2.92), Graham and Jones, 1962 (2.86), Thomas, 1964 (2.91) and Allen, 1938, (3.0).

Table 3.1.1 Actual length-weight relation of brown trout from the four study areas
in Ardon Peninsula, Newfoundland. (Number of fish in parentheses)

Fork Length (cm)	Average body weight (in grams)						Western Island Pond						Sedfour Lake					
	Male	Female	Mixed	Male	Female	Mixed	Male	Female	Mixed	Male	Female	Mixed	Male	Female	Mixed	Male	Female	Mixed
12.5	-	-	-	-	21.0 (1)	24.0 (1)	32.0 (1)	-	32.0 (1)	-	-	-	-	-	-	-	-	-
14.5	-	-	-	-	-	-	-	52.8 (2)	52.8 (2)	47.0 (1)	-	-	-	-	-	-	-	-
16.5	59.0 (1)	69.0 (2)	64.0 (3)	-	61.0 (2)	61.0 (2)	63.0 (1)	59.0 (1)	73.0 (2)	65.6 (5)	65.5 (2)	66.3 (7)	67.0 (1)	66.3 (7)	67.0 (1)	66.3 (7)	66.3 (7)	67.0 (1)
18.5	80.8 (35)	81.5 (69)	81.2 (84)	-	83.9 (14)	83.9 (26)	106.0 (2)	114.0 (1)	108.7 (3)	92.0 (5)	95.0 (2)	91.0 (7)	92.0 (5)	92.0 (7)	91.0 (7)	92.0 (5)	92.0 (7)	91.0 (7)
20.5	99.5 (32)	98.7 (43)	99.1 (75)	93.8 (12)	93.8 (12)	113.3 (39)	140.3 (3)	144.8 (4)	142.9 (7)	134.5 (5)	125.4 (4)	129.4 (9)	134.5 (5)	125.4 (4)	129.4 (9)	134.5 (5)	125.4 (4)	129.4 (9)
22.5	127.0 (18)	131.0 (32)	129.0 (56)	114.3 (23)	112.4 (16)	142.6 (39)	173.3 (10)	182.4 (10)	177.9 (20)	152.4 (5)	146.8 (6)	149.9 (11)	152.4 (5)	146.8 (6)	149.9 (11)	152.4 (5)	146.8 (6)	149.9 (11)
24.5	174.5 (22)	178.1 (31)	175.4 (35)	144.7 (8)	141.7 (16)	172.0 (24)	221.9 (12)	216.6 (13)	219.2 (20)	179.3 (13)	175.9 (9)	179.1 (27)	179.3 (13)	175.9 (9)	179.1 (27)	179.3 (13)	175.9 (9)	179.1 (27)
26.5	224.3 (21)	222.7 (23)	223.5 (46)	179.4 (9)	164.3 (4)	217.0 (9)	260.2 (9)	250.8 (13)	259.3 (24)	225.5 (12)	223.8 (12)	224.9 (26)	225.5 (12)	223.8 (12)	224.9 (26)	225.5 (12)	223.8 (12)	224.9 (26)
28.5	260.7 (8)	256.6 (23)	256.6 (33)	217.0 (1)	-	217.0 (1)	306.8 (9)	307.4 (14)	307.8 (24)	277.6 (16)	265.3 (12)	261.5 (14)	277.6 (16)	265.3 (12)	261.5 (14)	277.6 (16)	265.3 (12)	261.5 (14)
30.5	295.6 (5)	329.0 (9)	312.3 (14)	391.0 (1)	-	391.0 (1)	369.1 (7)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)	378.0 (9)
32.5	364.0 (5)	364.0 (5)	364.0 (5)	-	-	-	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)	409.4 (4)
44.5	-	-	-	-	-	-	-	-	-	1064.0 (1)	-	1064.0 (1)	-	-	1064.0 (1)	-	-	1064.0 (1)
46.5	-	-	-	-	-	-	-	-	-	1208.0 (1)	-	1208.0 (1)	-	-	1208.0 (1)	-	-	1208.0 (1)

TABLE 3.12 Variation in the values of
a and n in the length-weight relation-
ship of brown trout from Avalon Peninsula

LOCATION	a			n		
	Male	Female	Mixed	Male	Female	Mixed
Topsail Pond	0.006019	0.04250	0.01946	3.1904	2.5451	2.822
Long Pond	0.02321	0.03209	0.02948	2.7871	2.6935	2.715
Western Island Pond	0.01194	0.03280	0.01636	2.9773	2.6778	2.884
Windsor Lake	0.01427	0.01155	0.00724	2.9128	2.9609	3.100

The length-weight relationships for females and males from different locations are shown in Fig. 3.13a and Fig. 3.13b. The length-weight relationships are very similar between the sexes. Larger males are heavier than females of the same length in Windsor Lake, whereas at Long Pond, the larger females are slightly heavier than males of the same length. In Topsail and Western Island Ponds, young females are heavier than young males. At a larger size, males tend to be heavier than females of the same length. Wiseman (Personal Communication) in a study of brook trout

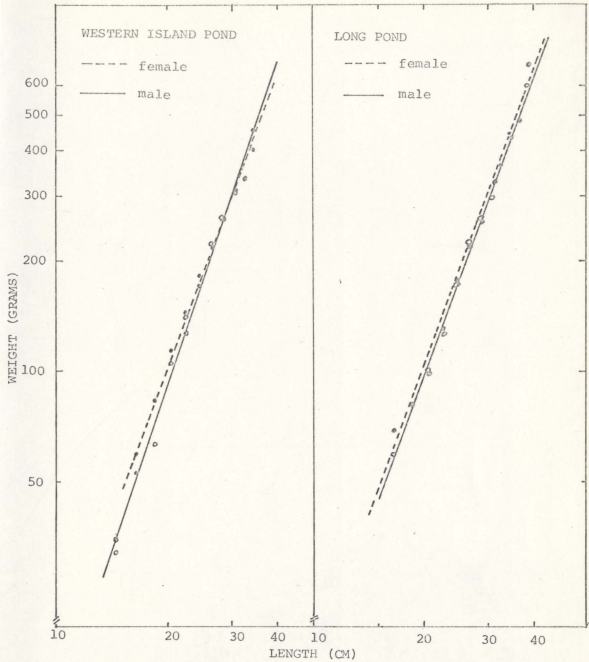


Figure 3. 13a The length-weight relationships of brown trout from Western Island Pond and Long Pond.

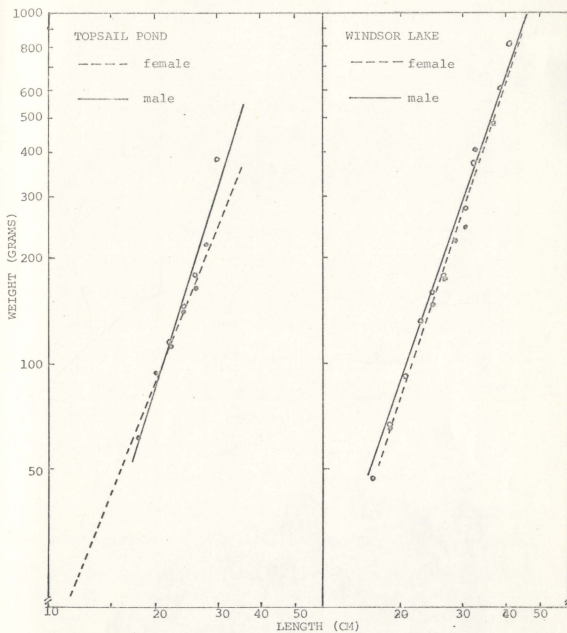


Figure 3.13b The length-weight relationships of brown trout from Topsail Pond and Windsor Lake

populations in Newfoundland found that male brook trout were heavier than females at least in the upper range of length. Because the difference between sexes in length and weight relationship was more pronounced in heavily fished areas, he regarded the differential removal of males at the upper range of lengths as one of the causes that induced the differences.

In the present study, the males were generally heavier than females and the above interpretation by Wiseman could not hold for brown trout in this area. It has been mentioned in the previous section, that the brown trout populations of these areas, with the exception of Topsail Pond are not heavily exploited. The differences between males and females might be caused by a real difference between sexes in these populations.

The length-weight relationships of sexes from different locations are shown in Fig. 3.14. Among the four study areas the growth in weight is fastest in Windsor Lake and slowest in Topsail Pond of corresponding lengths. The growth patterns of weight corresponding to length are very similar in different areas and the method of analysis of covariance is used to test if there is any difference between different areas. The results of the test are shown in Appendix, Table E.

The analysis of covariance for the length-weight relationship shows that there are significant differences

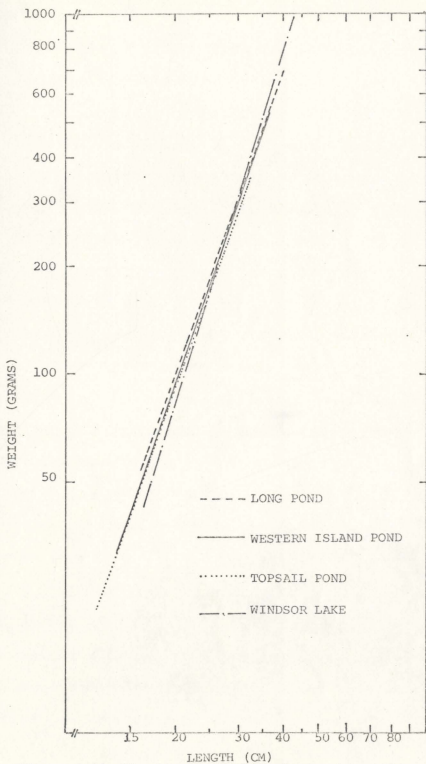


Figure 3.14 The length-weight relationships of brown trout from the four study areas.

in the slopes and intercepts for the four study areas at the 5% level. (Appendix, Table E)

In order to resolve the differences, the analysis was carried out further on the regressions of any 2 of the 4 study areas. The result of these tests are summarized in Appendix, Table F. There are no significant differences in either slopes or intercepts between samples from Windsor Lake and Topsail Pond, and between Long Pond and Topsail Pond at the 5% level. The slopes of regressions for samples from Long Pond and Western Island Pond, and from Topsail Pond and Western Island Pond are not significantly different but the intercepts of these regressions are significantly different at the 5% level. The growth in weight for corresponding lengths of fish from Western Island Pond and Windsor Lake is different at the 5% level; a similar difference occurs in fish from Long Pond and Windsor Lake.

In general, the fish from the four study areas are closely similar with respect to growth in weight for corresponding lengths. The differences which occurred in the length-weight relationships might be caused by the differences in food quantity and/or quality, available space, water qualities and other environmental factors in these study areas at different seasons of the year.

3.38 Condition Factor

The condition factor has widely been used to express the degree of well-being, fatness etc. It has also been used to indicate suitability of an environment or to compare fish from one lake or area with a general average for an entire region (Rounsefell and Everhart, 1953).

The present study, the condition factor is calculated for each fish on the basis of the formula:

$$K = \frac{W \times 100}{L^3}$$

where W is weight in grams, L is form length in centimeters and 100 is an arbitrary multiple to give K the magnitude of 1.

Table 3.13 shows the condition factor of brown trout collected during May to October from the four study areas.

TABLE 3.13 Condition factor for sex combined trout
in the four study areas
(number of fish in parentheses)

Age	LONG POND			WESTERN ISLAND POND	TOPSAIL POND	WINDSOR LAKE		
	May	October	Total	August	June	July	October	Total
2				1.225 (3)	1.460 (1)	0.99 (8)	1.100 (6)	1.053(14)
3	1.208(123)	1.078(11)	1.183(134)	1.199(17)	1.094(18)	0.996(25)	1.037(13)	1.023(38)
4	1.183(111)	1.067(16)	1.161(127)	1.175(46)	1.073(57)	1.039(32)	0.944(14)	0.973(46)
5	1.196(83)	0.963 (6)	1.179 (89)	1.103(21)	1.042(23)	1.109(17)	0.986(12)	1.037(29)
6	1.168(14)	1.070 (2)	1.150 (16)	1.041(26)	1.011 (3)	1.106 (4)	0.942 (5)	1.033 (9)
7	0.979 (1)	--	0.979 (1)	1.044 (7)	1.291 (1)	1.191 (2)	1.057 (5)	1.152 (7)
8	1.012 (1)	1.160 (1)	1.086 (2)					
GRAND TOTAL	1.124	1.1067	1.170	1.131	1.161	1.059	0.998	1.021

The condition factors for each area are very similar, with Windsor Lake trout having the lowest K. The K values ranged from 1.170 in Long Pond to 1.021 in Windsor Lake.

The values of K for each age group in each area show some variation. There is a tendency for the younger fish to attain higher K values especially the 2 year old fish in Western Island Pond and Topsail Pond. The selection introduced by the gill-net for the fatter and fast growing fish may have accounted for the higher condition factor found in the young fish. There is a similar trend for the fish in Western Island Pond, Long Pond and Topsail Pond where the younger fish are of a better condition. As the fish grow in age, the K values decrease except for one 7 year old fish in Topsail Pond which had a high value of K but this may not be representative of the 7 year old fish in that water due to the small number. The decrease in condition factor with increasing age has also been reported by Frost and Smyly (1952) in brown trout of British fishpond. It seems probable that these waters although rich in food may be unable to supply enough larger food organisms for a faster growth of larger fish. Klak (1940) reported that in Big Spring Creek, Virginia, the smaller rainbow trout grow better than the larger fish and he concluded that small streams, although rich in food, are unable to supply the

normal food requirements of larger fish. The condition factor of fish in Windsor Lake increase as the fish grow older. The K values of fish caught in July increases gradually from 0.99 for a 2 year old to 1.191 for a 7 year old. In Windsor Lake, the gradual increase in condition factor with age may indicate the larger fish could obtain enough larger food organisms to meet their basic requirements as well as some food for growth.

In Long Pond, the specimens obtained in October have lower K values for different age groups than the specimens obtained in May. The K values of Windsor Lake trout for the September/October sample also have a lower condition factor than the fish caught in July. The decrease of mean condition factor in September/October fish in Windsor Lake is certainly not due to the presence of poorly conditioned spent fish. The majority of the sample were in pre-spawning condition and some were immature or unripe fish. There was a general decline in conditions in October, unassociated with sexual maturity and spawning in most of the fish. The seasonal decline in condition of the fish before spawning was observed for brown trout by Cooper (1953), Went and Frost (1942), and for the lake whitefish by Van Ooston and Hile (1949).

The condition factor of brown trout varied with time of collection. Since the samples were collected at different times of the summer, no valid comparison could

be made for fish from different areas. In general, the mean values of K for all fish examined indicate that trout in these areas are, irrespective of age, in good condition.

3.39 Discussion

From the analysis of the data of age, length and weight, it is obvious that the growth of brown trout shows considerable differences in the four study areas. It has been shown that the Windsor Lake trout are always greater in length and weight than the fish from the other three areas, while the fish from Topsail Pond show a slower growth than the others.

Swynnerton and Worthington (1939), in a study of the growth of brown trout in British waters, stated that the growth of a fish population is influenced by the chemical contents of the water, the food supply, the predators, the population density, or a combination of these. Southern (1932) found that brown trout grew more rapidly in alkaline than in acid waters. But Wingfield (1940) found that the amount of dissolved calcium, which is more abundant in alkaline water than in acid water, is not the factor responsible for the differences in trout growth in hard and soft waters. He suggested that

"such differences may be affected not by differences in the concentration of any one specific ion, but by departures from the optimum ionic balance brought about by variations in the relative concentration of any of the ions present."

Swynnerton and Worthington (1939) and Campbell (1961) believed that growth rate of the trout they studied depended more on the density of the trout population and the food supply than on any direct influence of the chemical composition of the water. On the basis of pH readings, most of the present study areas could be classified as acid waters. The growth rate of brown trout among these areas varied, however; some of the fish did not grow slower than fish in alkaline water in England (Table 3.14). This might indicate that the growth of fish may be influenced more strongly by population pressure and food supply rather than by the acidity of the water.

TABLE 3.14 The growth of brown trout in acid and alkaline waters from different areas

AREA	pH	Length (in cm) at end of winters					
		1	2	3	4	5	6
¹ Loch Lanish	8.7	8.7	21.2	36.1	43.1		
¹ Lochan Dain	7.7	4.2	11.7	18.9	23.6		
¹ Fincastle	8.6	6.5	15.6	22.2	24.2		
¹ Unnamed Loch	5.7	8.6	20.2	30.6	39.5		
¹ Glutt Loch	4.9	6.3	13.7	20.8	33.6		
² Lough Derg	8.4 -						
	7.8	6.9	16.5	29.1	39.3		
² Lough							
Atorick	6.8	5.8	13.4	17.5	19.7		
Topsail Pond	6.4	6.5	10.7	17.3	20.9		
Western Island Pond	6.4	9.2	12.4	18.6	23.4		
Long Pond	6.9	8.5	12.9	18.2	22.5		
Windsor Lake	6.4	9.8	17.4	24.6	29.7		

1 After Campbell (1961)

2 After Southern (1932)

Some workers have related the growth of fish to the conductivity, alkalinity and total hardness of the water (McFadden et al, 1962; Scherer, 1963; Beyerle, 1959; Moyle, 1956, etc.). McFadden et al (1962) demonstrated a positive correlation between the growth rate and specific conductance of the water. However, Scherer (1963) pointed out that the effect of water chemical composition on fish growth may be more indirect rather than direct. Long Pond has the highest conductivity and total hardness readings among the four areas in the present study. Although Long Pond trout showed faster growth than fish in Western Island Pond and Topsail Pond, the growth rate was much slower than in Windsor Lake. Factors other than water composition, such as food and space, eventually have more influence on fish growth in these waters. Nevertheless, the water composition probably acts on fish growth indirectly by controlling food supply.

The food supply, either in quantity or quality or both, is probably one of the main reasons for the differences in growth of trout in the four study areas. Trout require a certain amount of food to provide for basal metabolism and to provide energy for their activity (Brown, 1957). They can gain weight only when they consume more food than is necessary to satisfy these requirements. Frost and Smyly (1952) reported poor growth of trout in waters depleted in food and good growth in waters with an abundance of food.

Stomach contents of trout revealed the presence of only small food organisms in Topsail Pond. There were also no large food organisms present in Western Island Pond, and yet the fish grow faster and reach a larger size than trout from Topsail Pond. This may be due to the fact that Western Island Pond is much shallower and has more aquatic vegetation than Topsail, thus there may be a greater supply of food in Western Island Pond resulting in a faster rate of growth.

The fish of Western Island Pond and Long Pond grow at more or less the same rate early in life. However, the Long Pond trout have a faster growth rate and reach a bigger size after 5 years of age. If it is assumed that big trout need more of the larger foods than smaller trout, the absence of larger organisms may limit the growth of larger fish. In Long Pond, the larger food organisms such as snails and leeches are apparently abundant in number and species as indicated by stomach analysis, and there also are forage fish present. Thus the fish in Long Pond would not appear to suffer from a shortage of larger food organisms. The quantity and quality of large food organisms are especially conducive to good growth in the older Long Pond trout.

Windsor Lake trout have a different pattern of growth from the other study populations. They grow faster than the pond trout from the 1 to 7 year old stage. As

indicated by the number of empty stomachs in the sample, the amount of food present in Windsor Lake might not be very large. Nonetheless, large food organisms such as dragonfly nymphs and adult damselflies as well as sticklebacks are numerous. It is well known that condition depends on the amount of food intake. The low values of condition for the younger Windsor Lake trout as compared to the larger ones is probably caused by a low availability of small food organisms for young fish, and the availability of forage fish for older fish.

Alm (1939) found that trout are usually bigger in large than in small lakes. This was also found to be the case in the present study. The Windsor Lake trout grow faster and reach a bigger size than trout in the three other ponds. Wiseman (personal communication) also found that the speckled trout in large lakes (over 1000 acres) in Newfoundland grow faster than fish from small lakes or ponds (less than 1000 acres). Ball et al (1960) found that lakes offer better conditions for trout growth than streams. As the young of Windsor Lake trout always live in the lake, this may explain the better growth in these fish as compared to young pond fish which inhabit streams. The living space might influence growth either via its effects on competition for food or more directly by its influence on appetite and efficiency of utilization of

ingested food (Brown, 1946). Lake (1957) in a survey of trout populations and habitats in New South Wales, found that acid streams provided good spawning conditions and that trout populations are possibly so dense that poor growth occurs in the first year. The fact that the Long Pond trout have sufficient large food organisms as well as forage fish but do not show better growth than fish in Western Island Pond is probably due to the large population present in this pond. That Long Pond contains a large population of trout was shown by the fact that one night's gill-netting, on the same scale as that carried out in the other three areas, produced 333 trout, while at the most 1/6 of this number was caught in other areas in one night's gill-netting.

Went and Frost (1942) who compared the growth of brown trout in acid and alkaline water by specific growth rates, stated that the size attained during the first year (0-1) determines the subsequent and final sizes of the trout. When the specific growth rates of the four areas are examined, similar results were also found in the growth of brown trout in the four areas. The specific growth rate was highest during the first year in Windsor Lake trout, followed by trout from Western Island Pond, Long Pond and Topsail Pond respectively. The growth rate of fish older than 3 years old is nearly the same in all waters. Trout in Windsor Lake have the fastest growth rate and reach

the largest size followed by those in Long Pond, Western Island Pond and Topsail Pond. It seems, therefore, that factors responsible for the slower growth in Topsail and other ponds must operate from the beginning of life. Of course, good first year growth is associated with the food as well as available space.

Sexual maturation in fishes is generally accompanied by a reduction in growth rate (Page and Veillet, 1938). This is because the growth and development of gonads demand a large supply of nutrients with the result that only a small part of the food can be utilized for increased growth of the body. However, Alm (1959) found that

"in fishes under natural conditions the inhibiting influence of maturity on continued growth is not as great as has been shown in other cases. The factors, both inner and outer, which regulate the growing ability are stronger than the growth-inhibiting sexual hormones."

In these areas most of the fish mature at the end of the 4th year. Fish in Windsor Lake mature earlier than the fish in other areas, but do not exhibit poorer growth than fish from other ponds. Thus, maturity does not explain the marked differences between the growth of fish in Windsor Lake as compared with that in fish from the three ponds.

In general, the differences in growth between fish from the three ponds and Windsor Lake can be attributed to a combination of factors such as the abundance of food, available space, the growth reached at 1 year old, water compositions and predator-prey relationships, etc. Any emphasis on a single factor might result in the overlooking of other factors which also exert an influence on the growth of fish.

CHAPTER IV

SEX AND REPRODUCTION OF BROWN TROUT

4.1 Introduction

In a study of fish populations, a knowledge of the reproduction of the species is of great importance. There is very little information available on the reproduction of brown trout, particularly in North America.

Since the brown trout is a naturalized species in this area, it is of considerable importance to have detailed information on the reproductive ability of such populations in the new environment and to compare these populations with previous reports on the reproduction of the species from other areas (Brown & Kamp, 1942; Allen, 1951; Cooper, 1953; Nicholls, 1958; McFadden, Cooper and Anderson, 1965).

The fish in this study were collected from Long Pond, Topsail and Western Island Ponds and Windsor Lake in the summer and fall of 1967. Only those specimens from Long Pond, Windsor Lake and Western Island Pond were used for fecundity study.

4.2 Methods

4.21 Sex Ratio

External sexual dimorphism is evident in the mature brown trout immediately prior to the spawning season. At this time the hooked jaw, rounded caudal fin and bright color of the males were used in separating them from females. However, as only a small portion of the samples were collected in this season, it was necessary to dissect out the gonads and examine them macroscopically in order to accurately sex them and determine the stage of maturity of each trout.

The sex ratio for each population was determined for each age group as a percentage of the females in the population. The observed sex ratios were tested against the theoretical 1:1 ratio by the adjusted chi-square distribution (Snedecor, 1956).

4.22 Maturation

The maturity of sexually mature fish could be determined easily by the presence of well developed eggs or testes. However, fish maturing for the first time were difficult to distinguish from mature resting fish. In an immature male, the testes are white, narrow or thread-like and are of uniform width for the greater part of its length, becoming very thin at the posterior end. The larger, highly vascularized testes are present in maturing males. In ripe fish the milt gives the testes a creamy-white colour. Spent

or resting males have shrunken pellucid and blood-shot testes (Brown and Frost, 1967).

Female trout were designated as immature if the ovaries were less than one-quarter the length of the body cavity, orange or yellow in colour, eggs small with a diameter of about 1 mm, and the follicles tightly packed together and of uniform size. The ovaries of a trout maturing for the first time, or in the resting stage, are similar in appearance to those of immature fish, but are longer (almost half the length of the body cavity) and wider.

The percentage of mature fish was calculated and compared by categories of age, size and sex.

4.23 Fecundity

Fecundity has always been regarded as the total number of ripe eggs present in the ovaries prior to spawning. Vladykov (1956) showed that the number of viable eggs contained in a brook trout is reduced by reabsorption during the maturation process. The rate of reabsorption decreases as the size of the eggs increase and is negligible after the eggs are 3.5 mm in diameter. This critical diameter would not necessarily be the same in other species of trout but it serves to emphasize the point that fecundity will be overestimated for egg counts from fish collected too early in the maturation process. No specimens collected earlier

than August 15 were used and fully ripe fish with no more than 20 free eggs in the coelom were accepted. The specimens collected from Western Island Pond in mid-August contained eggs ranging from 2.5 - 3.6 mm in diameter^{which} were included in the present data for comparison.

The ovaries of each fish from Long Pond, Windsor Lake and Western Island Pond were carefully removed, weighed to the nearest gram and then preserved in 10% formalin. The number of eggs contained in each female was determined by placing 30 mature eggs in a small measuring trough and measuring to the nearest millimeter. The mean egg diameter was calculated from the total measurement of the entire sample of 30.

In comparing the present data with data from other sources, relating the size of fish to the number of mature eggs produced by each individual, the total length was used instead of the fork length which was used in the growth study.

In relating the gonad weight to the number of eggs, both ovaries were combined. The sample from Long Pond was collected at one time, thus eliminating any error arising from the time factor.

Regression analysis was performed to obtain equations useful in predicting the numbers of eggs from fish length, fish weight, ovary weight and age. Statistical methods follow Croxton and Cowden (1956).

4.3 Spawning Time and Spawning Habits

The brown trout is a fall spawner. They usually spawn in fast flowing streams on a gravel nest or redd in the day-time between late October and early February (Fenderson, 1954). Cooper (1953) reported that the brown trout spawn from November 4 until November 25 in Michigan, but he believed that the actual spawning period was longer. Brown trout in Cowichan River, B.C., spawned from October 15 to November 16 (Carl, 1938). McFadden et al (1965) obtained their specimens for fecundity study between September 4 and December 20. Therefore, it seems reasonable to consider that brown trout spawn between September and the end of December or early January in Pennsylvania waters.

In British waters, brown trout may spawn during the period between October and February. Their normal spawning time is November and December, but there are local variations. For example, the chief spawning month is February in upper Avon, Wiltshire and Driffield Beck, Yorkshire, while in River Derwent, twenty miles away from Driffield Beck, spawning takes place in November and December (Frost and Brown, 1967). However, Stuart (1957) reported that spawning is completed by the end of November in Scottish waters.

In Horokiwi, New Zealand, brown trout spawn in all parts of the stream in June and spawning reaches a maximum in early July.

Kellett (MS., 1965) studied the brown trout in Long Pond, Newfoundland, and reported that they begin to spawn in the first week of October, reaching a peak in the first week of November, with some spawners still available on the 14th of November. In 1967, some observations were made on the spawning activity of brown trout in the streams leaving Long Pond. On the 10th of October, some spawners were found in the outlet of the pond. After 22nd of October, more spawners and some new redds were found, and the spawning reached a peak during the first week of November. In 1968, a pair of spawners were obtained on the 27th of November and they spawned in the aquarium five days after capture. This probably implies that their spawning period extends into December. In Middle Pond, which is about twenty miles from St. John's, trout spawn between 20th of October and the end of November, the peak in 1967 being reached between the 26th and 27th of October (Wiseman, personal communication).

Spawning usually takes place in running water and trout living in lakes or ponds migrate and spawn in streams. The spawning places are usually in fairly rapid flowing water of moderate depth but not in turbulent riffles. Stuart (1953) found that trout select gravels composed of stones up to 3 inches in diameter which contain a large porportion of smaller material which consolidates the mass while leaving it permeable to the water. When rapid spring

streams are not available, the fish are able to spawn in lakes or ponds. Eddy and Surber (1960) found that brown trout spawned in Lake Superior on rocky reefs close to shore. In Windsor Lake, there are no streams deep enough for the trout to spawn in and the fish have been found spawning on the shallow rocky shore of the lake. It seems, therefore, reasonable to conclude that the fish are able to spawn even where there is no suitable gravel available.

4.4 Observation of spawning activity in the aquarium.

Jones and Ball (1954) observed the spawning behaviour of brown trout in specially constructed tanks. They considered that despite the artificial conditions, the spawning behaviour they observed was normal. During the present study an opportunity had been obtained to observe the following spawning activity in an aquarium between November and December of 1967.

A pair of pre-spawning male and female brown trout were obtained by beach seine on November 27 from Long Pond. They were kept in an aquarium 48 inches long, 16 inches wide and 16 inches deep. Its bottom, sides and back were of fiberglass and the front was covered with plate glass. The bottom was covered with a layer of 1 to 2 inches of 0.5 to 1.0 cm gravel mixed with some 4 to 10 cm gravel. The depth of the water was 10 inches and the aquarium was aeriated by an air stone at each end. The water temperature was maintained between 10-13° C by a thermo-regulator. The

water was not circulated except for that caused by aeration.

When the fish were first introduced into the aquarium on November 27, they remained at one corner and did not feed until November 28. The female fish started digging a depression in the gravel at the left side of the tank on November 29. She repeated the digging at long intervals (over 15 minutes) during the first 24 hours. The digging was carried on continuously during the day and none were observed at night despite the fact that the aquarium was continuously lit. The intervals between diggings were 5 to 10 minutes on the third day (December 1). The male started short sequences of rapid quivers on November 29. He quivered either alongside the female or at some distance from her. The orientation of the male during each sequence was either parallel to or facing the female.

The female continued her digging even after the depression reached the bottom of the tank. From time to time she dropped down into the redd and tested it with her anal fin. The male attended the female while she was in the redd, swam alongside and quivered his body against her with increasing frequency as time passed. On December 2, 8 eggs were found but none were in the redd. Spawning occurred between 1 pm and 1:30 pm on December 3. About 138 eggs were laid 1 to 1½ feet away from the redd. It is of interest to note that the female didn't attempt to cover them (Fig. 4.2). This behaviour is completely different



Figure 4.1 A 25.2 cm brown trout (3+) with fully developed golden ova.



Figure 4.2 Picture showing eggs on the floor of an aquarium without cover.

from observations reported by Greeley(1932) on brown trout, Jones and King (1949, 1950) on Atlantic Salmon, Curtis (1949) on steelhead, Stuart (1953) on brown trout and Jones and Ball (1954) on brown trout. These authors observed that after spawning female salmonids covered the eggs with gravel.

After the first spawning, the fish swam actively and fed on the pieces of beef liver which were put in the aquarium daily. By late afternoon of December 3, the male resumed his quivers against the female and she resumed digging on the original redd. The female fish spawned another 156 eggs between 12:20 -12:50 pm on December 4. These eggs were laid at more or less the same place as before and were not covered.

After this spawning both fish swam actively and ate. It was observed on December 5 that some of the eggs were eaten by the spawners. As this suggested that the food supply may have been insufficient, more pieces of beef liver were put in. It was surprising to find out that most of the eggs had been eaten and that some of the pieces of liver were uneaten by the morning of December 7. It has been reported that the other fish eat their eggs (Curtis, 1949) but this has not previously been reported in salmonoids. It is unknown whether this act was caused by the long confinement of the spawners or was induced by other factors.

The male brown trout died after jumping out of the aquarium on December 7. The female fish remained under the cooler of the thermo-regulator and did not feed until December 13.

On the morning of December 13, another 89 eggs were found in the tank. These were laid without the presence of the male and without any evidence of digging. These eggs were either spawned during the night of December 12 or the early morning of December 13. During this interval the light was continuously on.

Stuart (1953) observing the reproduction of brown trout stated that

"before the release of the ova and spermatozoa takes place, and despite the rising level of internal stimulation suitable gravel must be present. Males have to be found, the territory chosen is to be guarded, the redds have to be excavated and the final release of ova will only take place in the presence of the male."

The present observation do not agree with this statement. The present study indicates that female brown trout may spawn in a place with no suitable gravel and may leave eggs uncovered. It is also apparent that female brown will release ova in the absence of a male and without digging a redd.

Due to the weather as well as the fact that the natural spawning period was more or less over when these observations were made, no specimens were available for

further observation. As the present observations were scanty, no further discussion of their significance will be made. Nevertheless, the differences between the present observations and information in the literature may be of interest to those working on the spawning behaviour of salmonids.

4.5 Results

4.51 Sex Ratio

Knowledge of the sex ratio of a fish population is important in estimating the numbers of potential spawning females and in determining whether a mortality differential exists between the sexes (McFadden et al, 1962).

Consistent deviations of the sex ratio from the ideal 1:1 ratio have been reported frequently for various species of fish. The most common case involves a progressive decrease in the proportion of males in older age groups.

Runnstrom (1959) reported that the sex ratio of the spawning brown trout in Lake Rensjon was close to 1:1. However, Gustafson (1951) found that females constituted 70% of all ascending spawning fishes from Damman, and a predominance of females has also been found in the sea-trout in the river Ava by Alm (1949). The sex ratio of 4443 individuals of Salmo trutta taken during the spawning season in Switzerland was given by Surbeck (1914) as 80.2 percent male, and 19.8 percent female.

In the streams of Pennsylvannia, essential 50:50 sex ratios were found in the age groups 0 to VI in both hard and soft water streams (McFadden et al, 1962).

The total sex ratio of brown trout in the four areas studied is 53 percent females, and no significant difference exists from the hypothetical ratio of 50 percent females at 0.05 probability level (Table 4.1). However, a preponderance of males occurred in the Windsor Lake population (65% male; $p < 0.005$). There is no reason to believe that the extremely unequal sex ratio of males could be the result of sampling in areas where males were more likely to be found. A breakdown of the sample from Windsor Lake by period of sampling showed a significant difference between males and females in the sample collected between the 12th and 19th of July. The sex ratio was 28:61 in favour of males (X^2 : 12.23). However, there was no significant difference at the 0.05 significance level between sexes of 55 fish collected between September 27 and October 4 (40%; X^2 : 2.2). This indicates that sexual segregation may exist in the brown trout population in Windsor Lake during the feeding period but not at spawning time.

Since Windsor Lake is a relatively unexploited area, another explanation, besides the aggregation of males in the fishing area, might be that the natural mortality is higher in the females.

TABLE 4.1 Sex ratio of brown trout from four waters given as the percentage of both sexes (Probability values on the hypothesis that the observed sex ratios were no different from the theoretical 1:1 ratio were based on the adjusted chi-square distribution following Snedecor(1956))

AREA	Total Sample	No. of Males	% Mature	% of		P
				No. of mature female	female	
Long Pond	369	144	39.0	225	61.0	$P > 0.025$
Topsail Pond	103	50	48.5	53	51.5	> 0.75
Western Island Pond	120	55	45.8	65	54.2	> 0.50
Windsor Lake	144	94	65.3	50	34.7*	< 0.005
Total	736	343	46.6	393	53.4	> 0.05

* significantly different between the sex-ratio from 1:1 ratio

When the sex ratio is broken down by age groups within the four areas, it is interesting to note that there was no significant difference from the 50% females at 0.01 level of significance in most of the age groups except age VII, where the males were more abundant (Table 4.2 and Fig. 4.3).

The sex-ratio for all trout collected was 393:343 in favour of females (53.4%; $p > 0.05$). It is therefore concluded that the sex ratio of 1:1 holds for brown trout population in this area.

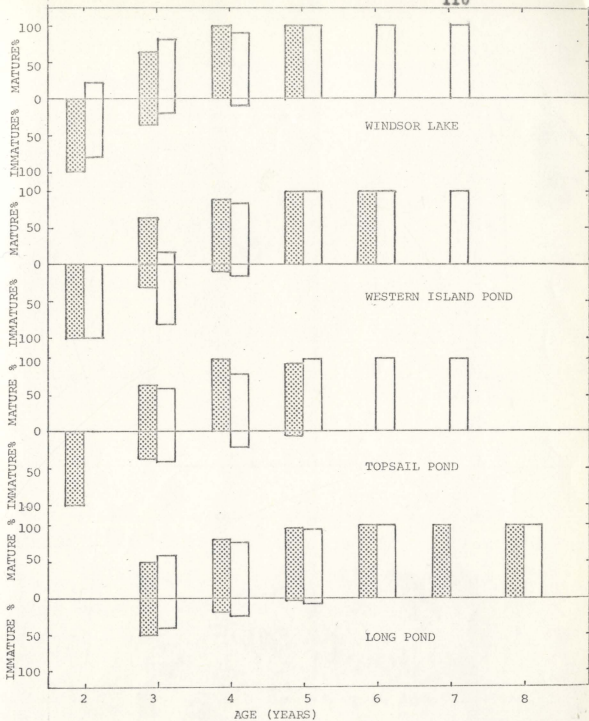


Figure 4.3. Percentage of mature and immature brown trout by age class in samples from four study areas (stippled female; white male).

TABLE 4.2 Sex ratios of brown trout by age groups for various localities combined

Sex	II+	III+	IV+	V+	VI+	VII+	VIII+	Total
Male	10	95	133	67	34	14	1	343
Female	8	112	143	96	31	1	2	393
% Female	44.4	54.1	51.8	58.9	47.7	6.7	66.6	53.
X ² Value	0.222	1.396	.3622	5.1594	.1384	11.36*	.3332	3.39
P	P>.5	P>.1	P>.5	P>.01	P>.5	P<.005	P>.5	P>.0

* significantly different between the sex-ratio from 1:1 ratio

4.52 Sexual Maturity

Table 4.3 shows the data concerning the maturity and age of fish from four areas in the 1967 collection. The data of age groups II, II and IV were broken down into component size groups to indicate the importance of fish size on the maturation of a fish population.

In most cases, the brown trout were mature by the end of the 5th year of life (4+) although many males and females matured at the 4th year and some males matured even during their third year of life (2+). but No females were found mature at 2 years old.

Alm (1959) found very few mature females in age group II in Swedish waters. The slower growing small river trout (Salmo trutta fario) matured in their 4th to 5th year

Table 4.3. The relationship of size and age to sexual maturity in brown trout from the four study areas on Avalon Peninsula, Newfoundland. (Total number of individuals(T); number of mature fish (M)).

Age group	Total length(cm)	Female										Male									
		Long P.		Topsail P.		Western Island		Windsor P. L.		Total streams		Long P.		Topsail P.		Western Island		Windsor P. L.		Total streams	
		T	M	T	M	T	M	T	M	T	M	T	M	T	M	T	M	T	M	T	M
II	11.0 - 12.9			1	0																
	14.0 - 15.9									1	0					1	0			1	0
	16.0 - 17.9					2	0			2	0							1	0	1	0
	18.0 - 19.9							2	0	2	0					4	1	4	1	4	25
	20.0 - 21.9							2	0	2	0					3	1	3	1	3	33
	22.0 - 23.9							1	0	1	0					1	0	1	0	1	0
	Total			1	0	2	0	5	0	8	0					1	0	9	2	10	20
III	16.0 - 17.9											1	0							1	0
	18.0 - 19.9	24	11	1	0	1	0			26	46.1	12	5			1	0			13	38.5
	20.0 - 21.9	33	16	4	2					37	67.5	33	20	2	1	1	0			36	58.3
	22.0 - 23.9	17	9	2	2	3	1	1	0	23	56.5	8	7	8	5	1	0	3	2	20	70.0
	24.0 - 25.9	2	2	1	1	4	3	9	6	16	81.2	3	2			2	1	4	3	9	66.7
	26.0 - 27.9					3	3	3	2	6	83.3	1	1			1	0	10	8	12	75.0
	28.0 - 29.9							2	1	2	50.0							4	4	4	100.0
	30.0 - 31.9							2	2	2	100.0										
	Total	76	38	8	5	11	7	17	11	112	54.5	58	35	10	6	6	1	21	17	95	62.1
IV	18.0 - 19.9	1	1	1	1	3	2			5	80.0	2	0							2	0
	20.0 - 21.9	14	10	4	4	10	9			28	82.1	12	8	5	3					17	64.7
	22.0 - 23.9	21	16	12	12	7	7			40	87.5	16	14	11	7					27	77.7
	24.0 - 25.9	25	19	10	10	1	1			36	83.3	8	6	11	11	4	4			23	91.3
	26.0 - 27.9	15	15	1	1			1	1	17	100.0	10	8	2	2	11	8	2	1	25	76.0
	28.0 - 29.9	1	1					9	9	10	100.0	2	2			10	9	13	11	25	88.0
	30.0 - 31.9							7	7	7	100.0							9	9	9	100.0
	32.0 - 33.9																	5	5	5	100.0
V	Total	77	62	28	28	21	19	17	17	143	88.1	50	38	29	23	25	21	29	26	133	81.2
VI	57	55	16	15	13	13		10	10	96	96.8	32	30	7	7	8	8	20	20	67	97.0
	13	13			18	18				31	100.0	3	3	3	3	8	8	9	9	34	100.0
VII	1	1						1	1	2	100.0			1	1	7	7	6	6	14	100.0
	1	1								1	100.0	1	1							1	100.0

of life and practically all males reached maturity at five years. The faster growing big brown trout (*S. trutta ferox*) which occupied large lakes attained sexual maturity for the first time at VI to VIII years (Alm, 1959). In Straffan and Ballysmattan, Ireland,, a small proportion of males were mature in their 2nd year, but most of the males and females matured in their 4th year (Frost, 1942), a case very similar to the finding in the present study. However, in Pennsylvania, fish start maturing at the end of the first year and are completely mature at the age of three (McFadden et al, 1965). Similarly, all the two year olds collected by Allen (1951) were mature.

Within each age in each area, there was a tendency for a higher percentage of the larger fish to be mature. This emphasizes the importance of growth rate in determining the reproductive capacity of a population. Alm also reported that in specimens of the same age maturity is reached earlier by larger specimens than by smaller ones.

In general, the males mature at an earlier age than females. Although males show only a very slightly higher percentage of mature individuals in the present data, the tendency of males to mature earlier does exist.

4.53 Frequency of Spawning

Vladykov (1956) found that brook trout of either sex could remain from one to several years in stage 0 or 1 (egg diameter smaller than 1 mm or around 1 mm). As

soon as an individual develops eggs of 2 mm in diameter, it will definitely spawn the same autumn. This could also be the case in brown trout. Of course, there are fish which had ova that reached 1 mm in diameter but didn't spawn in the fall. In Long Pond and Windsor Lake, the youngest trout of either sex were ripe at 24 cm in total length. The samples collected in the spawning period are shown in Table 4.4. This table shows that some fish of large size do not spawn regularly each year. Stuart (1953) reported that considerable numbers of trout do not spawn annually in some of the British waters and that not all trout are biennial spawners. This is also true for the fish from this area. It is demonstrated by some maturing female fish which retain few non-extruded ova in the body cavity from the last spawning.

4.54 Fecundity

Most investigators define the fecundity of a fish as the number of ripening eggs found in the female just prior to spawning. McFadden et al (1965) regarded the number of eggs produced by a brown trout to be dependent to a great extent upon the size of the fish and they defined fecundity either as the weight, or the number, of eggs produced by a female. The usual definition is adopted in the present study.

Table 4.4. Relationship between ripe and immature* specimens of Salmo trutta, taken between 29th September and 6th October 1967 in Windsor Lake and Long Pond

Total length (cm)	Windsor Lake						Long Pond					
	No. of females			No of males			No of females			No of males		
	Ripe	Imm.*	Total	Ripe	Imm.	Total	Ripe	Imm.	Total	Ripe	Imm.	Total
18.0 - 19.9	0	1	1	0	2	2						
20.0 - 21.9	0	2	2	0	0	0						
22.0 - 23.9	1	0	1	1	1	2	1	5	6	0	1	1
24.0 - 25.9	0	0	0	0	0	0	4	7	11	2	3	5
26.0 - 27.9	1	2	3	1	6	7	2	0	2	0	3	3
28.0 - 29.9	3	2	5	1	2	3	0	1	1	0	1	1
30.0 - 31.9	3	1	4	0	1	1	0	0	0	3	0	3
32.0 - 33.9	0	0	0	4	1	5	1	0	1			
34.0 - 35.9	3	1	4	4	0	4	1	0	1			
36.0 - 37.9	1	0	1	2	0	2	0	0	0			
38.0 - 39.9	0	0	0	1	0	1	0	0	0			
40.0 - 41.9	0	0	0	3	0	3	1	0	1			
42.0 - 43.9	0	0	0	1	0	1						
44.0 - 45.9	1	0	1	1	0	1						
46.0 - 47.9	0	0	0	1	0	1						
Grand total:	12	10	22	20	13	33	10	13	23	5	8	13
Percentage	54.5	45.5	100	61	39	100	43.5	56.5	100	38.5	61.5	100

* Imm. = immature.

* All those specimens with immature gonads caught between 29th September and 6th October were grouped into the immature group irrespective of their sexual maturity.

The left ovary is generally longer and heavier than the right one and usually contains more eggs. Brown and Kamp's (1942) data explain the disproportion in the size of the two ovaries as follows:

"In the brown trout, the posterior of the intestine usually bends strongly to the right, thus crowding the right ovary at its caudal end. The length of the ovary is inversely proportional to the degree of crowding. However, the ovary is not always the longer. One fish was observed to have longer right ovary and it was interesting to note that this specimen had an intestine which bent to the left instead of the right. In one or two fish the ovaries were of approximately equal length, with the intestine bending neither to the right nor the left."

In the combined data for Long Pond and Windsor Lake (20 pre-spawning females), 14 had a larger left ovary, 5 had a larger right ovary and only 1 had ovaries of approximately equal size. Eight fish out of nine from Long Pond had a larger left ovary. However, the sample from Long Pond is too small to indicate that the population has a consistently larger left ovary. Chi-square tests on the combined data of Long Pond and Windsor Lake substantiated the hypothesis that differences in egg number existed between left and right ovaries. It was decided, therefore, to use the total number of mature ova in a female to explore the relation between fecundity and size, and weight, of fish in the hope of avoiding the complications arising from the difference in numbers of ripe eggs in the left and right ovaries.

4.55 Fecundity and Length

The number of eggs produced by a brown trout depends to a great extent upon the size of the fish. As reported by McFadden (1962) and other authors on salmonoids, there is always a positive correlation between the length of females and number of eggs produced. The relationship between egg content and fish length has been expressed as

$$F = a L^b$$

where F is the number of mature eggs contained in a fish, L is the total length of fish in centimeter, a and b are constant and exponent derived from F and L variables. When a logarithmic transformation is applied to the two variables, the formula is expressed as

$$\log F = \log a + b \log L$$

The resulting fecundity-length curve for the data is shown in Fig. 4.4. The regression coefficient b and intercept values $\log a$ for the separate and combined data are given in Table 4.5 together with the corresponding correlation coefficients r. The relation between fecundity and fish length is curvilinear. Allen (1951) and Nicholls (1957) also showed curvilinear relationship between fecundity and length for brown trout from both New Zealand and Tasmania. This relation indicates that fecundity of brown trout in this area increases at ^{the} rate of 2.1845 power of the total length. However, there is a poor relationship between fecundity and fish length of Western Island Pond fish. As

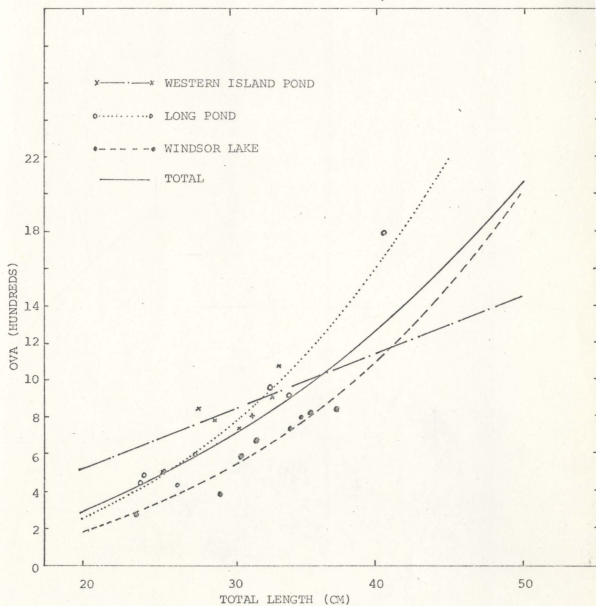


Figure 4.4 Relationships between mean number of eggs and the total length of fish from the three study areas.

Table 4.5. Relationship between fecundity and total length of brown trout from Long Pond, Western Island Pond and Windsor Lake . (Ova from mature females with ovaries still intact. Values for constants determined empirically from relationship $F = a L^n$, where F = number of ova, L = total length of female and r = correlation coefficients of F and L.)

	Collection date	Number of females	Mean ovum diameter (mm)	log a	b	r	Calculated number of eggs for females of	
							25 cm	35 cm
Long Pond	6th Oct., 1967	9	4.2	-1.1713	2.7277	0.97	438	1097
Western Island Pond	16th Aug., 1967	14	3.0	1.2474	1.1298	0.46	670	981
Windsor Lake	29th Sept., 1967	11	4.4	-1.3244	2.7245	0.95	304	760
	to 4th Oct., 1967							
Total		34		-0.3998	2.1845	0.86	451	941

indicated by the correlation coefficients, only 21 percent ($r = 0.47$) of the variation in number of eggs is associated with change in length of the fish. In Western Island Pond, the low correlation between the fecundity and fish length ^{being} may be due to the sample /collected too early and some of the ova may become atretic during the period between August and October. Vladykov showed an atresia rate of more than 50% in most wild brook trout populations. Wydoski et al (1965) also showed a decrease in the number of ova in brown trout from August to October.

However, contradictory results were reported by Brown and Kamp (1942). They found no marked correlation between the size and weight of fish and the number of eggs produced. Their data show a negative correlation between egg numbers and length. Nevertheless, they made no explanation of their negatively correlated data and their results have not been substantiated by other workers.

Among the three study areas, fish from Long Pond have the highest fecundity and fish from Windsor Lake have the lowest fecundity. The fertility of the water and abundance of food may be the major factors influencing the fecundity.

When all data are combined, there is a fairly good correlation between fecundity and fish length ($r = 0.86$). Owing to the small sample from each station,

no further test on the difference between the fecundity of different locations was attempted.

Bagenal (1966) in discussing fish fecundity stated that

"the actual value of the exponent b has been calculated for a variety of fish and although it has been found to range from 2.34 to 5.28, the most usual values are a little above 3".

Pope et al (1961) in analysing the fecundity of the Atlantic Salmon (Salmo salar) found that the regression coefficient varied from 1.8103 for ones from the River Canon to 3.2035 for those from the River Carry. The pooled estimates for their six rivers was 2.3345 ± 0.1003 .

McFadden et al (1965) found that the number of eggs of brown trout increased with size at the same rate in different Pennsylvanian streams ($b = 2.44$).

The regression coefficients for the present study vary from 1.1298 to 2.7277 (Table 4.5). The number of eggs of Windsor Lake fish increases with size at more or less the same rate as those from Long Pond except at a lower level. Fig. 4.5 shows the egg number and fish length relationship for brown trout from seven different areas.

Figure 4.5 lists the calculated logarithmic relationship for brown trout from the present data with those found in other areas. It seems that the fish from the Avalon Peninsula are no less fecund than those from other

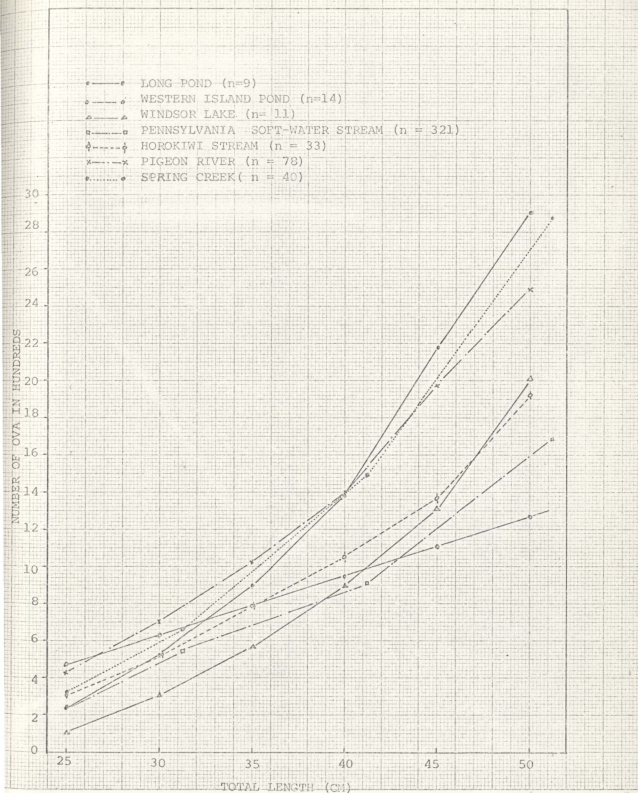


FIGURE 4.5 THE RELATIONSHIP OF THE NUMBER OF MATURE OVA ON TOTAL LENGTH OF BROWN TROUT FROM SEVEN DIFFERENT AREAS. (MICHIGAN DATA ARE FROM COOPER, 1953; THE OTHER DATA ARE TAKEN FROM McFADDEN, 1962)

parts of the world except for fish from Windsor Lake which apparently have a lower fecundity.

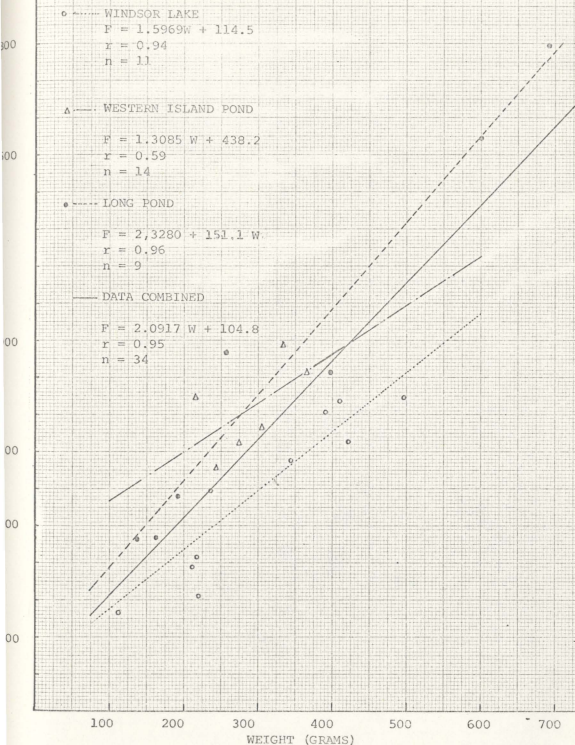
Nicholls (1958) reported that the brown trout from Great Lake (Tasmania) do not yield the expected number of eggs at larger size. It must be remembered that the egg numbers of larger fish in the present data (51.25 cm) were derived from the regression line, and the reading could vary from the actual number produced by the fish.

4.56 Fecundity and Weight

Fecundity has often been related to the fish weight since it might be supposed that weight is more closely connected with the condition of a fish than length. The regression line fitted to the pooled data of three locations gives the relationships as $F = 104.8 + 2.0917 W$ where W is the total weight of the fish in grams. A quite significant correlation coefficient ($r = 0.95$) was obtained (Fig. 4.6).

4.57 Relation of Age to Number of Eggs

Berg and Grimald (1965) reported ^{that} the number of eggs increases with age in Whitefish (Coregonus sp.) of Lake Maggiore. Fry (1949) showed that egg production in lake trout is related to the age of fish. Wiseman (personal communication) also finds that egg number is approximately proportional to the square of the fish age in brook trout (Salvelinus fontinalis).



are 4.6 Relationships between the mean weight and fecundity of brown trout from the three study areas.

Appendix, Table G shows the mean number of eggs produced by each group of mature fish. The data of three locations were fitted to a logarithmic regression and the relationship between age and fecundity is

$$\text{Log } F = 1.7604 + 1.577 \log A$$

where A is the age of the fish. The log-log plot of age against egg number is shown in Fig. 4.7.

Gerking (1959) in reviewing the relation of fecundity and age of haddock, long rough dab, herring and plaice found that the fecundity of these fish does not increase in proportion to the gonad weight. Longer ovaries produce larger and fewer eggs, or connective tissue increases disproportionately in the ovaries of larger fish. However, this is not the case in brown trout from Long Pond where fecundity increases with the gonad weight.

4.58 Relation of Ovary Weight and Number of Eggs

In salmon, larger fish have larger ovaries as well as more single ova than salmon of smaller size (Belding 1940). Ovary weight of Long Pond fish was related to the total length of fish, and ^{the} regression line was given as

$$OW = 5.8763 L - 173.53$$

where OW is the weight of ovaries (Fig. 4.8).

A similar relation exists between the numbers of mature ova and the weight of the ovary in fish from Long Pond. The log-log regression is

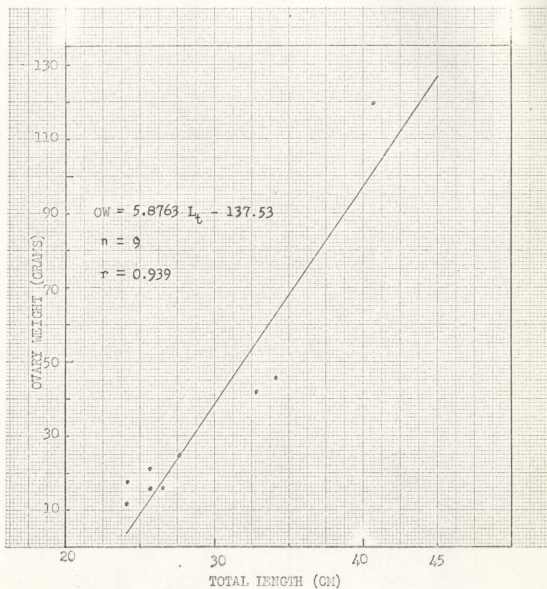


Figure 4.8 Regression of the ovary weight on total length of brown trout from Long Pond .

$$\text{Log } F = 1.7341 + 0.6906 \log \text{GW}$$

where GW is gonad weight. This indicates the egg numbers increase with the weight of the gonads. (Fig. 4.9)

In general, the bigger fish in Long Pond have heavier gonads than the smaller ones and have more eggs as well. It seems, therefore that the bigger fish produce more eggs than the smaller ones.

4.59 Variation in Egg Size

The ripe ova of brown trout are a light amber color (Fig. 4.2). The diameter of pre-spawning ova of 9 mature females obtained from Long Pond varied from 3.5 to 5.1 mm with a mean of 4.2 mm. The average diameter of ripe eggs from 12 Windsor Lake trout was 4.4 mm. (ranged 3.8 - 5.2 mm).

The egg size is partially dependent on fish size (Svardson, 1949) and it seems that the age number is not dependent on the egg size. This was illustrated by a very poor correlation coefficient ($r = 0.005$) of egg size against egg numbers. However, in trout from Long Pond and Windsor Lake, the egg size increases proportionately with the length of the fish (Fig. 4.10). This means that older fish produce larger eggs. However, Scott (1962) found that the egg size is not affected by diet. He regarded egg size to be controlled by natural selection operating through intraspecific competition.

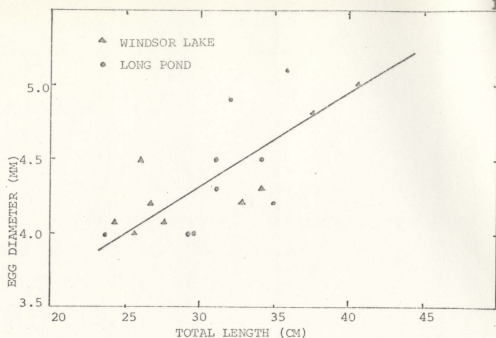


Figure 4.10 Variation in sizes of ripe ova with body length of brown trout from Long Pond and Windsor Lake.

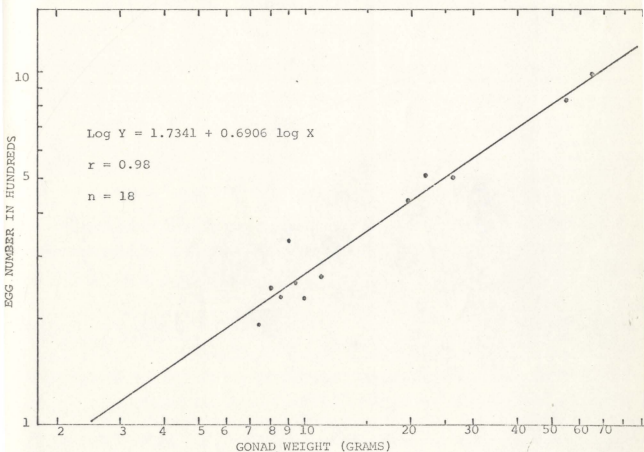


Figure 4.9. Regression of the number of mature ova on ovary weight of brown trout caught on 6th October, 1967 from Long Pond

4.6 Discussion

4.61 Maturation

It has been shown by the present data that female brown trout are able to mature and spawn at three years in this area. Male trout mature at a younger age than females and some maturing at two years old were found. The time of maturation may be affected by many factors, perhaps including inheritance and growth rate.

McFadden et al (1965) mentioned that brown trout attain sexual maturity earlier in fertile than in infertile waters. This emphasizes the importance of growth rate in determining the reproductive capacity of a population. Both food supply and population density are important in determining the proportion of fish of a given age which attain sexual maturity. Scott (1965) demonstrated that starvation suppressed maturation in rainbow trout (Salmo gairdneri) while Alm (1959) demonstrated that in brown trout of every age group the growth rate and the attainment of a certain size decide the maturity.

In the present study, the data obtained from Windsor Lake substantiate Alm's finding that maturity is decided by the growth rate and the attainment of a certain size. Windsor Lake fish have a higher growth rate and thus reach a larger size per age group than fish in other areas. Some Windsor Lake trout mature in their second year, but

this does not occur in other areas. Larger fish of the same age also show a higher ratio of sexual maturity. However, delayed maturation in some populations of brown trout may be an inherited characteristic. (Aim, 1949).

4.62 Variation in Fecundity

Variation in egg production by different populations of brown trout is high, this is shown by Table 4.6 and Fig. 4.5. Such variability also exists among the populations on the Avalon Peninsula. Rounsefell (1957) showed differences in fecundity between populations of chinook salmon (Oncorhynchus tshawytscha) from different localities. For Atlantic salmon Pope et al (1961) also found differences in fecundity between Scottish rivers but Belding (1940) did not find such differences among fish of the Gulf of St. Lawrence rivers. Svardson (1949) explained the differences in fecundity in terms of natural selection by environmental factors. Under conditions of low intraspecific competition for food and space, there would be selection towards females with an inherent capacity to produce the larger number of eggs. Heavy exploitation of the adult population and a resultant low total production of eggs would serve to maintain selection toward an increased fecundity. However, Wydoski et al (1965) did not find any distinctive evidence to establish whether the reduced fecundity in high fish density streams is either genetically-determined or caused

Table 4.6. Comparison of fecundity of brown trout in various areas expressed as average number of eggs per mature female. Horokiwi data converted to total length with factors derived from Long Pond sample.

Total length (cm)	Spring Creek Pennsylvania	Pennsylvan- ia soft water streams	Michigan streams	Madison River	Horokiwi streams, N. Z.	Windsor Lake	Long Pond	Western Island Pond
21.25	336	290	488	-	369	195	281	364
31.25	862	741	974	1364	778	558	806	766
41.25	1694	1458	1704	1131	1329	1189	1718	1309
51.25	2874	2474	2857	804	2021	2147	3106	1990

by environmental factors. In present studies, the fish of Windsor Lake have the lowest egg production. It has been discussed in the previous section that the younger fish in Windsor Lake have a consistently lower condition factor than older fish; this may indicate the scarcity of smaller organisms and abundance of larger food organisms in Windsor Lake.

The straight line fit of the Western Island Pond's data is probably due to the relatively short range of fish lengths (27.8 - 33.5 cm) as compared to the lengths for Long Pond and Windsor Lake. This is similar to Nicholl's explanation of the contradiction between his Plenty River data and Allen's results for Horokiwi Stream. Over a short range, the data fit well to a linear regression because of the great variability in numbers at any one length. However, an interesting conflict between Nicholl's data from Plenty River and the data from Long Pond and Windsor Lake is noted. The range of fish length between these areas are more or less the same, the curvilinear relationship occurred in Long Pond and Windsor Lake data but not in those from Plenty River. If Nicholl's explanation is valid for all cases, then theoretically the Long Pond and Windsor Lake data should also give a straight line as happened in Plenty River. The difference is probably due to the range of fish length over which a curvilinear relationship will occur, ^{this} being different in different localities.

In general, the fecundity of fish increases proportionately with length. The larger fish usually produce more and larger eggs, but this may not always be true. The data obtained by Brown and Kamp (1942) show a tendency for the longer fish to produce fewer eggs than the smaller fish.

The linear regressions for the weight relationship of the brown trout (Fig. 4.6) show the true relationship in all cases. The correlation of weight and fecundity ^{the} are very close to those of length-fecundity relationship. Since weight is more variable than length, it will not be more representative than the length relationship.

CHAPTER V

FOOD AND FEEDING OF BROWN TROUT

5.1 Introduction

Very little work has been done in Newfoundland on the food of brown trout. Wiggins (1950) in a review on the food of brown trout in North America stated that it consists of plankton, Gordiaceans (roundworms), spiders, mollusks, salamanders, frogs, lampreys, fishes and mice. The investigation of Kellett (MS, 1965) on the brown trout in Long Pond showed that aquatic insect larvae, mollusks, annelids, crustaceans and fish were the main foods.

Phillips (1929) examined the food of brown trout from Wellington District, New Zealand and found that trichopterans, ephemeropterans and mollusks were the main foods. He also concluded that variations in diet occurred from one stream type to another. Thomas (1964) found the differences between the food of brown trout from various habitats in West Wales were due to faunistic differences of the different waters.

Neill (1938) in his study of the food of brown trout relative to the bottom fauna, concluded that

" The trout feeds on the whole range of animals present in whatever type of habitat it finds itself, to an extent dependent on their representation in the fauna. This is sufficient to account for the nature of its stomach contents without invoking discrimination on the part of the fish."

This conclusion has also been substantiated by other authors (Allen, 1938, 1951; Frost, 1939, 1945, 1950; Frost and Smyly, 1952; Nilsson, 1955; Thomas, 1962, 1964). Idyll (1942) in Cowichan River found no close correlation between numbers of organisms present in the bottom fauna and the numbers taken by the trout. In addition, the size of fish is also importance in food intake. As the trout grows it takes larger food organisms, the larger fish tending to be exclusively piscivorous (Allen, 1938, 1951; Swynnerton and Worthington, 1940; Idyll, 1940; Nilsson, 1955; Ball, 1961; Thomas, 1964).

In general, the brown trout is an indiscriminate carnivore. Ball (1961) in a study of brown trout concluded that " The relative extent to which different animals are eaten depends mainly on their numerical representation in the fauna, though their habits and mobility are probably also important."

In view of wide range of food organisms which occur in different types of environments, the feeding habits of brown trout were studied in a variety of habitats. Owing to lack of information on the faunistic distributions in

these habitats and in view of previous studies on brown trout, it is hoped that this preliminary investigation on the food of brown trout will help to show the faunal compositions in these locations.

5.2 Methods of Study

The methods of collecting samples for this and other studies have been described in Chapter II. From the collections of each location, a random sample of 50 fish was examined. To facilitate the identification of ingested food, only the stomach contents were studied.

As soon as possible after capture, the stomachs, from the lower esophagus to the pyloric sphincter, of the fish were removed and preserved in 10% formalin. During examination, each gut was dissected out, the contents were emptied into a petri dish and examined under a dissecting microscope. The numerical method, occurrence method, and the gravimetric method were used to quantitize each sample.

By the numerical method, all organisms present were counted individually. In ^{the} case of disintegrated animals, the available heads were counted since these are relatively resistant to digestion and quite distinctive. Bottom living animals were identified to family. Aerial insects

were usually identified to order.

Some organisms (e.g. Daphnia, amphipods etc.) were often found in large numbers. Their number was estimated by placing them in a petri dish on a sheet of filter paper on which had been drawn a number of equal sectors. After the members of animals were evenly spread over the dish, the ^{number of} /organisms in one sector was then determined. The total numbers of individuals present could then be derived by proportionality. The total numbers of individuals were expressed as percentages of the total number of animals found in all fish examined (Allen, 1938, 1951; Neill, 1938; Frost, 1946; Ball, 1961 and others).

By the occurrence method, the contents in each stomach were noted and the number of fish in which each food item occurred was expressed as a percentage of the total number of guts examined (Hartley, 1947; Frost, 1946).

To determine the weight of food found in stomachs, food items were dried at 65°C for three days before weighing. The result was expressed as percentage dry weight (Iagler, 1952).

In order to examine the difference in the food preferences of various size groups, the food of these groups were compared in terms of number and frequency.

Hynes (1950), in reviewing the methods used in

some studies of food of fishes mentioned that the numerical and the occurrence methods tend to over-estimate the importance of small organisms, or those present in small numbers. The weight method is preferable for studying the relation between the amount of food taken and the rate of growth and the productivity of the trout production, since it is less subject to variations due to differences in the size of the food organisms (Allen, 1951). However, Leonard and Leonard (1946) suggest that weight data may be misleading unless used in conjunction with the number and occurrence methods. For a fish with a generalized food, provided a large number of stomachs are examined, all methods will give substantially the same result (Hynes, 1950).

5.3 Results

5.31 The percentage composition of the food of brown trout

The percentage composition of the food, assessed by the three methods are shown in Table 5.1. The major food items forming more than 1 per cent of the diet are also shown in Fig. 5.1.

The principal food taken by brown trout were trichopterans, ephemeropterans, odonates, dipterans, mollusks, crustaceans and fishes. As Metzelaar (1929) reported, some

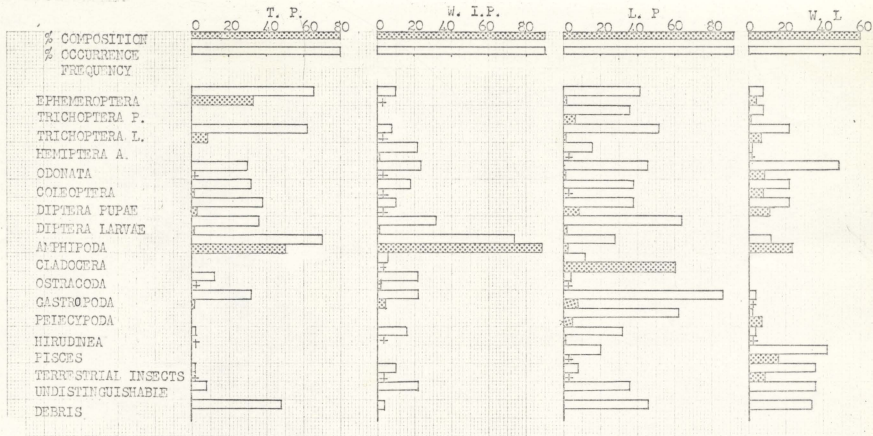


FIGURE 5.1. THE PERCENTAGE COMPOSITION OF THE FOOD AND THE PERCENTAGE FREQUENCY OF OCCURRENCE OF FOOD ITEMS OF THE BROWN TROUT FROM THE FOUR STUDY AREAS. ONLY THE IMPORTANT ITEMS ARE LISTED. T.P. = TOPSAIL POND; L.P. = LONG POND; W.L. = WINDSOR LAKE; W.I.P. = WESTERN ISLAND POND.

(+ INDICATES THAT THE PERCENTAGE COMPOSITION IS LESS THAN 1 PER CENT)

Table 5.1 Percentage occurrence, composition and weight of various categories of contents in the guts of brown trout from the four study areas (based on 50 stomachs).

Food organisms	Topsail Pond			Western Island Pond			Long Pond			Windsor Lake		
	Occur.	Comp.	Weight	Occur.	Comp.	Weight	Occur.	Comp.	Weight	Occur.	Comp.	Weight
<u>Temporary bottom fauna</u>												
Anisoptera nymphs	2	.02	.15	12	.2	10.29	14	.10	.82	40	7.5	8.26
Chironomid larvae	36	1.28	.10	32	.76	.19	46	1.94	.31	-	-	-
Tubificidae larvae	-	-	-	-	-	-	12	.63	.19	-	-	-
Tubifera larvae	-	-	-	-	-	-	6	.08	1.39	-	-	-
Coeloptera larvae	20	.94	.07	12	.29	.77	6	.06	.04	4	4.7	.52
Ephemeroptera nymphs	66	32.55	30.34	10	.20	1.30	42	2.03	4.05	8	4.03	.65
Trichoptera larvae	62	8.94	30.73	8	.26	.23	44	1.26	12.70	-	-	-
Zygoptera nymphs	28	.50	.65	8	.18	.63	28	.64	1.11	-	-	-
Corixidae	-	-	-	22	1.02	1.49	16	.12	.12	2	.19	.01
Total		44.23	62.04		6.24	14.90		6.24	20.73		16.12	9.44
<u>Permanent bottom fauna</u>												
Ampipoda	70	50.21	5.82	74	89.12	38.21	26	2.17	.36	12	23.46	3.04
Isopoda	-	-	-	-	-	-	4	.28	1.59	-	-	-
Amecole	32	1.78	.94	18	3.98	10.71	44	2.94	4.62	4	.36	.1*
Amydidae	-	-	-	-	-	-	-	.11	.20	-	-	-
Hydridae	-	-	-	-	-	-	30	4.65	6.41	-	-	-
Planorbidae	-	-	-	4	.38	.65	4	.04	.02	-	-	-
Pisidium	-	-	-	-	-	-	62	4.76	6.78	2	7.3	.77
Musculinae	2	.02	.15	16	.38	1.47	32	7.04	8.25	4	.57	.20
Total		52.01	6.91		93.86	51.04		16.29	28.23		31.71	4.71
<u>Surface & midwater food</u>												
Hydrocorina	2	.05	.01	-	-	-	4	.03	+	2	.57	.01
Chironomid pupae	38	2.75	.48	10	.32	.17	38	8.61	.89	22	11.34	.62
Coeloptera adults	12	.33	.22	6	.18	.69	32	3.39	1.44	18	3.7	.6
Trichoptera pupae	-	-	-	-	-	-	36	7.13	1.38	8	.70	+
Odonata	12	.55	.01	22	1.49	1.15	4	.03	-	-	-	-
Glaucocera	-	-	-	6	.64	.02	12	60.8	+	-	-	-
Chironomids	-	-	-	-	-	-	2	.01	.05	-	-	-
Epidora	-	-	-	-	-	-	6	.14	.12	-	-	-
Total		3.68	.72		2.63	2.03		77.14	4.68		16.37	.73
<u>Fishes</u>												
Gasterosteus aculeatus	-	-	-	-	-	-	14	.14	7.78	42	15.06	74.86
Salmonids	-	-	-	-	-	-	6	.06	29.80	-	-	-
Total		-	-		-	-		.20	37.58		15.06	74.86
<u>Serial insect</u>												
Diptera adults	2	.02	.06	4	.35	.04	2	.11	.04	14	3.65	.62
Hydroptera adults	-	-	-	-	.09	8.27	-	-	-	-	-	-
Zygoptera adults	-	-	-	-	-	-	4	.02	.32	8	1.34	.13
Trichoptera adults	-	-	-	2	.09	.86	-	-	-	14	4.61	.77
Ephemeroptera adults	-	-	-	4	.06	.42	-	-	-	-	-	-
Total		.02	.06		.59	9.59		.13	.36		9.6	1.62
<u>Miscellaneous food</u>												
Indistinguishable	8	-	4.04	22	-	32.02	36	-	7.53	36	-	5.4
Debris	40	-	26.16	4	-	.40	46	-	.83	34	-	1.23
Empty	-	-	-	-	-	-	2	-	-	10	-	-
Total of food organisms		4138			3421			10544			520	
Total weight of food			13.57 gm.			4.763 gm			25.20 gm			15.406 gm
Time of collection			June, 1967			August, 1967			May & October, 1967			July & October, 1967

*+ indicates the presence of food organisms less than 1%.

plants, plant remains, gravel and other indigestible debris were found in the stomachs. The vegetation, mainly Spirogyra found in the stomachs of fish from Long Pond and Western Island Pond, was always mingled with twigs and caddis fly larvae cases, presumably it was taken together with the larval Trichoptera and other bottom food organisms. Neill (1938) found that plant stems were ingested accidentally by trout feeding on pupae of Simulium. The debris was composed mainly of twigs, pieces of bark, stones and conifer needles. It is of interest to note that gravel up to 16 mm in length half-filled the stomachs of two fish which were 20.1 cm and 23 cm in length from Topsail Pond. It is doubtful that these stones could have been excreted from the fish.

Fish remains, especially the threespine stickleback (Gasterosteus aculeatus) were present in fish from Long Pond and Windsor Lake. This species forms an important food item for the fish in Windsor Lake. Six unidentified half-digested salmonids were also found in the fish from Long Pond. The presence of fish in the diet of brown trout is not uncommon and is reported by many authors (Metzelaar, 1929; Neill, 1938; Allen, 1938, 1951; Frost and Smyly, 1952; Nilsson, 1955, 1957; Ball, 1961; Graham and Jones, 1962). The fish from Western Island Pond and Topsail Pond were not piscivorous, probably due to the scarcity of forage fish

in these waters.

The food present in the samples from the different areas is presented in Table 5.1 and Fig. 5.1 and is discussed below.

5.31a Topsail Pond. The most important food items of Topsail Pond in June were larval Trichoptera, ephemeropteran nymphs and amphipods. The zygopterans, coleopterans, dipteran larvae and pupae and Amnicola were important. Anisopterans, leeches and cladocerans were not important food items.

5.31b Long Pond. The main components of stomach contents in Long Pond were mollusks, trichopteran larvae and pupae, dipteran larvae and pupae and ephemeropteran nymphs in the month of May, and mostly Daphnia in October. Amphipods, fish, leeches, beetles, odonates and hemipteran adults were the other common food items. Among the mollusks, Amnicola, Physa and Pisidium were found quite frequently in considerable numbers. The larvae and pupae of chironomids were common food items and the tubiferan larvae which could live in badly polluted waters were also found. Terrestrial insects and ostracods were insignificant parts of the diet.

5.31c Western Island Pond. Unlike the trout from other ponds, those of the Western Island Pond fed mainly on

amphipods, dipteran larvae and pupae and adult corixids. Zygopteran nymphs, gastropods, ostracods, beetle larvae and adults, terrestrial insects and ephemeropteran nymphs were other common food items.

5.31d Windsor Lake. Of fish caught from Windsor Lake, sticklebacks were the most important food items. Anisopteran nymphs and terrestrial insects were fairly common. Larval trichopteran, adult coleopterans, dipteran pupae and amphipods were also frequently found. Leeches, clams and hemipteran adults were insignificant in the diet of Windsor Lake brown trout.

5.32 Differences in the Food of the Trout from the Four Locations

As no samples of the fauna were taken, no correlation between food items and their availability could be made. In comparing the general food organisms found in the stomach contents, Thomas(1964) showed that the animals that were numerous or abundant in the fauna also became important in the food of trout. Neill (1938) found that 98.9 per cent of the food eaten by trout came from the adjacent fauna and thus only slightly over 1 per cent of the food organisms were of casual origin from elsewhere.

A comparison of the percentage composition and

percentage composition and percentage weight of the food of the fish on the basis of habitat and size shows some interesting differences between the four stations (Table 5.1). These differences could be caused by faunistic differences, as well as by the time of collection.

5.321 Comparison on the basis of habitat

5.321a Transient bottom fauna. The transient bottom fauna consists of those benthic organisms which are available only during certain period of the year.

The insect larvae, pupae or nymphs are an important part of the food of trout. It formed 44.2% of the ingested food in Topsail Pond and 16.1%, 6.2% and 2.9% in Windsor Lake, Long Pond and Western Island Pond respectively. Allen (1938), Frost and Smyly (1952), Ball (1961) and Thomas (1962) showed that Trichoptera and Ephemeroptera were abundant in the stomachs of trout during May and June. The sample from Topsail Pond was collected in June, so the appearance of these insects more or less occurred at the same time as in British waters. Dragonfly nymphs were relatively abundant in Windsor Lake and scarce in other areas. The number of corixids eaten in different waters was low except in Western Island Pond where trout consumed relatively more corixids than those in other waters. Frost and Smyly showed that this insect is usually not acceptable

to the trout and the numbers eaten in different waters were low.

5.321b Permanent Bottom Fauna. Allen (1938) regarded permanent fauna as those food organisms which are available throughout the the year and are the most abundant during the winter months. It comprises mainly the arthropods, mollusks, leeches and others. Ball (1961) and Thomas (1962) also found these organisms were most numerous in the trout food during the winter months. In contrast to their results, the permanent bottom fauna was important in the food of brown trout in these areas, especially in Western Island Pond, in summer. It formed 93.8%, by composition, of the food from Western Island Pond, 52% in Topsail Pond, 31.7% in Windsor Lake and 16.3% in Long Pond. The food composition of Western Island Pond trout differed from other locations by the presence of great numbers of amphipods. Amphipods also formed 50% in number of the food in trout from Topsail Pond. Dunn (1961) reported that the permanent food organisms were more abundant in summer than in winter months.

Mollusks were found to be present in the fauna throughout the year in Windermere (Allen, 1938; Frost and Smyly, 1952), but rarely occurred in Ball's (1961) sample for the whole year from Llyn Tegid, Wales. Number of Sphaeriidae, Physidae and Amnicolidae were often consumed

by trout from Long Pond where they formed 12.8% in number and 18% in weight of the food. However, they were less important in other areas. Thomas (1962) found that genera of mollusks such as Limnaea, Sphaerium and planorbis were commonly found in silt, mud, on stones or vegetation in slow flowing water or in backwater. They were of little importance to the salmon parr and brown trout except for Limnaea which occurred more often in the food of older trout. This is also true in the fish from Long Pond where mollusks occurred more often and in greater numbers in the larger fish.

Hirudinea was quite important in Long Pond, forming 1.04% in number and 8.2% in weight of the total food consumed. However, leeches were seldom found in the stomach of trout from other waters.

5.321c Surface and Mid-water Food. The surface and mid-water food constitutes 77.1% of the food of Long Pond trout and 16.4%, 3.7% and 2.6% of the food of Windsor Lake, Topsail and Western Island Ponds trout respectively. The large numbers of Daphnia in 6 fish from Long Pond caught in October showed it to be the major food component. This, of course, may be an illustration of the overestimation of the importance of the small organisms in the food. However, the surface and mid-water food is most abundant

in weight among the total food consumed in all areas.

In view of the great abundance of various aquatic insect adults and pupae in the food of Long Pond trout, the greater differences in food between Long Pond and other areas could probably be due to the great abundance of aquatic insect adults and pupae of different orders in this habitat. The small-sized trichopteran pupae which appeared in great numbers in Long Pond, and lesser numbers in Windsor Lake, were not found in other areas. Chironomid pupae as well as beetle adults were taken in all waters. In Western Island Pond, ostracods were found to be an important food item but were absent in the stomachs of Topsail Pond and Windsor Lake trout.

5.321d Fishes. In the present study, fish formed 16% in number of the food in Windsor Lake and 0.2% in Long Pond, but formed 74.8% and 35.6% respectively of the total weights of food consumed. No forage fish were found in the stomachs of fish from Topsail and Western Island Ponds. Allen (1938) found that a few trout of all sizes in Windsermere had eaten very small fishes (usually minnows), and Swynnerton and Worthington (1940) found that trout in Haweswater fed mainly on sticklebacks and probably minnows.

In Windsor Lake and Long Pond, three-spined sticklebacks are the chief forage fish. The trout in Long

Pond also feed on young salmonids to a considerable extent as was found by Metzelaar (1929). In view of the larger size of fish in Windsor Lake, it is not surprising to find these fish feeding more intensively on forage fish (42% in occurrence) than those from Long Pond (16% in occurrence).

5.321e Aerial Insects. Aerial insects were found most frequently in Windsor Lake trout and formed 9.6% in composition of the diet. They formed only 0.6%, 0.13% and 0.02% in composition of the food of the fish from Western Island Pond, Long Pond and Topsail Pond respectively. The main insects present were dipterans and trichopterans. Dragonflies formed 8.2% by weight of the diet from Western Island Pond but no dragonflies were found in other localities. In spite of the reports by previous workers (Metzelaar, 1929; Allen, 1938; Frost, 1939; Frost and Smyly, 1952; Holmes, 1960; Ball, 1961; Thomas, 1962, 1964; Graham and Jones, 1962) that aerial insects were the main food of trout during summer months, the aerial insects were not the main food for trout in these study areas.

5.322 Comparison Based on the Size of Food Organisms.

The organisms in the stomach contents were divided arbitrarily into the following size groups and the

comparisons were made on their abundance on the basis of percentage weight of the food (Table 5.1 and Fig. 5.2).

5.322a Large Organisms. Animals in this category are those which reached three centimeters or more in length. They include dragonfly nymphs which formed 8.7% and 10.29% of the food contents of the fish at Windsor Lake and Western Island Pond respectively. Dragonfly adults, which formed 8.2% of Western Island Pond trout food, were unimportant in the food of fish at the other locations. Centipedes, tubiferan larvae and big trichopteran larvae were present in Long Pond only. The zygopteran nymphs were present in Topsail Pond (0.6%), Western Island Pond (0.6%) and Long Pond (1.1%) and absent in Windsor Lake while damselfly adults were present in Long Pond and Windsor Lake in small numbers. Forage fish were important in the diet of trout from Long Pond (37.6%) and Windsor Lake (74.8%) but were absent in the other two areas. Hirudinea were more important in the diet of trout at Long Pond (8.2%) and Western Island Pond (1.4%) than at Topsail Pond (0.15%) and Windsor Lake (0.2%). The seasonal fluctuation in size and accessibility limit the importance of insect nymphs and adults to the fish. Yet, the other large organisms like fish and leeches were available to the trout throughout most of the year. It is evident, therefore

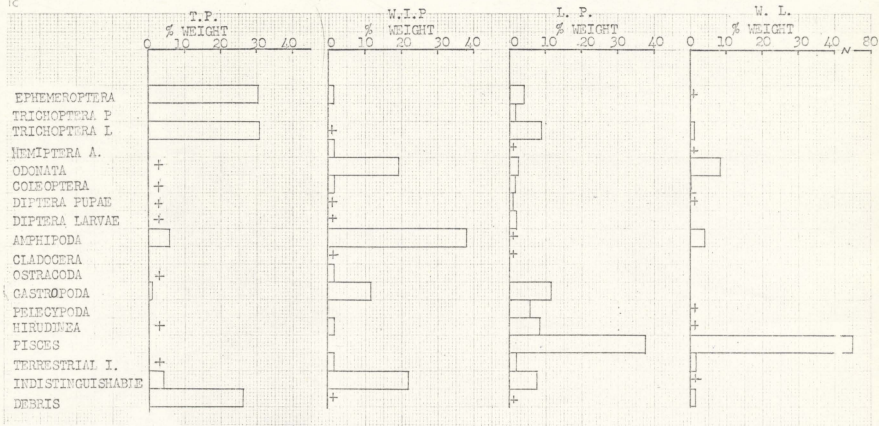


FIGURE 5.2. THE PERCENTAGE WEIGHT OF FOOD ITEMS OF BROWN TROUT FROM TOPSAIL POND (T.P.), WESTERN ISLAND POND (W. I. P.) , LONG POND (L.P.) AND WINDSOR LAKE (W.L.).

(+ INDICATES THAT THE PERCENTAGE COMPOSITION IS LESS THAN 1 PER CENT)

that large organisms are far more important in the food of trout at Windsor Lake and Long Pond than at the other locations.

5.322b Small Food Organisms. This group of animals comprised those which are below 5 mm in length. They include chironomid larvae which were more important in Long Pond (0.3% in weight) than Topsail Pond (0.1%) and Western Island Pond (0.2%). No chironomid larvae were found in Windsor Lake. Amnicola was very important at Western Island Pond (10.7%) and formed 4.6% and 0.9% of the food of trout at Long Pond and Topsail Pond respectively. Physa was present only in Long Pond (6.4%) and Pisidium was more important in the food of trout at Long Pond (6.8%) than at Windsor Lake (0.8%).

Amphipods were very important in the food of fish at Western Island Pond (38.2% in weight) and common at Topsail Pond (5.8%) and Windsor Lake (3.9%), but were scarce in Long Pond. Daphnia was present only in Long Pond (0.8%) and Western Island Pond (0.02%). Ostracods were important in Western Island Pond (1.15%). Most of the organisms except the chironomids were present throughout the year. This is the case particularly with the permanent bottom fauna such as Amnicola, Physa, and Pisidium etc. at Long Pond and Western Island Pond.

5.322c Medium-sized Food Organisms. Among this group of organisms, ephemeropterans, trichopterans, coleopterans and corixids were ^{more} numerous than the Tipulidae larvae, isopods and spiders. The ephemeropteran nymphs were the most important food in Topsail Pond. They also formed an important food source in Western Island Pond and Long Pond but not in Windsor Lake.

Trichopteran larvae were one of the main food items in Topsail Pond and formed 30.73% (dry weight) of the food. They formed 12.7% of the stomach contents of Long Pond fish but were less important to the Western Island Pond and Windsor Lake trout. The coleopterans were more abundant in Long Pond and Western Island Pond than in the other two areas. However, the corixids were important only in Western Island Pond and absent in Topsail Pond. Owing to the seasonal fluctuations of these organisms, especially trichopterans and ephemeropterans, they were important and available during only part of the year. Dominy (1965) indicated that the ephemeropterans and trichopterans were abundant in June and July in the food of rainbow trout of Murray's Pond. This is also the case in the present study. They were more abundant in the stomach contents of Topsail Pond and Long Pond trout which were collected between May and July. It is therefore assumed that these food organisms were more important to the fish

in the early summer than other periods of the year in this area.

5.33 Variation in Food with Size of Brown Trout.

It has been reported in previous literature that brown trout change their feeding habits as the fish increase in size (Metzelaar, 1929; Allen, 1938; Swynnerton and Worthington, 1940; Idyll, 1942; Nilsson, 1955, 1957; Ball, 1961; McCormack, 1962). Metzelaar suggested that brown trout up to 9 inches were insect feeders, "as they grow larger, they distinctly turn to crab and fish diet and end their career as predaceous fish, living almost entirely on a fish diet". In Windermere, Allen (1938) found that all the trout he examined showed little difference in diet (bottom living invertebrates) except for fish over 40 cm in length which fed mainly on fish. Swynnerton and Worthington (1940) also found a change over to fish-eating by the large trout in Haweswater. The same result were shown in Cowichan River, British Columbia by Idyll (1942), in Swedish lakes by Nilsson (1955, 1957), in Welsh lakes by Ball (1961) and in Lancashire becks by McCormack (1962).

McCormack found that the fry and young fish fed on ephemeropteran nymphs, chironomids, shrimps and dipteran larvae and trout 10 cm long ate trout eggs and alevins. In Horokiwi Stream, the small trout consumed more soft-bodied

animals, such as ephemeropteran nymphs and chironomid larvae and the larger trout ate more mollusks and trichopteran larvae etc. (Allen, 1951). The same result had also been reported by Swynnerton and Worthington (1940) and Nilsson (1955).

Table 5.2 show a comparison of the food eaten by brown trout of various sizes in Windsor Lake and Western Island Pond. The occurrence and composition methods were used to illustrate the differences between food items taken by different sizes of fish. It shows that within the size range between 15-35 cm, there is an increase in the consumption of sticklebacks by trout in Windsor Lake. Forage fish formed the main food of the trout over 35 cm in length. There is no consistent change with size in diet of trout from Western Island Pond and all the trout examined were probably in the insect-feeding stage. The smaller trout feed mainly on smaller organisms, while the larger organisms such as trichopteran larvae, aerial insects and odonates are consumed by larger fish.

5.4 Discussion

It is clear from the present results that the brown trout is essentially carnivorous, taking mainly aquatic animals and varying amounts of terrestrial animals, whenever they were accessible. The same conclusion was reached by

Table 5.2 Analysis of food of brown trout, caught in Windsor Lake (October, 1967) and Western Island Pond (August, 1967), arranged according to size of fish and type of organisms eaten. A - percentage in occurrence; B - per cent of composition. sign + indicates 0.1% or less

Area	Windsor Lake									Western Island Pond					
	length (cm)	15-20	20-25	25-30	30-35	35-40	40-45	45-50	Total	15-20	20-25	25-30	30-35	35-40	Total
No. of fish		2	3	6	12	4	3	1	32	1	2	2	21	1	50
No of organisms		67	19	72	50	25	12	12	257	20	975	15	794	26	1407
Diptera	A	-	-	16.7	16.7	25.0	-	-	12.5	-	25.0	4	38.0	-	32.0
	B	-	-	1.4	22.0	16.0	-	-	6.2	-	1.4	2	15.0	-	1.3
Coleoptera	A	-	-	50.0	9.3	-	-	-	12.5	-	-	2	14.2	-	14.0
	B	-	-	9.3	2.0	-	-	-	2.7	-	-	2	1.0	-	.5
Trichoptera	A	66.0	66.0	33.0	16.7	-	33.0	-	28.1	-	-	2	9.5	-	10.0
	B	20.9	47.4	16.7	4.0	-	16.7	-	15.2	-	-	2	.6	-	.3
Ephemeroptera	A	-	-	16.7	9.3	-	-	-	6.3	-	-	10	14.2	-	10.0
	B	-	-	6.9	4.0	-	-	-	2.7	-	-	10	.5	-	.2
Odonata	A	66.0	-	50.0	50.0	25.0	66.0	-	43.8	-	25.0	15	28.6	-	20.0
	B	10.4	-	12.5	39.0	4.0	16.7	-	14.8	-	.2	15	1.1	-	.5
Hemiptera	A	-	-	-	-	-	-	-	-	-	25.0	31	19.0	-	24.0
	B	-	-	-	-	-	-	-	-	-	.4	1	1.3	-	1.1
Pelecypoda	A	33.0	-	16.7	-	-	-	-	6.3	-	-	10	-	-	4.0
	B	56.7	-	1.4	-	-	-	-	15.2	-	-	10	-	-	.4
Gastropoda	A	-	-	-	-	-	-	-	-	-	37.5	24	4.0	-	10.0
	B	-	-	-	-	-	-	-	-	-	.7	7	.6	-	4.0
Amphipoda	A	-	33.0	33.3	9.3	25.0	-	-	15.6	-	97.5	69	76.2	100.0	74.0
	B	-	21.0	14.0	2.0	9.0	-	-	6.6	-	96.6	95	77.4	96.0	89.4
Ostracoda	A	-	-	-	-	-	-	-	-	-	25.0	15	24.6	-	22.0
	B	-	-	-	-	-	-	-	-	-	1.4	3	3.0	-	1.5
Gnathocera	A	-	-	-	-	-	-	-	-	100.0	-	-	54.0	-	6.0
	B	-	-	-	-	-	-	-	-	100.0	-	-	.1	-	.6
Hirudines	A	33.0	-	-	-	-	-	-	3.1	-	25.0	21	7.5	-	16.0
	B	3.0	-	-	-	-	-	-	.8	-	.3	2	.4	-	.4
Miscellaneous organisms	A	-	66.0	93.3	25.0	-	-	-	31.0	-	-	10	8	100.0	2.0
	B	-	10.4	19.4	9.0	-	-	-	7.8	-	-	10	1	4.0	+
Unidentified	A	-	-	16.7	-	25.0	-	-	6.3	-	-	-	-	-	-
	B	-	-	16.7	-	4.0	-	-	5.1	-	-	-	-	-	-
Empty	A	33.0	33.0	-	16.7	-	-	-	12.5	-	12.5	10	.2	-	12.0

Pentelows (1932), Neill (1938), Nilsson (1955), Ball (1961) and Thomas (1962, 1964). Ball showed that the brown trout is an indiscriminate carnivore, the most important animals eaten being those which were most readily accessible in the fauna. Therefore, as has been stated by Thomas (1964), the variation in the food of trout from one area to another could be attributed to faunistic differences. The time of collection, which influences the occurrence of certain aquatic insects, probably also has some effects on the food compositions in the different areas. Allen (1938) commented that seasonal changes in the diet could be explained by changes in the availability of the fauna.

In the food of brown trout, insects are the main constituents at every location. In a study of food and feeding of brown trout in North America, Wiggins (MS, 1950) concluded the insects such as Trichoptera, Ephemeroptera, Diptera and other orders are numerically and volumetrically important in the food of brown trout. This also has been reported in New York by Needham (1938), in Michigan by Metzelaar (1929), in British Columbia by Idyll (1942) and in Newfoundland by Kellett (MS, 1965).

In Britain, the trout in limestone waters eat insects, crustaceans and small fish but fish from acid waters eat only insects and crustaceans (Southern, 1932). Pentelow (1932) found that trichopterans, ephemeropterans, dipterans,

crustaceans and mollusks were the most important food items for brown trout in River Itchen. In general, the insects such as trichopterans, dipterans, ephemeropterans and coleopterans together with mollusks and crustaceans were eaten very often by trout in British waters (Allen, 1938; Frost, 1939; Frost and Smyly, 1952; Holmes, 1960; Ball, 1961; Graham and Jones, 1962; Thomas, 1962, 1964).

Phillips (1929) in his investigation of the rivers of Wellington District, New Zealand found that trichopterans and ephemeropterans were the dominant food, and that dipterans and plecopterans were also common in the diet of brown trout. Allen (1951) showed that the most important constituents of the diet of trout in Horokiwi stream were trichopterans, ephemeropterans and dipterans.

The results of this study show that the food organisms eaten by trout belong to the bottom fauna, such as ephemeropterans, trichopterans, dipterans and amphipods. Mollusks are also important diet of trout. The food of trout from Topsail Pond, Western Island Pond and Windsor Lake contained numerically more bottom fauna than those from Long Pond which contained mainly surface and mid-water organisms. The organisms of terrestrial origin did not form an important part in the food of trout and they were only relatively important in the diet of fish from Windsor Lake. Thomas (1964) found that the large quantities of terrestrial food present in his low product-

ivity streams during the summer months were due to the terrestrial food which were brought into the streams from overhanging vegetation by constant winds. In the present study, the samples were collected from May to October, yet, very few aerial insects with aquatic larvae were present. Allen (1938) suggested that when all classes of food were available the trout feed on the surface food rather than on the bottom fauna and if no surface food were present they would feed on temporary bottom fauna rather than on the permanent bottom fauna. Therefore, there is no reason to believe that the fish would feed mainly on bottom fauna if there was plenty of surface food available. The scarcity of aerial insects present in this area is probably the main cause of their infrequent occurrence in the diet. Surface feeding had been found to predominate in trout in Malham Tarn and Llyn Tegid from May to September (Holmes, 1960; Ball, 1961). Brown and Frost (1967) showed that older trout eat more surface food of aquatic origin such as caddis flies, winged midges and the duns and spinners of may-flies, than do younger fish.

Due to the selectivity of the gill nets, no fish under 21 cm were examined. Therefore, no data on the food of young trout were examined. However, McCormack (1962) reported that the fry eat ephemeropteran nymphs, chironomid larvae, Gammarus and dipteran larvae; while yearlings eat

aquatic animals similar to those eaten by fry but in different proportion, and consume some terrestrial organisms. Nilsson (1957) showed that the fry feed mainly on planktonic crustaceans carried out by the current in the outflow of the lake.

Older trout eat much the same kinds of animals as younger fish but take a greater variety of bottom living organisms, both larvae and adults (Brown and Frost, 1967). In addition, mollusks and vertebrates may be included in the diet.

Insects were the major food at all four locations. The ephemeropteran nymphs and trichopteran larvae formed an important food of trout. They dominated the diet of Topsail Pond trout. It is no doubt that their presence in the diet could be attributed to their abundance and ready accessibility in this area. The dominant food was amphipods, cladocerans and fish in Western Island Pond, Long Pond and Windsor Lake respectively. As the insects tend to attend their seasonal maximum over a restricted period, organisms other than insects would provide the trout with a more reliable food supply. Thomas (1964) pointed out that the occurrence of arthropods, mollusks and fish in the food of trout appears to be a good index of growth. The amphipods are important in the Topsail and Western Island Ponds; cladocerans, Daphnia,

mollusks and fish (sticklebacks and salmonids) are important at Long Pond while the stickleback is important in Windsor Lake.

The planktonic crustaceans & cladocera were present in the stomachs of Long Pond trout. The fish which consumed more Daphnia than other organisms were collected in October which may indicate the abundance of this organism and scarcity of other organisms at that time of the year. Wiggins (1950) suggested that plankton is eaten by brown trout up to four years of age (accurate lengths were not available). In this study, the length of those fish which feed on Daphnia varies from 21cm to 27.6cm (three to five years old).

In Windermere, Allen found that the brown trout ate very little zooplankton but it was the main food eaten by trout of about 340 grams in weight, caught in one-inch gill-net during the summer months. Southern (1932) found that 53% of trout from Lough Inchiquin ate cladocerans, but all trout larger than 340grams (12 ounces) caught at the same time were not feeding on zooplankton. Therefore it is thought that perhaps trout in lakes at about this size pass through a phase when they feed on zooplankton (Frost and Brown, 1967).

The appearance of a high proportion of Oligochaetes

(mainly terrestrial) in the stomachs of trout from Llyn Tegid were reported by Graham and Jones (1962). However, no *Oligochaetes* were found in trout stomachs from the four areas in this study. Frost and Smyly (1952) also found that *Oligochaetes* were absent in trout stomachs of moorland fish-ponds. The scarcity of *Oligochaetes* in the food was also reflected in the findings of Phillips (1929), Pentelow (1932) and Southern (1932).

In the present survey it has been shown that larger- or medium-sized food items are more important in the food of trout at Windsor Lake and Long Pond than in Western Island and Topsail Ponds. The trout grow faster in Windsor Lake where the larger organisms, especially sticklebacks, are available during all seasons. In Windsor Lake and Long Pond where fish and mollusks are available, trout grow faster than those from areas like Topsail and Western Island Ponds where they live mainly on insects and amphipods. It may be suggested that, the dearth of large organisms at the latter stations is one of the factors which is responsible for the relatively slow growth of trout compared with those from Long Pond and Windsor Lake (see chapter on growth). It has been shown by Frost and Smyly (1952) that in Windermere, where the trout achieve a large size,

there is a plentiful supply of larger food organisms such as forage fish which are being selected by the larger fish.

SUMMARY AND CONCLUSION

1. The browntrout, Salmo trutta Linn. was first imported from Scotland to Newfoundland in 1886 for recreational purposes. Since then it has become established in the Avalon Peninsula with its range extending to East Trinity Bay and the east coast of the Burin Peninsula.
2. The brown trout has been reported to be replacing the native trout (Salvelinus fontinalis) in waters where both occurred. A general biological study was undertaken in the summer and fall of 1967 in four different environments to provide life history information on this species.
3. The purpose of the present study was to examine different aspects of the biology of brown trout in the four areas and to compare them with the biology of brown trout from other areas.
4. The four study areas selected were Long Pond, Topsail Pond, Western Island Pond and Windsor Lake. These areas range in size from 16 acres (Long Pond) to 1216 acres (Windsor Lake). Some of the physico-chemical characteristics of these waters were determined.
5. A total of 737 specimens were collected from the four study areas. The largest fish occurred in Windsor Lake,

followed by Western Island Pond, Long Pond and Topsail Pond respectively. This may indicate that fish size is related to the size of the body of water.

6. The age of the trout was determined from the scales. The scale length was used to back-calculate the length attained by fish of a given age by using the direct-proportion method corrected with the intercepts of the body-scale length relationship. A regression of body length-scale length of sex combined data was used for each area.

7. The age of brown trout in the present study ranged from 2 to 8 years. In Long Pond, the modal age-group was 3 years while the modal group for other areas was 4 years. The annual survival rate was 0.47 for all areas. An annual survival rate of 0.50 in Windsor Lake is regarded as representative of the annual survival of an unexploited population in Newfoundland.

8. The von Bertalanffy growth curve $L_t = L_{\infty}(1 - e^{-K(t-t_0)})$ was fitted by computer to male, female and combined-sexes data of brown trout from each area. Only the sex-combined results were used due to the non convergence in iteration of some of the male and female data. The growth curves showed the same result as the straight forward plots of the age against back-calculated length.

9. Comparison of the

9. Comparison of the annual growth in length among the four areas showed that Windsor Lake trout have the fastest growth, followed by Long Pond, Western Island Pond and Topsail Pond fish respectively.

10. The Windsor Lake trout showed a faster growth in length than some British lake trout but after the 5th year a slower growth than the Windermere trout. The Newfoundland pond trout showed a much slower growth than fish from the U.S.A. but a better growth than some of the British tarn and river fish.

11. The specific growth rate of fish indicated that the fish grow fastest in their first two years of life. The growth rate slowed down after the 3rd year and remained at a low level. The fish that spent their early life in streams showed a high growth rate during their first and second years. The fish that lived in a lake from hatching showed a continuously decreasing specific growth rate.

12. The value of n , in the length-weight relationship was found to vary between 2.7 and 3.1. By using analysis of covariance, the length-weight relationships of the four study areas were found to be significantly different at the 5% level. However, the regressions of the body weight on body length between any two of the four study areas were tested and no consistent differences were found between them.

13. The Windsor Lake trout showed lower mean condition coefficients than the trout from other study areas, while the Long Pond trout had the highest K values. The fish collected in the early summer were in better condition than fish collected in the fall.

14. The growth of fish probably depends on the size of the habitat, the population pressure, the abundance of food, length attained by the first year and the water composition. When the size of the habitats is similar, the abundance of food organisms and time of migration from stream to pond or lake are perhaps the most important factors which determine the growth of the fish.

15. It was found that the brown trout populations deviated little from a 1:1 sex-ratio. The ratio was in favour of females in all areas except in Windsor Lake where males were more abundant than females. This might be due to the selectivity of the fishing gear or sexual segregation in the Windsor Lake population.

16. Male fish tend to mature at an earlier age and smaller size than females. Most of the fish were mature at 4 years. The fecundity varied between 400 ova per female at three years to 1797 ova per female at 8 years. Egg numbers increased with increasing size and age of female. A linear logarithmic

fecundity-length relationship fitted the data of the Western Island Pond sample while exponential curves fitted the data of Long Pond and Windsor Lake trout. Number of eggs were also proportionate to egg size and gonad weight.

17. The stomach contents of trout from the four study areas were analysed by the weight, number and occurrence methods. The brown trout is an indiscriminate carnivore. Basic food consisted mainly of larvae, nymphs and pupae of ephemeropterans, trichopterans and dipterans; amphipods; cladocerans; forage fish, gastropods, odonates, coleopterans, surface insects were also frequently eaten.

18. Relative importance of the various food items reflected the differences in availability of organisms in different environments. In all areas, the trout fed mainly on bottom fauna except in Long Pond where surface and mid-water foods were more important. Some aquatic insects and amphipods were utilized by brown trout of all sizes. The large organisms such as gastropods, odonates and forage fish formed the main food of fish over 35 cm .

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APPENDIX

Table A. The conversion factors for the fork length and total length of brown trout based on 159 specimens from Long Pond

Length intervals (cm)	Fork Length x Factor	Total Length x Factor
	= Total length	= Fork length
18.0 - 27.9	1.0587	0.9445
28.0 - 29.9	1.0512	0.9453
over 30.0	1.0383	0.9630

Table B Specific growth rates for length (as % per annum) for each year of life for the brown trout from the four study areas in Newfoundland.

Area	Specific growth rates (% per annum)							
	0 - I	I - II	II - III	III-IV	IV-V	V-VI	VI-VII	VII-VIII
Long Pond	122.4	41.7	34.4	21.2	18.6	13.1	15.0	5.7
Topsail Pond	94.0	51.4	48.1	17.0	14.5	14.5	9.1	-
Western Island Pond	129.2	30.1	40.8	23.5	15.8	8.7	8.6	-
Windsor Lake	130.3	54.1	39.7	21.0	13.8	13.5	5.9	-

Table C. Comparison of the regressions of age-weight relationship by analysis of covariance for the four study areas.

Test	Source of variation	Errors of Estimation			F
		Degree of freedom	Sum of squares	Mean squares	
Between localities, Long P., Western Island P., Topsail P. & Windsor L.	Within Samples	16	0.11235	0.00702	0.5897
	Regression Coeff.	3	0.01244	0.00414	
	Common Regression	19	0.12479	0.00656	
	Adjusted Means	3	0.58076	0.19358	
	Total	22	0.70555	0.03207	29.5091*

* significant difference

At d.f. 3,16, $F(0.05) = 3.24$; d.f. 3, 19, $F(0.05) = 3.13$.

Table D. Comparisons of the regressions of body weight on age by analysis of covariance between any two of the four study areas.

Test	Source of variation	Errors of Estimation			F
		Degree of freedom	Sum of squares	Mean squares	
Between localities, Long P., & Western Island P.	Within Samples	8	0.03441	0.00430	2.12558
	Regression Coeff.	1	0.00914	0.00914	
	Common Regressions	9	0.04355	0.00483	
	Adjusted Means	1	0.00993	0.00993	
	Total	10	0.05348	0.00535	2.0559
Between localities, Long Pond & Topsail Pond	Within Samples	8	0.07815	0.00976	0.1680
	Regression Coeff.	1	0.00164	0.00164	
	Common Regressions	9	0.07979	0.00886	
	Adjusted Means	1	0.05552	0.05552	
	Total	10	0.13531	0.01353	6.2664*
Between localities, Long Pond & Windsor Lake	Within Samples	8	0.00931	0.00116	1.5517
	Regression Coeff.	1	0.00018	0.00018	
	Common Regressions	9	0.00949	0.00105	
	Adjusted Means	1	0.24128	0.24128	
	Total	10	0.25077	0.02508	229.7905*
Between localities, Western Island P. & Topsail P.	Within Samples	8	0.10304	0.01288	0.3098
	Regression Coeff.	1	0.00399	0.00399	
	Common Regressions	9	0.10702	0.01189	
	Adjusted Means	1	0.13989	0.13989	
	Total	10	0.24691	0.02469	11.7653*
Between localities, Western Island P. & Windsor L.	Within Samples	8	0.03420	0.00427	2.0468
	Regression Coeff.	1	0.00874	0.00874	
	Common Regressions	9	0.04294	0.00477	
	Adjusted Means	1	0.44233	0.44233	
	Total	10	0.18527	0.01853	29.8356*
Between Localities, Topsail P. & Windsor L.	Within Samples	8	0.07794	0.00974	0.0944
	Regression Coeff.	1	0.00092	0.00092	
	Common Regressions	9	0.07886	0.00876	
	Adjusted Means	1	0.56135	0.56135	
	Total	10	0.64021	0.06402	64.0810*

* significant difference

At d.f. 1,8, $F(0.05) = 5.32$; d.f. 1,9, $F(0.05) = 5.12$.

Table E. Comparison of the regressions of body weight on body length by analysis of covariance for the four study areas.

Test	Source of variation	Errors of Estimation			F
		Degree of freedom	Sum of squares	Mean squares	
Between	Within Samples	39	0.0583	0.0013	3.7333*
Localities,	Regression Coeff.	3	0.0169	0.0056	
Long P.,	Common Regressions	42	0.0752	0.0018	2.6111*
Western Island	Adjusted Means	3	0.0142	0.0047	
P., Topsail P. & Windsor L.	Total	45	0.0894	0.0020	

* significant difference

At d.f. 3,39, $F(0.05) = 2.34$; d.f. 3,42, $F(0.05) = 2.34$

Table F. Comparisons of the regressions of body weight on body length by analysis of covariance between any two of the four study areas.

Test	Source of variation	Errors of Estimation			F
		Degree of freedom	Sum of squares	Mean squares	
Between	Within Samples	19	0.01520	0.00080	1.8500
localities,	Regression Coeff.	1	0.00148	0.00148	
Long P. &	Common Regressions	20	0.01668	0.00083	7.7590*
Western Island	Adjusted Means	1	0.00644	0.00644	
P.	Total	21	0.02312	0.00110	
Between	Within Samples	16	0.03230	0.00201	0.4079
localities,	Regression Coeff.	1	0.00082	0.00082	
Long P. &	Common Regressions	17	0.03312	0.00194	1.8814
Topsail P.	Adjusted Means	1	0.00365	0.00365	
	Total	18	0.03677	0.00204	
Between	Within Samples	24	0.02540	0.00200	7.150*
localities,	Regression Coeff.	1	0.01430	0.01430	
Long P. &	Common Regressions	25	0.03970	0.00160	7.125*
Windsor L.	Adjusted Means	1	0.01140	0.01140	
	Total	26	0.05110	0.00200	
Between	Within Samples	15	0.00329	0.00021	140.8571*
localities,	Regression Coeff.	1	0.02958	0.02958	
Western Island	Common Regressions	16	0.03287	0.00205	1.7609
P. & Topsail P.	Adjusted Means	1	0.00361	0.00361	
	Total	17	0.03648	0.00214	
Between	Within Samples	23	0.02600	0.00113	5.3982*
localities,	Regression Coeff.	1	0.00610	0.00610	
Western Island	Common Regressions	24	0.03210	0.00130	9.538*
P. & Windsor L.	Adjusted Means	1	0.01240	0.01240	
	Total	25	0.04450	0.00180	
Between	Within Samples	20	0.04310	0.00215	2.6930
localities,	Regression Coeff.	1	0.00579	0.00579	
Topsail P. &	Common Regressions	21	0.04889	0.00232	2.0733
Windsor L.	Adjusted Means	1	0.00481	0.00481	
	Total	22	0.05370	0.00245	

* significant difference

At d.f. 1,15, $F(0.05) = 4.54$; d.f. 1,16, $F(0.05) = 4.49$;d.f. 1,17, $F(0.05) = 4.45$; d.f. 1,19, $F(0.05) = 4.38$;d.f. 1,20, $F(0.05) = 4.35$; d.f. 1,21, $F(0.05) = 4.32$;d.f. 1,23, $F(0.05) = 4.28$; d.f. 1,24, $F(0.05) = 4.26$;d.f. 1,25, $F(0.05) = 4.24$

Table G. The variation between the fecundity and age of fish from the three study areas (number of fish in parentheses).

Age	Long Pond	Windsor Lake	Western Island Pond	Total
3	-	400 (5)	-	400 (5)
4	483 (6)	389 (1)	810 (4)	593 (11)
5	968 (1)	812 (5)	756 (5)	801 (11)
6	915 (1)	-	867 (5)	875 (6)
7	-	-	-	-
8	1797 (1)	-	-	1797 (1)

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