COMPARATIVE ECOLOGY OF THE BROOK TROUT (*Salvelinus fontinalis* MITCHILL) IN TWO NATURAL AND ONE FERTILIZED LAKE IN CENTRAL INSULAR NEWFOUNDLAND

SEAN RICHARD CLANCY

Comparative Ecology of the Brook Trout (*Salvelinus fontinalis* Mitchill) in Two Natural and One Fertilized Lake in Central Insular Newfoundland.

by

© Sean Richard Clancy B. Sc.

Department of Biology
Memorial University of Newfoundland

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

2001

St. John's **Newfoundland**

Abstract.

This study compares aspects of the feeding, physiological, population dynamics, ecology, and the life history of the brook trout, *Salvelinus fontinalis* Mitchill in three ponds of the Experimental Ponds Area (EPA), central Newfoundland. Two of the ponds were natural control ecosystems while the third had been fertilized with nitrogen and phosphorus each summer since 1991.

Analysis of stomach contents was used to evaluate feeding intensity and diet composition. Feeding intensity generally decreased throughout the summer. Brook trout were predominantly benthic feeders and switched from a diet dominated by odonate nymphs (Corduliidae) in the spring to one composed of snails (Gastropoda), smaller-sized insect taxa (Trichoptera, Corixidae) and organisms found on or near the surface waters of the pond later in the summer and early fall (Diptera, Hymenoptera). Modest variation in the prey groups selected by male and female trout indicated spatial differences where each gender feeds within the lake ecosystem. Large fish fed on larger-sized prey taxa and had a greater mean ration in comparison to small fish.

Analysis of somatic-visceral percent lipid content was used to document the seasonal change in physiological condition of large, maturing male, and female trout. The monthly mean lipid content increased from spring to a maximum in mid-summer, then decreased through to fall for each gender. Lipid accumulation coincided with the period when mean ration was greatest, while lipid depletion coincided with a decrease in feeding intensity, an increase in metabolism inferred from higher water temperatures and

the diversion of lipid into gonadal mass. Percent lipid content was positively correlated with two indices of condition and negatively correlated with water content which can be used to predict lipid content.

Analysis of annual seasonal population census data from 1991 to 1996 and electro-fishing data collected in 1996 facilitated the description of the life history and growth characteristics of brook trout in the three ponds. Young-of-the-year were most predominant in the streams and cohort patterns indicated trout enter the ponds at ages 1+ and 2+. The lack of older fish in the streams suggests that death may be the principle source of loss for pond fish aged 2+ and older. The maximum age observed was age 5+. Male trout matured at a smaller size and at a younger age, on average, than females; the majority of reproductive individuals were age 3+. Female brook trout produced an average of 236 eggs per female with a mean egg diameter of 3.23 mm. EPA brook trout displayed generally smaller fork lengths at age than fish in other lakes on the mainland and insular Newfoundland.

Comparison of the temporal change in the brook trout population abundance, population structure and growth characteristics in the experimental pond relative to the controls facilitated the investigation of the potential effects of the whole-lake fertilization experiment. There was an increase in brook trout density in the experimental pond relative to the controls during the fourth year of fertilization, consistent with an expected 'bottom-up' response to increased macroinvertebrate abundance, followed by increased mortality rates possibly attributable to a 'top-down' impact by loons. Fertilization appears not to have increased growth rates of fish in the experimental pond, as indicated

by the comparisons of age-class fall weight, however the growth patterns of experimental pond fish varied less among individuals than those of the control ponds across years.

Acknowledgements.

I would first like to thank my supervisor, Dr. Roy Knoechel, for his guidance, patience, support, and supervision throughout this study. I would also like to thank him for granting me the freedom to become involved with graduate student government and issues, and to help teach other students about marine and freshwater biology. Funding for this study was provided by a Memorial University of Newfoundland Graduate Fellowship from the School of Graduate Studies, by a research grant from the Natural Science and Engineering Research Council to Dr. Knoechel, and grant from the Canada-Newfoundland Agreement for Salmonid Enhancement and Conservation to Dr. Knoechel.

I wish to thank my supervisory committee members, Dr. Richard Haedrich and Dr. John Green, for their expertise and advice throughout this study, and for reviewing this thesis.

I wish to acknowledge the following individuals for their help throughout my study: Danny, Trevor, Jennifer, Shawn and Derek for their assistance while in the field; Pat Ryan (Department of Fisheries and Oceans) for part of the population data; Keith Clarke (Department of Fisheries and Oceans) for the electrofisher training and for data from earlier work completed at the EPA; Dr. Robert Dunbrack for lab space; Eric Baggs and Dr. Gary McGowan for information about lipid analysis, Kevin Mercer for lab space and equipment at the Marine Institute; all the technical and office staff of the Biology Department.

Thanks to my fellow graduate students in Biology for giving me the honour of representing them as Chairperson of the Biology Graduate Students Association and as a member of the Graduate Students' Union of the Memorial University of Newfoundland Board of Directors. Thanks also to Trevor, Kent, Jose and Dwayne for your support and to the BBQ gang and Mike for all the great memories.

I would like to thank Jennifer Lawlor for her love and support during the final years of this thesis. She helped me regain the courage and focus I had lost, and gave me a kick when I needed it the most.

Finally, I wish to thank my parents Derm and Gail, whose patience and support while I was away from home helped me continue on.

Dedication.

I dedicate this study in memory of my Uncle Robert (Bobby) Boone who passed away December 12, 2000.

The Cast of a Lifetime...

Everything looks grand,
When I peer from the land,
Into the waters fished by few.
I'll be thinking of you.

Everything feels fine,
When I cast my one line,
Into the waters clear and blue.
I'll be thinking of you.

Everything flows nice,
As I watch my line splice,
Into the waters clean and true.
I'll be thinking of you.

Everything grows bright,
When I feel my fish bite,
From these waters fine and new.
I'll be thinking of you.

Everything looks grand,
With my fish now at hand,
From these waters fished by few.
I'll be thinking of you.

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Chapter 1. General Introduction.

The brook trout, *Salvelinus fontinalis*, is a dominant species in many insular Newfoundland lakes, locally known as ponds, and supports an important recreational fishery. These lakes are generally more acidic and of lower productivity than those of mainland North America and Europe (Kerekes 1975, Knoechel and Campbell 1988). They have a depauperate fish community consisting primarily of three species: threespine stickleback (*Gasterosteus aculeatus*), Atlantic salmon (*Salmo salar*), and the brook trout (*Salvelinus fontinalis*) which relies heavily on the benthic invertebrate community for their food (Baggs 1985, Brown 1993, Clarke and Knoechel unpublished data). Other fish species found in Insular Newfoundland lakes include the introduced brown trout (*Salmo trutta*), rainbow trout (*Oncorrynchus mykiss*), and lake whitefish (*Coregonus clupeaformis*), the banded killifish (*Fundulus diaphanus*), and the arctic charr (*Salvelinus alpinus*). However, these species are not as widely distributed throughout the island. The reason for the depauperate fauna is a contribution of the island's isolation from the mainland of North America and the effects of the last glaciation (Larson and Colbo 1983).

Little is known about the ecology of brook trout in the lakes and rivers of Central Newfoundland. Most knowledge concerning brook trout in Newfoundland comes from studies of fluvial and lacustrine habitats of the Avalon Peninsula and the island's north-eastern coast. Wiseman (1969) described the morphology, population ecology, life history, growth characteristics, parasitology, and feeding ecology of brook trout from river and lake sites on the Avalon Peninsula and the Northeastern region of the island. Later studies include an investigation of selected life history parameters of lake-dwelling brook trout (Big Northern Pond, Avalon Peninsula: Baggs 1985) and a study on the feeding strategies of trout in a river (Wings Brook, Avalon Peninsula: Thonney and Gibson 1989). Studies in the last decade include an investigation on life history variation of stream dwelling brook trout (Trepassey area, Avalon Peninsula: Hutchings 1991), a brief account on physiology of lake dwelling trout (Avalon Peninsula: Mayo 1994), an investigation into the movement patterns of brook trout (Copper Lake, Western Newfoundland: McCarthy 1997), and a very recent study on the overwintering of trout in rivers (Indian Bay, Eastern Newfoundland: Hutchings *et al.* 1999).

Central Newfoundland differs from the eastern and western regions of insular Newfoundland. The central region has the highest summer and lowest winter temperatures and an annual precipitation ranging from 900 mm in the north to over 1250 mm to the south (Damman 1983). The main physiographic divisions are the North East Trough in the north and the Central Plateau in the south, which include the areas drained by the Gander and Exploits rivers along with thousands of small shallow lakes interspersed with ribbed fen bogs and balsam fir-black spruce forests. It is also geologically distinct in that it separates the remnants of the ancient continents of Laurentia (Humber Zone: Western Newfoundland) and Gondwana (Avalon Zone: Avalon region) (Rogerson 1983). The island of Newfoundland supported its own ice cap during the last late-Wisconsin glacial maximum (15 000 yr B.P.). The thickest ice and the greatest amount of rebound probably occurred in the interior of the island (Rogerson

1983). This suggests that the freshwater habitats of the central plateau were probably the last to be colonized by the brook trout and associated invertebrate fauna.

The Department of Fisheries and Oceans Experimental Ponds Area (48°19'N; 55°28'W) includes 8 small brown water lakes and their watersheds at the headwaters of the Northwest Gander River, on the central plateau of central Newfoundland. Limnological data have been collected from this area since 1977 by the Department of Fisheries and Oceans, Forestry Canada, Conservation and Protection Branch of the Canadian Wildlife service and Memorial University to document and understand the physical, chemical and biological factors which affect the production of Atlantic Salmon (Ryan *et al.* 1994). Studies on brook trout include an early report on the size and growth of these fish (Ryan *et al.* 1981), a description of their parasites (Cone and Ryan 1984), and descriptions of population status and movement ecology within the area (Ryan 1984, Ryan 1990, Knoechel and Ryan 1994, Ryan and Knoechel 1994).

A whole-lake fertilization experiment was initiated in 1991 as part of a Memorial University of Newfoundland project (headed by Dr. Roy Knoechel) funded by NSERC and the Department of Fisheries and Oceans, Canada. Whole-lake fertilization should enhance the productivity of a lake ecosystem through 'bottom-up' processes. One impact of the addition of nitrogen and phosphorous fertilizers was a 2–4 fold increase in the total abundance of macroinvertebrates (Moore 1999). It was hypothesized that this increase should enhance the productivity of the brook trout through community food web interactions. These enhancements might include increased population size, increased survivorship and increased growth.

The primary objective of this study was to describe the ecology of brook trout residing in three ponds of the Experimental Ponds Area, central Newfoundland. A secondary objective was to compare brook trout in the natural ponds to the experimental pond to evaluate how brook trout have responded to whole-lake fertilization. Chapter 2 describes the study sites and the whole lake fertilization procedure. Chapter 3 presents results of a study on brook trout feeding ecology and physiological condition in the experimental pond compared to that of a control pond over the summer of 1996. Chapter 4 describes the general life history and growth characteristics of brook trout in the Experimental Ponds Area and presents comparisons of population size, structure and growth in the experimental pond relative to the controls.

Chapter 2. The Study Site.

The brook trout of three ponds, Coles Pond (48° 17.4' N 55° 31' W), Spruce Pond (48° 19' N 55° 28' W) and Headwater Pond (48° 19' N 55° 29' W) were studied. These ponds are located in the Department of Fisheries and Oceans Experimental Ponds Area (EPA) at the headwaters of the Northwest Gander River in central Newfoundland (Figure 2.1). They are small (surface areas ranging from 25.7 - 76.9 ha), shallow (mean depths 1.0 - 1.3 m), and typical for this area (Table 2.1) (Ryan and Wakeman 1984, Ryan *et al.* 1994) and for insular Newfoundland in that they are oligotrophic (Knoechel and Campbell 1988) and have a depauperate fauna. The fish community of the ponds include the threespine stickleback (*Gasterosteus aculeatus*), the brook trout (*Salvelinus fontinalis*) and the Atlantic salmon (*Salmo salar*). The American eel (*Anguilla rostrata*) has only been captured a few times near the inlet / outlet of Spruce Pond and thus, is considered rare for this area.

A whole-lake fertilization experiment was conducted from 1991 to 1996. Nitrogen, in the form of sodium nitrate (1991 - 1992) or ammonium nitrate (1993 - 1996) and phosphoric acid were added to Coles Pond during the summer in each year (see Table 2.2 for fertilizer dosages). Both Spruce Pond and Headwater Pond remained unfertilized and served as control sites to investigate the responses of brook trout. Spruce Pond served as the primary control for plankton and benthic macroinvertebrate comparisons.

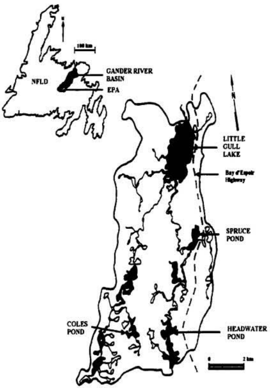


Figure 2.1. A map of the location of the three study ponds.

Table 2.1. Physical characteristics of Coles, Headwater and Spruce pond (data from Ryan and Wakeman (1984) and Knoechel (unpublished data)).

Parameter	Coles Pond	Headwater Pond	Spruce Pond
Surface Area (ha)	25.7	76.1	36.5
Volume ($m^3.10^3$)	322	872	364
Maximum depth (m)	3	3.3	2.1
Mean depth (m)	1.3	1.1	1
Catchment Area (ha)	331	596	2 006

Table 2.2. Annual dosage and duration of nutrient addition to Coles Pond, 1991-1996.

	N (kg)	P(kg)	N (g / m^2)	P (g / m^2)	Duration (Days)
1991	49.2	6.9	0.191	0.027	79
1992	70	9.4	0.272	0.037	96
1993	195.3	25.8	0.76	0.1	100
1994	195.3	25.8	0.76	0.1	100
1995	195.3	25.8	0.76	0.1	100
1996	195.3	25.8	0.76	0.1	100

Chapter 3. Studies on the feeding ecology and physiological condition of *Salvelinus fontinalis* Mitchill during the ice-free season in ponds of the Experimental Ponds Area, insular Newfoundland.

3.1 Introduction.

This chapter presents the feeding ecology of brook trout in terms of feeding intensity and diet composition during the ice-free season and then relates these variables to observed changes in brook trout physiological condition as estimated by lipid content.

3.1.1 Feeding Ecology.

The analysis of fish stomach contents provides fundamental information on the quantity and type of prey selected, which allows researchers to examine how feeding and food habits vary among individuals (Momot 1965, Baggs 1985, Chapman *et al.* 1989), throughout time (daily, monthly, seasonal) (Needham 1932, Allen and Claussen 1965, Allan 1981), and across aquatic habitats (Ricker 1932, Wiseman 1969, Allen *et al.* 1994). Stomach content analysis also provides information on where fish feed within an aquatic environment. For example, diets from lake-dwelling salmonids may be comprised of benthic, pelagic or surface-associated organisms.

Brook trout have been described as opportunistic generalists that feed on a wide variety of invertebrate and vertebrate animals (Scott and Crossman 1973, Power 1980).

This wide prey variety is primarily due to differences among the availability of prey types found in various aquatic habitats. For example, studies in Ontario (Ricker 1932) and Quebec (Lachance and Magnan 1990, Lacasse and Magnan 1992) indicated fish and plankton were important prey items whereas diet was dominated by benthic invertebrates in lakes with depauperate invertebrate and vertebrate fauna due to isolation (high altitude: Swift 1970; insular Newfoundland: Wiseman 1969, Baggs 1985, Knoechel unpublished data).

Brook trout diet also responds to changes in the availability of prey through time. For example, diel peaks in the number of prey types consumed by stream-dwelling trout corresponded with times when the number of prey found in the drift was increasing (Allan 1981). Several studies have documented seasonal declines in the insect component of the diet as the insects emerge and become less available to trout predation (Needham 1932, Elliot 1973, Thonney and Gibson 1989). The few studies that have documented the change in the diet composition of brook trout across the ice-free period in lake habitats indicate that the seasonal change or shift among functional groups of prey (example: benthic prey to surface prey) is due to declines in the abundance and/or availability of one prey group relative to another (Allen and Claussen 1965, Momot 1965, Lacasse and Magnan 1992, Venne and Magnan 1995). Only two studies have documented the brook trout diet for insular Newfoundland lakes on the Avalon Peninsula (Wiseman 1969, Baggs 1985). This present study is the first to document brook trout feeding ecology in the central region of insular Newfoundland.

The feeding and food habits of fish may also vary due to gender and to different size classes of fish. Differences in the physiology and behaviour of male and female brook trout may affect the types of prey each selects. For example, the energy requirements needed for the production of gametes in female salmonids are generally higher than those for males (Love 1970). Female fish may therefore require prey of higher nutritional quality compared to male fish or they may need a greater range of prey types or greater amount of prey. Large fish possess the functional capability and experience required for the capture of larger-sized prey and/or greater amounts of prey in comparison to small fish. Studies have shown a positive correlation between prey size and gape length in Atlantic salmon (Keeley and Grant 1997) and a positive relationship between ration and fork length of brown trout (Elliot 1976a). Thus it is expected that diets of larger brook trout should include larger prey and should contain greater amounts of prey items compared to smaller trout.

The present study uses stomach content analysis to document the feeding intensity and diet composition of brook trout from the Experimental Ponds Area, and to describe the pattern of each across the ice-free period. Diet composition and seasonal diet selection are compared between the genders, between two size-classes of brook trout, and between two ponds, one of which has been experimentally fertilized.

3.1.2 Physiological Condition.

Lipids are an important source of potential chemical energy and their relative level reflects the physiological condition of fish (Love 1970, Jobling 1994). Lipids stored in somatic and visceral tissue usually constitute the greatest proportion of lipid reserves in salmonids. These reserves have been shown to vary seasonally during the periods of lipid accumulation and depletion associated with the reproductive cycle in salmonids (Jobling 1994, Mayo 1994) and coregonids (Lizenko *et al.* 1973). Gonadal tissue accumulates lipids throughout the reproductive maturation period usually at the expense of somatic-visceral reserves (Love 1970, Nassour and Léger 1987, Encina and Granado-Lorencio 1997).

Seasonal patterns in the lipid content of salmonids have been attributed to changes in food availability (Elliot 1976a, Cunjak and Power 1987) and quality (Love 1970), to changes in metabolic rates due to seasonal variation in water temperature (Elliot 1976a, Elliot 1982) and to developmental changes such as gonad maturation (Nassour and Leger 1987, Jobling 1994) and smoltification (Sheridan *et al.* 1983, Birt and Green 1986). Percent lipid content has also been shown to be negatively correlated with percent water content (Elliot 1976a, Cunjak 1988, Jonsson and Jonsson 1998) and positively correlated with condition factor (Caulton and Bursell 1976, Elliot 1976a).

A consistent seasonal pattern of lipid change has been observed throughout the salmonids. Lipid accumulation in visceral and somatic tissue coincides with increased feeding from spring to mid-summer (Elliot 1976b, Cunjak and Power 1986). Depletion of visceral-somatic lipid coincides with gonad maturation and spawning in reproductive fish (Nassour and Léger 1989), with decreased food availability late in the ice-free season and with physiological acclimation to cold water habitation during the overwinter period both in reproductive and non-reproductive fish (Cunjak and Power 1986, Cunjak 1988).

Fertilization of a lake ecosystem should impact the fish community through food chain effects. One impact of the addition of nitrogen and phosphorous fertilizers to a small shallow lake in central Newfoundland was a 2 - 4 fold increase in the total abundance of benthic macroinvertebrates (Clarke 1995, Clarke *et al.* 1997, Knoechel *et al.* 1999, Moore 1999). It was hypothesized that the increase in prey abundance would enhance the productivity of the brook trout. Another impact of whole-lake fertilization might be the enhancement of the nutritional quality of benthic prey organisms. Thus, it was also hypothesized that trout feeding on greater amounts of prey similar in 'nutritional quality' or feeding on prey of higher 'nutritional quality' in the experimental pond would have greater somatic - visceral lipid reserves relative to those in the control pond.

The present study describes the pattern in percent lipid content for male and female brook trout across the ice-free period and then compares the observed seasonal changes in lipid content to those observed for feeding intensity (mean ration and percentage empty stomachs), surface water temperature and gonadal-somatic index. Lipid contents are compared between fish from the fertilized pond and the control ponds to evaluate the potential impact of whole-lake enrichment. The relationships among lipid content, water content and two morphometric condition factors are determined.

3.2 Methods and Materials.

3.2.1 Sample Collection and Treatment.

Diet composition, lipid content, water content, gonadal-somatic index and condition factor of brook trout were evaluated monthly in two of the study ponds (Coles and Headwater) during the summer (May - September) season in 1996. Additional specimens were collected from Spruce Pond in May and September only. Fish were collected using 15 - 19 mm stretch-mesh fyke nets set overnight from shore for a duration no greater than 15 hours, with one exception: the fyke net sample collected from Coles Pond in June 1996 was set for a 6- hour daylight duration. Fork length (mm) and weight (g) were recorded for a sample of fish representative of the total range of lengths caught during each sampling period.

Individual fish were sacrificed using cervical dislocation, then frozen for further laboratory analysis. Upon dissection, stomachs were cut free at the esophagus and at the constriction of the duodenum, opened, and then cleared of all contents. Contents were stored in 95 % ethanol, identified, and then were weighed to the nearest 0.1 mg after drying for 48 hours at 65 °C. Stomachs void of content and those containing only mucus were recorded as empty. Gonads were removed from each fish, stored in 75 % ethanol and were later weighed to the nearest 0.1 mg wet weight. Upon removal of stomach content and gonad, the wet weight of each fish was measured and then re-weighed after drying for 72 hours at 65 °C to determine dry weight. The difference between the dissected wet weight and the dry weight gave the water content which was expressed as a percentage of the dissected wet weight. Gonadal somatic index (GSI) was calculated as the gonad weight (g wet weight) divided by the whole wet weight excluding the stomach contents.

Lipid content was gravimetrically determined similar to the method described by Bligh and Dyer (1959) with a change in the extraction solvent from chloroform to hexanes. Individual dried samples were ground to a grain size less than 3 mm in diameter and were thoroughly mixed in a Waring blender before the extraction process since studies have documented variation in the lipid content of liver, heart, white muscle, and visceral tissue (Lizenko 1973, Nassour and Léger 1987, Mayo 1994). Lipid was extracted from dry samples using a Soxtec Fat Extraction Unit with hexanes as the extraction solvent (Egan 1981). The lipid content was expressed as a percentage of the dry weight of the original sample used. Duplicate samples and both positive and negative controls were also run through the extraction procedure to test the accuracy of the extractor unit.

Morphometric condition factors were calculated using the dissected wet weight, the dissected weight plus the weight of the gonad, and the whole weight of those fish used in the lipid analysis. Condition factor was measured as a function of the relationship between the length and weight of an individual fish and was calculated using the formula for Fulton's condition factor (LeCren 1951):

$$K = 100\ W / L^3,$$

and the formula for relative condition factor (LeCren 1951):

$$Kn = 100\ W / L^b.$$

Relative condition (Kn) factor differs from Fulton's in that the coefficient b is the slope from the least squares relationship between $\log_{10}$ weight and $\log_{10}$ length of all fish used for lipid analysis. Thus, relative condition (Kn) is specific to this group.

3.2.2 Feeding Ecology.

3.2.2.1 Feeding Intensity.

Monthly mean ration and percentage empty stomachs were used as indicators of brook trout feeding intensity. Ration was determined as the total amount of food found per stomach sample measured to the nearest 0.1 mg dry weight. The relationship between ration and fish size (length) was evaluated for each pond and then was compared between ponds using analysis of covariance (ANCOVA, Sokal and Rohlf 1995). The analysis of covariance facilitated the estimation of adjusted mean rations for each pond and gender, with correction for the covariate length and the variation due to the nominal scale variables: pond, gender and month. Seasonal patterns in the feeding intensity were evaluated by graphing the observed mean ration (summed weight of all contents / total number of fish with food), the adjusted mean ration estimated from the ANCOVA model and the percentage of fish with empty stomachs (total number of empty stomachs / total number of fish sampled per sampling date) across the five-month study period.

3.2.2.2 Percentage Diet Composition.

Stomach content items were identified at least to order and usually to family. Further taxonomic division was used to emphasize the relative importance of individual genera within specific orders or families. A small portion of the stomach contents items (< 0.4 % by weight) that could not be identified at least to order were omitted from further calculations and analyses. Diet composition for each taxonomic group was calculated as percentage of total ration for each fish separately and then averaged over all fish, hereafter referred to as percentage diet composition. This method reduces the influence of heavier but rare diet items and facilitates comparisons among fish of different sizes as compared to the common method of calculation which sums the total ration over all fish before calculating percent composition. For example, a single three-spine stickleback was a large diet item eaten by only one of thirteen fish from Coles Pond in September. This prey item represented 30 % of the total summed ration of all fish but constituted a percentage diet composition of only 7 % when averaged across the total number of fish sampled (91 % of ration in one fish and 0 % for the other 12).

Diet data for each pond was pooled across the five-month sample period to facilitate graphic comparisons of the percentage diet composition of prey groups between Headwater Pond and Coles Pond. Once pooled, individual taxa were ranked in descending order of percentage diet composition to identify taxa common to Headwater Pond and Coles Pond, and to identify prey taxa unique to each pond.

3.2.2.3 Seasonal Pattern in Selection of Prey Categorized by Habitat and/or Behaviour.

Brook trout diet selection relative to prey ecological characteristics was evaluated by sorting stomach content items into four functional prey types based on prey habitat type (Benthic, Pelagic or Surface) and, for the Benthic group, prey behaviour (Evasive or Passive) (Table 3.1). Benthic prey which can evade predators via quick escape responses were categorized as Benthic Evasive and included the Odonata, Ephemeroptera, Trichoptera, Hemiptera, Amphipoda and Hydracarina. Benthic Gastropoda, Pelecypoda, Annelida and aquatic dipteran larvae were classed as Benthic Passive prey, prey which can evade predators but with slower escape responses relative to Evasive prey. Pelagic prey types were those organisms living freely in the water column, such as the threespine stickleback. The Surface prey group included an aquatic component (dipteran pupae and adults) and a terrestrial component (Insecta and Hymenoptera) of winged insects which were assumed to be on or near the surface when feed on by the trout. Graphical analysis was used to compare the seasonal patterns in prey type for each pond.

Graphical analysis of the percentage diet composition (prey type and prey group) and seasonal diet pattern was used to compare between gender (male and female) and size-classes (small < 180 mm, and large ≥ 180 mm). The size-classes were separated

Table 3.1. Stomach content items sampled from Experimental Ponds Area brook trout.

Prey Type	Prey Group	Common Name	Prey Taxa
Benthic Evasive	Odonata	Dragonfly nymphs	*Cordulia* spp.
			Aeshna spp.
			Unidentified Odonata
		Damselfly nymph	*Enallagma* spp.
	Ephemeroptera	Mayfly nymphs	Ephemeroptera
		Burrowing mayfly nymph	*Hexagenia rigida*
	Trichoptera	Caddisfly larvae	Trichoptera
	Hemiptera	Pygmy backswimmer	Corixidae
	Other Aquatic	Amphipods and mites	Amphipoda/Hydracarina
Benthic Passive	Gastropoda	Snails	*Amnicola* spp.
			Heliosoma spp.
			Physa spp.
	Pelecypoda	Fingernail clam	Pelecypoda
	Annelida	Aquatic worms	Annelida
	Diptera	Aquatic dipteran larvae	Diptera larvae
Pelagic	Fish	Three-spined stickleback	*Gasterosteus aculeatus*
Surface	Diptera	Pupae and adults of aquatic origin	Aquatic Diptera
Terrestrial Insecta	Hymenoptera	Winged ants	Hymenoptera
	Insecta	Insects of terrestrial origin	Terrestrial

based on the median fork length observed for all fish sampled during the ice-free season.

3.2.3 Physiological Condition.

The percent lipid content measured in this study represents the somatic-visceral lipid reserve because gonad and stomach contents were removed prior to extraction. Monthly mean percent lipid values were graphed to qualitatively characterize lipid variation. Analysis of variance (ANOVA, Sokal and Rohlf 1995) of somatic-visceral lipid content was used to quantify how percent lipid varied across season, between genders and among ponds. Further statistical analyses were performed to quantify the difference in lipid content from spring to mid-summer and from mid-summer to fall (Tukey post-hoc test, Sokal and Rolf 1995). Graphical techniques were used to evaluate how the seasonal pattern in percent lipid content corresponded with that observed for adjusted mean ration, percentage empty stomachs, surface water temperature, and gonadal somatic index. Emphasis was placed on the patterns for female fish because data were available for each month of the study only for females.

The percent lipid content values for each fish sampled was transformed to percent wet weight to facilitate the comparisons among somatic-visceral lipid content, water content and morphometric indices of condition. The percent lipid wet weight per fish was calculated using the formula:

$$\% \text{ Lipid (wwt)} = [(\% \text{ Lipid (dwt)} / 100) \times (W_{(\text{Fish dwt})} / W_{(\text{Fish wwt})})] \times 100\ \%,$$

where $W_{(Fish\ dwt)}$ is the dissected dry weight and $W_{(Fish\ wwt)}$ is the dissected wet weight per fish. Correlation analysis (Sokal and Rohlf 1995) was used to measure the association of water content, Fulton's condition factor and relative condition factor to lipid content. Graphical analysis was used to compare the seasonal patterns for each variable and the association among patterns was measured using correlation analysis. Ordinary least squares regression (Ricker 1973, Sokal and Rohlf 1995) was used to determine the relationships of lipid content to water content, to Fulton's condition factor (K) and to relative condition factor (Kn) (K and Kn calculated using dissected wet weight).

Stepwise multiple linear regression was used to examine whether percent lipid content could be predicted from percent water content, K and Kn. K and Kn were calculated using each measure of weight (dissected, dissected + gonad, whole) to determine which measure would best predict percent somatic-visceral lipid content. Binary dummy variables were created for gender (1 variable) and each month (5 variables), and then used to determine whether or not these variables contributed significantly to the prediction of somatic-visceral lipid content. The binary dummy variable for gender coded females as 0 and males as 1. Each of the monthly binary dummy variables coded data from the month selected as 1 and all other data as 0. The adjusted r^2 value was used to compare which model best predicted lipid content.

The level of statistical significance for all statistical procedures used was set at $\alpha = 0.05$, and residuals from each procedure were examined to meet the error assumptions of the general linear model (Sokal and Rolf 1995).

3.3 Results and Discussion.

The following discussion focuses on results of studies conducted on brook trout collected during the 1996 field season. In total, 264 brook trout were sampled from the fertilized Coles Pond (N = 146) and one of the control ponds, Headwater Pond (N = 118) over the 5-month study period beginning in May. In addition, 70 fish were sampled from Spruce Pond, the second control pond, in May (N = 46) and September (N = 24). The first section discusses the results from the comparative study on the feeding ecology of brook trout while the second section focuses on the comparison of the changes in the physiological condition of reproductively maturing male and female brook trout during the ice-free season.

3.3.1. The Feeding Ecology of Brook Trout in the EPA.

Analysis of the stomach contents was used to evaluate feeding intensity and diet composition of brook trout from the Experimental Ponds Area, Newfoundland. This discussion initially presents the results on brook trout feeding intensity to address the relationship between ration and fish size, and whether average ration varies with time, habitat, or gender. Subsequent comparisons of diet composition and seasonal diet selection are made among habitats, genders and two size - classes of fish.

3.3.1.1 Feeding Intensity.

Analysis of covariance (GLM ANCOVA SPSS 8.0) was used to model the linear relationship between ration and brook trout length, and to test if the relationship between ration and length varied due to habitat, time or gender. All 2 - way, 3 - way and 4 - way interactions between the fixed variables and the co-variate were also tested for significance. The initial step in the ANCOVA was to run a model with all variables (Appendix A) to determine which could be removed due to non-significance.

The expected positive relationship between ration and fish length was observed for brook trout from the Experimental Ponds Area (Figure 3.1) and was statistically highly significant (Table 3.2). ANCOVA was employed to determine if there was further significant variance in the ration that could be attributed to pond, month or gender, or to interactions among these variables and the covariate, length (Table 3.2). For example, [Gender x Length] was the interaction factor representing the slope parameter comparing each gender. None of the interactions between nominal variables and the co-variate contributed significantly in the initial ANCOVA model (Appendix A). This was expected since the observed positive relationship between ration and fish size should be a function of an increase in the capacity of larger fish to hold more food.

Forty-nine percent (adjusted r^2) of the total variation in brook trout ration was explained by the ANCOVA model:

$$\log_{10}(\text{Ration (mg)}) = \beta_o + \beta_{Length}(\text{Length (mm)}) + \beta_{Pond}(\text{Pond}) + \beta_{Month}(\text{Month}) +$$

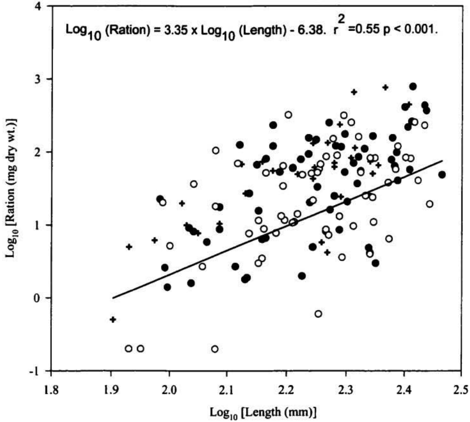


Figure 3.1. The relationship of ration (log_{10}(ration)) and fish size (log_{10}(fork length)) for brook trout sampled from the Experimental Ponds Area, insular Newfoundland. The symbol (○) represents trout from the fertilized Coles Pond (N = 61), (●) fish from Headwater Pond (N = 64) and (+) fish from Spruce Pond (N = 31). Fish with empty stomachs were omitted from this analysis.

Table 3.2. Summary table of ANCOVA model to predict brook trout ration in the Experimental Ponds Area. None of the interaction variables with the covariant ($\log_{10}$ (Length)) were significant, thus all were removed from the model. The percentage variance is the variance each factor contributes to the model and was calculated by dividing the adjusted sum of squares of each factor by the total model sum of squares. The adjusted $r^2 = 0.494$, $F_{1,18} = 10.065$, $p \leq 0.001$.

Factor	Degrees of Freedom	F - Statistic	Significance	Percentage Variance
Log_{10} (Length)	1	86.52	≤ 0.001	27.99
Month	4	3.91	0.005	3.80
Pond	2	5.88	0.004	5.06
Pond x Month	5	4.36	0.001	7.05
Sex x Month	4	3.43	0.003	5.54
Error	138			

$\beta_{\text{Pond x Month}}$ (Pond x Month) + $\beta_{\text{Gender x Month}}$ (Gender x Month) + ε;

where β_o is the grand mean, β_F is the parameter for each variable F (F = pond, month, gender) and ε represents the error. Ration varied significantly among ponds and across months after adjustment for the co-variate length (Table 3.2). Further investigation revealed that the adjusted mean ration for Coles Pond was significantly lower when compared to Headwater Pond and Spruce Pond separately (mean difference Coles - Headwater = -0.379 $p = 0.001$, df = 1; mean difference Coles - Spruce = -0.233, $p = 0.013$, df = 1).

Monthly mean ration was lowest during the last two months of the study period (Figure 3.2). A decline in the mean ration from spring to fall has been attributed to seasonal declines in prey abundance (Momot 1965, Allan 1981). Clarke (1995) observed a decline in the density of *Cordulia*, *Enallagma*, and *Amnicola*, estimated from benthic dredge samples, from May to August for ponds in the Experimental Ponds Area while abundance estimates from artificial substrate samplers showed an increase in Ephemeroptera and Gastropoda from spring to fall (Clarke 1995, Clarke *et al.* 1997).

The ANCOVA model (Table 3.2) was used to generate adjusted monthly mean ration for each pond and gender, thereby accounting for the significant co-variation due to fish size (27.99 % from Table 3.2). The significant interactions between the fixed variables, Gender x Month, and Pond x Month, indicated that the seasonal pattern in ration differed among ponds and between genders (Table 3.2). The pattern in the adjusted mean ration from May to July in Coles Pond was opposite to that observed in Headwater

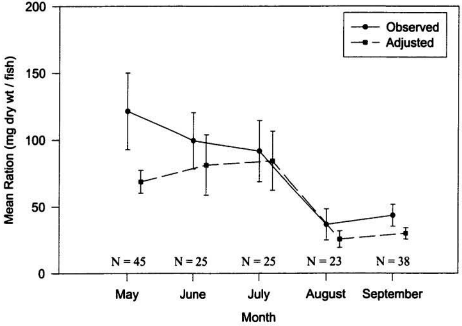


Figure 3.2. Observed and adjusted monthly mean ration (± 1 standard error) for all brook trout samples from the Experimental Ponds Area, insular Newfoundland. Adjusted mean ration is corrected for co-variation due to fish size variation among samples.

Pond (Figure 3.3 A.) in which mean ration was highest in June for Coles Pond trout compared to May and July peaks in Headwater Pond. The greater ration in June for Coles Pond trout may be due to differences in sampling duration and time. These trout were collected from a fyke net set for a 6 hour daylight duration (12:30h - 18:30h), while all other trout were collected from nets set overnight. Female trout ration steadily increased from May to July compared to a lower ration in male trout which peaked in June and then declined steadily (Figure 3.3 B.). Large standard errors about the adjusted mean within a pond (and gender) during June and July indicate high variability in the amount of food eaten among individual fish regardless of their size.

A greater percentage of trout fed actively in both Headwater Pond and Spruce Pond as compared to Coles Pond. Coles Pond trout had approximately 54% less ration after adjustment for differences due to fish size, and had twice the percentage of empty stomachs (Table 3.3). An earlier investigation in the summer of 1993 revealed a similar ration difference (~ 50 % less) but showed little difference between the percentage of empty stomachs in Coles Pond and Headwater Pond (24 % and 27 %, respectively, K. Clarke unpublished data). Thus, Coles Pond brook trout obtain lower ration during the overnight period regardless of the proportion of fish actively feeding. The percentage of empty stomachs was generally low in the initial months of the study, peaked in July then decreased through to September (Figure 3.4). This pattern was similar regardless of gender and size class within each pond and Coles Pond had greater percentages of empty stomachs in four of the five study months (Appendix B).

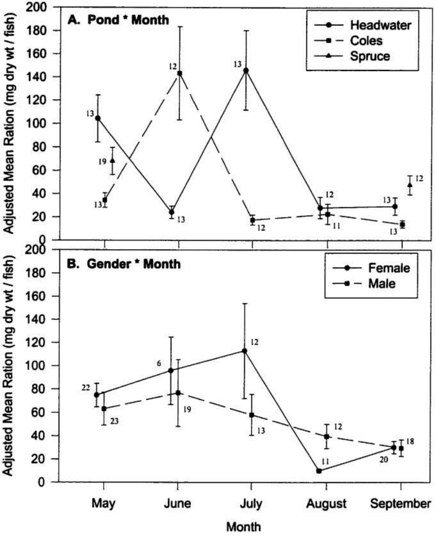


Figure 3.3. The seasonal patterns in adjusted mean ration (± 1 standard error) for brook trout separated by pond (A) and gender (B).

Table 3.3. Sample sizes and the percentage empty stomachs for brook trout samples collected over the summer in three ponds of the Experimental Ponds Area, insular Newfoundland. Percentage empty stomachs was calculated as the number of stomachs observed as empty divided by the total sample size of fish collected.

	Total Brook Trout			Observed Empty Stomachs (% empty)				
Pond	**N**	**Male : Female**	**Small : Large**	**Total**	**Male**	**Female**	**Small**	**Large**
Coles	145	73 :72	76 : 69	63 (43)	42 (42)	31 (43)	35 (46)	28 (41)
Headwater	117	70 : 47	58 : 59	23 (20)	12 (17)	11 (23)	12 (21)	11 (19)
Spruce	70	30 : 40	36 : 34	17 (24)	8 (24)	9 (23)	10 (28)	7 (21)

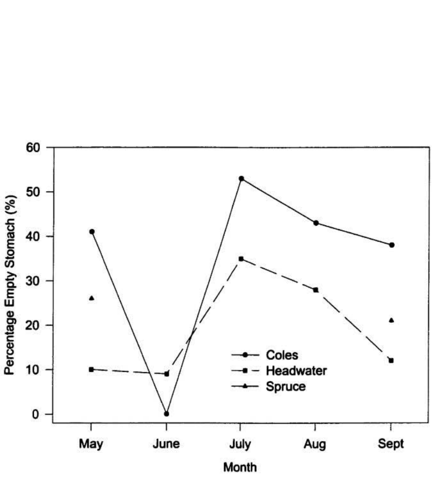


Figure 3.4. Comparison of the seasonal pattern in percentage empty brook trout stomachs for each of the three study ponds of the Experimental Ponds Area, insular Newfoundland.

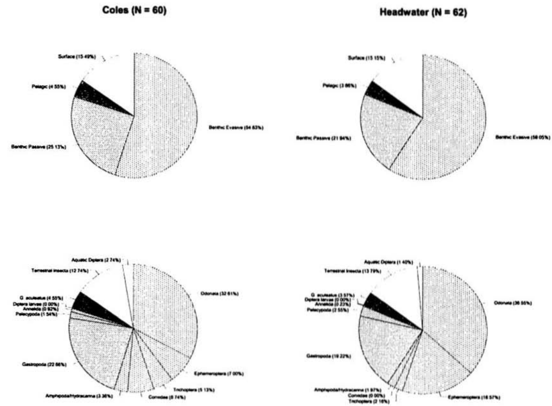
3.3.1.2 Percentage Diet Composition.

Seventy-nine percent (15 / 19 x 100%) of the diet items identified in this study were benthic invertebrates indicating brook trout of the Experimental Ponds Area are primarily benthic feeders (Benthic Evasive and Benthic Passive types, Table 3.1). Stomach contents also included the pelagic threespine stickleback and insects associated with the water-air interface. Dominance of benthic and terrestrial insects in brook trout diets have previously been shown in studies on riverine populations in Quebec (Cunjak and Power 1986), Ontario (Cunjak and Power 1987), insular Newfoundland (Wiseman 1969, Thonney 1984, Thonney and Gibson 1989), and on lake populations in Ontario (Ricker 1932), insular Newfoundland (Wiseman1969, Baggs 1985) and Labrador (Keats 1986). In contrast, studies in the Laurentian Shield lakes showed that Pelagic Prey (zooplankton and fish) were either equal to or more important than benthic prey in trout diet (Lachance and Magnan 1990, Lacasse and Magnan 1992, Venne and Magnan 1995), while a study in northern Ontario showed a dominance of fish prey in brook trout greater than 240 mm (Ricker 1932).

Fourteen of the fifteen benthic prey items have been previously observed in benthic dredge and rock-bag samples (Clarke 1995, Moore 1999, Knoechel unpublished data), and have previously been observed in stomachs of brook trout from an earlier investigation in the Experimental Ponds Area (Ryan unpublished data, Clarke and Knoechel unpublished data). The exception was *Hexagenia rigida*, commonly known as the burrowing mayfly, which spends most of its life history burrowing up to 20 cm deep in mud sediments of ponds making it difficult to detect with the sampling methods previously used.

Evaluation of the Headwater Pond and Coles Pond samples pooled over the five-month study period in 1996 revealed similar major dietary groups (Figure 3.5 bottom pie charts). Odonata dominated the percentage diet composition in both ponds. The next most prevalent groups were the Gastropoda followed by the Terrestrial Insecta, each of which had similar percentage diet composition in both ponds. Headwater Pond brook trout had more than twice the proportion of Ephemeroptera as compared with that found in Coles Pond (18.57 % to 7.00 %, respectively), largely due to the higher proportion of *Hexagenia* nymphs observed in a greater number of fish (5 more fish than in Coles) during the July sample from Headwater Pond. Stomach contents of brook trout from Coles Pond had greater proportions of Trichoptera, Amphipoda and Hydracarina and one unique prey group, Corixidae, compared to Headwater. The higher proportion of Trichoptera in Coles Pond was due to a greater trichopteran ration (mean = 7.65 mg / fish for N = 17) as compared to that found in Headwater (mean = 3.75 mg / fish for N = 20). Threespine stickleback represented less than 5 % of the total percentage diet composition in each pond. Only 8 of 262 fish sampled (includes those with empty stomachs) from both ponds had one stickleback each (5 from Coles and 3 from Headwater). Six of these eight specimens contained partially digested stickleback located in the forward cardiac portion of the stomach, suggesting the occurrence of sticklebacks might have been exaggerated due to their artificial concentration and confinement with the trout while in the fyke nets.

Figure 3.5. Comparison of pond-specific brook trout diet composition (%) pooled over the 5 month sampling period. Diet contents were sorted by functional prey type (habitat and behaviour) (upper pie charts) and by prey taxonomic group (lower pie charts).


Coles (N = 60)
Headwater (N = 62)
Surface (15.49%)
Pelagic (4.55%)
Benthic Passive (25.13%)
Benthic Evasive (54.83%)
Surface (15.15%)
Pelagic (3.86%)
Benthic Passive (21.94%)
Benthic Evasive (58.05%)
Aquatic Diptera (2.74%)
Terrestrial insecta (12.74%)
G. aculeatus (4.55%)
Diptera larvae (0.00%)
Annelida (0.92%)
Pelecypoda (1.54%)
Gastropoda (22.86%)
Amphipoda/Hydracarina (3.36%)
Corixidae (8.74%)
Trichoptera (5.13%)
Ephemeroptera (7.00%)
Odonata (32.61%)
Aquatic Diptera (1.40%)
Terrestrial insecta (13.79%)
G. aculeatus (3.57%)
Diptera larvae (0.00%)
Annelida (0.23%)
Pelecypoda (2.55%)
Gastropoda (19.22%)
Amphipoda/Hydracarina (1.97%)
Corixidae (0.00%)
Trichoptera (2.16%)
Ephemeroptera (18.57%)
Odonata (36.55%)

Ranking the relative contribution of each taxon within each pond provides a non-parametric means of comparing diet item importance between ponds (Table 3.4). Fourteen diet items were found to be common to both ponds in the 'Spring and Fall Rank', wherein, *Cordulia* (mean rank = 1.0), *Amnicola* (mean rank = 2.0), Terrestrial Insecta (mean rank = 4.5), *Heliosoma* (mean rank = 6.0), and Ephemeroptera (mean rank = 6.5) were the five highest ranked taxonomic groups (Table 3.4). Corixidae were found only in Coles Pond trout stomachs and were ranked third within the Coles Pond samples. Further analysis of preserved *Amnicola* revealed that 71.8% of the dry weight of this organism was shell, thus its nutritional importance is likely less than its rank suggests. Correcting for this bias drops the rank of *Amnicola* from 2.0 to 4.0 and decreases the percentage composition of the Benthic Passive group by 3 - 4%, however this correction does not substantially change the overall diet composition previously presented.

Pooling content data over the entire season (Spring thru Fall) revealed additional prey taxa common to both ponds (Table 3.4). These taxa were *Hexagenia rigida*, Hymenoptera, threespine stickleback and unidentified Odonata. The presence of *Hexagenia rigida* nymphs in July and winged ants (Hymenoptera) in August illustrate that the increase in the number of months through pooling enhances the detection of prey taxa which are available only for short periods of time during the summer. *Hexagenia rigida* nymphs become susceptible to trout predation during their mid to late July emergence period while the winged ants (Hymenoptera) become available in mid August. The three occurrences of stickleback predation observed for Headwater Pond brook trout illustrates that pooling also increases the total number of fish stomachs sampled

Table 3.4. Rank of brook trout stomach content taxa for each pond (HWP = Headwater, CP = Coles) based on percentage composition calculated across two seasons, and across five sampling months in order of declining percentages such that the greatest percentage composition equalled a rank of 1. Ranks for items common to both ponds were summed, then averaged (Mean Rank). Notes: nr = not ranked because percentage composition equalled zero; -- indicates an item unique to one pond.

		Spring and Fall Rank			Spring thru Fall Rank		
Type	Taxa	HWP	CP	Mean Rank	HWP	CP	Mean Rank
Benthic Evasive	*Cordulia*	1.0	1.0	1.0	1.0	1.0	1.0
	Aeshna	10.0	11.0	10.5	8.0	14.0	11.0
	Unidentified Odonata	9.0	nr	--	7.0	11.0	9.0
	Enallagma	13.0	14.0	13.5	11.0	9.0	10.0
	Ephemeroptera	3.0	10.0	6.5	5.0	5.0	5.0
	Hexagenia rigida	nr	nr	nr	3.0	17.0	10.0
	Trichoptera	12.0	6.0	9.0	13.0	6.0	9.5
	Corixidae	nr	3.0	--	nr	4.0	--
	Amphipoda / Hydracarina	7.0	7.0	7.0	14.0	10.0	12.0
Benthic Passive	*Amnicola*	2.0	2.0	2.0	2.0	2.0	2.0
	Heliosoma	4.0	8.0	6.0	6.0	13.0	9.5
	Physa	8.0	15.0	11.5	16.0	18.0	17.0
	Pelecypoda	6.0	12.0	9.0	12.0	15.0	13.5
	Annelida	15.5	13.0	14.3	17.0	16.0	16.5
	Diptera larvae	15.5	16.0	15.8	18.0	19.0	18.5
Pelagic	*Gasterosteus aculeatus*	nr	5.0	--	10.0	8.0	9.0
Surface	Aquatic Diptera	11.0	9.0	10.0	15.0	12.0	13.5
	Hymenoptera	14.0	nr	--	9.0	7.0	8.0
	Terrestrial Insecta	5.0	4.0	4.5	5.0	3.0	3.5

throughout the summer which in turn increases the probability of detecting rare predation events.

A majority of the taxa found in the diets of Experimental Ponds Area brook trout were benthic invertebrates in which the Odonata (primarily *Cordulia*) and the Gastropoda (primarily *Amnicola*) were most important. Terrestrial insects were the third most important group observed in brook trout diets while pelagic prey were found to be rare.

3.3.1.3 Seasonal Diet Patterns.

Diet selectivity and monthly diet patterns were evaluated by separating pooled data into their individual sampling dates. For both ponds, benthic prey types (Benthic Evasive and Benthic Passive) made up greater than 58 % of the percentage diet composition in any month (Figure 3.6, Table 3.5). Selection of prey on or near the surface occurred throughout the ice-free period and was generally greatest in August and September (Figure 3.6, Table 3.5). Selection of prey in the pelagic areas of these ponds was rare because only one group, the stickleback, was found in the gut contents and at very low percentages (Figure 3.6, Table 3.5).

The pattern of prey group selection across the ice-free period was similar in both ponds. Brook trout selected greater percentages of Benthic Evasive prey types in the first two months then switched to a diet composed of a greater proportions of Benthic Passive and Surface prey types in August and September (Figure 3.6). Studies have shown that brook trout switch from benthic prey to other prey types such as surface prey

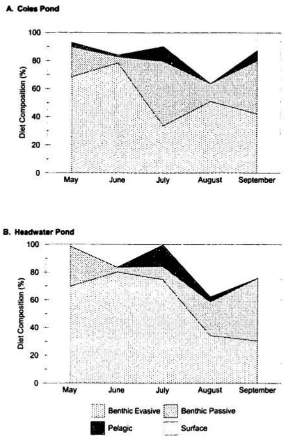


Figure 3.6. Comparison of the selection of functional prey types over the summer period observed for brook trout in Coles Pond and Headwater Pond.

Table 3.5. Monthly percent diet composition of the functional prey types found in brook trout stomach samples from the Experimental Ponds Area, insular Newfoundland.

Pond	Month and Year	N	Benthic Evasive	Benthic Passive	Pelagic	Surface
Coles	May, 1996	13	68.4	21.5	3.0	7.2
	June, 1996	12	78.5	4.4	1.2	15.9
	July, 1996	12	33.7	46.0	10.4	9.8
	August, 1996	10	51.0	12.7	0.0	36.4
	September, 1996	13	42.0	38.2	7.3	12.5
	Mean		54.8	25.1	4.6	15.5
Headwater	May, 1996	13	69.8	28.8	0.0	1.4
	June, 1996	13	80.1	3.5	0.0	16.4
	July, 1996	13	74.8	9.6	15.4	0.2
	August, 1996	11	34.1	24.5	3.6	37.8
	September, 1996	12	30.4	45.5	0.0	24.1
	Mean		59.1	21.9	3.9	15.2

(Needham1932, Wiseman 1969) and pelagic prey (zooplankton: Lacasse and Magnan 1992, Venne and Magnan 1995) as the availability of benthic prey declines throughout the season. The switch between the benthic prey types in this study suggests a seasonal decline in the availability of benthic evasive prey.

Brook trout seem to opportunistically utilize prey types in each pond when they become available. For example, the presence of aquatic dipteran pupae and adults in addition to *Cordulia* during May and June indicated trout utilized prey from different ecological zones (see Appendix C(a) and (b) for percentages of taxa found in stomachs from each pond). Similarly, the presence of terrestrial insects such as beetles, spiders, and wasps, indicates opportunism as brook trout take advantage of insects accidentally falling into the ponds from the surrounding vegetation. The August peak of Hymenoptera (winged ants, 25.8 % to 26.9 %) in each pond also demonstrates that trout select surface taxa when available even though benthic items were still predominant.

The seasonal patterns in the benthic diet taxa can be compared to previous seasonal observations of benthic macroinvertebrate densities (Clarke 1995) and relative abundances (Clarke 1995, Clarke *et al.* 1997). For example, the period of emergence for the damselfly, *Enallagma*, is between May to July (Clarke 1995), which corresponds with a June peak for *Enallagma* nymphs in trout diet for Headwater Pond (Appendix C(b)). *Cordulia*, the highest ranked diet taxon observed in this study, dominated trout diets during May and June when *Cordulia* densities have been shown to be greatest, then declined thru to September when *Cordulia* density is typically lowest (see Clarke 1995 for trend in *Cordulia* density). Trichopteran abundance was observed to be greatest in the benthos in fall (Clarke 1995, Clarke *et al.* 1997) which coincides with a higher percentage of Trichoptera in the September diet of Coles Pond fish when compared to that in the spring (Appendix C (a)).

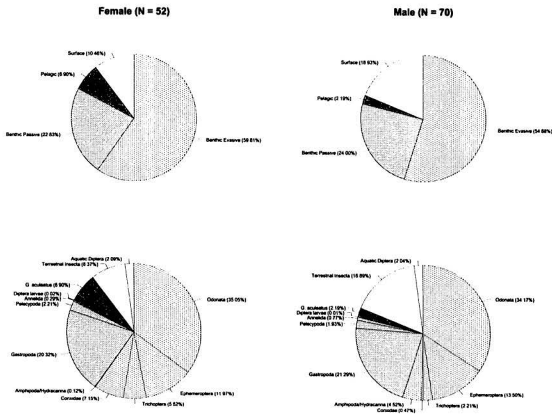
The greatest difference observed between the ponds was for *Hexagenia rigida*, which dominated the July trout diet in Headwater Pond (52 %) compared to only 2.4 % in Coles Pond. This may result from large differences in the abundances of this taxon between the ponds, but could also be a sampling artefact; Coles Pond was sampled two days earlier than Headwater and mayfly hatches can be of short duration.

Thus, the overall seasonal pattern in diet in both ponds was one of benthic predominance throughout the ice-free season but of declining strength as surface prey increased in availability over the summer.

3.3.1.4 Diet of Male versus Female Fish.

There is little information available on how diets compare between male and female brook trout throughout the ice-free season in lake habitats. The data for trout in the Experimental Ponds Area suggest there are modest differences between the genders. Female brook trout had greater proportions of Benthic Evasive and Pelagic prey compared to males whereas male brook trout had approximately twice the proportion of Surface prey (Figure 3.7: Top pie charts). The greater proportions of Trichoptera and Corixidae in the female diet accounted for the difference in Benthic Evasive prey, while the difference in Surface prey was due to males feeding on a greater proportion of

Figure 3.7. Percentage diet composition of male and female brook trout sampled from the Experimental Ponds Area, Newfoundland. Diet contents were sorted by prey type (upper pie charts) and then by prey group (lower pie charts).


Female (N = 52)
Male (N = 70)
Surface (10.46%)
Pelagic (6.90%)
Benthic Passive (22.83%)
Benthic Evasive (59.81%)
Surface (18.93%)
Pelagic (2.19%)
Benthic Passive (24.00%)
Benthic Evasive (54.88%)
Aquatic Diptera (2.09%)
Terrestrial Insecta (8.37%)
G. aculeatus (6.90%)
Diptera larvae (0.02%)
Annelida (0.29%)
Pelecypoda (2.21%)
Gastropoda (20.32%)
Amphipoda/Hydracarina (0.12%)
Corixidae (7.15%)
Trichoptera (5.52%)
Ephemeroptera (11.97%)
Odonata (35.05%)
Aquatic Diptera (2.04%)
Terrestrial Insecta (16.89%)
G. aculeatus (2.19%)
Diptera larvae (0.01%)
Annelida (0.77%)
Pelecypoda (1.93%)
Gastropoda (21.29%)
Amphipoda/Hydracarina (4.52%)
Corixidae (0.47%)
Trichoptera (2.21%)
Ephemeroptera (13.50%)
Odonata (34.17%)

Terrestrial Insecta (Table 3.6, Figure 3.7: Bottom pie charts). Female diets also had a greater proportion of sticklebacks when compared to males (6.9 % compared to 2.2 %) due to a greater number of stomachs with higher mean ration of stickleback (76.3 mg . $fish^{-1}$ N = 6, compared to 29.65 mg . $fish^{-1}$ N = 2).

Both genders selected the greatest proportion of Benthic Evasive prey in the first two months of the summer after which the proportion declined through to September (Figure 3.8). The Benthic Evasive group remained dominant over time for females because of a switch from *Cordulia* in May and June, to Ephemeroptera in July, then to Trichoptera and Corixidae in the remaining months. The seasonal pattern of Surface prey was similar in both ponds but the percentage diet composition was greater in magnitude for male fish four out of five months (Figure 3.8), especially in August where terrestrial insects were the dominant group. The pelagic taxon, *G. aculateus*, was selected at low proportions by a total of six female trout compared to only two male fish, both in July.

Thus, male and female brook trout were predominantly benthic feeders with the greatest difference in diet occurring in late summer at which time males selected a greater proportion of terrestrial prey from the surface in comparison to female trout. This modest difference may be due to males feeding more at the surface or feeding in shallow near-shore habitats where terrestrial insects should be more readily available.

Table 3.6. Mean percent diet composition of the functional prey types found in brook trout stomach samples from the Experimental Ponds Area, insular Newfoundland.

Prey Type	Prey Group	Size Class		Gender	
		Small	Large	Male	Female
Benthic Evasive	Odonata	35.5	33.6	34.2	35.1
	Ephemeroptera	8.1	17.9	13.5	12.0
	Trichoptera	3.5	3.7	2.2	5.5
	Corixidae	5.0	1.5	0.5	7.1
	Amphipoda / Hydracarina	4.9	0.2	4.5	0.1
Benthic Passive	Gastropoda	18.9	23.0	21.3	20.3
	Pelecypoda	0.5	3.8	1.9	2.2
	Annelida	1.1	< 0.1	0.7	0.3
	Diptera larvae	0.0	< 0.1	< 0.1	< 0.1
Pelagic	*G. aculeatus*	0.6	8.0	2.2	6.9
Surface	Terrestrial Insecta	18.4	7.8	16.9	8.4
	Aquatic Diptera	3.5	0.5	2.1	2.1

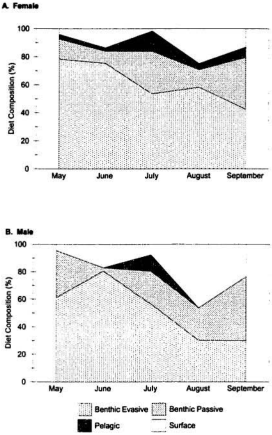


Figure 3.8. Comparison of the seasonal diet pattern for female and male brook trout sampled from the Experimental Ponds Area, Newfoundland.

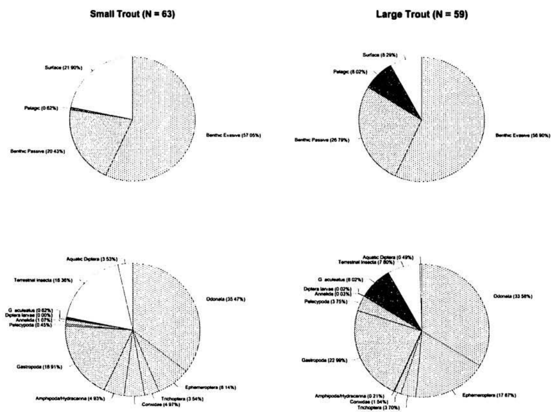
3.3.1.5 Diet of Small versus Large Fish.

Prey selection may be affected by a size-related ability to capture prey of different sizes or to size-related habitat differences. The diet composition and seasonal pattern of two size ranges of brook trout were determined to compare prey type, prey taxa and prey size. The two size classes used were all fish below the median size (< 180 mm) versus the remaining fish (≥ 180 mm).

The diets of each size-class of fish were composed of similar proportions of Benthic Evasive and Passive prey but differed in the proportions of Pelagic and Surface prey consumed (Figure 3.9 top pie charts). Small trout selected more terrestrial insects and aquatic diptera while large trout had a greater proportion of stickleback (Table 3.6, Figure 3.9 bottom pie charts). The seasonal pattern was similar for both sizes in that Benthic Evasive prey were selected in greater proportions in May and June, then declined over the last three months during which they were displaced by greater proportions of Benthic Passive and Surface prey (Figure 3.10).

The higher proportion of surface prey observed in the small trout could be due in part to the fact that males, which were previously shown to select more surface prey (Figure 3.8), were over represented in the sample. Males constituted 63.5 % of the small fish sample size (40 of 63) wish is significantly greater than the expected 50 % ($p = 0.026$, d.f. = 1). A breakdown of the small fish diet by gender shows that small males selected 25.5 % surface prey compared to 15.6 % for small females which is still greater than the 8.3 % surface prey selected by large trout (Table 3.6). There was no gender

Figure 3.9. Percentage diet composition of small and large brook trout sampled from the Experimental Ponds Area, Newfoundland. Diet contents were sorted by prey type (upper pie charts) and by prey group (lower pie charts).


Small Trout (N = 63)
Surface (21.90%)
Pelagic (0.62%)
Benthic Passive (20.43%)
Benthic Evasive (57.05%)
Aquatic Diptera (3.53%)
Terrestrial insects (18.36%)
G. aculeatus (0.62%)
Diptera larvae (0.00%)
Annelida (1.07%)
Pelecypoda (0.45%)
Gastropoda (18.91%)
Amphipoda/Hydracarina (4.93%)
Corixidae (4.97%)
Trichoptera (3.54%)
Ephemeroptera (8.14%)
Odonata (35.47%)
Large Trout (N = 59)
Surface (8.29%)
Pelagic (8.02%)
Benthic Passive (26.79%)
Benthic Evasive (56.90%)
Aquatic Diptera (0.49%)
Terrestrial insects (7.80%)
G. aculeatus (8.02%)
Diptera larvae (0.02%)
Annelida (0.03%)
Pelecypoda (3.75%)
Gastropoda (22.99%)
Amphipoda/Hydracarina (0.21%)
Corixidae (1.54%)
Trichoptera (3.70%)
Ephemeroptera (17.87%)
Odonata (33.58%)

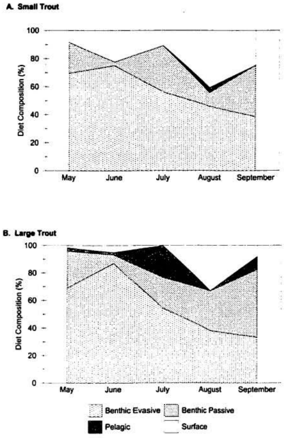


Figure 3.10. Comparison of the seasonal diet pattern for small and large brook trout sampled from the Experimental Ponds Area, Newfoundland.

imbalance in the large fish sample (30 males : 29 females).

Large trout selected larger-sized prey taxa than those selected by small trout. For example, the proportion of the gastropod prey was similar between the size classes however the taxa selected within the gastropod group differed. The small trout diet was composed primarily of *Amnicola*, a small snail 1-3 mm wide, while *Heliosoma*, the largest snail found in the Experimental Ponds Area (up to 15 mm wide), was selected only by large fish. The stickleback content found in one small-sized trout was of a young of the year stickleback (3.0 mg dry wt. / fish) in comparison to greater mean stickleback ration found in seven large trout (73 mg dry wt. / fish). *Hexagenia rigida*, a large mayfly, were also selected in greatest proportion by large fish (99 % of the total weight of *Hexagenia*, the 1% was from one small-sized fish) as opposed to the selection of smaller mayfly nymphs (primarily *Leptophlebia* and *Stenonema*) by small fish.

Both size classes of brook trout predominantly fed on benthic prey throughout the season. Small fish selected a greater proportion of terrestrial insects and aquatic diptera late in the season and fed on smaller-sized prey taxa in comparison with that observed for large size fish.

3.3.2 The Physiological Condition of EPA Brook Trout.

Analysis of somatic-visceral percent lipid content was used to document the seasonal change in physiological condition of large male and female brook trout as they reproductively matured. Female fish were investigated further to determine if the seasonal change in lipid could be explained by gonad maturation, seasonal change in feeding intensity, or by changes in metabolism inferred from the seasonal change in water temperature. Lipid patterns were also compared between the experimental pond (Coles Pond) and the control pond (Headwater Pond) in order to determine if whole-lake fertilization may have affected the physiological condition of brook trout.

3.3.2.1 The Seasonal Pattern in Percent Lipid Content.

Salmonid visceral and somatic lipid usually accumulates from spring to mid-summer (Elliot 1976b, Cunjak and Power 1986, Mayo 1994) and then declines to the end of the ice-free season (Cunjak and Power 1986, Cunjak 1988, Nassour and Léger 1987). A similar seasonal pattern of lipid content was observed in this study. Specifically, the mean percent lipid content of brook trout from the Experimental Ponds Area increased from spring to a maximum in mid-summer (Figure 3.11: May to July), then decreased through to fall for each gender (Figure 3.11: July to September). Mean percent lipid content was highest in mid-summer compared to spring and fall percentages (Tukey test; difference (May to July) = 8.299 $p < 0.001$ df = 1, difference (July to September) = -6.595 $p < 0.001$ df = 1). Male trout had significantly less somatic-visceral lipid in the spring and mid- summer than females (Table 3.7 lists monthly lipid contents for each gender, $F_{1,1} = 4.69$, $p < 0.001$). A recent study by Hutchings *et al.* (1999) on a riverine population of brook trout of the Avalon Peninsula, Newfoundland reported a similar difference between male and female brook trout in April and found no statistical

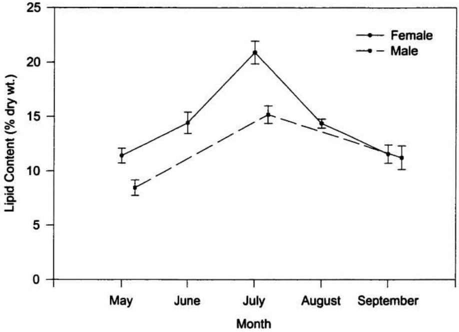


Figure 3.11. Seasonal trend in somatic-visceral lipid content (% dry weight) for male and female brook trout sampled from the Experimental Ponds Area. Vertical bars represent 1 standard error about the mean.

Table 3.7. Mean (± 1 standard error) fork length (mm), somatic - visceral lipid content (% dry wt.), ration (mg dry wt / fish), empty stomachs and gonadal-somatic index ((g gonad / (g fish + g gonad)) * 100 %) for brook trout sampled from the Experimental Ponds Area, Newfoundland. Numbers in parenthesis are the sample sizes used to calculate each statistic. Mean rations were adjusted for the observed co-variation due to fish size.

Gender	Factor	Sampling Month				
		May	June	July	August	September
Female	Length	205.46 ± 6.91 (13)	195.13 ± 13.76 (8)	217.13 ± 10.79 (8)	203.25 ± 5.33 (8)	208.69 ± 6.87 (16)
	Lipid	11.42 ± 0.68 (13)	14.43 ± 0.98 (8)	20.91 ± 1.04 (8)	14.36 ± 0.65 (8)	11.57 ± 0.84 (16)
	Ration	74.83 ± 10.01 (22)	95.85 ± 29.25 (6)	113.04 ± 41.03 (12)	9.95 ± 0.65 (11)	30.08 ± 5.35 (20)
	Empty	25.53 (12)	0.00 (0)	57.14 (20)	40.00 (10)	23.81 (10)
	GSI	0.41 ± 0.04 (13)	0.69 ± 0.19 (8)	0.62 ± 0.08 (8)	1.90 ± 0.54 (8)	6.96 ± 0.89 (16)
Male	Length	226.31 ± 8.60 (13)		235.44 ± 9.31 (9)		198.83 ± 5.30 (16)
	Lipid	8.47 ± 0.72 (13)		15.18 ± 0.81 (9)		11.24 ± 1.08 (16)
	Ration	68.18 ± 13.99 (23)		58.04 ± 17.55 (13)		29.47 ± 7.10 (18)
	Empty	30.36 (17)		44.12 (15)		54.84 (17)
	GSI	0.06 ± 0.01 (13)		0.16 ± 0.03 (9)		0.89 ± 0.24 (16)

difference in somatic or total lipid (%wet weight) between reproductive male and female fish in late fall (October). An earlier study in Ontario by Cunjak (1988) also reported no difference in the lipid content of male and female trout or between reproductively mature and immature trout during the fall season but also found no difference in the lipid content of males and females in the spring.

The increase in mean lipid content from May to July suggests active feeding during the spring to mid-summer period. Female brook trout mean lipid content increased by 9.49 % dry weight from spring to mid-summer compared to smaller 6.71 % dry weight increase in male fish. Furthermore, the increase in mean lipid content of female trout was approximately linear when plotted against elapsed time (Figure 3.12), suggesting stable feeding rates during the spring to mid-summer period. The seasonal trends for mean ration and percentage empty stomachs were used as indicators of brook trout feeding intensity. Thus, it was expected that mean ration would be greatest from spring to mid-summer and that the percentage empty stomachs would be lower and less variable for that same period. The adjusted mean ration for female fish was indeed greatest during the observed period of lipid accumulation (Figure 3.13 A, B) however the percentage empty stomachs was low only in May and June (Figure 3.13 C). The month-to-month variability in percentage empty stomachs (range of 0 - 60 % during the period of lipid accumulation) along with the large variation in the June and July ration, as indicated by the wide standard error bars, is not reflected in the lipid accumulation pattern. This suggests that feeding 'snapshots' may be insufficient to characterize seasonal trends of feeding intensity.

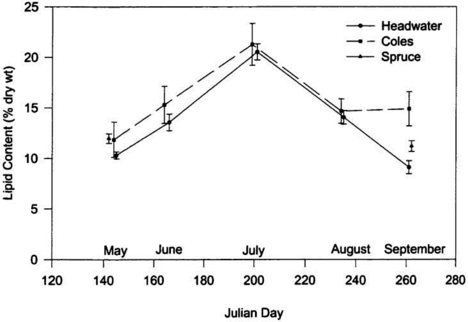
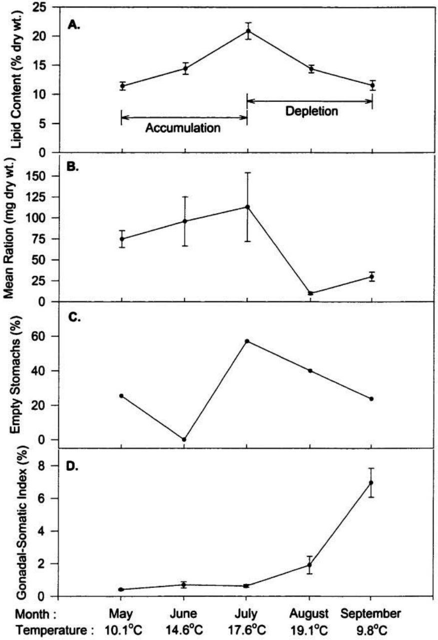


Figure 3.12. Seasonal trends in somatic-visceral lipid content (% dry weight) for female brood trout sampled from three ponds of the Experimental Ponds Area. Vertical bars represent 1 standard error about the mean.

Figure 3.13. Comparison of the seasonal patterns for female brook trout; A. somatic-visceral lipid content (% dry weight), B. adjusted mean ration (mg dry wt.), C. empty stomachs (% empty), and, gonadal-somatic index (% wet weight). Surface temperatures are listed for each sampling period and vertical bars represent 1 standard error about the mean.



Lipid Content (% dry wt.)
A.
Accumulation
Depletion
Mean Ration (mg dry wt.)
B.
Empty Stomachs (%)
C.
Gonadal-Somatic Index (%)
D.
Month : May June July August September
Temperature : 10.1°C 14.6°C 17.6°C 19.1°C 9.8°C

Depletion of somatic-visceral lipid content from mid-summer to fall could be due to decreases in feeding intensity, increases in metabolism due to higher water temperature, and to gonad maturation. The monthly mean lipid content for all females decreased by 6.39 % of dry weight from mid-summer to fall compared to a decrease of 3.94 % of dry weight for males. Female fish generally invest more somatic-visceral energy derived from lipid reserves into gamete production than do males (Love 1970, Jobling 1994), consistent with the present observations. The greatest decline in female somatic-visceral lipid content occurred from July to August and corresponded with a significant drop in mean ration, a high percentage empty stomachs, a small increase in the gonadal-somatic index and with high surface water temperatures (Figure 3.13 A, B, C, D). This suggests that female fish utilize somatic-visceral lipid reserve primarily to offset the higher maintenance requirements due to increased metabolism as a result of high water temperatures during a period of low food ration. Lipid depletion from August to September was less (2.79 % of dry weight compared to 6.55 % of dry weight) and corresponded to a period of declining water temperature to 9.8 ° C, a small increase in mean ration, a small decline in percent empty stomach and a sharp increase in the gonadal-somatic index (Figure 3.13 A, B, C, D). This suggests that lipid reserves may have been primarily utilized for the development of the gonad since maintenance requirements would be lower due to the drop in water temperature and feeding intensity increased.

The utilization of somatic-visceral lipid reserve during reproductive maturation was further investigated by reconstructing the ovarian lipid content for female fish in

Headwater Pond and Coles Pond. Ovarian lipid content was calculated as a percentage of the sum of the dissected plus the gonadal weight (wet weights only) per trout using the formula:

$$\% \text{ ovarian lipid} = [(P \times Wt_{gonad}) / (Wt_{Dissected} + Wt_{gonad})] \times 100\,\%;$$

where P is the ovarian lipid content as a proportion of gonad weight determined from a study of riverine brook trout on the Avalon Peninsula, Newfoundland (P = 0.096 Hutchings *et al.* 1999). This proportion was assumed constant during the period from July to September; the ovarian lipid content of an aquaculture strain of rainbow trout varied only from 12 - 14 % during the slow growth and rapid growth physiological stages of reproductive maturation (Nassour and Léger 1987).

The depletion pattern of somatic-visceral lipid for female fish differed between Coles Pond and Headwater Pond. Lipid content in Headwater Pond declined throughout the July - September period whereas in Coles Pond the decline was confined to the July - August period (Figure 3.12). The gonadal-somatic index and the estimates of ovarian lipid content were similar in both ponds from July to September indicating that reproductive maturation patterns were similar (Table 3.8). More lipid (% wwt) was transferred to the ovaries of Coles Pond fish during the August to September interval than was lost in the somatic-visceral reserve (0.45 % compared to 0.17 %, respectively). Thus, the September increase in ovarian lipid in Coles Pond did not come at the expense of somatic-visceral reserves and was likely derived from ingestion. In contrast the

Table 3.8. Comparison of the monthly mean lipid content (% wet wt. ± 1 standard error) and mean gonadal somatic index (GSI ± 1 standard error) from July to August for female brook trout residing in two ponds of the Experimental Ponds Area. Ovarian lipid estimates are explained in section 3.3.2.

Pond			Sampling Month		
			July	August	September
Coles	Lipid	Somatic - Visceral	5.88 ± 0.68	3.81 ± 0.35	3.64 ± 0.53
		Ovarian A	0.06 ± 0.01	0.15 ± 0.10	0.60 ± 0.10
	GSI		0.68 ± 0.13	1.60 ± 1.07	6.24 ± 1.42
	N		4	4	5
Headwater	Lipid	Somatic - Visceral	5.18 ± 0.23	3.58 ± 0.27	2.01 ± 0.17
		Ovarian A	0.05 ± 0.01	0.21 ± 0.04	0.58 ± 0.12
	GSI		0.56 ± 0.11	2.21 ± 0.38	6.01 ± 1.29
			4	4	6

ovarian lipid increase (0.36 % wwt) in Headwater Pond was less than one-quarter of the somatic-visceral lipid loss (1.57 % wwt).

The increased September lipid in Coles Pond (Figure 3.14: somatic-visceral + ovarian) is inconsistent with the observation that Coles Pond female brook trout had a lower mean ration than Headwater trout (Appendix D) and a higher percent empty stomachs (Appendix B) in both August and September. It may be that fertilization of Coles Pond resulted in prey of higher nutritional quality however no chemical analyses of prey are available to test this hypothesis.

In summary, the accumulation of somatic-visceral lipid (% dry wt) occurred from May to July and corresponded with a period of high mean ration, while depletion occurred from July through to September when feeding intensity decreased (low mean ration with high percentage empty stomachs) and when water temperatures were highest. Similar estimates of the monthly ovarian lipid content (% dry wt) were observed for female fish in each pond which increased greatly from August to September. This increase coincided with a significant decline in the somatic-visceral lipid content for Headwater Pond fish only.

3.3.2.2 Relationships Between Lipid Content, Water Content and Condition Indices.

The assessment of somatic-visceral lipid content is both time-consuming and expensive. The average time from initial dissection to final determination of lipid content for this study was 78 hours (½ hr dissection + 72 hr drying + ½ hr sample prep + 5 hr

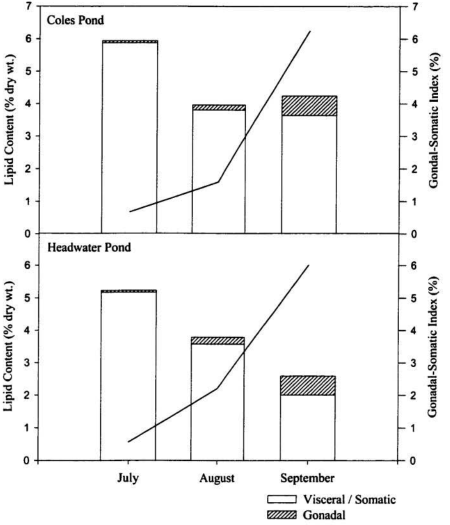


Figure 3.14. Comparison of the change in somatic-visceral lipid, gonadal lipid and gonadal-somatic index (solid line) of female brook trout sampled from the Experimental Ponds Area, insular Newfoundland.

extraction) per batch of 10 samples with a materials cost of $7 per sample. Percent water content, Fulton's condition factor (K) and relative condition factor (Kn) have been shown to be correlated with lipid content and can be measured more rapidly and with less expense. It thus seemed worthwhile to explore the relationship between somatic-visceral percent lipid content (males and females combined) and each of the above variables for brook trout to determine if lipid content could be predicted from water content, K and Kn.

A significant negative correlation was observed between percent lipid content and percent water content for Experimental Ponds Area brook trout (Table 3.9). Similar correlations have been documented for brook trout in northern Quebec (Cunjak and Power 1986), Wyoming USA (Novinger and Martinez del Rio 1999), and the Avalon Peninsula, Newfoundland (Mayo 1994, Hutchings *et al.* 1999), and for other salmonids (brown trout: Elliot 1982, Elliot 1976a; rainbow trout: Weatherley and Gill 1983; Atlantic salmon: Mayo 1994, Sutton *et al.* 2000). Ordinary least squares regression was used to quantify the negative relationship between lipid content and water content (Figure 3.15. A). A significant positive correlation was observed between percent lipid content and each of the condition factors, Fulton's (K) and relative condition (Kn) (Table 3.9). Positive correlations have also been reported for brown trout (Elliot 1976a) and Atlantic salmon parr (Sutton *et al.* 2000). The ordinary least squares relationships shown in Figure 3.15 C and D quantify the positive predictive relationships between lipid content and the morphometric condition indices.

The seasonal pattern for water content was the inverse of that for lipid content (Figure 3.16 A and B, $r_{A \cdot B} = -0.915$, $p = 0.03$, $N = 5$) (Table 3.10). Similar patterns have

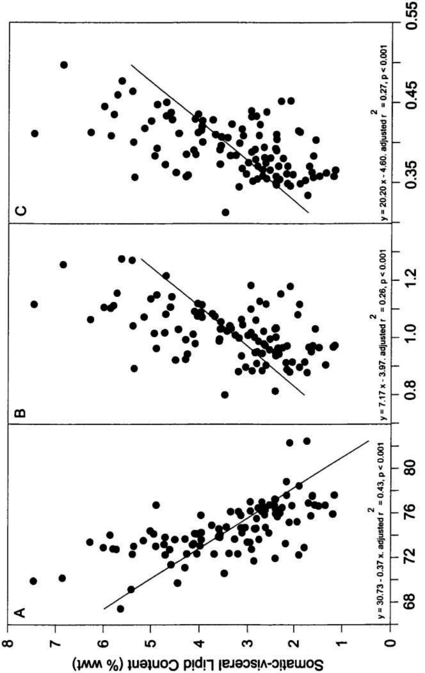
Table 3.9. Pearson correlation coefficients for comparisons of brook trout percent somatic - visceral lipid content (% lipid) to percent water content (% water) and to two condition factor indices (K and Kn). Values in parenthesis are the significance p-values calculated for sample N = 104 and an alpha = 0.05.

	% Water	K	Kn
% Lipid	- 0.66 ($p \leq 0.001$)	0.51 ($p \leq 0.001$)	0.50 ($p \leq 0.001$)

Table 3.10. Mean (± 1 standard error) percent somatic-visceral lipid content (% wet wt.), percent water content (% wet wt.), Fulton's condition factor (K), and relative condition factor (Kn) for brook trout sampled from the Experimental Ponds Area, Newfoundland. Numbers in parenthesis represent the sample sizes.

Statistic	Sampling Month				
	May	June	July	August	September
Lipid Content	2.57 ± 0.15 (33)	3.76 ± 0.30 (8)	5.00 ± 0.25 (21)	4.07 ± 0.27 (10)	2.77 ± 0.16 (32)
Water Content	74.83 ± 0.48 (33)	74.08 ± 0.44 (8)	72.51 ± 0.47 (21)	73.69 ± 0.35 (10)	76.11 ± 0.25 (32)
K	0.97 ± 0.01 (33)	1.07 ± 0.02 (8)	1.11 ± 0.02 (21)	1.02 ± 0.02 (10)	1.00 ± 0.02 (32)
Kn	0.37 ± 0.005 (33)	0.42 ± 0.01 (8)	0.42 ± 0.01 (21)	0.40 ± 0.01 (10)	0.39 ± .01 (32)

Figure 3.15. The relationships between: A. Somatic-visceral lipid content and water content, B. Somatic-visceral water content and Fulton's condition factor (K), and C. Somatic-visceral lipid content and relative condition factor (K) for brook trout of the Experimental Ponds Area, insular Newfoundland. K and Kn were calculated using dissected wet weight.


A
B
C
Somatic-visceral Lipid Content (% wwt)
Water Content (% wwt)
K
Kn
y = 30.73 - 0.37 x. adjusted r2 = 0.43, p < 0.001
y = 7.17 x - 3.97. adjusted r2 = 0.26, p < 0.001
y = 20.20 x - 4.60. adjusted r2 = 0.27, p < 0.001

been observed for brook trout in Ontario (Cunjak and Power 1986), Quebec (Cunjak 1988), and Newfoundland (Mayo 1994), and for Atlantic salmon (Sutton *et al.* 2000). The observed seasonal pattern in mean condition generally corresponded to lipid content trends: condition was low in May and September and peaked in July (Figure 3.16 A, C, and D. $r_{A \cdot C} = 0.898$ $p = 0.04$, $r_{A \cdot D} = 0.835$ $p = 0.08$). However, both condition indices displayed less change from June to July and from August to September than did lipid content. Similar correspondence between the seasonal trend in percent lipid content and those for condition have also been observed for Atlantic salmon (Sutton *et al.* 2000) and the barbel, *Barbus sclateri* (Encina and Granado-Lorencio 1997).

The observed differences in somatic-visceral lipid content between the genders and across months suggests that these variables might provide additional predictive power beyond that provided by water content or condition factor alone. This possibility was examined using multiple linear regression. Three models were constructed: one using the dissected weight (gonad and stomach contents removed) to calculate the condition factors, one using dissected weight with gonad weights added back in, and one using whole weight. The latter two models were intended to determine if variability in gonad and/or stomach contents reduced predictive power. The month and gender information was incorporated into the regression by using binary dummy variables (see methods).

Stepwise regression analysis had much higher predictive power (adjusted r^2 from 0.69 to 0.72, see Table 3.11) than the water content and condition factors alone (adjusted r^2 from 0.26 to 0.43, see Figure 3.15). For each model, water content accounted for the greatest proportion of the explained variation followed by the binary dummy variables for

Figure 3.16. Comparison of the seasonal patterns for brook trout of A. Somatic-visceral lipid content (% wet weight), B. Water content (% wet weight), C. Fulton's condition factor (K), and, D. Relative condition factor (Kn). Vertical bars represent 1 standard error about the mean.

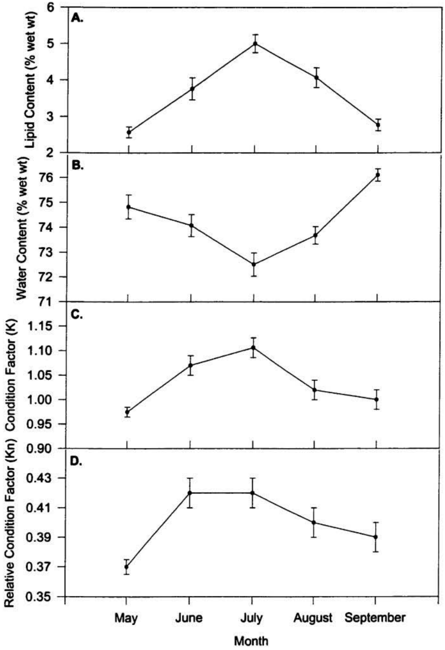

A.
B.
C.
D.
Lipid Content (% wet wt)
Water Content (% wet wt)
Condition Factor (K)
Relative Condition Factor (Kn)
6
5
4
3
2
76
75
74
73
72
71
1.15
1.10
1.05
1.00
0.95
0.90
0.43
0.41
0.39
0.37
0.35
May
June
July
August
September
Month

Table 3.11. Comparison of three models to predict somatic-visceral lipid content (% wet weight) as determined using stepwise multiple regression. Each model was based on one of three weight measures (Dissected, Dissected + Gonad and Whole) used to calculate condition factors (K and Kn). The general equation for each model is: $Y = M_1X_1 + M_2X_2 + M_3X_3 + M_4X_4 + M_5X_5 + b$, where Y is percent lipid content, M_n is the coefficient at step n, and X_n is the variable entered at step n.

Dissected Weight Model: N = 104, r = 0.854, Adjusted r^2 = 0.716, p < 0.001.

Step	Variable	Coefficient ± 1 s. e.	t-statistic	Significance	r^2 change
	Constant	17.453 ± 2.867	6.089	< 0.001	
1	% Water	- 0.233 ± 0.034	- 6.944	< 0.001	0.438
2	July	1.025 ± 0.216	4.753	< 0.001	0.138
3	Sex	- 0.766 ± 0.153	- 5.021	< 0.001	0.076
4	Kn	8.865 ± 2.419	3.677	< 0.001	0.064
5	May	- 0.402 ± 0.174	- 2.315	0.023	0.015

Dissected + Gonad Weight Model: N = 104, r = 0.849, Adjusted r^2 = 0.707, p < 0.001.

Step	Variable	Coefficient ± 1 s. e.	t-statistic	Significance	r^2 change
	Constant	16.011 ± 2.712	5.903	< 0.001	
1	% Water	- 0.221 ± 0.034	- 6.521	< 0.001	0.438
2	July	1.322 ± 0.215	6.148	< 0.001	0.138
3	Sex	- 0.682 ± 0.154	- 4.426	< 0.001	0.076
4	Kn	10.328 ± 2.434	4.243	< 0.001	0.057
5	August	0.562 ± 0.256	2.197	0.030	0.014

Table 3.11 (continued).

Whole Weight Model: N = 104, r = 0.842, Adjusted r^2 = 0.694, $p < 0.001$.

Step	Variable	Coefficient ± 1 s. e.	t-statistic	Significance	r^2 change
	Constant	19.600 ± 2.905	6.746	< 0.001	
1	% Water	- 0.246 ± 0.035	- 7.095	< 0.001	.438
2	July	1.145 ± 0.220	5.217	< 0.001	.138
3	Sex	- 0.696 ± 0.157	- 4.440	< 0.001	.076
4	May	- 0.439 ± 0.187	- 2.348	0.021	.041
5	Kn	4.980 ± 2.134	2.334	0.022	.016

the month of July and Gender as indicated by the magnitude of the change in the r^2 at each step. The dummy variable for July and Gender correspond with the July peak in monthly mean lipid content in July (see Figure 3.16 A) and with the difference between male and female trout (see page 28), respectively. The model based on whole fish weight accounted for slightly less variation (adjusted $r^2 = 0.69$) which was expected since differences in stomach contents and/or gonad weights among individuals should increase the error variance.

Thus, percent lipid content was positively correlated with both indices of condition and negatively correlated with water content. Percent water content and condition factor can be used to predict lipid content, and predictive power is much improved when differences due to gender and to season are accounted for.

3.4 Chapter Summary.

To summarize:

1. Ration increased with brook trout size and generally declined from spring through summer. Fish in fertilized Coles Pond fed less and had significantly lower mean ration when compared to those for Headwater Pond and Spruce Pond.
2. Benthic invertebrates were the most prevalent prey in brook trout diets throughout the season although there was a switch from the Evasive to the Passive prey type. This result was similar across gender, size-class and the two study ponds. The Surface prey were the third-most prevalent component of brook trout diet and were increasingly selected as specific taxa (e.g. Hymenoptera) became available in late summer - early fall.
3. There were two main differences in the seasonal diet patterns for male and female trout. Firstly, female brook trout continued to select a greater percentage of Benthic Evasive prey throughout the season due to the selection of a greater percentage of corixids and trichopterans in August and September. Secondly, males selected a greater percentage of surface prey especially later in the season. These results suggest that male and female trout may be feeding in different habitats within the lake ecosystem.
4. Large brook trout fed on larger prey taxa compared to small trout. Small trout fed upon greater proportions of surface prey and smaller benthic prey. The seasonal patterns in prey type selection were similar for each trout size class.

5. Somatic-visceral lipid content increased from May to July and then declined through to September. The accumulation of somatic-visceral lipid occurred when mean ration was greatest while lipid depletion occurred when feeding intensity decreased, metabolism increased (inferred from higher water temperatures) and das gonads matured. Differences in the depletion patterns between ponds in somatic-visceral lipid was not due to reproductive maturation differences because GSI and ovarian lipid estimates were similar in each pond. Coles Pond trout displayed very little lipid content depletion from August to September. This was inconsistent with observations that fish in Coles Pond fed less actively and had less ration during that period when compared to that for Headwater Pond.

6. There does not appear to be any dramatic effect of the whole-lake fertilization on the feeding and physiological condition of brook trout in Coles Pond. The September increase in total lipid content of Coles Pond trout suggest that fertilization resulted in prey of higher nutritional quality however no chemical analyses of the prey are available to test this hypothesis.

7. Somatic-visceral lipid was negatively correlated with percent water content and was positively correlated to both of the morphometric indices of condition: Fulton's condition (K) and relative condition (Kn). Percent water content and relative condition factor were used to predict lipid content, however, predictions were greatly improved with the addition of dummy variables that accounted for variation due to gender and season.

Chapter 4. General life history, growth characteristics and the impact of whole-lake fertilization on the ecology of brook trout in the Experimental Ponds Area, insular Newfoundland.

4.1 Introduction.

This chapter describes the general life history and growth characteristics of brook trout in three ponds of the Experimental Ponds Area, then analyzes the annual trends in the population size, structure, and growth characteristics among the ponds to explore the potential impacts of the whole-lake fertilization experiment.

4.1.1 Life History and Growth Characteristics.

The life histories of salmonids can be summarized into three general categories. The first are the salmonids that migrate from streams to lakes or to the sea immediately after emergence (e.g. some *Oncorhynchus* species). The second are the salmonids that remain in streams for a year or more and then migrate to the sea or to lakes to grow (e.g. Atlantic salmon and anadromous/adfluvial forms of rainbow trout and brown trout), while the third category includes those which spend their entire lives in streams. The brook trout fall into either the second (anadromous: Wiseman 1969, adfluvial: Saunders and Power 1970, McCarthy 1997) or the third general category (Hutchings 1991, Wydowski and Cooper 1966 as two examples).

Power (1980) suggests that brook trout that reside in streams and rivers are generally short-lived, up to Age 3+, with most of the egg production occurring at Age 2+. In comparison, brook trout that utilize both fluvial and lacustrine habitats are generally longer lived (5 - 7 years), mature at older ages (Age 3+ and up) and spawn annually for at least two years after maturity has been attained. Saunders and Power (1970) suggested that the availability of lake habitat to riverine brook trout populations reduces mortality, increases growth and augments production. Hutchings (1986) indicated that lake habitat provided conditions for increased growth of Atlantic salmon parr and greater survival to the smolt stage.

Very little is known about the utilization of both stream and pond habitat by brook trout on the island of Newfoundland. Most studies have focussed on describing the life history and growth characteristics of populations inhabiting coastal lakes (Wiseman 1969, Baggs 1985) and streams (Hutchings 1991). One study has documented movements of brook trout from streams to lake habitats (McCarthy 1997), while another inferred migrations to and from lake habitat from observed differences in seasonal age-structures (Ryan and Knoechel 1994).

Growth in weight and/or length may change due to the spatial and temporal variation in the abiotic and biotic conditions of the environment. Seasonal patterns in growth should reflect the gains due to somatic growth and lipid storage for all fish when food resources are available, and losses due to reproduction and basal metabolism during periods when resources are scarce (Love 1970). Yearly patterns in growth may indicate larger-scale environmental or community impacts on the growth of fish. Spatial patterns would include differences in the average size of fish in similar and/or differing habitats. For example, larger habitats usually produce older and bigger fish (Ricker 1932, Power 1980).

The main goal of this section is to describe the general life history and growth characteristics of Experimental Ponds Area brook trout. This includes a description of how these book trout utilize both stream and pond habitat and a description of the seasonal changes in population structure within a pond. Also included is the determination of the age of reproductive maturation, fecundity and ova size, the mean weight- and length-at-age, the seasonal changes in weight and length, and a comparison of these characters with those of other populations locally and continentally.

4.1.2 Impact of Whole-Lake Fertilization.

The addition of nutrients should increase the productivity of an aquatic ecosystem by increasing the biomass at all trophic levels through 'bottom-up' processes. Studies have linked the increase in nutrients to responses in the phytoplankton (Reinertssen 1982, Stockner and Shortreed 1985), zooplankton (Langeland and Reinertssen 1982) benthic invertebrate (Smith 1961, Dougherty and Morgan 1991) and fish communities (Hyatt and Stockner 1985, Mills 1985).

A few examples of the responses of the fish community to increases in prey abundance due to nutrient addition include observation of increases in the in-lake growth of juvenile sockeye salmon and larger outmigrant smolts, *Oncorhynchus nerka*, (Hyatt and Stockner 1985), increased growth and condition of whitefish, *Coregonus clupeaformis*, (Mills 1985), and increased production and biomass of arctic charr, *Salvelinus alpinus*, (Langeland 1982). Brook trout from the Experimental Ponds Area are predominantly benthivorous (Chapter 3) and the fertilization of Coles Pond has resulted in a 2 - 4 fold increase of the benthic macro-invertebrate abundance in the experimental pond (Clarke 1995, Clarke *et al.* 1997, Knoechel *et al.* 1999, Moore 1999). Other impacts of the fertilization experiment included a 4.6 % increase in the average weight of Coles Pond sticklebacks (up to 1993: Brown 1993), and, an increase in the size of overwintering juveniles and 33 % higher length-specific fecundity by 1994 (Simmonds 1999). The observed increase in prey density was expected to enhance the growth and subsequently, the abundance of their salmonid predators.

The effects of nitrogen and phosphorus additions on brook trout were investigated from 1991-96. Numerical response was evaluated through the comparison of the yearly spring and fall population density and biomass estimates for the experimental lake (Coles Pond) to those for each of the two control lakes (Headwater Pond and Spruce Pond). Structural responses were evaluated through the comparison of year class structures within and among the ponds. Growth responses were evaluated through the comparison of annual fall mean weight-at-age, and comparison of the change in weight over age per year class among the ponds.

4.2 Methods and Materials.

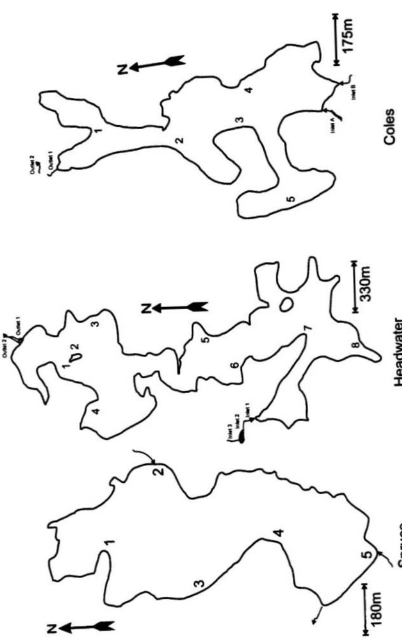
4.2.1 Data Collection and Treatment.

4.2.1.1 Field Sampling.

Spring and fall (May and September) salmonid population censuses were conducted annually from 1991 through 1996 in Spruce, Headwater and Coles Pond. Census data from 1991 to 1995 were provided by Dr. Roy Knoechel. Fish were captured in 13mm or 19mm stretched-mesh fyke nets set from shore during each population census. The locations of nets in each pond in 1996 are shown in Figure 4.1. Nets were fished over a short period of 9 - 11 days in order to minimize potential bias due to migration and/or mortality over the duration of each census (Knoechel and Ryan, 1994). All fish captured were measured for fork length (mm) and were marked by clipping the caudal fin with a hole punch. This mark provides a means of estimating the population abundance in each pond during a census. Weight (g), and scale samples were obtained from a sub-sample of fish representative of the total size range of brook trout in each pond. All fish captured during the spring census of 1996 in Headwater Pond and Coles Pond were secondarily marked by removal of the adipose fin. This mark does not regenerate and provides a means of estimating mortality over the period between censuses.

A survey of the trout utilizing inlet and outlet stream habitat of Headwater Pond

Figure 4.1. Net positions and inlet / outlet electrofishing sites used during the 1996 field season in each pond.


Spruce
180m
N
1
2
3
4
5
Headwater
330m
N
Outlet 1
Outlet 2
Inlet 1
Inlet 2
Inlet 3
1
2
3
4
5
6
7
8
Coles
175m
N
Outlet 1
Outlet 2
Inlet A
Inlet B
1
2
3
4
5

and Coles Pond was conducted in August - September 1996. Not all the stream habitat could be electrofished due to dense vegetation, narrow stream widths (< 30 cm), and muddy stream beds. Thirty to sixty metre long stream sections were enclosed using barrier nets, then repeatedly fished using a Smith-Root single anode backpack electro-fisher until catches reached or approached zero. All captured fish were measured for fork length and released downstream from the fished section. Once a section had been fished, a new section was created by removing the lower barrier net and placing it 30 - 60 metres upstream from the previous upper barrier net. This procedure was followed for the inlet and outlet survey for Headwater Pond (3 inlet sections: Figure 4.1). Outlet 2 and Inlet B of Coles Pond were surveyed in early September while all other sections were sampled in late August. Stream width was measured at 5 metre intervals starting at the lower barrier net in each section after fishing.

4.2.1.2 The Estimation of Population Abundance and Density.

The population abundance of brook trout residing in each of the three ponds was calculated using the Schnabel multiple mark-recapture method (Ricker 1975, Ryan 1984, Ryan 1990). The final abundance estimates were reported as density per hectare to facilitate comparisons among ponds. Ninety-five percent confidence intervals about each density estimate were calculated according to Ricker (1975). A density estimate for one pond which is outside the 95% confidence limits of another is significantly different at the 5% level.

Population abundance of brook trout residing in inlet and outlet streams was calculated by summing the total number of fish captured per section within a stream. The totals were then divided by the total area of the sections in each stream to provide density estimates (# . 100^{-1} m^{-2}) for comparisons among streams.

4.2.1.3 The Estimation of Population Age Structure.

Age composition was determined for each lake during each census according to methods described in Ricker (1975), Ryan *et al.* (1981) and Ryan (1990). Ages were assigned to each scale sample and then segregated into 50 mm interval length classes to determine the proportion each age-class contributed to each length interval. These proportions were then applied to the census estimate for each length interval to estimate the overall age composition.

The age composition was also determined for the stream-dwelling brook trout. These trout were provisionally assigned to age categories based on their length because only a small sample were actually aged using scales (N = 7). The median of the fall length minima and maxima of Age 1+ pond trout over the 1991 to 1996 period was used as conservative estimates of the length range for three age categories (Table 4.1). The length frequency distribution of the stream trout shows clear separation between the Age 2 + category and the younger categories, and no clear separation between the young-of-the-year (YOY) and Age 1+ (Figure 4.2). The majority of trout in the younger categories were smaller than the smallest age 1 + pond fish (77 mm) and were similar in size to aged

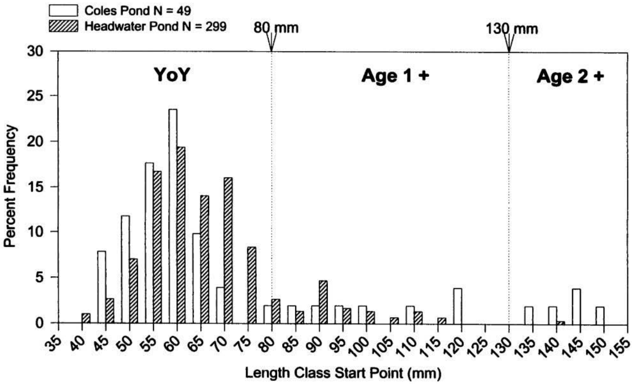


Figure 4.2. Length frequency distributions of fish captured from streams surrounding Headwater and Coles ponds. Arrows (and lines) represent medians of the length minima and maxima of Age 1 + pond fish from the period of 1991–1996.

YOY trout (43 - 74 mm, includes 30 YOY pond trout), thus, were assigned to the YOY age category. It has been documented for the Experimental Ponds Area that stream-resident 1+ Atlantic salmon parr have maximum lengths that only slightly overlap the minimum lengths of pond-resident 1+ parr (Alcock 2000). Thus, any errors in the age assignments will likely over-estimate the number of fish categorized as YOY, and underestimate those fish classed as Age 1+.

4.2.1.4 Estimates of Mortality.

A mortality estimate was calculated from the 1996 adipose fin clip survey data for Headwater Pond and Coles Pond. All fish captured in the spring of 1996 were adipose clipped and assigned to age classes based on the size distribution of scale-aged fish following the method of Tesch (1971). The number of adipose-clipped fish in each age class was divided by the age-class abundance estimated in the fall census to yield the proportion of fish expected to be marked with adipose clips if all fish had survived throughout the summer. The difference between the proportion of adipose-clipped fish actually recaptured in the fall and that expected was used to estimate the combined effects of mortality and emigration as a source of population loss:

$$\text{Loss} = [\ 1 - (\ \#\ \text{actual} - \#\ \text{expected})\ ]$$

Given that there were no fish older than age 2 + in the streams in fall 1996 (see section

4.3.1.2), it is assumed that the primary source of population decline was mortality.

4.2.2 Life History and Growth Characteristics.

4.2.2.1 Habitat Utilization.

Graphical analysis was used to compare the population age structure of brook trout utilizing stream and pond habitats. Frequency histograms were constructed from the 1996 age composition data for each habitat (inlet, outlet and pond). This facilitated the comparison of the age distribution of stream fish to that observed in the adjoining ponds (Headwater Pond and Coles Pond). The age composition data from each census was tabulated for each pond and then used to infer the age at which brook trout are most likely to enter the ponds and to provide a general description of the range of age-classes captured in the EPA ponds. The age composition data from all censuses were utilized for cohort analysis of the 1990 through 1993 year classes. These data were graphically analysed to identify general patterns in how brook trout utilize pond habitat and to compare patterns among ponds. Year classes were identified by the year of alevin emergence.

4.2.2.2 Maturation.

A sample of brook trout sacrificed at the end of each fall population census were internally examined to determine their gender and maturity status. Female ovaries with ova at Stage III to Stage IV (Vladykov 1956) and males with enlarged whitish testes were recorded as mature. Size at maturity was calculated for the male and female samples collected from 1992 to 1996. Age at maturity was calculated for each gender as the average age in relative years (example Age 3 + = 4th year of life). Ages for samples collected before 1996 were assigned according to the length-at-age classes of the corresponding fall census. Scale samples from each mature fish in the fall of 1996 were used to determine the age according to methods described in Tesch (1971).

Fecundity was measured as the total number of maturing ova in each female. Egg size was calculated as the average of three diameter (mm) measurements taken from 5 to 10 randomly chosen ova. Regression analysis was used to determine how the size (diameter (mm)) or the number of ova ($\log_{10}$ number) was related to maternal length (fork length (mm)). Analysis of covariance (ANCOVA) was used to test if habitat (ponds) or time (years) significantly contributed to the variance in size or number of ova while controlling for co-variance due to maternal length.

4.2.2.3 Growth Characteristics.

Mean weight-at-age was calculated by averaging the weights of individual fish within an age class during each census. For example, in the fall of 1996, 18 Coles Pond fish aged 1+ had a mean weight of 14.83 g with a standard deviation of 7.58 g. The weight-at-age was calculated as the weighted average of the yearly estimates of the mean weight-at-age in each season (fall and spring) for Headwater Pond and Spruce Pond fish. Coles Pond fish were not included in this calculation due to the possible influences of the fertilization experiment. Graphical analysis was employed to describe the change in weight over age, to compare between the seasons, and to compare this study to an earlier one on the EPA and to other locations in Newfoundland. The change in mean weight-at-age over the summer and winter periods was calculated using the formula:

$$\text{Growth} = [(\text{weight at } t_2) - (\text{weight at } t_1)] / (t_2 - t_1) \text{ (Ricker 1975)}$$

where, $(t_2 - t_1)$ for the summer = 4 months and $(t_2 - t_1)$ for the winter = 8 months. The mean rate of change per period was calculated across years for each age class within a pond then compared graphically.

Growth data in the literature are frequently reported as length-at-age. To facilitate comparisons, the length-at-age was estimated from the 1991 - 1996 fall season brook trout log length : log weight relationship for Spruce and Headwater;

$$\text{Length(mm)} = 50.466 \times (\text{Weight(g)})^{0.310},$$

by substituting the weight-at-age for ages 1 +, 2 +, 3 + and 4 +, and solving for length. Spring length-at-age were calculated using the formula:

$$\text{Length(mm)} = 49.545 \times (\text{Weight(g)})^{0.317}.$$

The length at age for age 2+ trout in each season was then graphically compared to that for localities across North America.

4.2.3 Impacts of the Whole-Lake Fertilization.

Response to whole lake fertilization was evaluated by comparing the yearly patterns in population density and biomass of the experimental pond (Coles Pond) to those of the two control ponds (Headwater Pond and Spruce Pond). Biomass (kg $.ha^{-1}$) was calculated as the sum of the total weight (kg) of each age class divided by the surface area of the pond. The age-specific density was graphically compared among the ponds to determine how specific age classes contributed to annual changes in population density.

Changes in growth were assessed through the comparison of the fall mean weights of fish aged 1 +, 2 + and 3 +, and the change in weight over age for each year class among ponds. Ninety-five percent confidence limits were constructed about the annual fall mean weights for Coles Pond fish to facilitate a visual measurement of the statistical difference between the experimental pond and each of the control ponds. The mean weight for fish in one pond which is outside the 95% confidence limits of another is significantly different at the 5% level.

4.3 Results and Discussion.

This study focuses on data collected during the ice-free season in 1996 and during annual spring and fall salmonid population assessments conducted from 1991 through 1997 in three ponds in the Experimental Ponds Area (EPA), insular Newfoundland. Comparison of the population age structure of brook trout in the ponds with that in the stream habitat provides insight into the relative importance of these habitats to each age class. Comparisons of the mean weight-at-age and length-at-age among the study ponds with those determined in studies of other areas places the growth characteristics of EPA brook trout into a global context. Comparison of the age and size structure among the ponds permits identification of general trends as well as departures from those trends in the manipulated pond which may indicate the impact of whole lake fertilization.

4.3.1 Life History and Growth Characteristics.

4.3.1.1 Age-Specific Habitat Utilization.

Brook trout can be either sedentary, remaining in stream or pond habitat, or mobile, utilizing stream and lake (pond) habitat at different points in their life history. Reproductively mature trout generally migrate into stream habitat in the fall to breed while the young of the year (YOY) remain in the streams for at least a year and then migrate to deeper pools within the river system or to adjoining pond and lake habitat

(Scott and Crossman 1973). Brook trout may also migrate from river to pond habitat to feed, to avoid increasing river water temperatures and to overwinter (Power 1980, Saunders and Power 1970).

Graphical analysis of the age frequency distributions in the two headwater ponds and their adjacent stream habitat reveal differences in the fish age composition. Younger age classes (YOY and Age 1+) were predominant in the streams while pond age distributions were dominated by ages 2 + and 3 + (Figure 4.3). Brook trout density in outlet stream habitat far exceeded that of inlet streams (Table 4.1). Outlet streams generally had coarser substrate (small-sized boulders, gravel and pebble), greater amounts of pool and riffle area, and greater amounts of flow compared with inlet streams, all of which are important stream characteristics for supporting salmonids (Elliot 1994).

Density differed among inlet streams probably due to differences in habitat quality. No fish were captured in Coles Pond Inlet A which consisted largely of wide, shallow habitat with very slow flow and little vegetative overhang, while density in Coles B was comparable to that for Headwater's inlet (Table 4.1). Coles Inlet B had a narrow, deeper channel with higher flow velocity and was totally covered by vegetation. Section 1 of the Headwater Pond Inlet had conditions similar to that of Coles Inlet A and lower density than those sections similar in habitat to Coles Inlet B (Section 2 and Section 3).

Experimental Ponds Area brook trout spend a majority of their life utilizing pond habitat. Young of the year (YOY) trout were usually absent in ponds during the spring season, and were observed at very low density ($\leq$ 1.44 $fish.ha^{-1}$) in 9 of the 18 fall

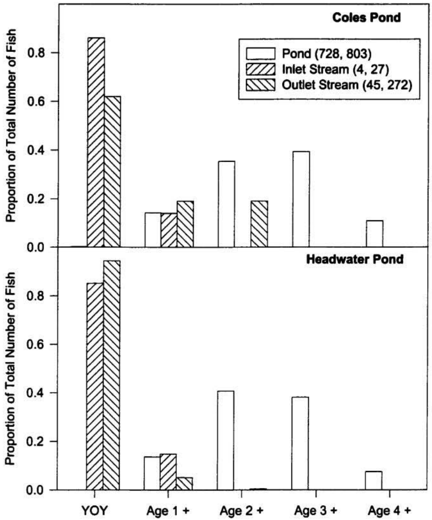


Figure 4.3. Comparison of the age frequency distributions of fish in stream habitats to that in ponds. Bars are the proportion each age class contributes for each of three habitat types (pond, inlet stream and outlet stream). Numbers represent sample sizes for each pond (CP, HP).

Table 4.1. Results of electro-fishing stream habitat surrounding Headwater Pond and Coles Pond of the Experimental Ponds Area, insular Newfoundland. The site number reflects increasing distance from the pond habitat. See figure 4.1 for stream locations.

			Stream Statistics			Age Structure		
Pond	Type	Section	Area (m^2)	Catch (#)	Density (# / 100m^2)	YOY	1+	2+
Coles	Inlet A		475.0	0.0	0.0			
	Inlet B		41.5	4.0	9.6	3	1	
	Total		516.5	4.0	0.8	3	1	
	Outlet	1	207.5	25.0	12.0	22	3	
		2	82.5	21.0	25.4	13	6	3
	Total		290	45.0	15.5	35	9	3
Headwater	Inlet	1	275.0	5.0	1.8	4	1	
		2	172.5	7.0	4.1	3	4	
		3	85.0	15.0	17.6	7	8	
	Total		532.5	27.0	5.1	14	13	
	Outlet	1	585.0	230.0	39.1	210	19	1
		2	262.5	42.0	16.0	28	14	
	Total		847.5	272.0	32.1	238	33	1

censuses (Table 4.2). Trout aged 1 + to 4 + were captured during each pond census, with age 3+ usually the most abundant in spring censuses (11 out of 15) and age 2+ most abundant in the fall censuses (12 out of 18). These results are consistent with earlier investigations in the Experimental Ponds Area (Ryan *et al.* 1981, Ryan 1990, Ryan and Knoechel 1994) and with studies in Newfoundland (Wiseman 1969, Baggs 1989, O'Connell and Dempson 1996), Quebec (Saunders and Power 1970), and New York (Josephson and Youngs 1996).

Brook trout have the shortest lifespan of the species in the genus *Salvelinus* and usually do not live past the fifth year (Scott and Crossman 1973). The maximum age of brook trout observed in this study was age 5 +. This age class was rare during the spring censuses and usually did not survive through to the fall (Table 4.2). A life span of 5 years (Age 5+) has also been observed in ponds of similar surface area across the Avalon Peninsula and Eastern Newfoundland (Wiseman 1969). In comparison, Saunders and Power (1970) observed a life span of 9 years (Age 9+) for brook trout of much larger Matamek Lake, Northern Quebec.

4.3.1.2 Seasonal Change in Population Structure in the Ponds.

Seasonal changes in the structure of brook trout populations can result from movements of younger fish into ponds and losses of older fish via emigration or mortality (Ryan 1990, Ryan and Knoechel 1994). Cohort analysis reveals a general pattern of increase in brook trout density from age 1 + to a maximum usually at age 3+ in the ponds

Table 4.2. Brook trout density (# / ha) by age class for three ponds of the EPA. The density-at-age for the 1992 year class is highlighted for each pond (boxed areas).

Pond	Season + Year	Age Class 0+	1+	2+	3+	4+	5+	Total	Year	Mean
Coles	Fall 1991	0.54	14.05	19.42	8.40	5.18	0.19	47.78		
	Spring 1992	0.08	2.30	11.13	12.41	9.53	0.86	36.30	1992	40.21
	Fall 1992	1.44	9.26	19.38	12.30	1.75	0.00	44.12		
	Spring 1993		2.26	21.01	22.92	2.14	0.08	48.40	1993	60.00
	Fall 1993	0.86	14.59	37.90	17.59	0.66		71.60		
	Spring 1994		2.65	36.61	56.34	6.11	0.23	101.95	1994	130.72
	Fall 1994		32.57	70.23	51.25	5.45		159.49		
	Spring 1995		1.79	40.12	35.14	13.70	1.17	91.91	1995	102.14
	Fall 1995	0.66	19.69	57.70	25.60	8.72		112.37		
	Spring 1996		1.79	12.22	41.48	14.28	0.51	70.27	1996	73.21
	Fall 1996	0.16	10.82	26.96	29.92	8.29		76.15		
Headwater	Fall 1991		7.48	8.91	6.64	0.72	0.05	23.80		
	Spring 1992		0.74	6.16	5.34	2.96	0.35	15.55	1992	18.18
	Fall 1992	0.13	3.94	10.66	5.01	1.08		20.81		
	Spring 1993		4.66	13.81	9.96	1.71	0.11	30.25	1993	35.89
	Fall 1993		6.73	22.21	11.48	1.10		41.52		
	Spring 1994		2.08	13.73	25.02	8.33	0.28	49.43	1994	44.82
	Fall 1994		5.22	17.25	15.87	1.59	0.26	40.20		
	Spring 1995		1.06	12.90	19.42	8.07	0.16	41.62	1995	42.35
	Fall 1995		4.77	13.38	18.38	4.65	1.91	43.09		
	Spring 1996		0.53	7.53	16.71	9.91	1.24	35.91	1996	40.99
	Fall 1996		6.28	18.74	17.56	3.48		46.06		
Spruce	Fall 1991		4.68	10.90	14.68	1.10		31.37		
	Spring 1992		2.11	10.41	11.64	3.86	0.63	28.66	1992	27.23
	Fall 1992	0.19	8.30	8.47	8.08	0.77		25.81		
	Spring 1993		7.40	18.99	9.18	2.33		37.89	1993	38.86
	Fall 1993	0.68	7.59	19.34	11.53	0.68		39.84		
	Spring 1994		2.47	26.05	43.12	10.19	1.75	83.59	1994	66.51
	Fall 1994	0.16	4.11	20.88	21.97	2.30		49.42		
	Spring 1995		2.03	9.48	32.90	14.27	0.08	58.77	1995	49.29
	Fall 1995		2.41	9.64	20.14	6.68	0.93	39.81		
	Spring 1996		1.07	6.38	29.42	18.99	2.47	58.33	1996	52.45
	Fall 1996		7.95	9.64	26.68	2.30		46.58		

followed by a decline (Figure 4.4). Seasonal increases in density were proportionally greatest over the period from spring age 1 + to spring age 2 + (Table 4.4) indicating that the bulk of immigration into pond habitat occurs during the second summer and third winter of life. Similar movements have been documented for brook trout in earlier studies of Spruce Pond and Headwater Pond (Ryan 1990, Ryan and Knoechel 1994) and in Lake Matamek, Quebec (Saunders and Power 1970), and for juvenile Atlantic salmon in Newfoundland (Hutchings 1985, Ryan 1990). In contrast, Josephson and Youngs (1996) observed emigration of small numbers of yearling trout from March to June from five stocked Adirondack lakes.

Variation in the cohort patterns among ponds may reflect differences in how young brook trout utilize pond habitat. The pattern for Spruce Pond as judged by eye was different from that of the two headwater ponds. Most trout entered Spruce Pond over the winter period (1+ to 2+, and 2+ to 3+) while in the two headwater ponds the greatest increases were during summer (Figure 4.4, Table 4.3). Trout in Spruce Pond have greater access to inlet and outlet stream habitat due to the ponds position within the watershed (downstream from Headwater Pond).

Brook trout density in all three ponds declined after age 3 + indicating losses due to mortality or to emigration. The loss of older fish is more likely due to mortality than to emigration given that no fish older than 2+ were captured in the fall stream electrofishing surveys. There is evidence that the summer period may also be more stressful to older, larger trout in these shallow pond environments. Spring censuses were usually conducted in May when water temperatures are low (typically 8 - 15°C). Muddy roads rendered

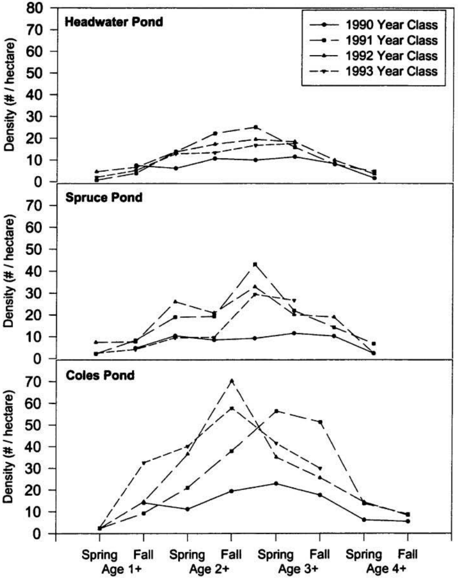


Figure 4.4. Comparison of cohorts of four year classes (1990, 1991, 1992, 1993) in three ponds of the Experimental Ponds Area.

Table 4.3. Average (range) summer and winter period change (%) in age-specific density over three year classes (1991, 1992 and 1993; 1990 was excluded because there was no spring sample for Coles Pond) of brook trout in the Experimental Ponds Area. Coles Pond fish in the later year classes would be more influenced by the fertilization experiment due to greater exposure of age classes to enhanced conditions.

Pond	**Season and Age**			
	Summer (Age 1+)	**Winter (Age 1+ to Age 2+)**	**Summer (Age 2+)**	**Winter (Age 2+ to Age 3+)**
Coles	660.3* (303 - 1130)	100.3 (23.2 - 150.9)	72.0 (43.8 - 91.8)	-9.8 (-50.0 - 48.7)
Headwater	210.4 (44.2 - 435.7)	167.3 (104.1 - 250.3)	30.4 (3.7 - 60.8)	16.7 (12.6 - 25.0)
Spruce	121.2 (2.6 - 293.5)	167.6 (128.7 - 243.3)	-5.4 (-19.1 - 1.9)	128.6 (57.6 - 205.1)

* may be inflated due to a large increase in trout density over the summer of 1994.

Coles Pond inaccessible in May of 1997 and the census was conducted in July when water temperature reached as high as 23°C, near the upper lethal limit for brook trout (~ 25°C Fry *et al.* 1946). Mortalities during capture and handling amounted to 7.5 % of the July catch, far in excess of the previously observed maximum of 0.4 % at lower water temperatures, and more than 80 % of those fish that died were greater than 150 mm, equivalent to fish aged 3+ and older (Figure 4.5).

4.3.1.3 Maturity, Fecundity and Egg size.

Experimental Ponds Area brook trout matured as early as their third year of life (Age 2 +) while the majority of mature trout were age 3+. Similar results were noted in other ponds in Newfoundland (Wiseman 1969) and in Matemak Lake (Saunders and Power 1970), while studies on rivers and streams typically observe lower ages at maturity (Wydowski and Cooper 1966, Hutchings 1991). Samples from the three ponds were pooled to increase sample size of each gender per year. Mature females tended to be older and of greater fork-length than males although only the age difference was significant for data from all years combined (Table 4.4). This was largely due to a greater proportion of reproductive males aged 2 + compared to females (37 % versus 22 %, respectively). Similar differences in average fork length of reproductive fish have been observed in stream (Wydowski and Cooper 1966) and lake habitats (Blanchfield and Ridgeway 1997).

Female brook trout of the Experimental Ponds Area had an average of 236 ± 10

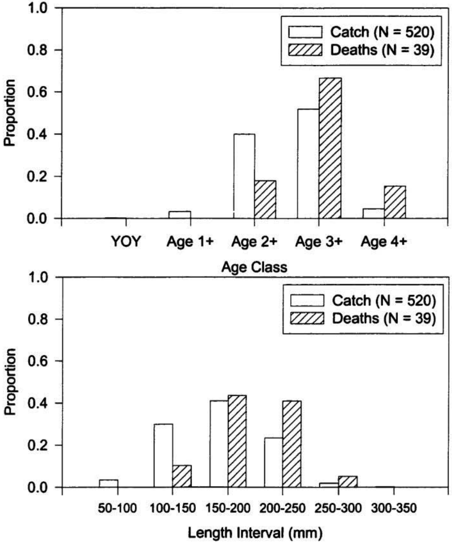


Figure 4.5. Comparison of the composition of fish which were captured and those which died during the July 1997 population census in Coles Pond. Panel A. presents the calculated proportions per age-class and panel B. those per 50 mm length interval.

Table 4.4. Average age (group ± 1 standard error) and size (mm ± 1 s.e.) of reproductively mature male and female brook trout from the Experimental Ponds Area.

		Year					
		1992	1993	1994	1995	1996	1992 to 1996
Male	Size	182 ± 12	177 ± 14	185 ± 6	188 ± 10	198 ± 9	188 ± 5
	Age	2.6 ± 0.3	2.5 ± 0.2	2.5 ± 0.3	2.4 ± 0.2	2.8 ± 0.1	2.6 ± 0.1
	N	5	6	4	7	10	32
Female	Size	205 ± 10	201 ± 12	185 ± 5	193 ± 11	200 ± 5	196 ± 3
	Age	2.9 ± 0.2	2.7 ± 0.2	2.7 ± 0.1	2.7 ± 0.2	2.9 ± 0.1	2.8 ± 0.1*
	N	11	6	15	10	22	64

*Females were significantly older than males $p < 0.05$, Wilcoxon Signed Ranks Test.

ova per female with an average diameter of 3.23 ± 0.49 mm. The average number of ova, corrected for significant co-variance due to length (see Figure 4.6 for equation), did not vary significantly among ponds ($F_{1,2} = 0.660$, $p = 0.521$), consistent with gonadal-somatic index and ovarian lipid estimates (see Section 3.3.3), nor across years ($F_{1,5} = 0.987$, $p = 0.422$). There was no significant correlation between ova diameter and maternal fork length (Figure 4.7). Similar positive relationships between fecundity and maternal length have been observed for other brook trout populations throughout insular Newfoundland and mainland North America (Table 4.5). The slope parameter for EPA brook trout was within the wide range observed for other lake locations, was lower than that for mainland North American streams but was greater than slopes determined for trout from streams in Newfoundland (Table 4.5). The estimated ova number was also within the range from other lake studies and from stream studies in Newfoundland but was much lower than estimated in other mainland North American streams.

4.3.1.4 Growth Characteristics.

Brook trout growth was assessed by graphically comparing the fall and spring mean weight across age classes and through the calculation and comparison of the winter and summer growth rates. Comparison of the weight-at-age to that determined in a previous study of the EPA place these growth characteristics in a historical context. Comparisons to other locations in Newfoundland and the rest of North America place the growth characteristics into a regional and continental context.

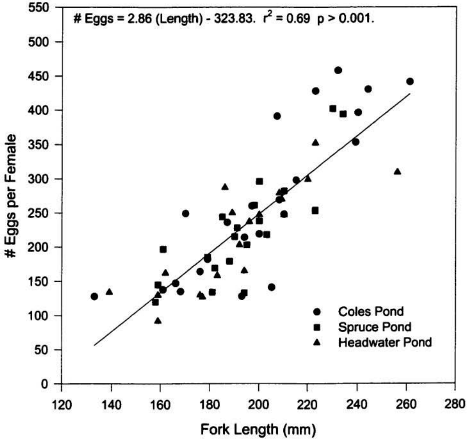


Figure 4.6. The relationship of the number of ova per female (# of ova) to maternal fork length (fork length) for brook trout captured in three ponds of the Experimental Ponds Area.

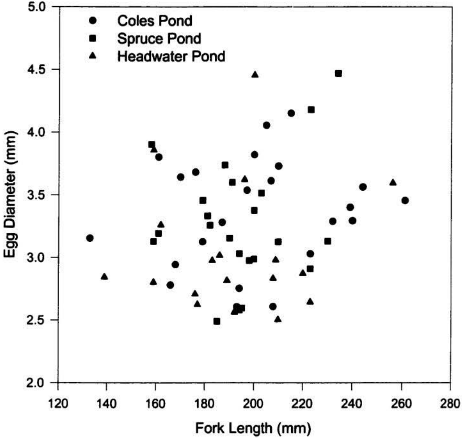


Figure 4.7. The relationship of ova size (diameter mm) to maternal length (mm) for brook trout captured in three ponds of the Experimental Ponds Area.

Table 4.5. Comparison of the slope, intercept and estimated number of ova of various brook trout populations (length range similar to that of this study) sampled from various river and lakes in Newfoundland and North America. The estimated number of ova in each study was calculated for a 200 mm fish using the regression parameters given. Regression parameters are based on the linear regression of ova number on length as calculated by Hutchings (1991).

Location	Study	Slope	Intercept	Estimated Number of ova
Lake Studies				
Experimental Ponds Area, Newfoundland	This Study	**2.86**	**-323**	**249**
Matamek Lake, Quebec	Saunders and Power (1970)	2.60	-270	250
Lauentide, Quebec	Vladykov (1956)	2.37	-240	234
Mad and Nipigon Lakes, Ontario	Ricker (1932)	5.11	-561	461
Beaver Pond, Wyoming	Allen (1956)	3.34	-286	382
Stream Studies				
Lawrence Creek, Wisconsin	McFadden (1961)	4.10	-388	432
Tomtit Run, Pennsylvania	Wydoski and Cooper (1966)	4.11	-455	367
Pigeon River, Michigan	Cooper (1953)	4.71	-464	478
Dunk River, Prince Edward Island	Hutchings (1991)	8.36	-455	438
Cripple Cove, Newfoundland	Hutchings (1991)	2.66	-281	251
Drook River, Newfoundland	Hutchings (1991)	1.89	-155	223

The increase in weight over the summer is a reflection of the weight gain due to somatic growth and lipid storage for all fish, and additional weight gain due to gonad growth for reproductively maturing individuals. The weight of brook trout of the Experimental Ponds Area increased with age and was greater in the fall than the spring for each age class (Figure 4.8). Monthly weight gains were generally greater in the summer than in the winter and tended to increase with increasing age (Figure 4.9, Appendix E).

The mean monthly weight gain across the summer for Coles Pond Age 1+ trout exceeded that of both control ponds (Appendix E). Greater dipteran and gastropod densities have been observed in Coles Pond relative to Spruce Pond (Moore 1999) which suggests that greater amounts of these types of prey are available to trout in Coles Pond. The Age 1+ trout from Coles Pond had greater percentages of gastropods and dipteran pupae/adults in their diet when compared to both control ponds (Table 4.6).

Decadal variance in mean weight-at-age may indicates changes in environmental conditions within the Experimental Ponds Area and in Newfoundland. The fall weight-at-age for ages 2+ and older was on average 25 % greater during the period from 1977 to 1980 when compared to that from 1991 to 1996 (Figure 4.10, 1977 to 1980 data from Ryan *et al.* 1981). Trout from three similar-sized ponds in eastern Newfoundland sampled in the late 1960's also grew heavier with age when compared to EPA trout in the spring (Figure 4.10). The mean weight at age 4 + for Angle Pond may have large error due to a small sample size of only 4 trout.

Brook trout growth varies greatly throughout its geographical range. Hutchings

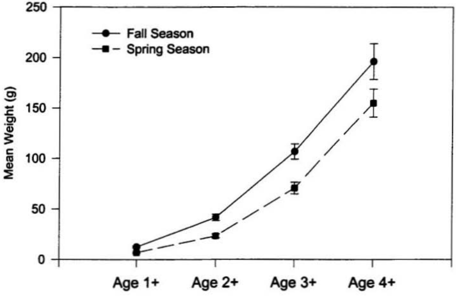


Figure 4.8. Comparison of the fall weight-at-age to that of the spring for Spruce and Headwater Ponds combined. Note: Summer Period N =6 per age class, Winter Period N = 5 per age class.

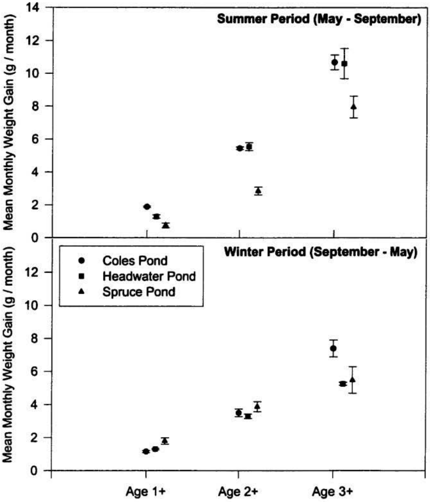


Figure 4.9. Comparison of the rates of change in weight versus age over the summer and winter period for ponds in the Experimental Ponds Area. Vertical bars represent 1 standard error. Note: Summer Period N =6 per age class, Winter Period N = 5 per age class.

Table 4.6. Comparison of the mean monthly weight gain and the percentage stomach content of Age 1+ brook trout from three ponds of the Experimental Ponds Area.

Pond	**Monthly Weight Gain (g / month)**	**Percentage Diet Composition (%)**	
		Gastropods	Diptera Pupa / Adults
Coles	1.9	30	11
Headwater	1.3	16	6
Spruce	0.7	17	3

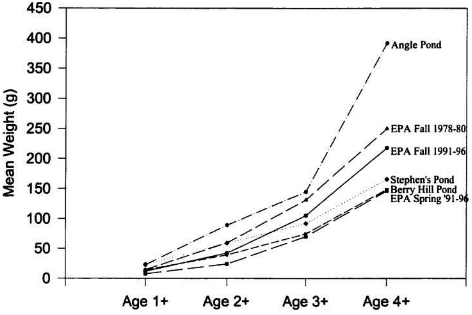


Figure 4.10. Comparison of the weight at age of Experimental Ponds Area trout (Spruce + Headwater Pond) to that from an older study of the EPA and to other locations in insular Newfoundland.

(1991) calculated a 3.4 fold range in the fork length of Age 2+ brook trout from 34 locations throughout North America. For insular Newfoundland, all of the lake sites lie above the spring mean length of EPA brook trout aged 2+, while a majority of river sites lie at or below the fall mean length (Figure 4.11). Furthermore, 2+ brook trout in the fall were generally shorter in fork length than most of the lake sites around North America and were within the length range of the river sites (Figure 4.11).

Experimental Ponds Area brook trout fork lengths were smaller than those reported for natural populations in mainland North American lakes of similar size (Figure 4.12). Subsequent annual length increments in the EPA were similar to those for Northern Quebec and Wisconsin, as denoted by the similarity in slopes, while length increments were noticeably higher in Ontario trout aged 2+ and older.

4.3.1.5 Life History and Growth Summary.

In summary, young-of-the-year were the most predominant age class in the streams and cohort patterns indicate trout enter the ponds predominantly at ages 1+ and 2+. The lack of older fish in the streams suggests that death is the principle source of loss for pond fish aged 2+ and older. The maximum age observed during this study was age 5+. Male trout mature at a smaller size and at a younger age, on average, than females, although the majority of reproductive individuals are age 3 +. Female brook trout produced an average of 236 eggs per female with a mean diameter of 3.23 mm. EPA

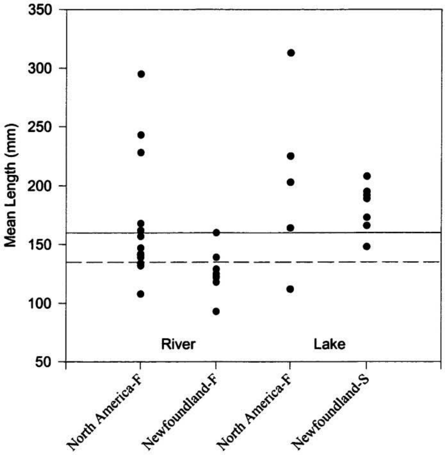


Figure 4.11. Comparison of the mean length of age 2+ trout from river and lake sites in insular Newfoundland and the mainland North America to that of the Experimental Ponds Area (Spruce + Headwater). Non-EPA data are from Hutchings 1991. Solid line represents the mean fall length-at-age while the broken line represents spring length-at-age for EPA brook trout (F = Fall season, S = Spring season).

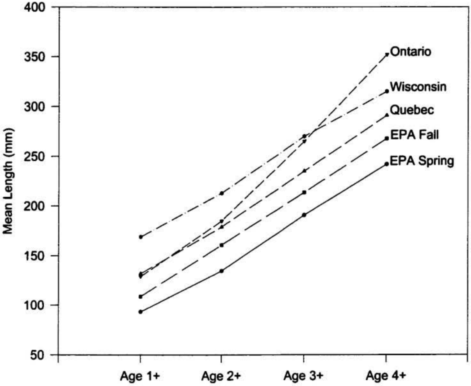


Figure 4.12. Comparison of the length at age of Experimental Ponds Area brook trout (Spruce + Headwater Pond) to that from similar sized ponds from various locations on the mainland North America. Note references: Ontario; Ricker 1932, Wiconsin; McFadden 1961, Quebec; Saunders and Power 1970.

brook trout were generally smaller in fork length than those in other lakes on the mainland and in eastern insular Newfoundland.

4.3.2. Impacts of the Whole-Lake Fertilization Experiment.

In this section, the temporal changes in the population size, population structure and growth characteristics of the experimental pond are compared to those in two control ponds to investigate the potential effects of the whole-lake fertilization experiment.

4.3.2.1 Population Size and Structure.

Fertilization of Coles Pond has led to a 2-4 fold increase in the abundance of benthic macroinvertebrates (Figure 4.13) leading to the expectation of increased benthivorous brook trout density relative to the control ponds over time. Brook trout density displayed generally similar trends among the ponds from the fall of 1991 through spring of 1994 (Figure 4.14 A and B, Appendix F for values). The densities in spring 1994 were, on average, 98 % greater than that observed in the spring of 1992 (90 % Coles Pond, 96 % Spruce Pond and 108 % Headwater Pond) and the differences were statistically significant (difference between Spring 1992 and Spring 1994, $p < 0.05$). This suggests that the increase in density was largely due to factors which affected all ponds in common. Analysis of the cohort patterns indicates a very strong 1991 year class that peaked in pond density in spring of 1994 at age 3 + in each pond (Figure 4.4).

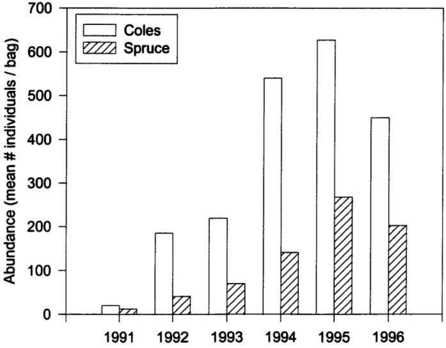


Figure 4.13. Annual spring macroinvertebrate abundances for Coles Pond and Spruce Pond based on counts from artificial substrates. Data adapted from Moore (1999).

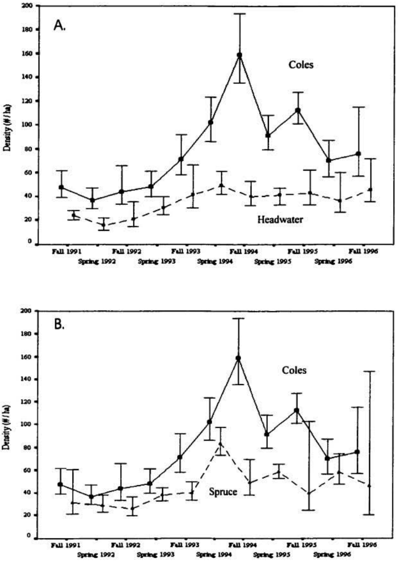


Figure 4.14. Comparison of the temporal pattern in brook trout density of Coles Pond to that of Headwater Pond (A) and Spruce Pond (B). Vertical bars represent the 95 % confidence limits of each population estimate.

Trout density in fertilized Coles Pond diverged from that in the control ponds during summer 1994 reaching a maximum of 159.5 fish / ha, a density approximately 3 - 4 times greater than that observed in the controls (40.20 fish / ha and 49.42 fish / ha for Headwater Pond and Spruce Pond). Similar trends were observed for brook trout biomass (Figure 4.15). The increase in the density of Coles Pond trout over the summer of 1994 and 1995 was due largely to influxes of age 1 + and age 2 + fish (arrows in Figure 4.16) which coincided with the highest recorded macroinvertebrate abundances (Figure 4.13). Enhanced prey abundances may have attracted younger fish into the experimental pond as well as increased survivorship rates. Both the 1992 and 1993 year classes were very strong in Coles Pond compared to Headwater and Spruce ponds (Figure 4.4). Age 3 + trout also provide evidence for enhanced survivorship in that they declined only by 9 % in Coles Pond during the summer of 1994 compared with declines in Headwater Pond and Spruce Pond of 37 % and 49 %, respectively (Table 4.2).

It was expected that density would diverge further in subsequent years as more cohorts became exposed to the enhanced prey abundance for longer periods of their life cycle however Cole's Pond brook trout density actually declined from the 1994 fall peak in both 1995 and 1996 (Figure 4.14). This unexpected decrease coincided with a shift in the population structure to one that peaked at a younger age. The 1990 and 1991 year classes peaked at age 3+ in the spring whereas the 1992 and 1993 year classes peaked at age 2+ in the fall (Figure 4.17). These observations are consistent with increased mortality of larger fish reflected as declining densities over the winter and summer periods.

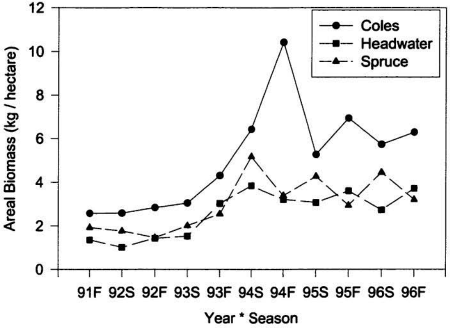


Figure 4.15. Comparison of the temporal trend in brook trout biomass of Coles Pond to that of Headwater Pond and of Spruce Pond.

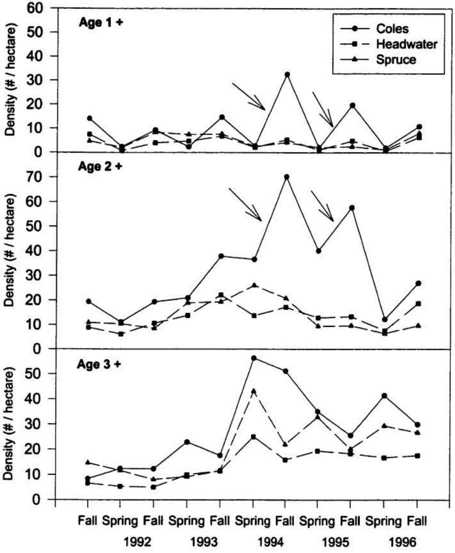


Figure 4.16. Comparison of the temporal trend in the density of three age classes of brook trout (1+, 2+, 3+) in Coles Pond to that of Headwater Pond and Spruce Pond.

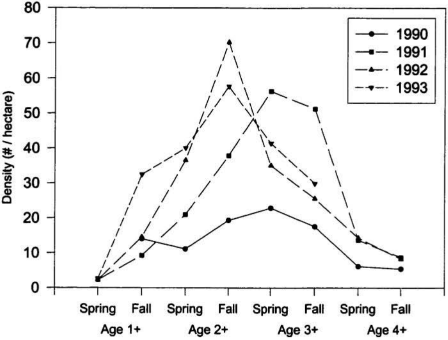


Figure 4.17. Comparison of age class strengths in Coles Pond for the 1990 through 1993 year classes.

The common loon (*Gavia immer*) can remove substantial amounts of fish from lakes (Matkowski 1989). Barr (1996) has estimated that a pair of loons with one chick require 370 kg of fish during a 15 week period from nesting to migration, a requirement that exceeds the maximum brook trout biomass in each of the study ponds (Headwater Pond = 293 kg; Spruce Pond = 189 kg; Coles Pond = 268 kg). Imputed fresh loon bites, bleeding circular wounds usually on both sides of the fish, were first noted on Coles Pond trout in the fall of 1994 and then increased dramatically in 1995 and 1996 (Table 4.7, data from Knoechel *et al.* 1999). This increase coincided with the unexpected decrease in brook trout density in Coles Pond and greater than 60 % of fish with loon bites in 1996 were older than age 3 + (66.7 % Aged 3+ and 4+, 33.3 % Aged 2 +).

Loons in insular Newfoundland tend to distribute their feeding over a number of nearby lakes unlike the mainland where they usually feed solely within their territorial lake (Kerekes *et al.* 2000). It is thus possible that the great increase in Coles Pond trout biomass in 1994 (Figure 4.15) could have caused a behavioural shift in feeding strategy that increased predation pressure in Coles Pond relative to nearby Headwater Pond (Figure 2.1). Summer mortality estimates from adipose clip data in 1996 were higher for Coles Pond 3+ and 4+ trout when compared to Headwater trout (Table 4.8).

4.3.2.2. Growth Characteristics.

If enhanced macroinvertebrate abundance following fertilization (Figure 4.13) resulted in increased brook trout growth rate it should be reflected in greater weights at

Table 4.7. Comparison of the number and the percentage of fish captured with fresh loon bites in Coles Pond and Headwater Pond. Number of fish sampled and those with bites do not include fish marked for census purposes.

Pond		# of Bites	# of Fish Sampled	% Bitten
Coles	1994	1	1317	0.08
	1995	5	1060	0.47
	1996	15	639	2.35
Headwater	1994	0	603	0.00
	1995	0	695	0.00
	1996	1	684	0.15

Table 4.8. 1996 summer mortality estimates (%) for three age classes of brook trout (Age 2+, 3+ and 4+) from Headwater and Coles ponds. Mortality was calculated using adipose fin clip data described in section 4.2.1.4..

Pond	Age Class	# Adipose Clipped in Spring	Estimated Fall Abundance	Expected # Adipose Recaptures[1]	Actual # Adipose Recaptures	Summer Mortality Estimate[2]
Coles	2 +	97	693	44.24	31	29.9
	3 +	470	769	183.97	67	64.0
	4 +	59	213	16.43	1	93.4
Headwater	2 +	97	1426	26.66	18	32.5
	3 +	284	1336	65.90	45	31.7
	4 +	59	265	8.68	3	65.4

[1] Expected number if all adipose-clipped fish from the Spring still present in the population.
[2] See equation in section 4.2.1.4.

age over time. Observed weights-at-age in Coles pond did not show a tendency to increase over time, nor were they significantly greater than those in Headwater Pond in most years (Figure 4.18). Weights-at-age in both headwater ponds tended to exceed those observed in Spruce Pond. The growth curves for fertilized Coles Pond varied less among years than those in the control ponds (Figure 4.19). Thus one of the impacts of fertilization may have been to stabilize the growth rates across years.

4.3.2.3 Fertilization Impact Summary.

There was an increase in brook trout density in the experimental pond relative to the controls during the fourth year of fertilization, consistent with an expected 'bottom-up' response to increased macroinvertebrate abundance followed by apparent increases in mortality rates possibly attributable to a 'top-down' impact by loons. Fertilization appears to have not increased the growth rates of fish in the experimental pond, as indicated by the comparisons of age class fall weights, however the growth patterns in the experimental pond varied less among years than those of the controls across years.

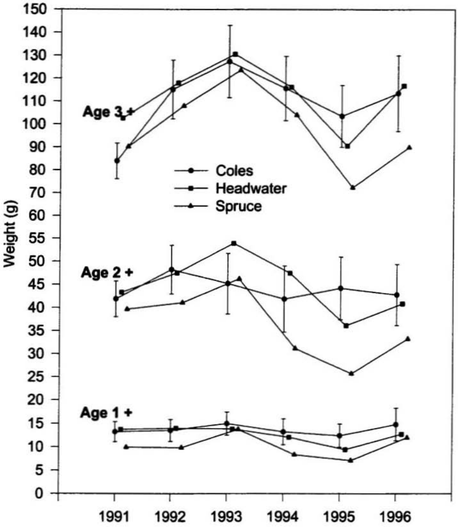


Figure 4.18. Comparison of the annual fall mean weights of three age classes of brook trout (1+, 2+, 3+) in Coles Pond to that of Headwater Pond and Spruce Pond. Vertical bars represent the 95% confidence intervals about the mean for Coles Pond fish.

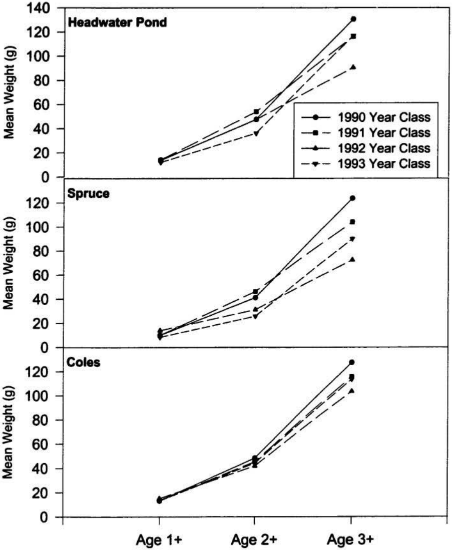


Figure 4.19. Comparison of the change in fall mean weight over age for four year classes of brook trout (1990, 1991, 1992, 1993) in Coles Pond to that of Headwater Pond and Coles Pond.

4.4 Chapter Summary.

To summarize,

1. Experimental Ponds Area brook trout older than YOY spend most of their life utilizing pond habitat to feed, to grow and to reproductively mature.
2. Young of the year brook trout generally remain in streams, then enter the ponds at ages 1+ and 2+. Pond cohort strength, the summation of pond immigration and survival less emigration and death, tended to peak at age 2+ fall and 3+ spring following which it rapidly declined. Very few fish reach five years of age.
3. Maturation can occur at age 2 +, although the greater proportion of reproductive individuals were age 3 + with earlier maturation of males, similar to findings elsewhere in Newfoundland and Quebec. Females produced an average of 236 eggs per female with mean diameter of 3.23 mm.
4. Brook trout were generally smaller than those in other Newfoundland ponds similar in size to those of the EPA. The mean length for age 2+ fish was within the range for other North American locations but was generally smaller compared to other lake-dwelling populations.
5. The brook trout population density in Coles Pond increased relative to the control ponds during the fourth year which was consistent with the 'bottom-up' response to the increased macroinvertebrate abundances. The population abundance declined thereafter due to an increase in mortality which was potentially attributable to a 'top-down' impact by piscivorous loons.

6. Growth rates appeared unaffected by fertilization although cohort growth patterns were less variable among years in the experimental pond compared to the controls.

Chapter 5. General Summary and Conclusion.

The main goal of this thesis was to describe the ecology and the life history of brook trout residing in three ponds of the Experimental Ponds Area, central Newfoundland. EPA brook trout enter the ponds at ages 1+ and 2+ where they feed, mature, and grow to a maximum age of 5 +. While in the ponds, EPA Brook trout predominantly feed on benthic organisms switching from a diet dominated by odonate nymphs in the spring to one composed of snails, smaller-sized insect taxa and organisms found on or near the surface waters of the pond later in the summer and early fall. They also accumulate lipid from spring to mid-summer when mean ration is greatest, then lose lipid from mid-summer thru to fall due to a decrease in feeding intensity, due to an increase in metabolism inferred from higher water temperatures, and due to the diversion of lipid into gonadal mass. Maturation occurred as early as age 2 +, although a greater proportion of reproductive individuals were age 3 +, with female trout producing an average of 236 eggs per female with a mean diameter of 3.23 mm. EPA brook trout displayed generally smaller fork lengths at age than fish in other lakes on the mainland North America and eastern insular Newfoundland.

A secondary goal was to compare brook trout in the two natural ponds to the experimental pond to evaluate how brook trout have responded to whole-lake fertilization. There was an increase in brook trout density in the experimental pond relative to the controls during the fourth year of fertilization, consistent with an expected 'bottom-up' response to increased macroinvertebrate abundance, followed by increased mortality rates possibly attributable to a 'top-down' impact by loons. Fertilization appears not to have increased the growth rates of fish in the experimental pond, however, the growth patterns in the experimental pond varied less among years than those of the control ponds.

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Chapter 7. Appendices.

Appendix A. Table of factors used in the initial ANCOVA model for the relationship between ration and length. The factors and interaction variables denoted with the superscript ([a]) were significant contributors for the final model listed in Table 3.1.

Main Factors		df	SS	Interaction Variables		df	SS
Dependant	Log_{10} (Ration)			2 - Way	Month x Pond[a]	5	1.76
					Month x Gender[a]	4	1.72
Covariate	Log_{10} (Length)[a]	1	5.64		Pond x Gender	2	0.04
					Month x Log_{10} (Length)	4	2.46
Fixed	Month (5)[a]	4	2.50		Pond x Log_{10} (Length)	2	0.22
	Pond (3)[a]	2	0.22		Gender x Log_{10} (Length)	1	0.40
	Gender (2)	1	0.39				
				3 - Way	Month x Pond x Gender	5	0.76
					Month x Pond x Log_{10} (Length)	5	1.66
Error		108	27.52		Month x Gender x Log_{10} (Length)	4	1.78
					Pond x Gender x Log_{10} (Length)	2	0.04
				4 - Way	Month x Pond x Gender x Log_{10} (Length)	5	0.67

Appendix B. Comparisons of brook trout sample sizes and percentage empty stomachs sampled from the Experimental Ponds Area, Newfoundland. Percentage empty stomachs is defined as the number of stomachs observed as empty divided by the total sample size of stomachs collected. For example, on the date 23-05-96, 10 of the 20 male brook trout sampled from Coles Pond had empty stomachs (50%).

		Total Brook Trout			# Empty Stomachs (%)				
Pond	Date	N	Male : Female	Small : Large	Total	Male	Female	Small	Large
	23-05-96	37	20 : 17	20 : 17	15 (41)	10 (50)	5 (29)	12 (60)	3 (18)
	13-06-96	14	8 : 6	7 : 7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Coles	17-07-96	43	19 : 24	19 : 24	26 (60)	10 (53)	16 (67)	10 (53)	16 (67)
	24-08-96	27	14 : 13	16 : 11	13 (48)	6 (43)	7 (54)	8 (50)	5 (45)
	17-09-96	24	12 : 12	14 : 10	9 (38)	5 (42)	4 (33)	5 (36)	4 (40)
	Total	145	73 : 72	76 : 69	63 (43)	31 (42)	32 (44)	35 (46)	28 (41)
	24-05-96	20	13 : 7	7 : 13	2 (10)	1 (8)	1 (14)	1 (14)	1 (8)
	14-06-96	22	18 : 4	16 : 6	2 (9)	2 (11)	0 (0)	1 (6)	1 (17)
Headwater	19-07-96	26	15 : 11	10 : 16	9 (35)	5 (33)	4 (36)	5 (50)	4 (25)
	22-08-96	24	12 : 12	9 : 15	7 (28)	4 (33)	3 (25)	4 (44)	3 (20)
	17-09-96	25	12 : 13	16 : 9	3 (12)	0 (0)	3 (23)	1 (6)	2 (22)
	Total	117	70 : 47	58 : 59	23 (20)	12 (17)	11 (23)	12 (21)	11 (19)
Spruce	21-05-96	46	23 : 23	30 : 16	12 (26)	6 (26)	6 (26)	9 (30)	3 (19)
	18-09-96	24	7 : 17	6 : 18	5 (21)	2 (17)	3 (18)	1 (17)	4 (22)
	Total	70	30 : 40	36 : 34	17 (24)	8 (27)	9 (23)	10 (28)	7 (21)

Appendix C (a). Monthly percent diet composition of taxonomic prey categories found in the stomach samples of Experimental Ponds Area brook trout.

Pond	Month and Year	N	Benthic Evasive					Benthic Passive				Pelagic	Surface	
			Odonata	Ephemeroptera	Trichoptera	Corixidae	Amphipod/Hydracarina	Gastropoda	Pelycopoda	Annelida	Diptera larvae	*G. aculeatus*	Terrestrial Insecta	Aquatic Diptera
Coles	May, 1996	13	53.9	6.5	0.4	0.0	7.6	17.3	0.1	4.1	0.0	3.0	0.4	6.7
	June, 1996	12	61.8	14.7	2.1	0.0	0.1	4.1	0.0	0.2	0.0	1.0	11.3	4.6
	July, 1996	12	13.7	4.0	5.3	0.0	8.3	45.7	0.3	0.0	0.0	12.8	8.7	1.1
	August, 1996	10	9.9	10.0	10.7	20.3	0.0	9.3	3.3	0.0	0.0	0.0	35.6	0.8
	September, 1996	13	18.1	0.0	8.2	15.5	0.1	34.0	4.2	0.0	0.0	7.3	12.5	0.0
	Total N	60												
	Mean		32.6	7.0	5.1	6.7	3.4	22.7	1.5	0.9	< 0.1	4.6	12.7	2.7
Headwater	May, 1996	13	25.3	34.5	1.8	0.0	8.1	27.8	0.9	0.0	0.0	0.0	0.5	1.0
	June, 1996	13	74.5	1.0	4.0	0.0	0.6	3.4	0.1	0.0	0.0	0.0	13.7	2.7
	July, 1996	13	19.7	52.7	2.5	0.0	0.0	9.6	0.0	0.0	0.0	15.4	0.2	0.0
	August, 1996	11	34.1	0.0	0.0	0.0	0.0	23.2	0.0	1.3	0.0	3.6	37.8	0.0
	September, 1996	12	27.5	0.0	2.2	0.0	0.6	33.5	12.1	0.0	0.0	0.0	20.8	3.3
	Total N	62												
	Mean		36.4	18.5	2.2	0.0	2.0	19.2	2.5	0.2	< 0.1	3.9	13.7	1.4

Appendix C (b). Monthly percent diet composition of specific prey types found in the stomach samples of Experimental Ponds Area brook trout.

Pond	Month and Year	N	Odonata				Ephemeroptera		Gastropoda				Terrestrial Insecta	
			Cordulia	*Aeshna*	Unidentified	*Enallagma*	Ephemeroptera	*Hexagenia*	*Amnicola*	*Helisoma*	*Physa*	*Gyrulus*	Hymenoptera	Terrestrial
Coles	May, 1996	13	49.0	4.7	0.2	0.0	6.5	0.0	10.1	7.3	0.0	0.0	0.0	0.4
	June, 1996	12	30.6	6.8	20.4	5.3	13.2	0.0	4.1	0.0	0.0	0.0	0.0	11.3
	July, 1996	12	12.4	0.0	1.4	0.0	4.0	2.4	42.3	3.4	0.0	0.0	0.0	8.7
	August, 1996	10	0.0	0.0	0.0	9.9	10.0	0.0	9.3	0.0	0.0	0.0	25.8	9.8
	September, 1996	13	17.8	0.0	0.3	0.0	0.0	0.0	33.9	0.0	0.1	0.0	0.0	12.5
	Total N	60												
	Mean		23.1	2.4	4.5	2.7	6.5	0.5	20.4	2.3	< 0.1	0.0	4.3	8.4
Headwater	May, 1996	13	20.6	1.7	1.7	1.3	34.5	0.0	17.8	9.7	0.4	0.0	0.0	0.5
	June, 1996	13	37.2	0.0	14.0	23.4	1.0	0.0	3.4	0.0	0.0	0.0	0.0	13.7
	July, 1996	13	10.1	8.5	1.1	0.0	0.7	52.0	8.8	0.8	0.0	0.0	0.0	0.2
	August, 1996	11	13.2	16.7	0.0	4.3	0.0	0.0	8.1	15.1	0.0	0.0	26.9	11.0
	September, 1996	12	17.9	3.3	1.7	4.6	0.0	0.0	17.4	9.5	6.6	0.0	3.3	17.5
	Total N	62												
	Mean		19.8	6.1	6.7	3.7	7.2	10.4	11.1	7.0	1.4	0.0	6.0	8.6

Appendix D. Monthly mean (± standard error) length (mm), percent lipid content (% dry wt.), percent water content (% wet wt.), gonadal-somatic index ((g gonad / g fish x 100%) and ration (mg dry wt / fish) for female and male brook trout sampled from the Experimental Ponds Area, Newfoundland. Mean Ration includes fish ≥ 180 mm and smaller fecund fish used for lipid content. The mean lengths are of those fish used to in the lipid analysis only.

Location	Sampling date	Female Brook Trout					Male Brook Trout				
		Length (n)	Lipid (n)	Ration (n)	Water (n)	GSI (n)	Length (n)	Lipid (n)	Ration (n)	Water (n)	GSI (n)
Coles Pond	23-05-96	202.60 ± 14.01 (5)	11.86 ± 1.75 (5)	66.65 ± 13.22 (6)	73.31 ± 0.79 (5)	0.33 ± 0.04 (5)	235.50 ± 14.01 (4)	8.25 ± 1.35 (4)	36.17 ± 14.13 (3)	73.61 ± 1.11 (4)	0.07 ± 0.02 (4)
	12-06-96	211.25 ± 15.12 (4)	15.30 ± 1.82 (4)	187.93 ± 68.65 (3)	73.11 ± 0.38 (4)	0.64 ± 0.17 (4)			212.93 ± 31.23 (3)		
	17-07-96	214.75 ± 17.36 (4)	21.29 ± 2.08 (4)	53.15 ± 15.05 (2)	72.30 ± 0.81 (4)	0.68 ± 0.13 (4)	233.75 ± 17.28 (4)	15.15 ± 1.08 (4)	18.13 ± 3.81 (3)	71.63 ± 0.95 (4)	0.23 ± 0.04 (4)
	24-08-96	199.00 ± 7.36 (4)	14.67 ± 1.50 (4)	5.63 ± 1.53 (3)	73.69 ± 0.49 (4)	1.60 ± 1.07 (4)			130.15 ± 126.55 (2)		
	17-09-96	215.80 ± 16.34 (5)	14.90 ± 1.69 (5)	52.63 ± 33.61 (3)	74.36 ± 0.81 (5)	6.24 ± 1.41 (5)	195.50 ± 7.86 (4)	11.29 ± 2.06 (4)	44.90 ± 37.90 (2)	77.56 ± 0.30 (4)	0.58 ± 0.32 (4)
Headwater Pond	24-05-96	213.50 ± 14.71 (4)	10.31 ± 0.33 (4)	132.40 ± 16.66 (3)	75.88 ± 2.37 (4)	0.53 ± 0.10 (4)	244.00 ± 10.32 (5)	7.78 ± 1.34 (5)	362.98 ± 25.68 (4)	77.90 ± 1.16 (5)	0.05 ± 0.01 (5)
	14-06-96	179.00 ± 21.94 (4)	13.57 ± 0.83 (4)	35.60 ± 28.90 (2)	75.04 ± 0.37 (4)	0.74 ± 0.38 (4)			152.45 ± 99.55 (2)		
	19-07-96	219.50 ± 15.45 (4)	20.53 ± 0.80 (4)	200.30 ± 43.05 (3)	74.61 ± 0.72 (4)	0.56 ± 0.11 (4)	236.80 ± 11.48 (5)	15.21 ± 1.28 (5)	176.53 ± 72.35 (6)	72.40 ± 1.25 (5)	0.10 ± 0.02 (5)
	22-08-96	207.50 ± 8.15 (4)	14.21 ± 0.67 (4)	9.25 ± 4.03 (4)	74.08 ± 0.72 (4)	2.21 ± 0.38 (4)			67.40 ± 22.63 (3)		
	17-09-96	204.67 ± 11.59 (6)	9.10 ± 0.65 (6)	59.97 ± 14.08 (3)	76.62 ± 0.50 (6)	6.01 ± 1.29 (6)	191.25 ± 6.88 (4)	9.75 ± 1.38 (4)	35.65 ± 19.45 (2)	76.22 ± 0.50 (4)	1.14 ± 0.46 (4)
Spruce Pond	21-05-96	201.00 ± 6.81 (4)	11.98 ± 0.47 (4)	210.98 ± 152.40 (4)	72.85 ± 1.74 (4)	0.38 ± 0.04 (4)	195.00 ± 6.81 (4)	9.55 ± 1.11 (4)	328.05 ± 174.01 (4)	75.42 ± 0.69 (4)	0.05 ± 0.01 (4)
	18-09-96	206.40 ± 8.87 (5)	11.20 ± 0.53 (5)	115.15 ± 48.68 (4)	77.08 ± 0.17 (5)	8.83 ± 1.93 (5)	209.75 ± 11.73 (4)	12.67 ± 2.30 (4)	53.70 ± 10.95 (4)	76.80 ± 0.92 (4)	.938 ± 0.53 (4)

Appendix E. Monthly rate of weight gain during summer and winter seasons for each age class.

	Summer Growth (May - September)				Winter Growth (September - May)			
Pond	Year	Age 1 +	Age 2 +	Age 3 +	Period	1 + to 2 +	2 + to 3 +	3 + to 4 +
Coles	1992	1.91	5.82	13.96	1991-1992	1.47	2.18	6.86
	1993	2.13	5.38	9.22	1992-1993	1.27	5.27	10.43
	1994	1.72	5.22	9.26	1993-1994	0.75	4.17	7.69
	1995	1.65	5.83	10.08	1994-1995	0.96	2.66	3.94
	1996	1.99	5.02	10.86	1995-1996	1.28	3.23	8.01
	Mean	1.88	5.45	10.68	Mean	1.15	3.50	7.39
	Std. Deviation	0.09	0.16	0.87	Std. Deviation	0.13	0.55	1.05
	c.v. (%)	10.36	6.67	18.32	c.v. (%)	22.60	32.61	36.27
Headwater	1992	1.75	5.71	12.58	1991-1992	1.37	3.05	4.83
	1993	1.23	6.85	12.26	1992-1993	1.57	4.24	5.24
	1994	1.17	6.00	9.46	1993-1994	1.20	3.05	5.67
	1995	0.64	3.94	4.01	1994-1995	1.04	3.38	5.67
	1996	1.65	5.23	14.69	1995-1996	1.32	2.73	4.83
	Mean	1.29	5.55	10.60	Mean	1.30	3.29	5.25
	Std. Deviation	0.20	0.48	1.85	Std. Deviation	0.09	0.26	0.19
	c.v. (%)	34.27	19.36	38.94	c.v. (%)	17.01	19.81	7.75
Spruce	1992	0.69	4.66	9.47	1991-1992	1.57	3.81	4.02
	1993	1.11	2.83	8.61	1992-1993	3.13	6.00	11.31
	1994	0.19	2.36	9.91	1993-1994	0.99	2.26	1.63
	1995	-0.01	1.94	3.23	1994-1995	1.20	3.53	5.48
	1996	1.75	2.45	8.51	1995-1996	2.04	3.77	4.93
	Mean	0.75	2.85	7.95	Mean	1.79	3.87	5.48
	Std. Deviation	0.32	0.47	1.21	Std. Deviation	0.38	0.60	1.60
	c.v. (%)	95.50	37.29	33.95	c.v. (%)	54.27	40.09	73.48

Weight Gain = $[(wt_2) - (wt_1)] / (t_2 - t_1)$; For summer growth $(t_2 - t_1) = 4$, winter growth $(t_2 - t_1) = 8$.

Appendix F. Population abundance, density and biomass estimates for three ponds of the EPA.

Pond	Season + Year	Abundance Estimate #	95 % C.I. Lower	95 % C.I. Upper	Density Estimate # / hectare	95 % C. I. Lower	95 % C. I. Upper	Biomass Estimate kg / hectare
Coles	Fall 1991	1228	1004	1582	47.78	39.05	61.55	2.58
	Spring 1992	933	757	1215	36.30	29.47	47.27	2.59
	Fall 1992	1134	850	1702	44.12	33.09	66.21	2.84
	Spring 1993	1244	1027	1578	48.40	39.95	61.40	3.05
	Fall 1993	1840	1520	2332	71.60	59.13	90.73	4.31
	Spring 1994	2620	2225	3186	101.9	86.56	124.0	6.43
	Fall 1994	4099	3481	4984	159.5	135.4	193.9	10.42
	Spring 1995	2362	2051	2784	91.91	79.80	108.3	5.27
	Fall 1995	2888	2588	3267	112.4	100.7	127.1	6.94
	Spring 1996	1806	1486	2302	70.27	57.81	89.58	5.73
	Fall 1996	1957	1466	2941	76.15	57.06	114.4	6.29
Headwater	Fall 1991	1811	1564	2150	23.80	20.56	28.25	1.36
	Spring 1992	1183	924	1645	15.55	12.14	21.61	1.02
	Fall 1992	1584	1118	2719	20.81	14.69	35.73	1.43
	Spring 1993	2302	1867	3000	30.25	24.54	39.43	1.53
	Fall 1993	3160	2261	5244	41.52	29.71	68.91	3.03
	Spring 1994	3762	3172	4621	49.43	41.69	60.72	3.85
	Fall 1994	3059	2466	4028	40.20	32.40	52.93	3.21
	Spring 1995	3167	2653	3927	41.62	34.87	51.60	3.07
	Fall 1995	3279	2511	4724	43.09	32.99	62.08	3.61
	Spring 1996	2733	1978	4423	35.91	25.99	58.12	2.73
	Fall 1996	3505	2632	5244	46.06	34.59	68.91	3.72
Spruce	Fall 1991	1145	770	2228	31.37	21.10	61.04	1.93
	Spring 1992	1046	842	1382	28.66	23.07	37.86	1.77
	Fall 1992	942	729	1333	25.81	19.97	36.52	1.46
	Spring 1993	1383	1196	1639	37.89	32.77	44.90	2.01
	Fall 1993	1454	1209	1821	39.84	33.12	49.89	2.55
	Spring 1994	3051	2677	3546	83.59	73.35	97.16	5.18
	Fall 1994	1804	1396	2548	49.42	38.25	69.82	3.39
	Spring 1995	2145	1940	2399	58.77	53.14	65.73	4.27
	Fall 1995	1453	901	3746	39.81	24.69	102.6	2.94
	Spring 1996	2129	1748	2722	58.33	47.90	74.57	4.45
	Fall 1996	1700	734	5358	46.58	20.10	146.8	3.20