EFFECT OF GENOTYPE, ENVIRONMENT AND GENOTYPE-ENVIRONMENT INTERACTIONS ON GROWTH OF RAINBOW TROUT (*Salmo gairdneri* RICHARDSON)

A thesis

submitted to

the Faculty of Graduate Studies

University of Manitoba

In partial fulfillment

of the requirements for the

degree of Master of Science

by

SUPATTRA URAIWAN

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To My Parents

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ABSTRACT

The study investigated how genotype, environment and genotype-environment interactions act on rainbow trout growth. Genetic differences between two strains of rainbow trout, Manx and Nisqually, and their hybrid were determined in the hatchery and field. The study also determined whether the observed differences between these two strains in field experiments could be attributed to genetic differences in maximum, optimum and maintenance rations, specific growth rate at maximum and optimum rations and net and gross conversion efficiencies at maximum and optimum rations. The field studies took place in ponds, pothole lakes and then under simulated commercial intensive aquaculture conditions. Laboratory experiments were interpreted as being true indicators of genetic differences since the environments (ration, temperature and initial size) were held constant.

Genetic differences in harvest weights appeared in pond, lake and tank experiments. On average, the Nisqually fish were 17 to 77% larger than the Manx fish grown in the same pond, lake or tank. Genotype-environment interactions also occurred in the pond experiments.

Variance component analysis in the definitive experiments showed that environmental differences accounted for between 53 and 68% of the variability in maximum, optimum and maintenance rations and specific growth rates and net and gross efficiencies of rainbow trout at maximum and optimum rations. Between 4 and 16% of total variation was due to genetic differences. Changes in temperature between 12 and 19°C increased food requirements at maximum, optimum and maintenance rations while specific growth rates and efficiencies were not markedly affected. As initial size of fish increased from 6 g. to 67 g., maximum, optimum and maintenance rations decreased. In a similar manner, specific growth rates and efficiencies decreased as fish grew larger.

Additive genetic differences between Manx and Nisqually in specific growth rates at maximum rations were high (10-11% of mid-parent values) and constant at temperatures of 12, 14.3 and 19°C. Values were low (4% of mid-parent values) at the optimum temperature, 16.7°C, i.e. growth rates of Manx and Nisqually fish were most similar at the optimum temperature. Additive genetic differences for specific growth rates at optimum rations were similar to those at maximum rations but there were no differences in maintenance ration requirements of the two strains of their hybrid. Additive and non-additive genetic differences between Manx, Nisqually and their hybrid in net and gross efficiencies at maximum and optimum rations were also observed.

Strain selection and hybridization are suggested as a means of genetic improvement of growth rates and efficiencies on the basis of experimental results. Consideration of genotype-environment interaction effects in any selective breeding program is also stressed.

A. INTRODUCTION

Studies of growth rates of fish can be very complicated. Rice et al (1970) stated that the variability among animals in any trait is influenced by the following factors: heredity, environment and heredity - environment interactions.

Numerous researchers have studied the relationship between the growth of salmonid fish and environmental factors. Environmental factors, such as temperature, ration, initial size, density, light and other factors have all been found to affect fish growth.

Perhaps the most complete work is that of Brett and his colleagues at the Pacific Biological Station at Nanaimo (Brett et al. 1969, Brett 1971 a, 1971 b, 1979, Brett and Higgs 1970 and Brett and Shelbourn 1975). Over a period of years they have defined the relationships between growth rates of sockeye salmon (Oncorhynchus nerka) and temperature, fish size, ration, etc. Similarly, at the Freshwater Biological Association, Windermere Laboratory, England, Elliott examined environmental factors affecting growth rates of brown trout (Salmo trutta L.) (Elliott 1975 a, 1975 b, 1975 c and 1975 d).

Studies of rainbow trout (Salmo gairdneri) have been carried out at numerous laboratories. Hokansen et al. (1977) compared the growth rate of juvenile rainbow trout in constant and fluctuating temperatures; Wurtsbaugh and Davis (1977 a) observed the effect of fluctuating temperatures and rations on juvenile rainbow trout growth and food conversion. Wurtsbaugh and Davis (1977 b) found a relationship between fish size and ration at optimum temperatures when studying the growth rate of rainbow trout. Kilambi et al. (1977) and Refstie (1977) studied the effect of density on growth, food conversion and production of rainbow trout. Li and Brocksen (1977) found that rainbow trout in high competition for space, had a low feeding rate while Wedemeyer (1976) said rainbow trout were physiologically stressed when moved and held at a density of 16 grams per liter, but still fed normally. Other environmental factors have also been shown to be important. For example Chaston (1968, 1969), Jenkins (1969) and Campbell (1971) found that light and dark influenced activity and feeding behaviour of salmonids and white sucker (Catostomus commersoni) . Of the controlling environmental factors (Fry 1947) temperature appears to have the greatest effect on the metabolic rate of fish.

Quantitative genetic studies of salmonids have not been nearly so extensive. The earliest and best publicized results are those of Donaldson at the University of Washington (Donaldson and Olson 1955, Donaldson et al 1956, Donaldson and Menasveta 1961, Donaldson 1970 and Hines 1976). Unfortunately Donaldson's apparent success at improving the growth rates, and other characteristics of rainbow trout and Chinook salmon (O. tshawytscha) is marred because no controls were maintained and it is therefore impossible to separate the genetic improvement from improved cultural conditions. The most complete studies of the genetics of salmonids have been those by researchers operating out of the fisheries research station at Sunndalsora, Norway on Atlantic salmon (Salmo salar) and other salmonids

(Gjedrem and Aulstad 1974, Gjedrem 1976, Kanis et al. 1976, Refstie et al 1977, Gjedrem and Gunnes 1978, Gunnes and Gjedrem 1978 and Edwards 1978). In recent years, numerous other researchers have contributed significantly to our understanding of the genetic factors affecting growth rates. Reinitz et al. (1979) found differences in body weight and body composition between strains of rainbow trout and applied artificial selection to a rainbow trout population (Kincaid et al 1977). Klupp (1979) studied genetic improvement in the growth of rainbow trout and found that heterosis appeared at the juvenile stage but was not statistically significant. Many workers have discussed which characters should be selected and agree that growth is one important trait that should be worked on (Donaldson and Olson 1955, Gjedrem and Aulstad 1974, Gjedrem 1976, Kincaid et al 1977 and McKay and Friars 1979). Weatherley (1976) has emphasized the importance of studying the physiological basis of genetic differences in growth rate.

Unfortunately, most of these breeding studies did not consider environmental factors. Even though the selection provided some genetic gains, the work was restricted to one or two environments and emphasized genetic effects. Environmental effects and genotype - environmental interactions that may have interfered with the variations were generally overlooked. Without consideration of all factors, attempted animal improvement will not be successful. The environmental factors which affect the physiological studies of fish growth such as metabolic rate, activity, feeding ration etc. should also be included in the genetic studies as suggested by Weatherley (1976). Bowman

(1974) stated that genotype - environment interaction may be defined as the change in performance of two or more genotypes measured in two or more environments. These interactions may change the rank order of genotypes from one environment to another. As well a change between different environments may result in a change in heritabilities. [a] One or a combination of these changes may be apparent. Gjedrem and Aulstad (1974) felt that the genotype - environment interactions for growth and survival are particularly important for a selective breeding program. In Kincaid's selection program (Kincaid et al 1977) weight gain variations at age 147 days were 30% due to genetics and 70% due to environments. They recommended that in future studies, breeders should consider both genetic and environmental factors as well as interactions between them. Heritabilities of growth rates in rainbow trout are quite low, between 0.1 to 0.2., suggesting to Gjedrem (1976) that there are other factors involved in the total variation. Recently, Bailey (1978) estimated the heritabilities of one strain of rainbow trout in different environments (2 hatcheries and 2 lakes). His work shows an effect of the environment, the genotype and genotype - environment interactions on heritabilities. Klupp et al. (1978) found that the interactions of strain and environments (net and pond environments) affected weight of rainbow trout. Moav et al 1975 found genotype - environment interactions when studying the Chinese carp and its crosses with European carp and changes in ranking of carp strains with seasons

[a]Heritabilities: a measure of the degree to which a phenotype is genetically influenced and can be modified by selection (King 1968)

(Moav and Wohlfarth 1973 and Moav et al 1975). Gall (1969) reported that interactions between strain and stocking density in rainbow trout growth and genotype - environment interactions, were high compared to other livestock. Similarly, Kallberg (1959) and Moav et al (1975) assumed that different stocking densities interact with strains of fish. Ayles (1975) studied the influence of genotype, environment and genotype - environment interactions on growth and survival of rainbow trout stocked in central Canadian aquaculture lakes and concluded that the observed differences in growth and survival were a function of all these factors. The genotype and genotype - environment interaction effects were statistically significant but smaller than the environmental effects. Ayles et al (1979) also found genotype-environment interactions in the percent of dry matter and lipid content of different strains of rainbow trout and their hybrids. Ihssen (1976) stated that genotype - environment interactions such as strain - hatchery and strain-lake effects are sometimes quite large for growth and survival. The above studies clearly indicate that genetic studies of rainbow trout should consider environmental effects and genotype - environment interactions as well.

The present study investigates how genotype, environment and genotype - environment interactions act on specific growth rates of rainbow trout. Specifically the study was to determine whether observed differences between strains of rainbow trout in field experiments could be attributed to genetic differences in maximum growth rates, growth rates at optimum rations, conversion efficiencies at maximum and optimum rations, or maintenance rations, and the extent to which these genetic differences varied under different environmental conditions.

The experiments of this study dealt with field studies, preliminary experiments and definitive experiments of growth rate (Table 1). The environmental factors involved in the study were temperature, ration and fish size. The genetic factors were genetic differences between strains. The work emphasized two strains (Manx and Nisqually) and their hybrid (Manx X Nisqually), while other strains were also used for the preliminary experiments and field studies.

Table 1. Experiment type, starting date, location and identification number of each experiment.

Experiment Type	Experiment Number	Starting Date	Location
Field	F.1 (79:H01*)	26/06/79,	Ponds at the Rockwood Experimental Hatchery
	F.2 (80:H03)	14/05/80,	Ponds at the Rockwood Experimental Hatchery
	F.3 (80:H08)	9/12/80,	Tanks at the Rockwood Experimental Hatchery
	F.4 (78:E02)	17/04/78;	Pothole Lakes at Erickson, Manitoba
Preliminary	P.1 (78:S01)	7/02/78,	Tanks at the Freshwater Institute
	P.2 (78:S02)	18/07/78,	Tanks at the Freshwater Institute
	P.3 (78:S03)	25/09/78 and 15/10/78,	Tanks at the Freshwater Institute
	P.4 (79:S04)	13 & 23/4/79 and 21/5/79,	Tanks at the Freshwater Institute
	P.5 (80:H01)	11-13/02/80;	Tanks at the Rockwood Experimental Hatchery
Definitive	D.1 (80:H06)	22-23/07/80,	Tanks at the Rockwood Experimental Hatchery
	D.2 (80:H07)	23-24/09/80,	Tanks at the Rockwood Experimental Hatchery
	D.3 (81:H01)	2-3/02/81.	Tanks at the Rockwood Experimental Hatchery

* indicates experiment code used by Aquaculture Project

B. GENERAL PROCEDURES

This section describes the general materials, methods and procedures of this study. The section is divided into subsections as follows: a general description of all experiments; a description of fish stocks used in the experiments; a description of all facilities and tanks used for the experiments; a description of general handling procedures for the experiments; a statistical analysis subsection which explains the statistical models used; a subsection describing genetic analyses used for some experiments and a subsection describing parameters of interested.

1. Experimental types

There were three types of experiments, field, preliminary and definitive. The field experiments were to determine growth and survival rates of different strains of rainbow trout in different types of commercial aquaculture operations. The preliminary experiments were to determine the preliminary parameters and handling techniques for laboratory experiments and provide ideas on how to do the definitive experiments. The definitive experiments were to specifically observe the effect of genotype (strain effect), environment and genotype - environmental interactions on specific growth rates of rainbow trout in laboratory conditions. Experiments took place between 1978 and 1981, in pothole experimental lakes at Erickson, Manitoba, in ponds or tanks at the Rockwood Experimental Hatchery and in tanks at the Freshwater Institute. The experiment number, starting dates and facilities used for experiments are outlined in Table 1. Brief descriptions and rationale for each experiment are given in Table 2.

2. Description of Strains of Fishes Used

Salmonids used in this study were rainbow trout (Salmo gairdneri), Artic charr (Salvelinus alpinus) and brook trout (Salvelinus fontinalis). The study was primarily of rainbow trout. Six purebred strains and two groups of inter-strain hybrids were used. The following strains and hybrids of rainbow trout were used:

Manx (M M [*1]) - domestic strain from Lake Fisheries Hatchery in the Isle of Man . The exact origins of these fish are unknown, but they are believed to have been taken to the Isle of Man in the 1940's and no new fish have been added to the hatchery since. This stock was originally received at the Rockwood Experimental Hatchery in February 1976. The eggs for the field experiments, F.1. and F.2. were spawned on January 24, 1979 in the Rockwood Experimental Hatchery. The eggs for the field experiment F.4. were spawned on November 3, 1977, in the Rockwood Experimental Hatchery. The eggs for the definitive experiments D.1., D.2., and D.3. and a field experiment F.3. were spawned on January 8, 1980 at the Rockwood Experimental Hatchery.

Nisqually (N N) - domestic strain from Nisqually Trout Farm Olympia Washington. The exact origins of these fish are unknown, but the hatchery had introductions of local strains and of the so-called Donaldson strain. This stock was originally received at the Rockwood Experimental Hatchery on February 5, 1974.

[*1] First letter indicates female parent, second letter indicates male parent.

Table 2. Brief descriptions and reasons for each experiment.

Experiment Type	No.	Name (Strain)		Brief Description	Reason for Experiment
Field	F.1	Manx Nisqually Idaho Sunndalsora	4 g 5 g 7 g 4 g	4 strains, 1 size, 4 still water ponds with 4 densities	Initial pond experiment to determine growth of different strains of rainbow trout and to examine effect of density on growths.
	F.2	Manx Nisqually	12 g 14 g	2 strains, 1 size, 4 still water ponds with 4 densities	Confirm F.1, emphasis on 2 strains showing greatest difference in growth.
	F.3	Manx X Manx Nisqually X Nisqually Manx X Nisqually	38 g 40 g 38 g	3 strain crosses, 1 size 12.5°C, maximum ration	Determine difference of specific growth rate between 3 strain crosses for large fish stocked together in 1,500 L. tank.
	F.4	Manx Nisqually	4 g 6 g	2 strains, 2 sizes, 2 pothole lakes with the same density	Determine differences of growth of 2 strains in central Canadian aquaculture conditions.
Preliminary	P.1	Idaho Nisqually	10 g 30 g	2 strains, 2 sizes, 10°C ration 0 - 5%	1. Initial experiment to learn how to handle fish 2. Define preliminary parameters
	P.2	Mt. Lassen Mt. Lassen	6 g 15 g	1 strain, 2 sizes, 10°C ration 0 - 5%	Initial experiment to determine effect of size on specific growth rates.
	P.3	Mt. Lassen Mt. Lassen	15 g 30 g	1 strain, 2 sizes, 10°C ration 0 - 5%	Initial experiment to determine effect of size on specific growth rate using the same strains as P.2 for the bigger size.
	P.4	Tunkwa X Tunkwa Idaho X Idaho Tunkwa X Idaho Idaho X Tunkwa	5 g 5 g 5 g 5 g	4 strain crosses, 1 size 10°C, ration 0 - 5%	Initial experiment to determine differences in growth in genotype (strain crosses) in common environment.
	P.5	Rainbow trout Arctic charr Brook trout	9 g 8 g 8 g	3 species, 1 size, temperature 10, 13, 16 and 19°C, ration 0 - 7%	Initial experiment to examine the differences of growth rates between salmonids in relation to temperatures and ration.
Definitive	D.1	Manx X Manx Nisqually X Nisqually Manx X Nisqually	8 g 7 g 7 g	3 strain crosses, 1 size, temperature: 12, 14.3, 16.7 and 19°C, ration 0 - 7%	Definitive experiment to examine effect of genotype, environment and genotype-environment interaction on specific growth rates.
	D.2	Manx X Manx Nisqually X Nisqually Manx X Nisqually	17 g 17 g 17 g	3 strain crosses, 1 size temperature: 12, 14.3, 16.7 and 19°C, ration 0 - 7%	Definitive experiment to examine effect of genotype, environment and genotype-environment interaction on specific growth rates.
	D.3	Manx X Manx Nisqually X Nisqually Manx X Nisqually	67 g 67 g 67 g	3 strain crosses, 1 size temperature: 12, 14.3, 16.7 and 19°C, ration 0 - 7%	Definitive experiment to examine effect of genotype, environment and genotype-environment interaction on specific growth rates.

The eggs for a preliminary experiment, P.1. were spawned on December 8, 1976; the eggs for field experiments, F.1. and F.2. on January 24, 1979; the eggs for the field experiment F.4. on October 20, 1977, while eggs for definitive experiments D.1., D.2. and D.3. and a field experiment F.3. were spawned on January 8, 1980, all at the Rockwood Experimental Hatchery.

Manx X Nisqually (MN) and Nisqually X Manx (NM) inter-strain hybrids from random matings of 3 - 6 females to 5 - 6 males of Manx and Nisqually strains. The matings were carried out on January 8, 1980 at the Rockwood Experimental Hatchery and offspring produced MM, NN, MN and NM. The eggs hatched in March 1980 and fry were kept in 4 nursery tanks at 13.5^{o} C until the end of May 1980. At the end of May, at an approximate size of 2.3 g. they were moved into 1,500 liter tanks at 6.5^{o}C. These fish, MN, were used in definitive experiments D.1.,D.2., and D.3. and field experiment F.3.

Mt. Lassen (LL) - domestic strain from Hildebrand's Mt. Lassen Trout Farm, Red Bluff, California. The exact origins of this fish are unknown but the Mt. Lassen Hatchery has received fish of the Kamloops strain from Coleman Fish Hatchery in Washington and Trout Lodge Fish Hatchery in Washington in 1962, and no new fish from other sources have been added since. These fish were received in 1978. The fish for preliminary experiments P.2. and P.3. were spawned in Hildebrand's Mt. Lassen Trout Farm and the eggs were sent to the Rockwood Experimental

Hatchery in January and February 1978.

Sunndalsora (SS) - domestic strain from a research hatchery in Sunndalsora, Norway. The exact origins of this fish are unknown, but the original stock which was introduced to Norway from North America were from a freshwater strain and rainbow trout culture in Norway began as far back as 1912 (Edwards 1978). The stock was received at the Rockwood Experimental Hatchery in April 1975. The eggs for field experiments F.1. and F.2. and preliminary experiment P.5. were spawned on January 24, 1979 in the Rockwood Experimental Hatchery.

Idaho (II) - domestic strain from Caribou Trout Ranch, Soda Spring Hatchery in Idaho. The origin of this stock is uncertain, but it was probably taken from a northern California stream many generations ago (Ayles 1975). The stock was received at the Rockwood Experimental Hatchery on November 17, 1971. The eggs for a preliminary experiment, P.1. were received from Idaho in April 1977 while the eggs for another preliminary experiment, P.4. were spawned in July 1978 at the Rockwood Experimental Hatchery.

Tunkwa (TT) - wild strain from Tunkwa Lake, B.C. These fish have been in Tunkwa Lake for several centuries (Ayles 1975). The original stock was received at the Rockwood Experimental Hatchery on June 10, 1972 from Summerland Hatchery British Columbia. The eggs for preliminary experiment, P.4. were spawned in July 1978 in the Rockwood Experimental Hatchery.

Tunkwa X Idaho (TI) and Idaho X Tunka (IT) - F_2 inter-strain hybrids between Tunkwa and Idaho. The original random mating system was in July 1975 in the Rockwood Experimental Hatchery. The eggs from this mating were II, TT, TI (F_1) and IT (F_1). The eggs for preliminary experiment, P.4. were from crosses of the F_1 TI and IT stocks in July 1978 at the Rockwood Experimental Hatchery.

The following other salmonids were also used:

Brook trout (BB) - wild strain from Gods River, Manitoba. The original stock was received at the Rockwood Experimental Hatchery as eggs in October 1974. The eggs for preliminary experiment, P.5. were spawned on August 30, 1978 at the Rockwood Experimental Hatchery.

Arctic charr (AA) - wild strain from Nauyak Lake, Kent Peninsula, North West Territory, Canada. The stock was originally received as eggs at the Rockwood Experimental Hatchery in November 1978. The parents of these fish were from the anadromus stock at Nauyuk Lake. The male parents averaged 675 m.m. in length and females 620 m.m. The eggs were taken to the Rockwood Experimental Hatchery in November 1978 and hatched at the end of December 1978. This stock was used in preliminary experiment, P.5.

3. Facilities

3.1. Ponds

Field experiments at the Rockwood Experimental Hatchery took place in four 0.05 hectare still water earthen ponds having a depth of 1 - 1.5 m. Each pond has an inlet and an outlet. Because of predator birds, especially terns (Sterna sp.), a mesh net covered 25% of each pond (2 meters above the water) around the feeding area while the rest of each pond was lined with cords 0.5 meters apart and two meters above the water. This method protected the fish in the first year of the pond experiments (F.1.), but the nets were destroyed over the winter resulting in lower survival rates in the 1980 experiments (F.2.)

3.2. Experimental tanks

In the Freshwater Institute, 22, 24 L. circular fiberglass tanks were used. The tanks were set up in four rows of 10 tanks, and a water temperature of 10°C maintained during experiments. The water flow averaged 0.5 litre m.m.$^{-1}$ in each tank and the tanks were aerated with airstones. Four 180 L. fibreglass tanks were used for holding fish before experiments.

In the Rockwood Experimental Hatchery the following experimental tanks were used:

1) 96, 60 L. square fiberglass tanks were used. They are set up in four rows of 24 tanks. Each row consists of a top and bottom level of 12 tanks hooked to a common filter/recirculation unit. The water temperature is the same for all tanks within a row, and water is recirculated at the rate of 90 - 95%. New water is supplied from

the hatchery reservoir to each row at a rate of 3.5 liter m^{-1}. Water flow to the tanks averages about 2 liter min^{-1}. Fish were held in 1,500 L. square fiberglass tanks prior to all experiments. Water temperatures of the holding tanks were maintained at 6.5°C. Flourescent lights above the experimental tanks were controlled by an automatic switch, set according to the daylight hour during the year. The light intensity on the top tanks averaged 0.69 microeinsteins. m^{-2} sec^{-1} [a], and on the bottom tanks 0.48 microeinsteins. m^{-2} sec^{-1}.

2) one 1,500 L. square fiberglass tank was used for experiment F3. The tank is one of the 12, 1,500 L. square fiberglass tanks for the pilot system in the Rockwood Experimental Hatchery (Ayles et al.1980). These tanks are mounted over filter units and the water temperature can be varied between 6 - 16°C. Water is recirculated at the rate of 45 liter min^{-1}.

3.3 Pothole Lakes

Field experiment F.4. took place in two of the experimental pothole lakes in Erickson, Manitoba. Lake 316 and 321 were used. The areas of these two lakes are 3.2 and 2.8 ha. with maximum depths of 2.4 and 1.5m., respectively (Sunde and Barica 1975). The geography of the area and the lakes have been described in Sunde and Barica (1975) and Barica (1975).

[a] The light was measured by underwater Quantum sensor. The sensor measures in units of microeinsteins. m^{-2} sec. $^{-1}$, where 1 microeinstein = 6.02×10^{-17} photons measured between a wave length band of 400 to 700 n.m.

4. Handling Procedures

4.1. Field experiments

The field experiments F1 and F2 were started shortly after the ice melt in spring. Fish were acclimatized in a 1 m^3 floating cage (1 cm. mesh) in each pond, and released after two weeks. Individual lengths and weights of 10 fish per strain in each pond were taken at release for experiment F.2., but only total weights of fish per strain in each pond were taken for experiment F.1. Every two weeks during the experiments, fish were caught with a seine and at least 10 fish per strain in each pond were sampled for total weights. Near the end of the experiment F.2., it was difficult to catch fish because they were big and fast, and occasionally it was not possible to catch 10 fish from each strain.

At harvest, the water was drained out of each pond, total weight and survival rates were measured and 20 fish per strain were sampled for individual length - weights.

Field experiment F.3. used a 1,500 L. tank under simulated commercial intensive aquaculture conditions. The experimental procedures such as stocking rate, feeding and fish sampling followed the procedure of the pilot - scale rainbow trout production (Ayles et al. 1980). Every four weeks, fish of each strain were anesthetized, brands examined and mean weights of 4 subsamples of the total weights for each strain were measured. At the end of the experiment mean weights and length of 20 individuals were measured.

Field experiment F.4. was carried out in two pothole experimental lakes in the Erickson - Elphinstone district of Manitoba. Shortly after the ice melt in spring, fish were transported to the lakes, acclimatized in floating cages, and then released. At the end of the experiment fish were harvested and mean weights of fish for each strain were determined. The experimental procedures have been described in detail in Lawler et al. (1974) and Ayles (1975).

4.2. Laboratory Experiments

General procedures in these experiments followed the procedures of Brett et al. (1969).

The densities of fish at the beginning of all experiments averaged 10 g. l^{-1}. Maximum densities reached at the end of any experiment did not exceed 27 g. l^{-1}. The number of fish varied depending on the experiment. Stocking was done when all tanks were at ambient temperatures. Temperatures were gradually raised to experimental levels over a two week period.

The total weight of fish in each tank was taken when fish were placed in the tank. At the beginning and end of the three definitive experiments 10 fish from each tank were anesthetized and sampled for individual lengths and weights and five of the 10 fish were frozen for subsequent dry weight analysis. In addition, the total weight of the remaining fish in each tank was measured when the samples were taken. The measurement error due to differences between pooled and individual weights was tested by measuring 96 lots of 10 fish for both total weights and individual pooled weights. There was no significant difference between the two ways of measurement. Every two weeks the total weight of each strain for each tank was taken and the number of fish per tank counted. Mortalities were recorded daily.

4.3. Food and Feeding

Commercial trout food (Silver cup [a]) was used in the field experiments F.1., F.2. and F.3. and the laboratory experiments. For each experiment, fish were fed three times a day with the exception of laboratory tanks receiving excess rations which were fed five times daily. For the field experiments F.1. and F.2., feeding followed standard feeding tables (Bardach et al. 1972). For the experiment F.3. feeding was 150% of the feeding tables. For the pothole experiment F.4., fish were fed on natural food only (Holmstrom 1972 and Bernard and Holmstrom 1978). For laboratory experiments, fish were fed 5.5% body weight. day^{-1} during the two week acclimation period and then, ration levels were adjusted according to the experimental design. The amount of food for each ration level was adjusted biweekly for changes in fish weight. Food for one week was measured in grams and divided equally by volume for daily feeding.

[a]Product from Murray Elevators. The dry weight of fish food no.2 and no. 5 were analysed by Nutrition Biologist of the Freshwater Institute as follows:

	Food Size No.2	Food Size No. 5
% protein	43.6	48.9
% lipids	17.5	14.2
% ash	12.3	13.0
% carbohydrate and fiber	25.6	24.0

Food for 14 days was fed in 13 days because fish were not fed on the day of measurements.

5. Statistical Analyses

A number of statistical tests were employed in this study.

The following statistical analyses used the computer program of Hewlett-Packard calculator model H.P. 85:

- One-way analysis of variance
- Two-way analysis of variance
- Linear regression

Three-way analysis of variance (Snedecor and Cochran 1967) was performed using an ordinary desk calculator.

6. Analysis of the Effect of Genotype, Environment and Genotype-Environment Interactions

The relative importance of genetic and environmental effects was analysesd for experiments employing different strains. Comparisons of genetic means as well as estimations of the relative variability associated with the genotypic and environmental effects and genotype-environment interactions were made. Genotype-environment interactions were assumed to be zero in the estimation of variance components; however, this assumption may not be valid in all cases as some graphs indicate the presence of genotype-environment interactions.

The initial observations of genetic differences in growth rate in an aquaculture system were in field experiments F.1. and F.2. in the pilot commercial experiment F.3. and in the pothole lake experiment F.4. Differences in size between strains were interpreted as being true genetic differences since the environments were held constant.

The relative importance of genetic effects, environmental effects (ponds) and genotype-environment interactions (strains x ponds) were estimated by determining the variance components in a two-way analysis of variance.

For the definitive experiments, genotype (strain) and environment (temperature and size) effects and genotype-environment interactions were analysed by means of three-way and two-way analyses of variance and the variance components estimated (Snedecor and Cochran 1967). Differences in maximum, optimum and maintenance rations and specific growth rates were analysed.

Differences in strain means were also examined directly. Additive genetic effects (A), non-additive genetic effects (D) and the relative values of additive and non-additive genetic effects were estimated for the Manx and Nisqually strains and their F_1 hybrid. The deviation of the higher values (NN) from the mid-parent values $\left(\frac{MM + NN}{2}\right)$ was interpreted as an additive genetic effect (A) and the deviation of hybrid values (MN) from the mid-parent values as a non-additive genetic effect (D) or dominance, or heterosis[a] (Falconer 1960). The relative values for each effect (A and D) were estimated as a percent of mid-parent values. Throughout this thesis additive genetic effect (A) will be used to denote the average genetic effects between the two strains, Manx and Nisqually. Non-additive genetic effect or dominance (D) is used to denote all effects due to heterosis.

The relative values of A and D for specific growth rate at maximum and optimum ration and for net and gross efficiencies at both ration

[a] Heterosis is the additional performance, if any, shown by the first generation of crossbred progeny above the mean performance of their parents P_1 and P_2. (Bowman 1973).

levels were compared in relation to environmental factors (initial sizes and temperatures). The comparisons are presented in graphic form only. A complete statistical analysis was not considered justified.

The genetic differences observed in the field experiments were compared graphically with those observed in the hatchery.

For the preliminary experiment P.5, genotype (species) and environment (temperature) effects were analysed by means of a two-way analysis of variance, and variance components were estimated (Snedecor and Cochran 1967). Differences in maximum, optimum and maintenance ration and specific growth rates were analysed. The genotype-environment interactions were also interpreted graphically.

7. Parameters of Interest

Specific growth rate (G) is the instantaneous rate of gain in weight per unit weight (percent change in weight/time) and can be described by the formula:

$$G = \frac{\log_e W_2 - \log_e W_1}{t} \times 100$$

where W_1 is the initial weight, W_2 is the final weight and t is the time interval (days) between W_1 and W_2 (Brett et al 1969, Ricker 1975 and Elliott 1975a).

A ration is normally expressed as the fraction of daily food fed to body weight per fish (Kono and Nose 1971). This fraction can be written as follows:

$$f = \frac{F}{\frac{W_1 + W_2}{2}} \times 100$$

where f is the ration (food fed) in percent of body weight per unit time (usually in a day) per fish and F is the daily amount of food fed per fish.

Growth rate can be plotted against ration and, in the absence of any tranformation, a smooth curve fitted by eye (Figure 1) (Brett et al 1969). Three parameters of interest can be taken from these curves (Brett et al 1969).

(1) The maximum ration: the ration that provides for the maximum growth rate.

(2) The optimum ration: the ration that provides for the greatest growth for least food fed. The optimum ration can be determined by drawing the tangent to the curve from the origin and is the ration at which growth is most energetically efficient.

(3) The maintenance ration: the ration that just maintains the fish without any weight change (zero growth rate) which can be considered maintenance metabolism (Brett et al 1969).

Food conversion efficiencies are the ratio of growth to ration in a given period of time (Paloheimo and Dickie 1966).

These efficiencies can be expressed in terms of net and gross efficiencies (Brett et al 1969).

Net efficiency was estimated from the formula:

$$Eni = \frac{Gi}{I - M} \times 100\%$$

and the gross efficiency was estimated from the formula:

$$Egi = \frac{Gi}{I} \times 100\%$$

where, Eni = net efficiency at the i^{th} ration level.

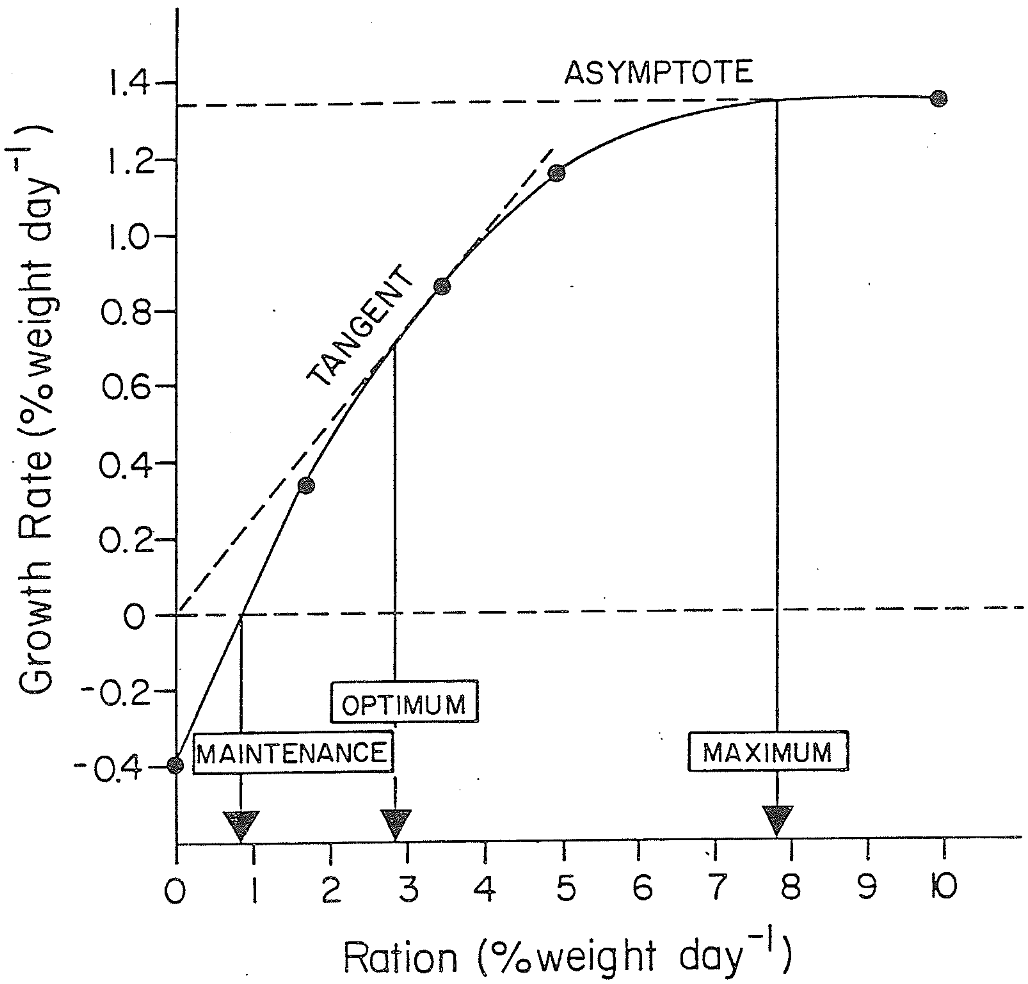
Egi = gross efficiency at the i^{th} ration level.

I = the i^{th} ration level corrected for moisture content for fish and food.

M = the maintenance ration obtained from the growth curve corrected for moisture content of fish and food.

Gi = specific growth rate at the i^{th} ration.

Figure 1. Geometric derivation of various parameters of growth with accompanying ration, using the data for fish at 10°C as an example (redrawn from Brett et al. 1969).


ASYMPTOTE
TANGENT
OPTIMUM
MAINTENANCE
MAXIMUM
Growth Rate (%weight day^{-1})
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
0
1
2
3
4
5
6
7
8
9
10
Ration (%weight day^{-1})

C. PROCEDURES AND RESULTS

In the following section, the specific experimental methods, statistical analyses and results are described for each experiment. Genetic interpretations are also included where appropriate.

1. Field Experiments

Field experiments (F.1 and F.2) were carried out in four still water ponds at the Rockwood Experimental Hatchery during the summers of 1979 and 1980. The experiments were to observe if there were differences in growth rate between different strains of rainbow trout in actual aquaculture conditions and to observe the differences in relation to densities in the ponds. The first experiment, F.1, was a study of four strains of rainbow trout, Nisqually, Manx, Sunndalsora and Idaho, while the second, F.2, concentrated on two strains, Nisqually and Manx which, according to the first experiment, differed significantly in growth rates. Differences between these two strains were examined more intensively in the definitive experiments in the hatchery. Field experiment F.3 was performed in a 1,500 L. tank at the Rockwood Experimental Hatchery. The experiment was to observe differences in growth between Manx, Nisqually and their hybrid under simulated commercial intensive aquaculture conditions. Experiment F.4 was a study of the differences between Manx and Nisqually strains planted in two pothole lakes near Erickson, Manitoba.

1.1 Experiment F.1

1.1.1 Method of Experiment F.1

Experiment F.1 began June 6, 1979 and ended October 31, 1979. The objective of the experiment was to determine the initial specific growth rate of different strains of rainbow trout in pond culture conditions. Subsequently, these observations were compared to laboratory observations on the same strains.

Each strain was branded with a hot wire branding apparatus two weeks before being stocked in the ponds (Bernard and Van der Veen 1974). Equal numbers of four rainbow trout strains were stocked at different densities in four ponds (Table 3). The mean weights of the four strains ranged between 3 and 10 grams when they were released from the floating cages. Procedures for fish sampling and feeding are described in Sections B. 4.1 and B. 4.3.

Daily measurement of water temperature and weekly measurements of dissolved oxygen (D.O.), nitrite (NO_2 - N), nitrate (NO_3 - N), ammonia (NH_3 - N), soluble reactive phosphorous (PO_4 -P), pH, water transparency and chlorophylla were made in each pond. When the water temperatures became close to rainbow trout's lethal temperature, cold well water was added to cool down the ponds. This was necessary on 11 different occasions.

In the fall at harvest time all fish were harvested by draining the ponds. Twenty fish per strain in each pond were sampled for individual lengths and weights. Total weight and survival rates were also determined. Unfortunately the water in pond no. 4 froze before the harvest was completed so that there was no survival record for this pond.

Differences in mean harvest weights between strains and between densities were tested by a two-way analysis of variance (Snedecor and Cochran 1967). The genetic and non-genetic variance components of harvested weight rates were also estimated (Snedecor and Cochran 1967). Specific growth rates of Manx and Nisqually were determined for each sampling period, and the additive

Table 3. Field Experiments F.1, F.2, F.3 and F.4, strains, initial weights and stocking rates of rainbow trout.

Experiment Number	Strain and Strain Crosses	Pond Number or Pothole Lake No.	Initial Weight Mean ± 2.S.E.	Stocking Rate: # Fish/Pond/Strain or # Fish/Tank/Strain or # Fish/Lake/Strain	Stocking Rate: # Fish/Ha. or g. $1.^{-1}$
F.1	Idaho Nisqually Sunndalsora Manx	1	10.2 2.8 4.9 2.8	351	25,436
	Idaho Nisqually Sunndalsora Manx	2	6.3 4.4 3.1 4.4	478	34,637
	Idaho Nisqually Sunndalsora Manx	3	6.1 5.5 3.6 5.0	136	9,856
	Idaho Nisqually Sunndalsora Manx	4	5.1 6.2 3.3 3.6	252	18,260
F.2	Nisqually Manx	1	10.3 12.3	306	22,174
	Nisqually Manx	2	12.1 10.4	146	10,544
	Nisqually Manx	3	18.0 12.5	553	40,036
	Nisqually Manx	4	15.3 12.5	393	24,442
F.3	Nisqually Manx Manx X Nisqually	*a	37.3 ± 2.1 37.8 ± 0.9 37.4 ± 0.4	400	30
F.4	Nisqually Manx	*b, 321	6.0 4.0	272	307
	Nisqually Manx	316	6.0 3.6	310	306

* a. Fish stocked in a 1,500 l. tank
* b. Fish stocked in two pothole lakes

genetic differences of these two were estimated as described in Section B.6.

1.1.2 Results of Experiment F.1.

The harvested weights of trout in the four ponds ranged from 23 to 207 g. (Appendix A; Table 1). The Idaho strain had the highest mean weight (106 g) followed by Sunndalsora (101 g), Nisqually (91 g.) and Manx (64 g.). The differences of harvested weight between Idaho, Sunndalsora and Nisqually were not significant, but Manx fish were significantly different from the other three strains ($P<0.05$). The differences (strain effects) accounted for 65% of the variation in mean weights (Table 4). The growth rates of each strain have been subjected to a more extensive analysis elsewhere (Appendix B - Papst et al. 1981). The specific growth rates of Manx and Nisqually are given in Appendix A; Table 2.

The relative values of additive genetic differences between Manx and Nisqually fish of different sizes ranged between 5 and 11% of the mid-parent values (Figure 2).

The physical and chemical observations on the ponds during the experiment are given in Appendix A; Table 3 and Figure 3.

1.2 Experiment F.2.

1.2.1. Methods of Experiment F.2.

Experiment F.2. began May 14, 1980 and ended October 1, 1980. This experiment was the continuation of experiment F.1. and the same two groups of Manx and Nisqually were used. The objective of the

Table 4. Field experiments F.1 and F.2, analysis of variance and variance components of mean harvested weights of different strains of rainbow trout stocked together in 4 ponds.

	F.1			F.2		
Source	d.f.	M.S.	Variance Component (%)	d.f.	M.S.	Variance Component (%)
Strains	3	1390.0**	65	1	3545.7	37
Ponds	3	338.7	12	3	1964.8	31
Error	9	114.6	23	3	678.6	32
Total	15			7		

Note:

1) Source — Expected Mean Square

Source	Expected Mean Square
Strains	$\sigma^2 + nb\ K^2A$
Ponds	$\sigma^2 + na\ K^2B$
Error	$\sigma^2 + nK^2AB$

2) ** indicates significant at $P < 0.01$

Figure 2. Relative values of additive (A) and non-additive (D) genetic effects for maximum specific growth rates of rainbow trout strains Nisqually, Manx and their hybrid (MN) for different temperatures and initial sizes in field and laboratory studies.

I. Definitive experiments D.1, D.2 and D.3 at 4 temperatures.
II. Definitive experiments D.1, D.2 and D.3 at 3 initial sizes.
III. Field experiments F.1 (○—○), F.2 (□--□) and F.3 (△---△ / ▲---▲) at various initial sizes.

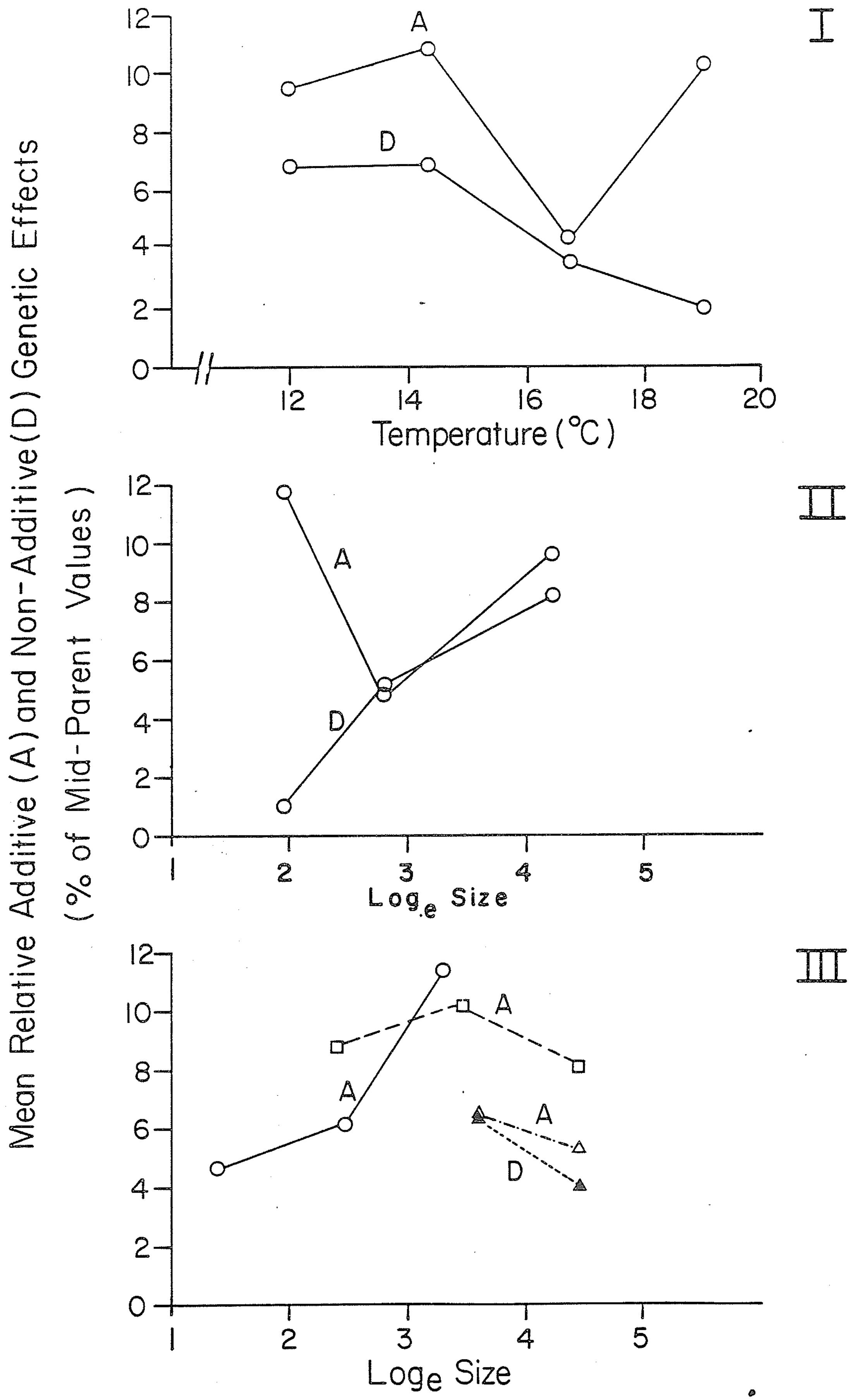
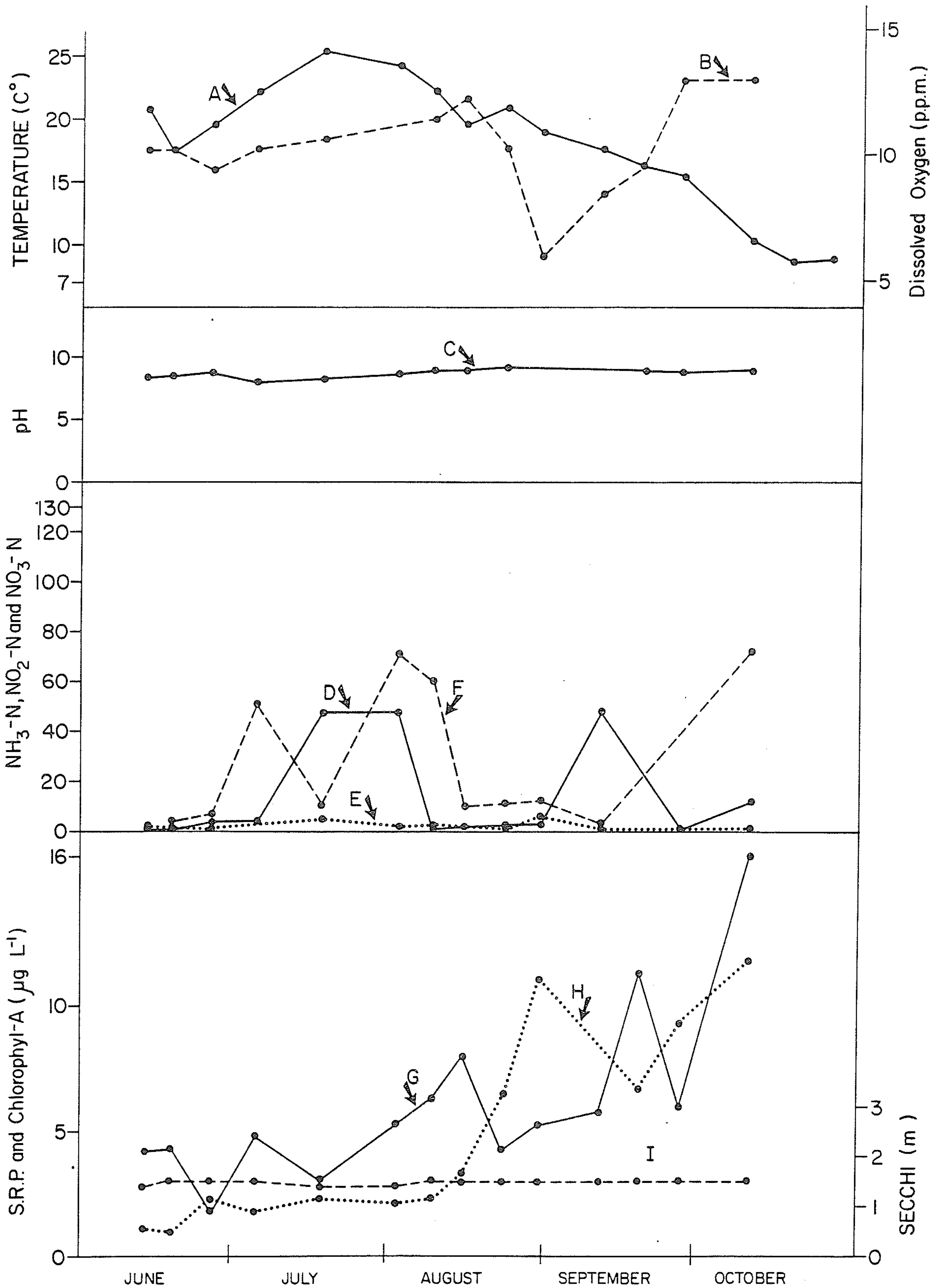

Mean Relative Additive (A) and Non-Additive (D) Genetic Effects
(% of Mid-Parent Values)
I
A
D
Temperature (°C)
II
A
D
Log$_e$ Size
III
A
A
A
D
Log$_e$ Size

Figure 3. Experiment F.1; seasonal variation in weekly means of water temperatures (A) , in pond 4, mean levels of Dissolved Oxygen (D.O.) (B) , pH (C) , Ammonia (NH_3-N) (D) , Nitrite (NO_2-N) (E) , Nitrate (NO_3-N) (F) , Soluble Reactive Phosphorous (PO_4-P) (G) , Chlorophylla (H) , and Secchi Depth (I) , in all ponds in 1979.


TEMPERATURE (C°)
Dissolved Oxygen (p.p.m.)
pH
(μg L⁻¹) NH3-N, NO2-N and NO3-N
S.R.P. and Chlorophyl-A (μg L⁻¹)
SECCHI (m)
A
B
C
D
E
F
G
H
I
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

experiment was to compare the specific growth rates of two strains in relation to different stocking densities and to confirm the observation of differences from the previous years experiment.

Similar to F.1., fish in each strain were branded with a hot wire branding apparatus two weeks before being stocked in ponds (Bernard and Van der Veen 1974). Equal numbers of each strain were stocked at four densities in the four ponds (Table 3). The mean weight of the two strains was between 10 and 18 grams when they were released from the floating cages. Fish sampling, feeding techniques and water analyses were similar to those for experiment F.1. The experiment lasted 4 months and at the harvest time all fish were caught by draining the ponds. Twenty fish per strain in each pond were taken for individual lengths and weights and total weights were taken.

The differences of mean harvested weights between strains were tested by means of a two-way analysis of variance. (Snedecor and Cochran 1967). A variance component analysis was used to separate the genetic (strains) and non-genetic (ponds) effect (Snedecor and Cochran 1967). Specific growth rates and genetic differences in specific growth rates of MM and NN were estimated similar to F.I.

1.2.2. Results of Experiment F.2.

The harvested weight of fish ranged between 65 and 460 g. (Appendix A; Table 4). The mean harvested weights of Nisqually (233g.) and Manx (189g.), although different, were not statistically significant (Table 4). The variation due to strain-pond interaction was high when compared to the genotypic variance. Genetic differences (strain effects) accounted for 37% of variation in mean weight (Table 4). The specific growth rates are given in Appendix A; Table 2 and analysed the same as for F.1.

The relative values of additive genetic differences between Manx and Nisqually fish of different sizes ranged between 8 and 10% of the mid-parent values (Figure 2).

The physical and chemical observation on the ponds during the experiment are given in Appendix A; Table 5 and Figure 4.

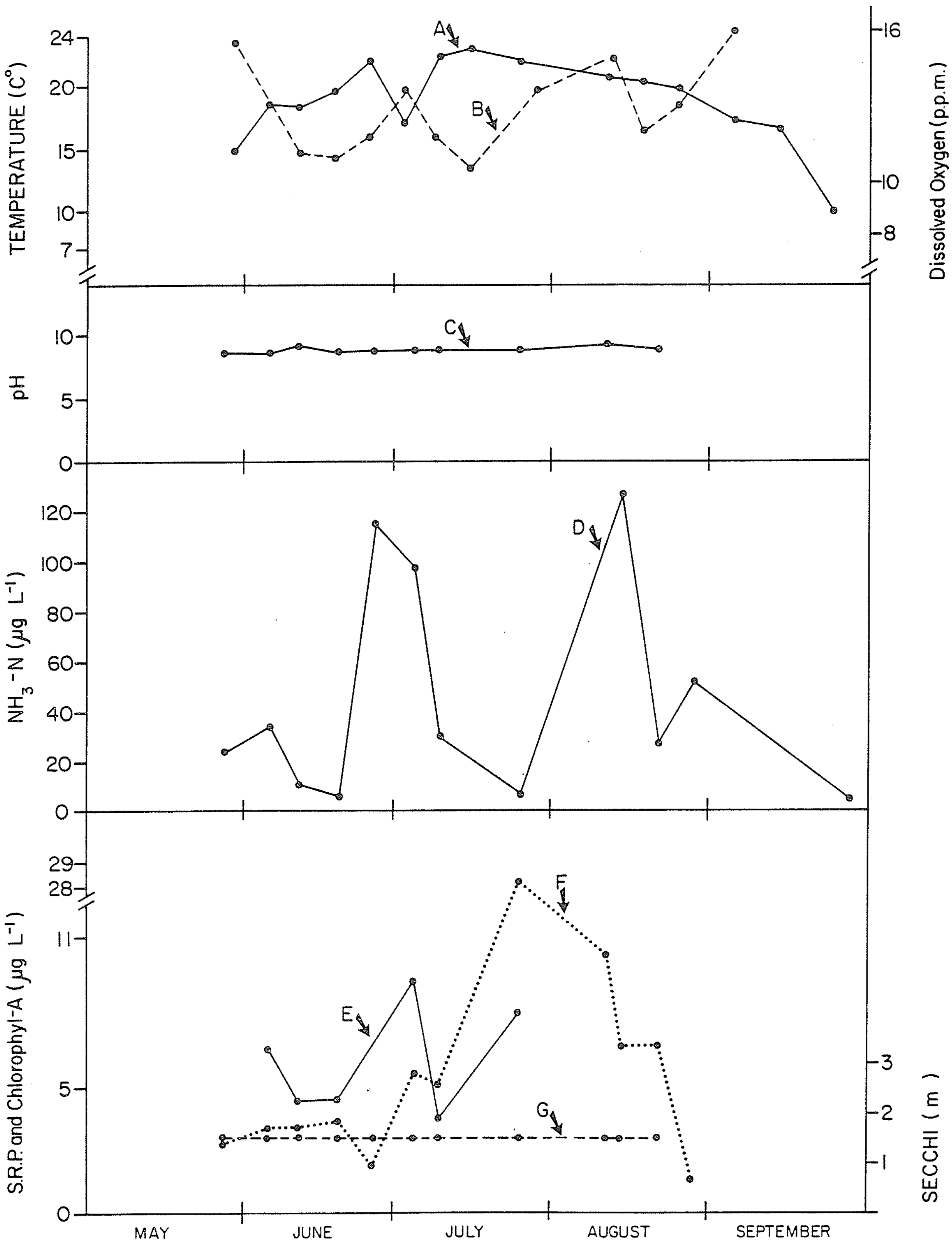
1.3 Experiment F.3.

1.3.1. Methods of experiment F.3.

Experiment F.3. began December 5, 1980 and ended April 29, 1981. The objective of this experiment was to test the differences of specific growth rates between Manx, Nisqually and their hybrid (MN) when grown in a 1,500 L. tank under simulated commercial intensive aquaculture conditions.

Fish of the three strain crosses were branded with a hot wire branding apparatus similar to the other field experiments (Bernard and Van der Veen 1974) and equal numbers of each strain stocked into a 1,500 L. tank. The mean weights of MM, NN and MN strains at stocking were 37.8, 37.3 and 37.4 g. respectively, at an initial stocking rate of 30 $g.l^{-1}$ (Table 3). The stocking rate and feeding rates were adjusted following the methods of the pilot scale rainbow trout production (Ayles et al. 1980) as described in Section B. The fish were culled periodically to keep

Figure 4. Experiment F.2; seasonal variation in weekly means of water temperature (A)●—● in pond 4, mean levels of Dissolved Oxygen (D.O.) (B)●---●, pH (C)●—● Ammonia (NH_3-N) (D)●—●, Soluble Reactive Phosphorous (PO_4-P)^3 (E)●—●, Chlorophylla (F)●—●, and Secchi Depth (G)●---● in all 4 ponds in 1980.



TEMPERATURE (C°)
Dissolved Oxygen (p.p.m.)
24
20
15
10
7
16
10
8
A
B
pH
10
5
0
C
NH$_3$-N (μg L^{-1})
120
100
80
60
40
20
0
D
S.R.P. and Chlorophyl-A (μg L^{-1})
29
28
11
5
0
E
F
G
SECCHI (m)
3
2
1
MAY
JUNE
JULY
AUGUST
SEPTEMBER

densities below 50 $g.l^{-1}$. The water temperatures were maintained at 12.5°C throughout the experiment.

The average specific growth rates for each strain cross were calculated for each sampling period (3 strain crosses x 5 periods). The additive genetic differences between Manx and Nisqually fish and the non-additive genetic differences between Manx, Nisqually and the hybrid (MN) fish were estimated for each period.

Differences in final mean weights of Manx, Nisqually and the hybrid were tested by means of a one-way analysis of variance (Snedecor and Cochran 1967).

1.3.2. Results of Experiment F.3.

Average mean weights and specific growth rates are given in Appendix A; Table 6. At harvest the MN and NN had mean weights of 155.5 and 150.5 g. respectively, and were significantly different ($P<0.05$) from MM at 133.4 g.

The relative values of the additive genetic effects ranged from 7.3 to 5.1% of the mid-parent value while the relative values of the non-additive genetic effects ranged from 7.3 to 4.0% of the mid-parent values (Figure 2).

1.4 Experiment F.4.

1.4.1. Methods of Experiment F.4.

The experiment started April 17, 1978 and ended near the end of September 1978 before freeze-up. The objective of the experiment was to determine the differences in growth between Manx and Nisqually under extensive fish culture conditions.

The experiment took place in pothole experimental lakes 316 and 321, in the Erickson - Elphinstone district of Manitoba. The experimental procedures have been described in detail elsewhere (Lawler et al. 1974 and Ayles 1975). The average initial weights of Manx and Nisqually were 3.7 and 6.0 g. at stocking respectively. At harvest, the average weights of each strain were again measured. As fish of each strain were stocked at a different size, the final harvested weight was adjusted to take this into account. The adjusted harvest weights were calculated by the formula:

$$\log_{10} \text{adjusted harvested weight} = \log_{10} \text{harvested weight} - 0.292 \log_{10} \text{stocking size} + 0.292 \log_{10} \text{adjusted stocking size (6g.)}$$

(Ayles personal communication)

1.4.2. Results of Experiment F.4.

The harvest weights, adjusted weights and initial size for each strain in each lake are given in Appendix A; Table 7. Manx fish had the lowest growth (adjusted harvest weight 121 to 159 g.) and Nisqually fish had the highest growth (adjusted harvest weight 213 to 271 g.). Nisqually fish were 70 to 77% larger than Manx fish.

2. Preliminary Experiments

The two groups of preliminary experiments consisted of initial observations on specific growth rates of rainbow trout in relation to genetic and environmental factors. The first set of preliminary experiments P.1., P.2., P.3., and P.4. occurred at the Freshwater

Institute in 1978 and 1979. The purpose of these experiments was to establish initial growth curves (Figure 1) for rainbow trout in the prevailing environment; and to provide estimates of maximum specific growth rates, optimum ration levels and maintenance ration levels at different fish sizes, with different strain crosses at one temperature. Each experiment used fish of different initial sizes or different strains and fish were fed at varying ration levels. The experimental designs are presented individually in Table 5.

The final preliminary experiment, P.5. took place at Rockwood Experimental Hatchery in 1980. This experiment examined the differences in specific growth rates between rainbow trout (Salmo gairdneri), brook trout (Salvelinus fontinalis), and Arctic charr (Salvelinus alpinus)in relation to genotype and environmental factors. The purpose of the experiment was to develop handling techniques for experiments in the 60 liter tanks in the hatchery, to determine the efficiency of the temperature control system prepared for the definitive experiments and to obtain preliminary observations on the effect of temperature on specific growth rates of 3 different species of salmonids fed at different ration levels.

These preliminary experiments served several functions. First, initial observations of all factors which affect the growth rate of rainbow trout were examined, and preliminary parameters such as maximum growth rate, optimum and maintenance ration were determined in various environmental conditions. Second, the preliminary experiments also provided an opportunity to refine experimental techniques before starting the definitive experiments. And third,

Table 5. Preliminary experiments, strains, initial weights, ration levels, stocking rates and temperature for rainbow trout, Arctic charr and brook trout.

Experiment Number	Strain and Strain Cross	Initial Weight Mean ± 2.S.E. (g.)	Ration (% Wet Weight day-1)	Temp. (°C)	Stocking Rate Fish/Tank	Stocking Rate g. l.$^{-1}$ (Mean ± 2.S.E.)
P.1[a]	Idaho Domestic Nisqually	10.8 ± 2.0 29.6 ± 4.0	0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0 5.5	10	37 17	14.8 ± 0.8 18.4 ± 1.0
P.2	Mt. Lassen Mt. Lassen	5.5 ± 0.5 15.4 ± 1.4	same as P.1	10	40 15	8.2 ± 0.2 8.9 ± 0.4
P.3	Mt. Lassen Mt. Lassen	15.1 ± 1.4 30.4 ± 2.5	same as P.1	10	10 12	5.5 ± 0.2 13.4 ± 0.4
P.4[b]	Tunkwa X Tunkwa	4.7 ± 0.6	0 1.5 3.5	10	15	2.7 ± 0.2
	Tunkwa X Idaho Idaho X Tunkwa	4.7 ± 0.1 4.8 ± 0.1	0 0.25 0.75 1.0 2.0 3.0 4.5 5.0	10	50 50	8.7 ± 0.1 9.0 ± 0.2
	Idaho X Idaho	5.0 ± 0.1	0 0.5 1.0 2.5 4.5 5.5	10	50	9.4 ± 0.2
			Top Tank / Bottom Tank			
P.5[c]	Rainbow trout (Sunndalsora) Arctic charr Brook trout	8.7 ± 0.4 8.2 ± 0.2 8.0 ± 0.5	0 / 0 3.0 / 1.5 4.5 / 6.0 7.0 / 7.0	10 13 16 19	100	13.2 ± 0.2

* a 2 strains X 2 sizes X 12 rations

* b 4 strain crosses X 1 size X 3-8 rations

* c 3 species X 1 size X 8 rations X 4 temperatures

the preliminary experiments were used as a guide for the design of the definitive experiments.

2.1 Preliminary Experiments P.1., P.2., P.3. and P.4.

2.1.1 Methods of Experiments P.1., P.2., P.3. and P.4.

Experiment P.1. began February 7, 1978 and ended March 21, 1978. The objective of this experiment was to learn how to handle the fish and to determine preliminary estimates of maximum growth rate, optimum ration and maintenance ration that could then be used to design a more definitive experiment.

Two rainbow trout strains were fed 12 different ration levels (0 - 5.5% body weight$\cdot$day^{-1}) at one temperature (10^{o}C) (Table 5) in 24 tanks (i.e. 24 lots). The mean weight of the Nisqually strain was 29.6 g and mean weight of Idaho strain was 10.8 g. The density at stocking was 14.8 g. l^{-1} and 18.4 g. l^{-1} for the Nisqually and Idaho respectively. The experiment lasted 6 weeks and at termination all fish were destroyed and mean weights measured.

The growth curve for each strain was fitted by eye from a graph plotting mean specific growth rates against mean ration level. Maximum specific growth rate, optimum ration and maintenance ration were read from the curves as shown in Figure 1.

Experiment P.2. began July 19, 1978 and ended August 29, 1978. The objective of the experiment was to determine maximum specific growth rate, optimum ration and maintenance ration of two size groups of the Mt. Lassen strain.

Two size groups of the Mt. Lassen strain were fed 12 different ration levels (0 - 5.5% body weight.day^{-1}), at one temperature (10^oC) (Table 5) in 12 tanks (i.e. 24 lots). The mean weight of the small size group was 5.5 g. and the mean weight of the large size group was 15.4 g. The density of stocking was 8.2 $g.l^{-1}$ and 8.9 $g.l^{-1}$ for the former and latter groups respectively. The experiment lasted 6 weeks and at termination all fish were destroyed and mean weights measured.

Maximum specific growth rate, optimum ration and maintenance ration of each size group were determined following the method described for Experiment P.1.

Experiment P.3. began September 25, 1978 and ended December 26, 1978. This experiment was a continuation of P.2. and used the same groups of Mt. Lassen fish grown to a larger size. Fish with an average size of 30.4 g. and 15.1 g. were used. The starting date of the former group was September 25, 1978 and the latter group was started October 15, 1978. The density at stocking was 5.5 $g.l^{-1}$ and 13.4 $g.l^{-1}$ for the large and small size groups respectively. The fish were fed 12 different ration levels (0 - 5.5% body weight.day^{-1}) at one temperature (10^oC) (Table 5) in 24 tanks (i.e. 24 lots). The experiment lasted 6 weeks and at termination all fish were destroyed and mean weight measured.

Maximum specific growth rate, optimum ration and maintenance ration of each size group were determined following the method described for Experiment P.1. A preliminary analysis of the effect of size of fish on specific growth rates was made using the data from Experiments P.2 and P.3. Regression analyses were carried out between $\log_e$ size of fish and $\log_e$ transformations of maximum specific growth rates, and between $\log_e$ size of fish and $\log_e$ transformations of specific growth rate at optimum rations.

Experiment P.4 was a preliminary examination of genetic differences in specific growth rates between different strains and their hybrids raised at one temperature ($10^{\circ}C$) and fed various ration levels.

The parental strains were Tunkwa (TT) and Idaho (II), and the hybrids were Tunkwa X Idaho (TI) and Idaho X Tunkwa (IT). All strains and hybrids were spawned July 7, 1978. Unfortunately the numbers of the different groups varied as there were only limited numbers of fish of the two parent strains. The start of feeding for each group was varied so the initial size would be the same (≈5 g.). The number of rations fed was restricted for TT and II fish (Table 5). Average initial stocking density for all groups was 7.4 $g.l^{-1}$.

Feeding of the IT and II groups began on April 13, 1979 and ended May 25, 1979, while feeding of the TI and TT did not start until April 23, 1979 and May 12, 1979 and ended on June 3, 1979 and July 1, 1979 respectively.

Growth curves were plotted and maximum specific growth rates, optimum ration levels and maintenance rations were determined following the method described in Experiment P.1. These observations provide an estimate of genetic differences between fish of one size and of one temperature and at various ration levels.

2.1.2 Results of Experiments P.1, P.2, P.3 and P.4

The biweekly mean weights of fish for each experiment and the average specific growth rates and rations are given in Appendix A; Tables 8-11. The relationship between specific growth rates and ration levels are shown in Figure 5.

Maximum, optimum and maintenance ration levels and specific growth rates at maximum and optimum rations observed in Experiments P.1, P.2, P.3 and P.4 are summarized in Table 6. No statistical tests were performed but genetic and environmental effects appeared to be present. When comparisons were made between Nisqually and Mt. Lassen fish of the same size, there were differences in maximum specific growth rate and maintenance ration level. There were also differences between the II, IT, TI and TT crosses. The TT had lower growth rates at both maximum and optimum rations. Similarly, different sized fish of the same strain, Mt. Lassen or Idaho, had different growth rates and ration requirements. Specific growth rates of the Mt. Lassen strain at maximum and optimum rations generally decreased as fish size increased (Figure 6) (maximum ration, $b = -0.22$ and optimum ration $b = -0.11$). The relationship between $\log_e$ initial size and $\log_e$ specific growth rate at maximum rations is significant ($r = 0.98$, $n = 3$), but not for optimum rations ($r = 0.75$, $n = 3$).

Figure 5. Experiments P.1, P.2, P.3 and P.4. Relationship between growth rates and ration levels.

I. P.1 and P.3 two strains at an initial size of 30 g.
II. P.2 and P.4. three strains plus two hybrids at an initial size of 5 g.
III. P.2 and P.3. one strain at initial sizes of 5, 15 and 30 g.
IV. P.1 and P.4. one strain at initial sizes of 5 and 10 g.

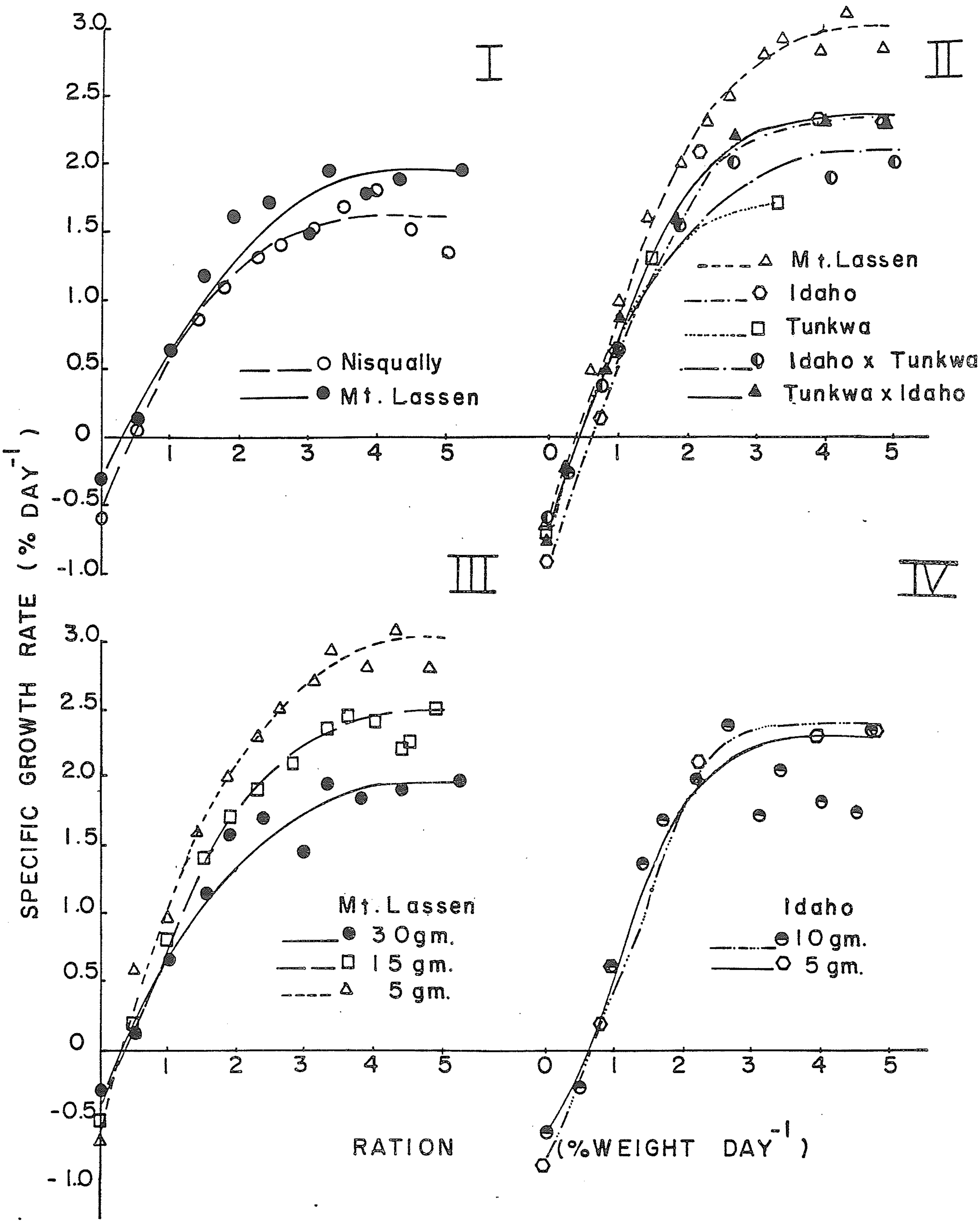

I
II
III
IV
SPECIFIC GROWTH RATE (% DAY^{-1})
Nisqually
Mt. Lassen
Mt. Lassen
Idaho
Tunkwa
Idaho x Tunkwa
Tunkwa x Idaho
Mt. Lassen
30 gm.
15 gm.
5 gm.
Idaho
10 gm.
5 gm.
RATION (%WEIGHT DAY^{-1})

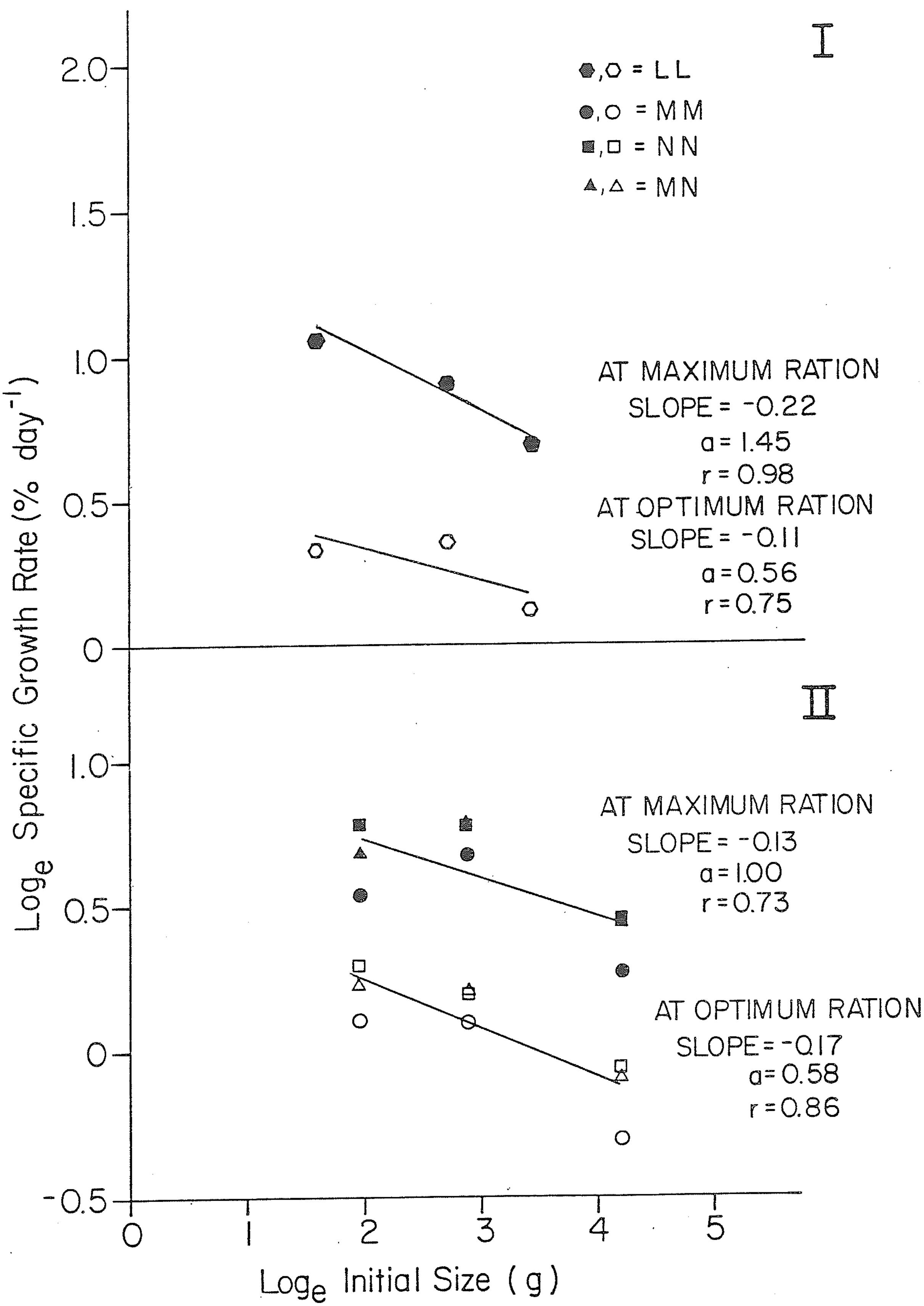
Table 6. Preliminary Experiments P.1 to P.4; maximum, optimum and maintenance rations, specific growth rates at maximum and optimum rations of different strains of rainbow trout.

Strain	Mean Initial Size (g)	Ration (% Wet Weight.Day^{-1})			Specific Growth Rate (%.day^{-1})	
		Maximum ration	Optimum ration	Maintenance ration	Specific growth rate at maximum ration	Specific growth rate at optimum ration
Nisqually (P.1)*	30	3.5	1.4	0.5	1.69	1.00
Mt. Lassen (P.2)	30	4.5	1.4	0.1	1.97	1.13
Mt. Lassen (P.2)	15	4.0	1.5	0.4	2.45	1.44
Mt. Lassen (P.2)	5	4.3	1.3	0.3	2.94	1.40
Idaho (P.1)	10	3.3	1.9	0.7	2.25	2.06
Idaho (P.4)	5	3.5	1.8	0.7	2.19	1.75
Tunkwa (P.4)	5	3.3	1.4	0.5	1.75	1.13
TI (P.4)	5	4.3	1.7	0.5	2.38	1.63
IT (P.4)	5	4.1	1.6	0.5	2.06	1.19

* number in brackets indicates experiment number

Figure 6. Relationship between $\log_e$ mean specific growth rates at maximum and optimum ration levels and $\log_e$ initial sizes of rainbow trout.

I. P.2 and P.3. one strain at 3 initial sizes.
II. Definitive experiments D.1, D.2 and D.3. three strains at 3 initial sizes.


I
●,○ = LL
●,○ = MM
■,□ = NN
▲,△ = MN
AT MAXIMUM RATION
SLOPE = -0.22
a = 1.45
r = 0.98
AT OPTIMUM RATION
SLOPE = -0.11
a = 0.56
r = 0.75
II
AT MAXIMUM RATION
SLOPE = -0.13
a = 1.00
r = 0.73
AT OPTIMUM RATION
SLOPE = -0.17
a = 0.58
r = 0.86
Loge Specific Growth Rate (% day-1)
Loge Initial Size (g)
2.0
1.5
1.0
0.5
0
1.0
0.5
0
-0.5
0
1
2
3
4
5

2.3 Methods of Experiment P.5.

The experiment started on February 11, 1980 and ended on April 9, 1980 and was the initial experiment in the 60 L. fiberglass tanks. The objective was to compare the specific growth rates of rainbow trout, brook trout and Arctic charr at four temperatures and eight rations (Total 96 lots, Table 5).

Four rows of 24 tanks per row consisting of a top and bottom level of 12 tanks were used. As described in Section B.3.2, each row had its own recirculation unit and the temperatures were constant within a row but variable between rows. Water temperatures were as follows: $10.1 \pm 0.1^{o}C$ (row C - odd), $13.0 \pm 0.1^{o}C$ (row C - even), $16.0 \pm 0.1^{o}C$ (row E - odd), and $18.9 \pm 0.1^{o}C$ (row E - even).

It was originally intended that there would be 8 ration levels from 0 to excess (approximately 7% based on preliminary experiments) with the ration levels within a temperature and within a species being applied at random to the upper and lower tanks. However, the top tanks are directly above the bottom tanks, resulting in some shading. In order to account partially for, and possibly minimize, any effect of differences in light level the procedures were altered. Excess rations (7% body $weight.day^{-1}$) and zero rations were each applied to two tanks of fish - one in the top and one in the bottom. The other ration levels were applied at random so that for each temperature and species the ration were as follows:

Tank level	Ration (% body weight.day^{-1})
Top	0, 4.5, 7, 3
Bottom	1.5, 7, 0, 6

Fish were started in all temperatures at an average density of 13.2 $g.l^{-1}$. The experiment lasted 8 weeks and, at the end of the experiment, 10 individuals per lot were sampled for lengths and weights.

The growth curves for each species were plotted, and the maximum specific growth rates, optimum ration and maintenance ration for each species were determined following the methods described for Experiment P.1. Differences in maximum specific growth rates, maximum ration and maintenance ration between species and temperature were tested separately by means of a two-way analysis of variance (Snedecor and Cochran 1967). The genetic variance components and non-genetic (temperature effect) variance components were also calculated (Snedecor and Cochran 1967).

2.4 Results of Experiment P.5.

The mean biweekly weights, rations and average specific growth rates for each species are given in Appendix A; Table 12. Maximum specific growth rates, maximum ration, specific growth rate at optimum ration, optimum ration and maintenance rations for Experiment P.5 are summarized in Table 7. Results of analysis of variance are given in Appendix A; Table 13.

Table 7. Preliminary experiment P.5; maximum, optimum and maintenance rations, specific growth rates at maximum and optimum rations for Arctic charr, brook trout and rainbow trout in various temperatures.

Temperature (°C)	Species	Ration (% Wet Weight.Day^{-1}) Maximum ration	Optimum ration	Maintenance ration	Specific Growth Rate (%.Day^{-1}) at maximum ration	at optimum ration
10	Arctic charr	4.70	0.55	0.15	2.00	0.50
	Brook trout	4.00	1.00	0.25	1.60	0.75
	Rainbow trout	4.35	1.10	0.25	1.80	0.80
13	Arctic charr	5.20	1.30	0.35	2.00	1.01
	Brook trout	4.00	1.60	0.35	1.90	1.25
	Rainbow trout	4.44	1.80	0.35	2.10	1.30
16	Arctic charr	5.40	1.70	0.32	1.85	1.00
	Brook trout	4.20	1.70	0.25	1.88	1.02
	Rainbow trout	5.05	2.30	0.50	2.10	1.45
19	Arctic charr	3.90	2.00	0.80	0.70	0.40
	Brook trout	3.60	1.60	0.50	1.08	0.60
	Rainbow trout	5.70	2.20	0.80	1.90	1.10

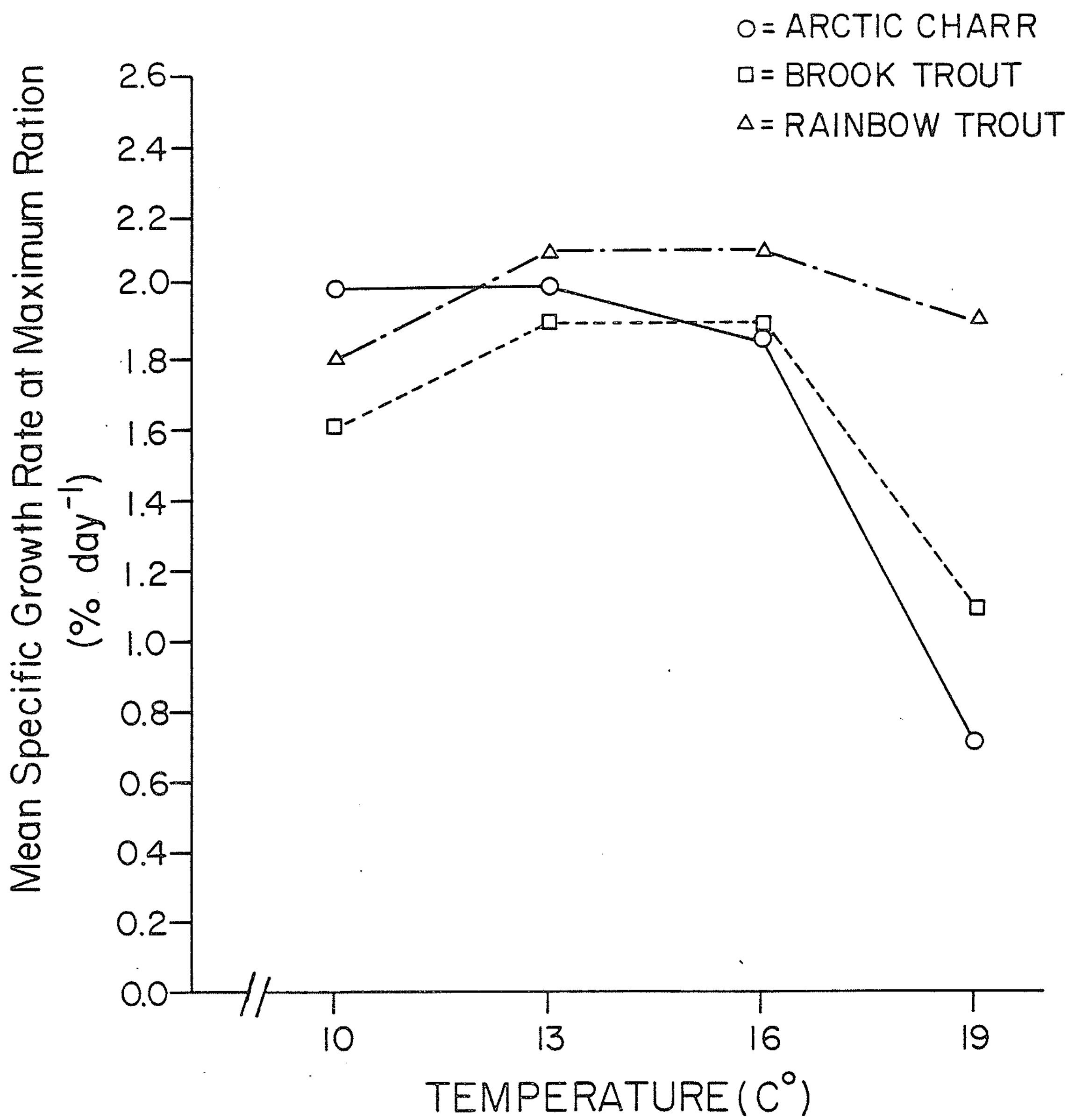
There were species and temperature differences in optimum ration and specific growth rate at optimum ration while temperature had the major effect on maintenance ration. Species differences in maximum ration and specific growth rate at maximum ration were not significant as the species-temperature interaction variations were large when compared either to species or temperature variation (Appendix A; Table 13).

All species showed the same general pattern of increasing food consumption and growth rates as temperatures increase and then a decline once the temperature optimum had been reached (Figure 7). The species-temperature interactions appear clearly in maximum ration and maximum specific growth rates (Table 7). At 10^{o}C Arctic charr had the highest maximum ration and growth (ration: 4.7% body weight.day^{-1}; growth: 2%.day^{-1}), but at 19^{o}C the rainbow trout had the highest maximum ration and growth (ration: 5.7% body weight.day^{-1}; growth: 1.9%.day^{-1}) (Table 7). Generally, temperatures between 13 and 19^{o}C are optimal for rainbow trout and brook trout while temperatures between 10 to 13^{o}C are optimal for Arctic charr (Figure 7).

3. Definitive Experiments

The field experiments demonstrated significant differences in growth between Manx and Nisqually but could not be used to identify the causative nature of those differences. For example, it was not possible to determine whether the observed differences were due to differences in maximum growth rate at all temperatures, or differences in temperature optima.

Figure 7. Preliminary experiment P.5, mean specific growth rate at maximum ration for Arctic charr, brook trout and rainbow trout at 4 temperatures.


○ = ARCTIC CHARR
□ = BROOK TROUT
△ = RAINBOW TROUT
Mean Specific Growth Rate at Maximum Ration
(% day⁻¹)
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
10
13
16
19
TEMPERATURE (C°)

Preliminary experiments provided the experimental techniques and the definitive experiments, the specific explanation for the differences. It was demonstrated in the field experiments, that differences between Manx and Nisqually were consistant and significant. Because it was possible to cross the Manx and Nisqually strains, differences between purebred lines and the hybrid were used to provide an estimate of genetic differences and heterosis in the definitive experiments.

3.1 Methods of Definitive Experiments

The definitive series of experiments took place at the Rockwood Experimental Hatchery. The objective of these experiments was to determine differences in growth rates of rainbow trout in relation to genotype and environmental factors and to determine what factors could explain the observed differences in harvest size of strains of fish in the field experiments.

Differences of specific growth rates between Manx, Nisqually strains and their hybrids in relation to ration, temperature and initial size were measured in 3 experiments (D.1, D.2 and D.3). Each experiment took 6 weeks. In each experiment, there were three strains or hybrids (MM, NN and MN), eight ration levels (0, 0, 1.5, 3, 4.5, 6, 7 and 7% wet weight.day^{-1}) and four temperatures (12, 14.3, 16.7 and 19^{o}C) (Table 8). Successive experiments used first 7 g, then 17 g, then 67 g fish to provide an estimation of the size effect (total 298 lots). The initial stocking density in each experiment averaged 10 g. l^{-1}. There was no culling or replacement of fish during the experiment.

Table 8. Definitive experiments D.1, D.2 and D.3; strains, initial weights, ration levels, temperatures and initial stocking rates of rainbow trout.

Experiment Number	Strain Crosses	Initial Size (g)	Ration (% wet weight.day^{-1}) Top Tanks	Bottom Tanks	Temperature (^{o}C)	Stocking Rate fish/tank	g.l.$^{-1}$
D.1	Manx	7	0.0	0.0	12.0	90	10.9
	Nisqually		1.5	3.0	14.3		
	Manx X Nisqually		4.5	6.0	16.7		
			7.0	7.0	19.0		
D.2	Manx	17	0.0	0.0	12.0	40	11.2
	Nisqually		1.5	3.0	14.3		
	Manx X Nisqually		4.5	6.0	16.7		
			7.0	7.0	19.0		
D.3	Manx	67	0.0	0.0	12.0	10	10.9
	Nisqually		1.5	3.0	14.3		
	Manx X Nisqually		4.5	6.0	16.7		
			7.0	7.0	19.0		

Similar to P.5, the 8 ration levels were applied to 4 rows of 24 experimental tanks as follows:

Tank Level	Ration (% wet weight.day^{-1})
Top	0, 1.5, 4.5, 7.0
Bottom	0, 3.0, 6.0, 7.0

The growth curves of each strain cross in each temperature and each initial size were plotted, and maximum, optimum and maintenance rations and specific growth rates at maximum and optimum rations were determined following the procedures described for Experiment P.1. In order to ensure impartiality three different people each fitted the 36 growth curves (3 strains x 3 sizes x 4 temperatures) and determined the 5 parameters from each curve. Results were based on the average value.

The other characters included in the study were the net and gross efficiencies at maximum and optimum rations (Brett et al. 1969). These efficiencies must be presented in terms of equal units. Since the moisture content of the food and fish differed and since the moisture content of the fish varied with temperature level, it was necessary to develop an appropriate correction factor. True ration level (dry weight of food.day^{-1} per dry weight of fish . day^{-1} as %) was calculated using the correction factor given in Appendix A; Table 14.

The genotype, temperature and initial size differences for all parameters under consideration were tested by means of a three-way analysis of variance (Snedecor and Cochran 1967). The variance components for genotypes, environments and genotype-environment interactions were estimated. When size interactions were found in the three-way analysis of variance, a two-way analysis of variance was used to test the differences of genotype and temperature for each initial size (i.e. D.1, D.2 and D.3 were analyzed separately).

The additive genetic effect (A), the non-additive genetic effect (D) and relative values were also estimated. The differences of mean relative values were compared for each temperature and initial size to observe the effect of environment on genetic values as well as genotype-environment interactions.

Experiment D.1. started July 22-23, 1980 and ended September 2-3, 1980. This initial definitive experiment was to determine genotype and temperature differences in specific growth rate, ration and conversion efficiency for small fish (initial size 7 g.). Water temperatures were as follows: $12.2 \pm 0.4^{\circ}C.$ (E - even), $14.3 \pm 0.3^{\circ}C.$ (E - odd), $16.6 \pm 0.2^{\circ}C.$ (C - even), and $19.0 \pm 0.5^{\circ}C.$ (C - odd). Each strain was raised under 4 temperatures and fed 8 different ration levels (total 96 lots, Table 8). The stocking density averaged $10.9\ g.l^{-1}$.

Experiment D.2. started September 22-23, 1980 and ended November 24-25, 1980. The objective and procedures were similar to Experiment D.1, but initial fish size averaged 17g. (Table 8). Water temperatures were as follows: $11.9 \pm 0.5^{\circ}C.$ (E - odd), $14.3 \pm 0.5^{\circ}C.$ (E - even), $16.8 \pm 0.4^{\circ}C.$ (C - odd), and $18.9 \pm 0.2^{\circ}C.$ (C - even). The initial density averaged $11.2\ g.\ l^{-1}$.

Experiment D.3. started February 2-3, 1981 and ended March 30-31, 1981 with objectives and procedures similar to Experiment D.1, and initial fish size averaged 67 g. (Table 8). The water temperatures were as follows: 11.9 ± 0.5°C. (C - even), 14.2 ± 0.2°C. (C - odd), 16.7 ± 0.4°C. (E - even), and 18.5 ± 0.5°C. (E - even). The initial density averaged 10.9 g. l^{-1}.

3.2 Results of Definitive Experiments (D.1., D.2. and D.3.)

The results section presents an analysis of both the observed differences and the estimations of genetic parameters.

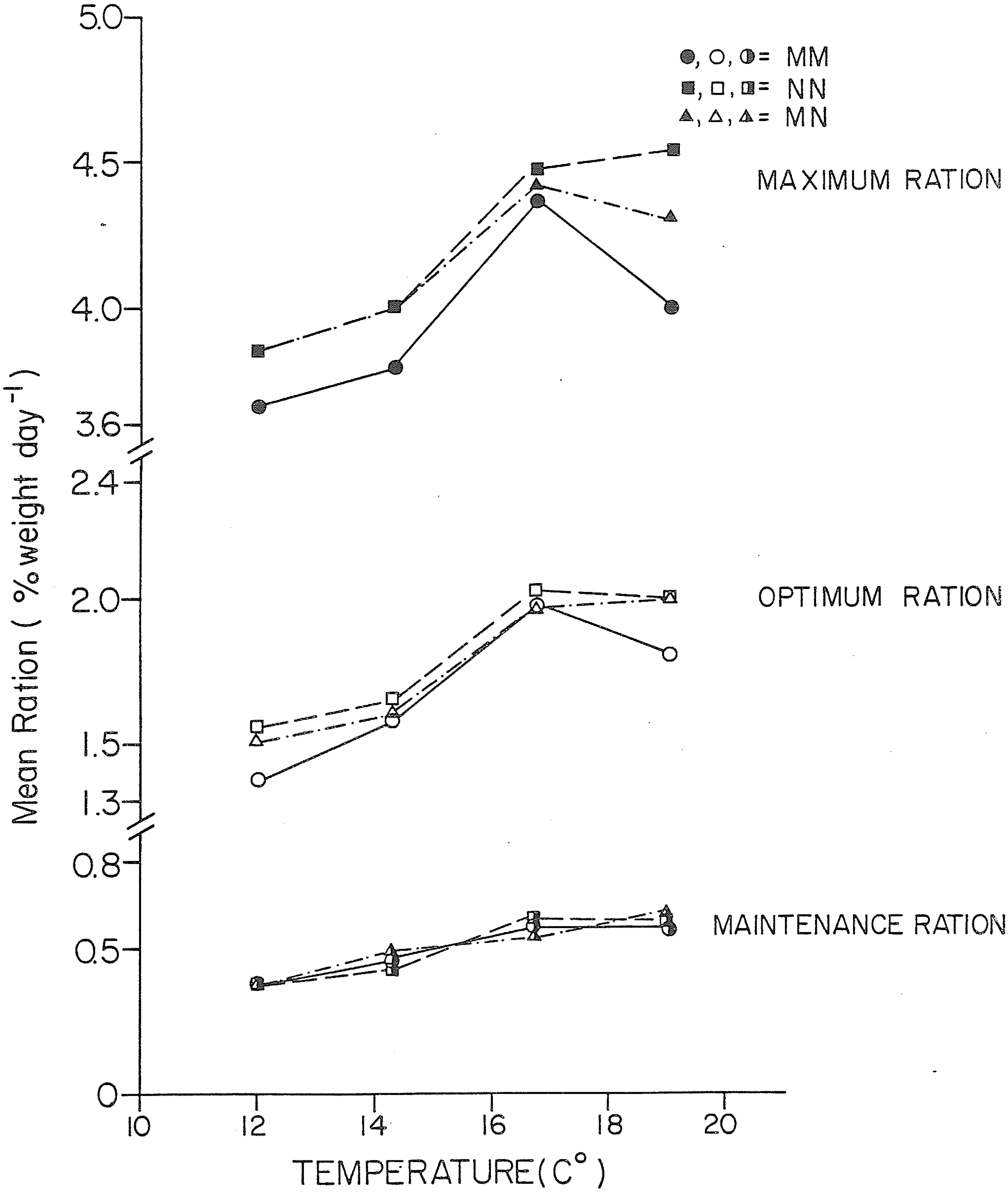
The maximum ration for NN, MN and MM fish averaged over all temperatures and initial sizes varied between 4.0 and 4.2% of fish body weight.day^{-1} (Table 9). NN fish consumed the most and MM the least with MN being intermediate. Variance component analysis showed that 30% of all variability at maximum rations was due to temperature, 23% due to differences in initial size and 6% due to genotype (Appendix A; Table 15). Consumption increased as temperature increased to 16.7°C but then decreased with a further rise in temperature (Table 9 and Figure 8). Consumption, as a percent of fish body weight.day^{-1}, decreased as fish size increased (Table 9, Figure 9). There were also significant temperature-initial size interactions.

The optimum ration for NN, MN and MM fish averaged over all temperatures and initial sizes only varied between 1.7 and 1.9% of fish body weight.day^{-1} (Table 9). NN fish consumed the most and MM the least with MN being intermediate. Variance component

Table 9. Definitive experiments D.1, D.2 and D.3; maximum, optimum and maintenance rations (% of body weight. day^{-1}) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

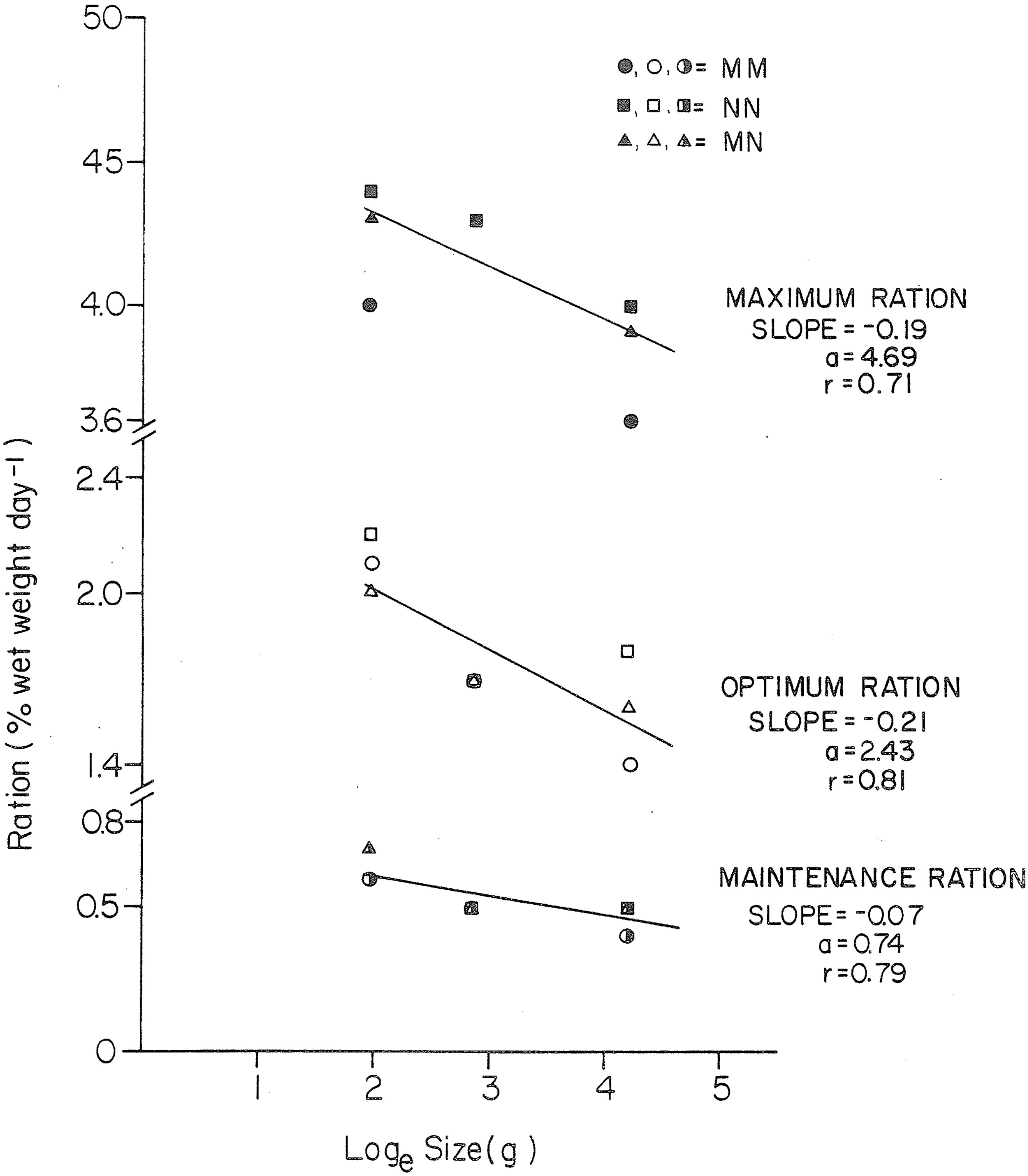
Size (g)			Temperatures 12.0	14.3	16.7	19.0	(^0C) Mean
7	MM	Maintenance	0.47	0.45	0.82	0.71	0.61
		Optimum	1.66	1.66	2.47	2.31	2.03
		Maximum	3.72	3.84	4.48	4.03	4.02
	NN	Maintenance	0.50	0.47	0.76	0.74	0.62
		Optimum	1.82	1.86	2.55	2.48	2.18
		Maximum	3.75	4.58	4.20	5.12	4.41
	MN	Maintenance	0.41	0.58	0.84	0.79	0.66
		Optimum	1.49	1.73	2.58	2.32	2.03
		Maximum	3.98	4.23	4.48	4.62	4.33
17	MM	Maintenance	0.32	0.57	0.55	0.52	0.49
		Optimum	1.31	1.68	2.06	1.69	1.69
		Maximum	4.05	3.76	4.73	4.40	4.24
	NN	Maintenace	0.27	0.46	0.47	0.49	0.42
		Optimum	1.41	1.63	1.83	1.79	1.67
		Maximum	4.14	3.78	4.93	4.34	4.30
	MN	Maintenance	0.27	0.48	0.45	0.57	0.44
		Optimum	1.41	1.63	1.90	1.89	1.71
		Maximum	3.89	3.82	4.98	4.38	4.27
67	MM	Maintenance	0.35	0.35	0.36	0.47	0.38
		Optimum	1.19	1.41	1.42	1.44	1.37
		Maximum	3.23	3.84	3.91	3.53	3.63
	NN	Maintenance	0.38	0.39	0.54	0.56	0.47
		Optimum	1.49	1.46	2.07	2.07	1.77
		Maximum	3.67	3.79	4.30	4.17	3.98
	MN	Maintenance	0.45	0.40	0.35	0.52	0.43
		Optimum	1.65	1.44	1.44	1.85	1.60
		Maximum	3.67	3.98	3.83	3.94	3.86
Mean	MM	Maintenance	0.38	0.46	0.58	0.57	0.50
		Optimum	1.39	1.58	1.98	1.81	1.69
		Maximum	3.67	3.81	4.37	3.99	3.96
	NN	Maintenance	0.38	0.44	0.59	0.60	0.50
		Optimum	1.57	1.65	2.15	2.11	1.87
		Maximum	3.85	4.05	4.48	4.54	4.23
	MN	Maintenance	0.38	0.49	0.55	0.63	0.51
		Optimum	1.52	1.60	1.97	2.02	1.78
		Maximum	3.85	4.01	4.43	4.31	4.15

Figure 8. Definitive experiments D.1, D.2 and D.3. Ration at maximum, optimum and maintenance levels at different temperatures for rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN).



●, ○, ◑ = MM
■, □, ◨ = NN
▲, △, ◭ = MN
MAXIMUM RATION
OPTIMUM RATION
MAINTENANCE RATION
Mean Ration (% weight day^{-1})
TEMPERATURE(C°)
5.0
4.5
4.0
3.6
2.4
2.0
1.5
1.3
0.8
0.5
0
10
12
14
16
18
20

Figure 9. Definitive experiments D.1, D.2 and D.3. Relationship between ration at maximum, optimum and maintenance levels and $\log_e$ initial sizes for rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN).



●, ○, ◑= MM
■, □, ◧= NN
▲, △, ◭= MN
MAXIMUM RATION
SLOPE = -0.19
a = 4.69
r = 0.71
OPTIMUM RATION
SLOPE = -0.21
a = 2.43
r = 0.81
MAINTENANCE RATION
SLOPE = -0.07
a = 0.74
r = 0.79
Ration (% wet weight day-1)
Loge Size(g)
50
45
4.0
3.6
2.4
2.0
1.4
0.8
0.5
0
1
2
3
4
5

analysis showed that 35% of the variability in optimum ration was due to temperature, 33% due to differences in initial size and only 4% due to genotype (Appendix A; Table 15). The genotype-size and temperature-initial size interactions were also significant. Consumption increased as temperature increased to 16.7^{o}C but dropped slightly at 19^{o}C (Table 9 and Figure 8). Consumption as a percent of fish body weight.day^{-1} decreased as fish size increased (Table 9 and Figure 9).

The maintenance rations for NN, MN and MM fish averaged over all temperatures and initial sizes was 0.5 % weight.day^{-1} for all strains (Table 9). There were, therefore, no significant genetic differences. Variance component analysis showed that 35% of variability in maintenance ration was due to initial size and 29% due to temperature differences (Appendix A; Table 15). Consumption increased as temperature increased to 16.7^{o}C and remained constant at 19.0^{o}C (Table 9 and Figure 8). Consumption, as a percent of fish body weight.day^{-1} decreased as fish size increased (Table 9 and Figure 9).

The mean specific growth rate at maximum ration for NN, MN and MM fish averaged over all temperatures and initial sizes varied between 1.7 and 2.0%.day^{-1}. NN and MN fish grew the fastest with MM being the slowest (Table 10). Variance component analysis showed that 63% of variability in mean specific growth rate was due to initial size, 16% due to genotype and 12% due to temperature-initial size interactions (Appendix A; Table 15). The temperature

Table 10. Definitive experiments, specific growth rates at maximum ration and the estimation of additive genetic effects (A) and non-additive genetic effects (D) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

		Mean specific growth rate at maximum ration (%.day^{-1})				
Temperature (°C) / Initial Size (g)		12.0	14.3	16.7	19.0	Mean
7	MM	1.65	1.66	1.80	1.75	1.72
	NN	1.86	2.31	2.14	2.43	2.19
	MN	1.80	2.03	2.06	1.97	1.97
17	MM	2.04	1.77	2.23	1.83	1.97
	NN	2.35	2.04	2.29	1.97	2.16
	MN	2.29	2.05	2.40	1.96	2.18
67	MM	1.16	1.30	1.43	1.33	1.31
	NN	1.58	1.55	1.53	1.66	1.58
	MN	1.55	1.58	1.48	1.62	1.56
Mean	MM	1.62	1.58	1.82	1.64	1.67
	NN	1.93	1.97	1.99	2.02	1.98
	MN	1.88	1.89	1.98	1.85	1.90

		Estimation of Genetic Value (%)									
		Absolute value (%)					Relative value (%) *a				
Temperature (°C) / Initial Size (g)		12.0	14.3	16.7	19.0	Mean	12.0	14.3	16.7	19.0	Mean
7	A	10.5	32.5	17.0	34.0	23.5	6.0	16.4	8.6	16.3	11.8
	D	4.5	4.5	9.0	-12.0	1.5	2.6	2.3	4.6	-5.7	1.0
17	A	15.5	13.5	3.0	7.0	9.8	7.1	7.1	1.3	3.7	4.8
	D	9.5	14.5	14.0	6.0	11.0	4.3	7.6	6.2	3.2	5.3
67	A	21.0	12.5	5.0	16.5	13.8	15.3	8.8	3.4	11.0	9.6
	D	18.0	15.5	0.0	12.5	11.5	13.0	10.9	0.0	8.4	8.2
Mean	A	15.7	19.5	8.3	19.2	15.7	9.5	10.8	4.4	10.3	8.7
	D	10.7	11.5	7.7	2.2	8.0	6.8	6.9	3.6	2.0	4.8

* a % of mid parent value

effect on growth (Table 10 and Figure 10) was not marked but there was a clear optimum at 16.7^{o}C. Growth rates decreased as fish size increased (Table 10 and Figure 6).

The specific growth rates at optimum ration for NN, MN and MM fish averaged for all temperatures and initial sizes varied between 1.0 and 1.2%.day^{-1}. NN fish grew the fastest, MN intermediate and MM having the slowest growth (Table 11). Variance component analysis showed that 60% of the variability in specific growth rate at optimum rations was due to initial size, 12% due to genotype, 10% due to differences in temperature and 10% due to temperature-initial size interactions (Appendix A; Table 15). The temperature effect on optimum growth (Table 11 and Figure 10) was less than for maximum growth. Growth at optimum rations, expressed in units of %.day^{-1}, decreased as fish size increased (Table 11 and Figure 6).

The net and gross efficiencies at maximum ration for NN, MN and MM fish averaged over all temperatures and initial sizes varied between 14 and 15% for net efficiency and between 12 and 14% for gross efficiency (Tables 12 and 13). NN and MN had the highest net efficiency while MM had the lowest. NN was highest in gross efficiency and MM was lowest with MN being intermediate. Variance component analysis showed that 61% of variability in net efficiency at maximum ration was due to initial size, 11% due to genotype and 16% due to temperature-initial size interactions. 63% of variability in gross efficiency at optimum rations was due to initial size, 14% due to genotype and 11% due to temperature-initial size interactions (Appendix A; Table 15). There were no consistent temperature

Figure 10. Definitive experiments D.1, D.2 and D.3. Specific growth rate at maximum and optimum ration levels at different temperatures for rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN).

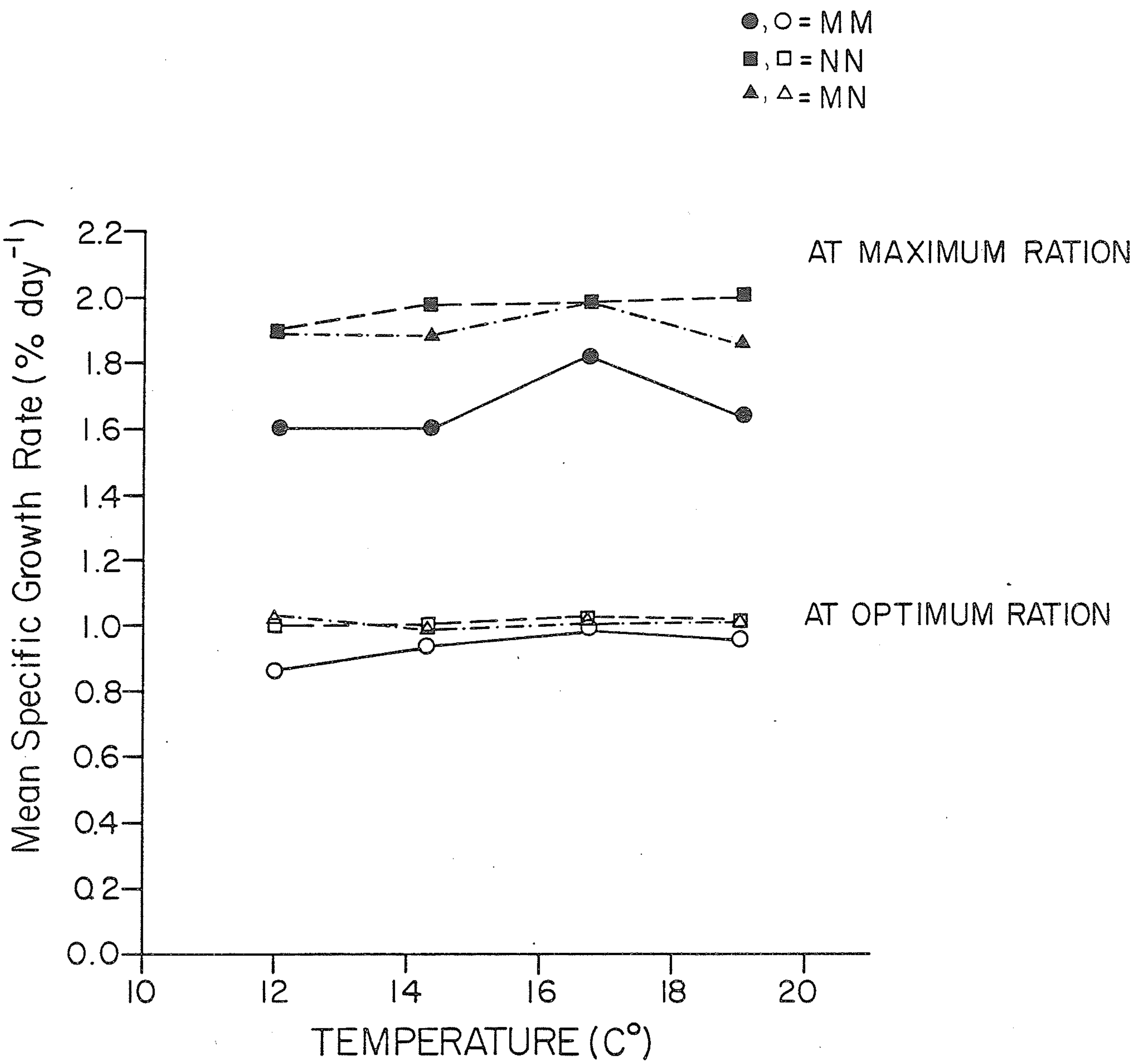

●, ○ = MM
■, □ = NN
▲, △ = MN
AT MAXIMUM RATION
AT OPTIMUM RATION
Mean Specific Growth Rate (% day^{-1})
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
10
12
14
16
18
20
TEMPERATURE (C°)

Table 11. Definitive experiments, specific growth rates at optimum ration and the estimation of additive genetic effects (A) and non-additive genetic effects (D) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

Temperature (°C) / Initial Size (g)		Mean specific growth rate at optimum ration (%.day^{-1}) 12.0	14.3	16.7	19.0	Mean
7	MM	0.93	1.01	1.37	1.16	1.12
	NN	1.17	1.22	1.49	1.45	1.33
	MN	1.23	1.05	1.39	1.28	1.24
17	MM	1.07	1.07	1.33	0.95	1.11
	NN	1.23	1.23	1.31	1.09	1.22
	MN	1.24	1.17	1.33	1.16	1.23
67	MM	0.62	0.73	0.80	0.80	0.74
	NN	0.89	0.88	1.00	1.00	0.94
	MN	0.93	0.83	0.89	0.95	0.90
Mean	MM	0.87	0.94	1.17	0.97	0.99
	NN	1.10	1.11	1.27	1.18	1.17
	MN	1.13	1.02	1.20	1.13	1.12

Temperature (°C) / Initial Size (g)		Estimation of Genetic Value (%) Absolute value (%) 12.0	14.3	16.7	19.0	Mean	Relative value (%)*a 12.0	14.3	16.7	19.0	Mean
7	A	12.0	10.5	6.0	14.5	10.8	11.4	9.4	4.2	11.1	9.0
	D	18.0	-6.5	-4.0	-2.5	1.3	17.1	-5.8	-2.8	-1.9	1.7
17	A	8.0	8.0	-1.0	7.0	5.5	7.0	7.0	-0.8	6.9	5.0
	D	9.0	2.0	1.0	14.0	6.5	7.8	1.7	0.8	13.7	6.0
67	A	13.5	7.5	10.0	10.0	10.3	17.9	9.3	11.1	11.1	12.4
	D	17.5	2.5	-1.0	5.0	6.0	23.2	3.1	-1.1	5.6	7.7
Mean	A	11.2	8.7	5.0	10.5	8.9	12.1	8.6	4.8	9.7	8.8
	D	14.8	-0.7	-1.3	5.5	4.6	16.0	-0.3	-1.0	5.8	5.1

* a % of mid parent value

Table 12. Definitive experiments, net efficiencies at maximum ration and the estimation of additive genetic effects (A) and non-additive genetic effects (D) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

Temperature (°C) / Initial Size (g)		Mean net efficiency at maximum ration (%) 12.0	14.3	16.7	19.0	Mean
7	MM	14.22	14.20	14.26	15.81	14.62
	NN	16.02	16.30	18.04	16.64	16.75
	MN	14.12	16.13	16.41	15.43	15.52
17	MM	15.31	16.09	15.47	14.15	15.26
	NN	17.00	17.82	14.89	15.35	16.27
	MN	17.71	17.80	15.36	15.43	16.58
67	MN	11.28	10.80	11.68	13.04	11.70
	NN	13.45	13.22	11.80	13.79	13.07
	MN	13.48	12.80	11.92	14.21	13.10
Mean	MM	13.60	13.70	13.80	14.33	13.86
	NN	15.49	15.78	14.91	15.26	15.36
	MN	15.10	15.58	14.56	15.02	15.07

		Estimation of genetic values (%)									
		Absolute values (%)					Relative values (%) *a				
Temperature (°C) / Initial Size (g)		12.0	14.3	16.7	19.0	Mean	12.0	14.3	16.7	19.0	Mean
7	A	0.9	1.1	1.9	0.4	1.2	6.0	6.9	11.7	2.6	6.8
	D	-1.0	0.9	0.3	-0.8	-0.2	-6.6	5.8	1.6	-4.9	-1.0
17	A	0.9	0.9	-0.3	0.6	0.5	5.2	5.1	-1.9	4.1	3.1
	D	1.6	0.9	0.2	0.7	0.9	9.6	5.0	1.2	4.6	5.1
67	A	1.1	1.2	0.1	0.4	0.7	8.8	10.1	0.5	2.8	5.6
	D	1.1	1.0	0.2	0.8	0.8	9.0	6.6	1.5	5.9	5.8
Mean	A	1.0	1.1	0.6	0.5	0.8	6.7	7.4	3.4	3.2	5.2
	D	0.6	0.9	0.2	0.2	0.5	4.0	5.8	1.4	1.9	3.3

*a % of mid parent value

Table 13. Definitive experiments, gross efficiencies at maximum ration and the estimation of additive genetic effects (A) and non-additive genetic effects (D) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

Temperature (°C) / Initial Size (g)		Mean gross efficiency at maximum ration (%) 12.0	14.3	16.7	19.0	Mean
7	MM	12.42	12.54	11.65	13.03	12.41
	NN	13.89	14.63	14.78	14.24	14.39
	MN	12.66	13.92	13.33	12.79	13.18
17	MM	14.10	13.65	13.67	12.48	13.48
	NN	15.89	15.65	13.47	13.62	14.66
	MN	16.48	15.56	13.98	13.43	14.86
67	MM	10.05	9.82	10.61	11.30	10.45
	NN	12.05	11.86	10.32	11.94	11.54
	MN	11.82	11.51	11.21	12.34	11.72
Mean	MM	12.19	12.00	11.98	12.27	12.11
	NN	13.94	14.05	12.86	13.27	13.53
	MN	13.65	13.66	12.84	12.85	13.25

		Estimation of genetic value (%)									
		Absolute Value (%)					Relative Value (%) *a				
Temperature (°C) / Initial Size (g)		12.0	14.3	16.7	19.0	Mean	12.0	14.3	16.7	19.0	Mean
7	A	0.7	1.1	1.6	0.6	1.0	5.6	7.7	11.8	4.4	7.4
	D	-0.5	0.3	0.1	-0.9	-0.3	-3.8	2.5	0.9	-6.2	-1.7
17	A	0.9	1.0	-0.1	0.6	0.6	6.0	6.8	-0.7	4.4	4.1
	D	1.5	0.9	0.4	0.4	0.8	9.9	6.2	3.0	2.9	5.5
67	A	1.0	1.0	-0.2	0.3	0.5	9.1	9.4	-1.4	2.8	5.0
	D	0.8	0.7	0.8	0.7	0.8	7.0	6.2	7.1	6.2	6.6
Mean	A	0.9	1.0	0.4	0.5	0.7	6.9	8.0	3.2	3.9	5.5
	D	0.6	0.6	0.4	0.1	0.4	4.4	5.0	3.7	1.0	3.5

*a % of mid parent value

effects on efficiencies (Tables 12 and 13, Figure 11), although efficiencies decreased as fish size increased (Tables 12 and 13, Figure 12).

The net and gross efficiencies at optimum ration for NN, MN and MM fish averaged over all temperatures and initial sizes varied between 22 and 24%, and 16 and 17% for net and gross efficiencies respectively (Tables 14 and 15). MN had the highest net efficiency, MM the lowest and NN were intermediate. Gross efficiency of MN and NN were the same while gross efficiency of MM was lower (Tables 14 and 15). Variance component analysis showed that 54% of the variability in net efficiency at optimum rations was due to initial size and 8% was due to temperature. Similarly, 46% of the variability in gross efficiency at optimum ration was due to initial size with 16% being due to temperature (Appendix A; Table 15). Genotypic differences were not significant and were small compared to common error.

There was no consistent temperature effect (Tables 14 and 15, Figure 13) and gross efficiencies decreased as fish size increased (Tables 14, 15 and Figure 14).

The genetic parameters were estimated for specific growth rate and efficiencies at maximum and optimum ration for each size and temperature (Tables 10-15). The additive genetic differences in maximum specific growth rate between Manx and Nisqually were relatively constant for fish initial size 7 to 67 g. while non-additive genetic effects (heterosis) seemed to increase as the

Figure 11. Definitive experiments D.1, D.2 and D.3. Net and gross efficiencies at maximum ration levels at different temperatures for rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN).

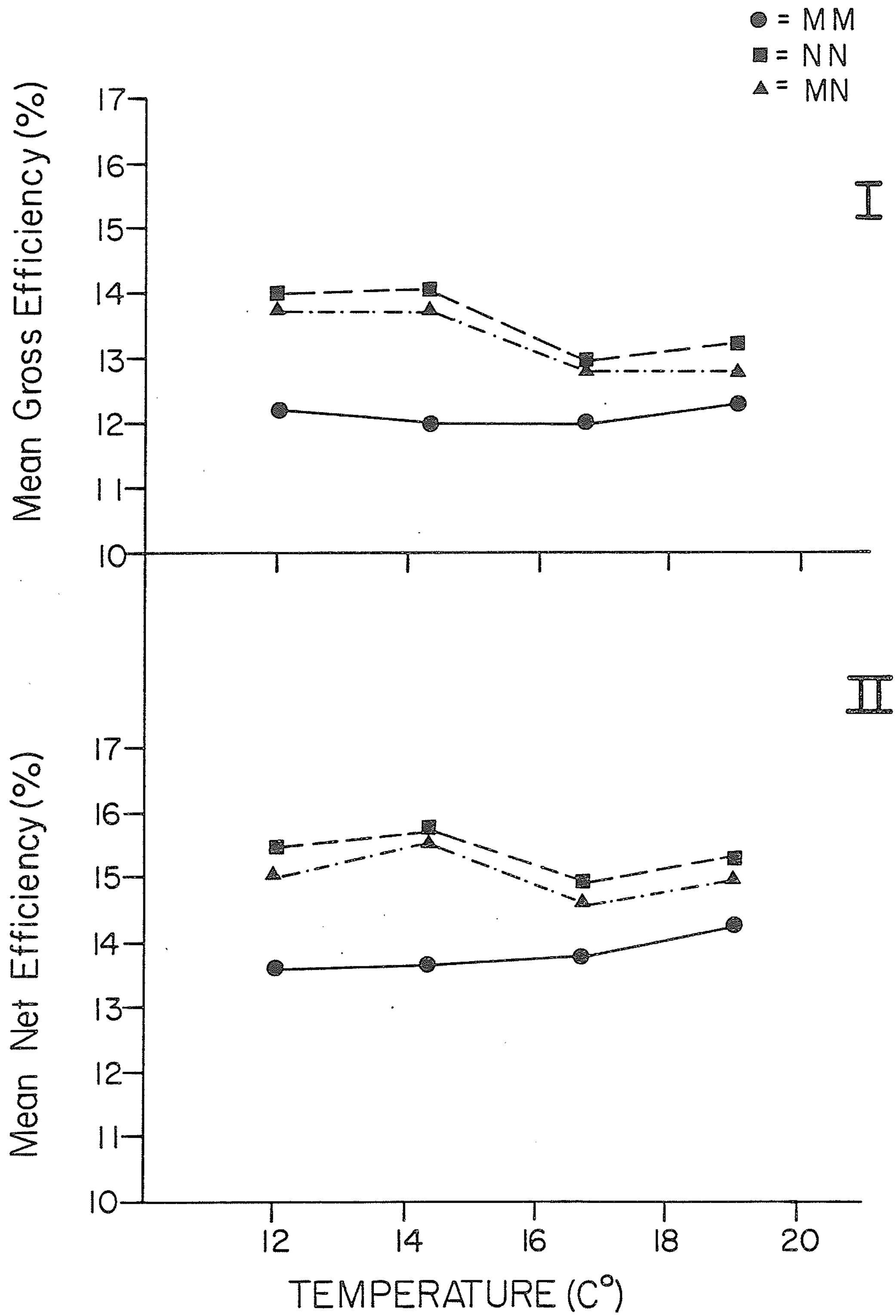
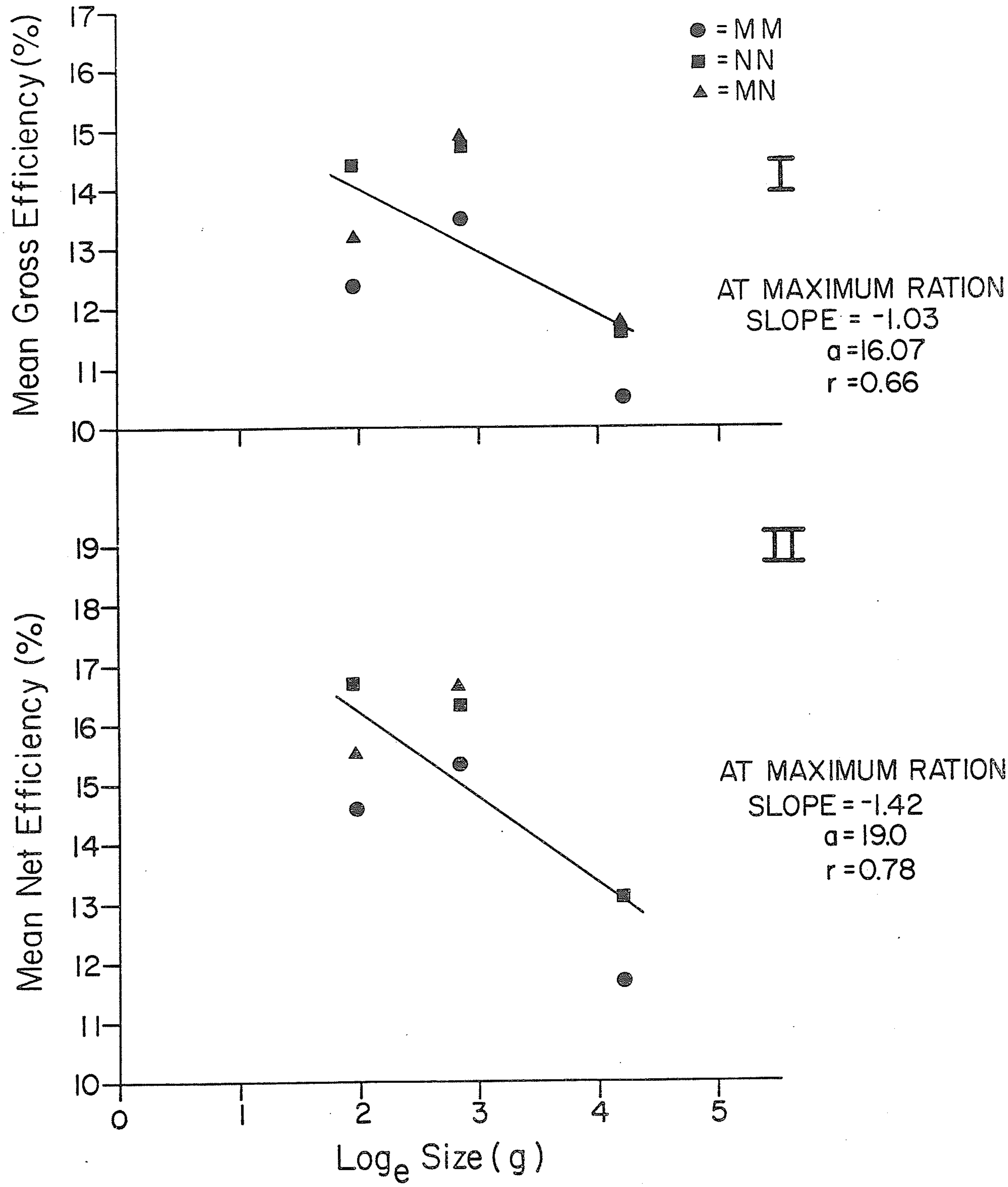

● = MM
■ = NN
▲ = MN
I
Mean Gross Efficiency (%)
17
16
15
14
13
12
11
10
II
Mean Net Efficiency (%)
17
16
15
14
13
12
11
10
12
14
16
18
20
TEMPERATURE (C°)

Figure 12. Definitive experiments D.1, D.2 and D.3. Relationship between net and gross efficiencies at maximum ration level and $\log_e$ initial size for rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN).



● = MM
■ = NN
▲ = MN
I
Mean Gross Efficiency (%)
17
16
15
14
13
12
11
10
AT MAXIMUM RATION
SLOPE = -1.03
a = 16.07
r = 0.66
II
Mean Net Efficiency (%)
19
18
17
16
15
14
13
12
11
10
AT MAXIMUM RATION
SLOPE = -1.42
a = 19.0
r = 0.78
0
1
2
3
4
5
Log$_e$ Size (g)

Table 14. Definitive experiments, net efficiencies at optimum ration and the estimation of additive genetic effects (A) and non-additive genetic effects (D) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

Temperature (°C) / Initial Size (g)		Mean net efficiency at optimum ration (%) 12.0	14.3	16.7	19.0	Mean
7	MM	20.32	21.70	23.25	19.58	21.21
	NN	23.05	22.82	23.31	22.50	22.92
	MN	29.61	23.74	22.37	22.59	24.58
17	MM	28.10	25.06	24.18	21.92	24.82
	NN	28.05	27.33	26.97	22.64	26.25
	MN	28.28	26.45	25.68	23.73	26.04
67	MM	19.03	17.91	21.13	22.27	20.09
	NN	20.85	21.38	18.30	17.88	19.60
	MN	20.15	20.75	22.86	19.29	20.76
Mean	MM	22.48	21.56	22.85	21.26	22.04
	NN	23.98	23.84	22.86	21.01	22.92
	MN	26.01	23.65	23.64	21.87	23.79

		Estimation of genetic value (%)									
		Absolute value (%)					Relative value (%)*a				
Temperature (°C) / Initial Size (g)		12.0	14.3	16.7	19.0	Mean	12.0	14.3	16.7	19.0	Mean
7	A	1.4	0.6	0.0	1.5	0.9	6.3	2.5	0.1	6.9	4.0
	D	7.9	1.5	-0.9	1.6	2.5	36.6	6.7	-3.9	7.4	11.7
17	A	0.0	1.1	1.4	0.4	0.7	-0.1	4.3	5.5	1.6	2.8
	D	0.2	0.3	0.1	1.5	0.5	0.7	1.0	0.4	6.5	2.2
67	A	0.9	1.7	-1.4	-2.2	-0.3	4.6	8.8	-7.2	-10.9	-1.2
	D	0.2	1.1	3.2	-0.8	0.9	1.1	5.6	16.0	-3.9	4.7
Mean	A	0.8	1.1	0.0	-0.1	0.4	3.6	5.2	-0.5	-0.8	1.9
	D	2.8	1.0	0.8	0.8	1.4	12.8	4.4	4.2	3.3	6.2

*a % of mid parent value

Table 15. Definitive experiments, gross efficiencies at optimum ration and the estimation of additive genetic effects (A) and non-additive genetic effects (D) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

Temperature (^oC) / Initial Size (g)		Mean gross efficiency at optimum ration (%) 12.0	14.3	16.7	19.0	Mean
7	MM	14.57	15.82	15.53	13.56	14.87
	NN	16.72	17.05	16.36	15.79	16.48
	MN	21.46	15.83	15.09	14.90	16.82
17	MM	21.24	16.56	17.82	15.18	17.70
	NN	22.68	19.62	20.04	16.44	19.70
	MN	22.86	18.66	19.60	16.57	19.42
67	MM	13.55	13.46	15.78	15.00	14.45
	NN	15.53	15.67	13.53	13.04	14.44
	MN	14.65	14.99	17.31	13.86	15.20
Mean	MM	16.45	15.28	16.38	14.58	15.67
	NN	18.31	17.45	16.64	15.09	16.87
	MN	19.66	16.49	17.33	15.11	17.15

		Estimation of genetic value (%)									
		Absolute value (%)					Relative value (%) *a				
Temperature (^oC) / Initial Size (g)		12.0	14.3	16.7	19.0	Mean	12.0	14.3	16.7	19.0	Mean
7	A	1.1	0.6	0.4	1.1	0.8	6.9	3.7	2.6	7.6	5.2
	D	5.8	-0.6	-0.9	0.2	1.1	37.2	-3.7	-5.4	1.5	7.4
17	A	0.7	1.5	1.1	0.6	1.0	3.3	8.5	5.9	4.0	5.4
	D	0.9	0.6	0.7	0.8	0.8	4.1	3.2	3.5	4.8	3.9
67	A	1.0	1.1	-1.1	-1.0	0.0	6.8	7.6	-7.7	-7.0	-0.1
	D	0.1	0.4	2.7	-0.2	0.8	0.8	2.9	18.1	-1.1	5.2
Mean	A	0.9	1.1	0.1	0.2	0.6	5.7	6.6	0.3	1.5	3.5
	D	2.3	0.1	0.8	0.3	0.9	14.0	0.8	5.4	1.7	5.5

*a % of mid parent value

Figure 13. Definitive experiments D.1, D.2 and D.3. Net and gross efficiencies at optimum ration levels at different temperatures for rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN).

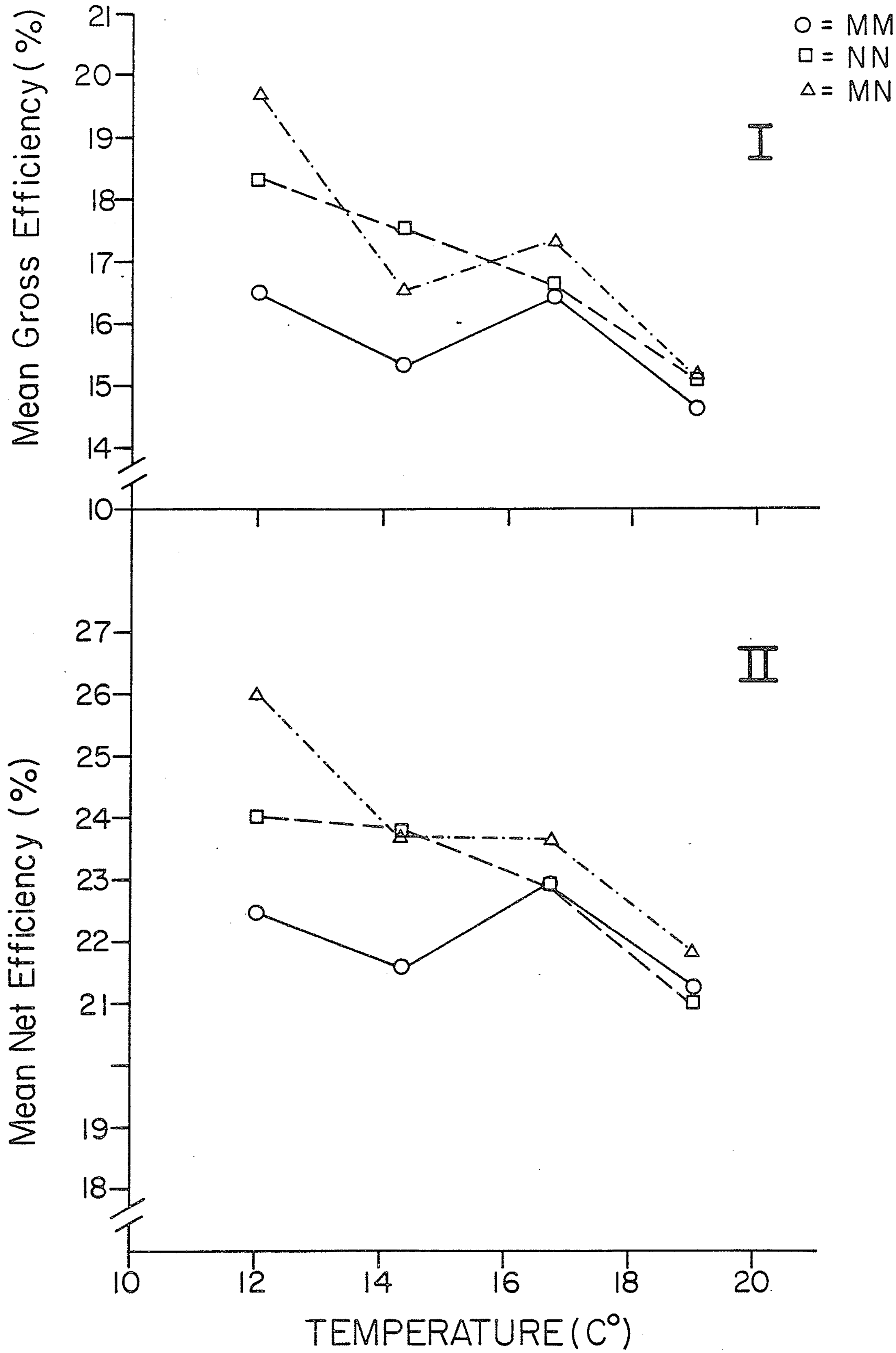
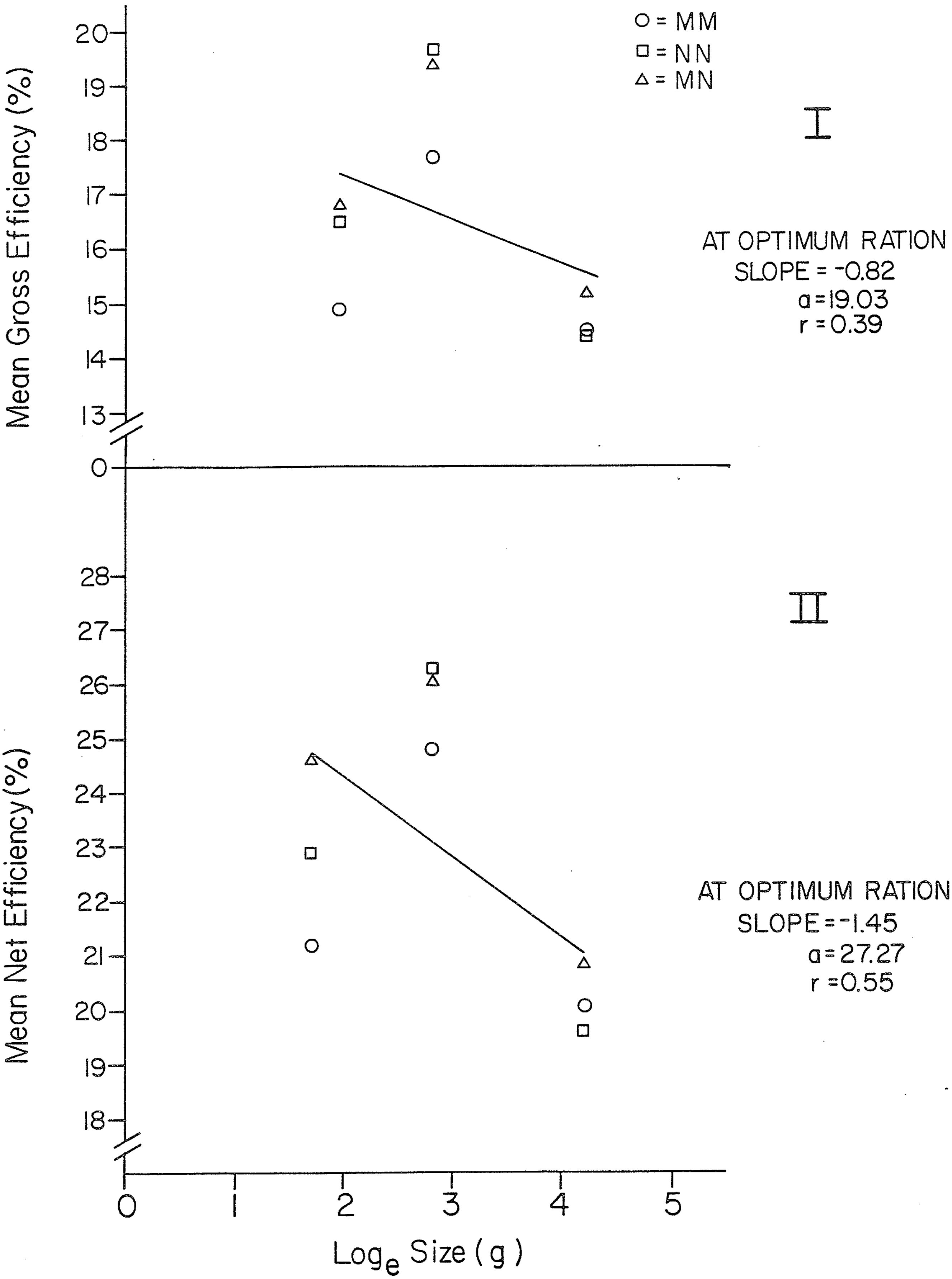

○ = MM
□ = NN
△ = MN
I
Mean Gross Efficiency (%)
21
20
19
18
17
16
15
14
10
II
Mean Net Efficiency (%)
27
26
25
24
23
22
21
19
18
10
12
14
16
18
20
TEMPERATURE (C°)

Figure 14. Definitive experiments D.1, D.2 and D.3. Relationship between net and gross efficiencies at optimum ration levels and $\log_e$ initial size for rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN).



○ = MM
□ = NN
△ = MN
I
AT OPTIMUM RATION
SLOPE = -0.82
a = 19.03
r = 0.39
Mean Gross Efficiency (%)
20
19
18
17
16
15
14
13
0
II
AT OPTIMUM RATION
SLOPE = -1.45
a = 27.27
r = 0.55
Mean Net Efficiency (%)
28
27
26
25
24
23
22
21
20
19
18
0
1
2
3
4
5
Log$_e$ Size (g)

fish grew larger (Table 10 and Figure 2). Changes in temperature outside the optimum range (16.7^{o}C.) had an effect on additive genetic differences in maximum specific growth rate. The relative values of additive genetic effect on maximum specific growth rate were high at temperatures of 12, 14.3 and 19^{o}C. (10 - 11% of mid-parent values) but low (4.4% of mid-parent values) at the optimum temperature, 16.7^{o}C.

Size and temperature affected additive genetic differences in growth rate at optimum ration in the same manner as they affected maximum specific growth rate. Additive genetic differences in specific growth rate at optimum ration between Manx and Nisqually were fairly constant between fish initial size 7 to 67 g. Non-additive genetic effects (heterosis) increased with increasing initial size (Table 11). Temperature changes seemed to alter the additive genetic effects. The relative additive genetic effects ranged between 9 and 12% of mid-parent values at temperatures of 12, 14.3 and 19^{o}C. while the value was only 5% of mid-parent values at 16.7^{o}C. Non-additive genetic effects were significantly affected by the changes of temperature. Dominance (non-additive genetic effect) occurred at temperatures 12 and 19^{o}C. (16 and 6% of mid-parent values respectively) while no dominance occurred at temperatures close to the optimum 14.3 and 16.7^{o}C. (-0.3 and -0.1% of mid-parent values respectively) (Table 11).

Additive genetic differences between Manx and Nisqually in net and gross efficiencies at maximum ration were relatively constant for fish of initial size 7 to 67 g. while the non-additive genetic effect (heterosis) seemed to increase as the fish grew larger (Tables 12 and 13). Changes in temperature clearly affected both additive and non-additive genetic effects. The genetic effects decreased as temperature increased (Tables 12 and 13). Additive genetic differences between Manx and Nisqually in net and gross efficiencies at optimum ration decreased as the fish grew larger while non-additive genetic effects (heterosis) were fairly constant for fish of initial size 7 to 67 g. (Tables 14 and 15). Temperature changes seemed to affect additive and non-additive genetic effects. Both genetic effects decreased as temperature increased.

In summary, there are clear indications of genetic differences between Nisqually and Manx fish and significant genotype-environment interactions. Additive genetic differences in specific growth rate at optimum and maximum rations and efficiencies at maximum ration remained constant as the size of the fish increased while the non-additive genetic effect increased. Changes in temperature from the optimum 16.7^{o}C had a significant effect resulting in higher additive genetic differences in specific growth rate at maximum and optimum rations while non-additive genetic effects decreased as temperature increased. Both additive and non-additive genetic effects on efficiencies at maximum and optimum ration decreased as temperature increased.

D. DISCUSSION

An understanding of the bioenergetics of fish growth has important implications for any attempt to genetically improve growth (Weatherley 1976). Weatherley (1976) suggested that the standard metabolic rate (S.M.R.) and specific dynamic action (S.D.A.) as well as the measurements of external factors that accounted for fish activity such as temperature, density and competition should be included in a selective breeding program for fish growth.

In the present study, environment and genetic factors affecting rainbow trout growth were combined. General genetic differences were initially observed in field or commerical type aquaculture operations and the specific physiological genetic differences were further analysed in laboratory experiments. Genetic differences in growth between strains of rainbow trout were evident. The Nisqually strain grew faster than the Manx strain in two years of pond culture experiments and one year of lake and tank culture experiments. The laboratory experiments showed that the differences between strains could largely be accounted for by genetic differences in specific growth rate and efficiencies at maximum rations. There were also small differences in specific growth rate at optimum rations, but no differences at maintenance ration levels. The results support Weatherley's contention that physiological studies can provide useful information for selective breeding of fish growth.

The findings from the present field experiments that there are significant genetic differences in growth rate between strains of rainbow trout are in complete agreement with the results of other workers. On the average, fish from the Nisqually strain were 17% to 77% larger than the Manx fish grown in the same ponds, lakes or tanks (Table 16). Results from other studies have also shown considerable differences between strains of fish (Table 16), mean size of some strains being up to 150% larger than others (Reinitz et al. 1979). Although there were significant genetic differences, there were also important genotype-environment interactions. In the two pond experiments the relative importance of genotype and environment effects and genotype-environment interactions were as follows:

	% Variance Components	
Source of Variation	Pond in 1979	Pond in 1980
Strain (Genotype)	65	37
Pond (Environment)	12	31
Error ÷ Strain x Pond (Error + Genotype x Environment)	23	32

Similarly, other workers have found genotype-environment interactions when studying the growth of rainbow trout of different strains (Gall 1969, Ayles 1975, Reisenbichler and McIntyre 1977 and Klupp et al. 1978). In the present field experiments the additive genetic differences in specific growth rates between Nisqually and Manx increased as size increased in F.1., but remained constant in F.2. and F.3. The non-additive genetic effect were fairly constant in F.3. as well (Figure 2). These inconsistances are presumed to be caused by

Table 16. Genetic differences in sizes of rainbow trout in various studies. Size of largest strain is presented as a % of smallest strain.

Mean weight of all fish (g)	Observed measurements	Size of largest strain as a % of smallest strain	Source	Comments
90	Harvested weight in F.1	166	Present study	Idaho and Manx
210	Harvested weight in F.2	123	Present study	Nisqually and Manx
146	Harvested weight in F.3	117	Present study	Hybrid (MN) and Manx
196	Harvested weight in F.4	174	Present study	Nisqually and Manx
270	Harvested weight	146	Ayles (1975)	Idaho and Pennask
270	Harvested weight	137	Ayles (1975)	Idaho and Tunkwa
119	Average weight for one year of study in sea water, in hatchery tanks	197	Clarke, Nanaimo, B.C. (unpublish)	Sunndalsora and Manx
675	Average weight 610-630 days	128	Gall and Gross (1978 a)	Hybrid (Domestic X Wild) and Wild
738	Female weight of post spawning	201	Gall and Gross (1978 b)	
749	Male weight of post spawning	190	Gall and Gross (1978 b)	
163	Final weight in net culture	162	Klupp, et al. (1978)	
90	Final weight in pond culture	145	Klupp et al. (1978)	
164	Weight at age 284 days	167	Klupp (1979)	
75	Weight at age 384 days	147	Klupp (1979)	
133	Average weight at one year	179	Rao and Chandrasekaran (1978)	Hybrid (Wild X Hatchery) and Wild
1, 143	Average % weights return/ weight plant in 3 lakes	160	Rawstron (1973)	Coleman Kamloop and Shasta
17	Weight gain for 168 days	143	Reinitz et al. (1978)	
15	Weight gain for 180 days	250	Reinitz et al. (1979)	
33*a	Length of juvenile stage reared in stream	125	Reisenbichler & McIntyre (1977)	Wild and Hatchery
33*a	Length of juvenile stage reared in a hatchery pond	138	Reisenbichler & McIntyre (1977)	Hatchery and Wild

*a = length in m.m.

unidentified genotype-environment interactions.

The differences in degree of variation between environment, genotype and genotype-environment interactions between different studies is not easy to interpret. Until the same genetic strain can be tested in the various geographical locations any real comparison will be problematical. In the field experiments there were uncontrolled differences in pond temperature, size of fish, annual climatic variation, etc. as well as the controllable but unknown effects of tank vs. pond.

Factors causing differences in growth of fish may be grouped into biotic and abiotic factors (Brett 1979). Examples of abiotic factors are temperature, light, salinity, oxygen, etc. Among the environmental factors, temperature, size and ration seem to be most important (Haskell 1959 and Stauffer 1973). Temperature is classified as a "controlling factor" (Fry 1954). The metabolic rate is controlled by this external environmental factor. Ration and size are classified as "limiting factors". The metabolic rate is also limited by the limiting factors (Fry 1954 and Brett 1979). There may be significant interaction between biotic and abiotic factors. For example, while increasing temperature causes a general increase in digestion rate and metabolic rate, each strain or species has different genes controlling these biological mechanisms. Brett (1979) suggested that the various forms of curves relating specific growth rate to ration level depend on environmental conditions and species. The experiment on charr, brook trout and rainbow trout confirms Brett's suggestion while the rainbow trout experiments indicate the importance of genetic differences within a species.

In order to refine the analysis of growth differences observed in pond and tank culture experiments, the effect of rations, fish sizes, temperatures and genes were analysed in a series of physiological genetic experiments on growth rate under laboratory conditions. In these experiments, there was evidence of the effect of genes, size and temperature, on ration and growth of rainbow trout. Genetic differences between strains were measured for maximum, optimum and maintenance ration, specific growth rate and net and gross efficiencies at maximum and optimum rations. These observations allow us to examine some of physiological parameters which, according to Weatherley (1976), are important to genetic studies of fish growth. The standard metabolic rate (S.M.R.) corresponds to zero activity or zero growth. In this study it is synonymous with the maintenance ration (Brett et al. 1969 and Brett 1979). Specific dynamic action (S.D.A.) had been defined as the energy expense during ingestion and deamination of amino acids (Beamish 1974, Brett 1976, Weatherley 1976 and Tandler and Beamish 1980) and it is difficult to dertermine. However, net and gross efficiencies are related to S.D.A. (Kerr 1971) and they were calculated for maximum and optimum rations in this study.

Variations in daily ration has the greatest effect in growth rates. Unfed fish lost as much as 0.9% of their body weight.day^{-1} while at maximum ration, fish of the same size and strain and at the same temperature gained up to 2.2%.day^{-1}. As the initial size of fish increased from 6 g. to 75 g., maximum rations decreased significantly from 4.3 to 3.9% of their body weight.day^{-1}, and optimum ration 2.05 to 1.5% body weight.day^{-1} while maintenance ration only decreased from 0.6 to 0.4% body weight.day^{-1} (Figure 9). Wurtsbaugh and Davis (1977b) also found that over a temperature range of 7 to 23^{o} C. maintenance ration decreased as the fish sizes increased. Similarly, Brett and Shelbourn (1975) reported that at an optimum temperature of 15^{o} C. rations that were restrictive for small sockeye salmon become excess rations as fish grew larger, i.e. the maximum, optimum and maintenance rations decreased as fish grew bigger.

In a similar manner the specific growth rate at maximum and optimum rations decreased as the fish grew larger (Figure 6). The relationship between specific growth rate at maximum ration and fish size has been demonstrated for rainbow trout in nature (Tavarutmaneegul 1978), sockeye salmon (Brett and Shelbourn 1977), brook trout (Haskell 1959 and Cooper 1961 in Brett and Shelbourn 1977) and brook trout (Elliott 1975c). The slopes of regression relating growth rates and fish sizes were slightly less for the present study than in other studies. (Table 17).

The probable reason for this is that the smallest fish, initial size 7 g. (D1), did not grow at the maximum rate possible. This was a result of the fish being stressed from excess waste products in the tanks during the fourth to sixth weeks of the experiments. This resulted in the mean specific growth rates at maximum rations being under estimated. This problem occurred in all tanks in this experi-

Table 17. Comparison of slope (b) and intercept (a) for the relationship of $\log_e$ maximum specific growth rate (Y) and $\log_e$ fish size (X) between salmonids.

Species	Weight Range (g)	Temperature (°C)	Intercept (a)	Slope (b)
Brook trout	1.5 - 60	11.0	4.66	-0.33 (Haskell 1959 in Brett & Shelbourn 1975)
Brook trout	2.5 - 350	10.0	6.49	-0.47 (Cooper 1961 in Brett & Shelbourn 1975)
Brown trout	5 - 300	15	2.50	-0.31 (Elliott 1974)
Sockeye salmon	3 - 45	15	4.47	-0.42 (Brett & Shelbourn 1975)
Rainbow trout	2 - 250	variable	10.30	-0.47 (Tavarut-maneegul 1978)
Rainbow trout	5 - 70	10	1.45	-0.22 (Present study P.2 to P.3)
Rainbow trout	7 - 200	12 - 19	1.00	-0.13 (Present study D.1 to D.3)

ment and it is assumed that the effects were equal on all strains at all temperatures and did not mask or cause differences between strains.

The differences in food conversion efficiences between strains of rainbow trout were measured in terms of gross and net efficiencies after Brett et al. (1969) at maximum and optimum rations. Both gross and net efficiencies at maximum ration for all strains and temperatures seemed to decrease as the initial size increased. For example, at initial size 6 to 75 g., the gross efficiency decreased from 14.2% to 11.6% and the net efficiency from 16.5% to 12.9% (Figure 12). These results agree with previous studies on growth efficiencies in salmonids (Paloheimo and Dickie 1966, Brett et al. 1969, Elliott 1975d and Wurtsb augh and Davis 1977 a and b). Unfortunately, the changes of efficiencies at optimum ration over initial sizes were not consistent. This is probably because the estimation error at optimum rations was high when compared to other characters. (Figure 14)

Changes in temperatures outside the optimum range for a species can have a major effect on fish growth. In this study changes were restricted to within the optimum range for rainbow trout. It was felt that if there were ecologically significant differences in temperature response between strains they would be most apparent at temperatures close to optimum. In general over the range 12^{0} C. to 17^{0} C. the effects of temperature were small. Maximum and optimum rations for rainbow trout increased slightly as temperatures rose from 12^{0} C. to 17^{0} C. and decreased as temperatures reached 19^{0} C. (Figure 8).

Similar results were found for sockeye salmon and brown trout (Brett et al. 1969 and Elliott 1975d). Maintenance rations increased as temperature increased from 12^{o} C. to 19^{o} C. (Figure 8). This is in agreement with other studies of the relationship between temperature and maintenance rations of rainbow trout (Wurtsbaugh and Davis 1977 a), and other salmonids (Brett et al. 1969 and Elliott 1975 d). The increase of maintenance rations is associated with an increase in metabolic rates as temperatures increase (Brett et al. 1969). Temperature did not have a marked effect on growth rates and efficiencies over the range of 12^{o} C. to 19^{o} C. The highest specific growth rates at maximum ration for all strains and initial sizes (1.9% day^{-1}) occured at 16.7^{o} C. The results agree with other studies of optimum temperatures of salmonids (Table 18). Species optimum range from 10 to 17^{o} C. with the optimum for rainbow trout being 16^{o} to 17^{o} C.

It is clear that differences in size, temperature, etc. can account for the differences in growth rate observed between ponds, tanks, years but not the differences between strain as all strains were grown under the same conditions. The laboratory experiments also demonstrated how these environmental factors affect specific growth rate, ration and efficiencies of rainbow trout. Therefore, in strain selective breeding programs, one should include an assessment of the effect of differences in fish size, optimum temperature and ration requirements as they affect genetic differences in growth.

Alternative environmental factors to be considered include maternal effects. Falconer (1960) stated that the maternal effect is the pre-

Table 18. The optimum temperature providing maximum specific growth rate at excess ration for salmonids.

Species	Optimum Temperature (°C)	References
Sockeye salmon	15	Brett et al. 1969
Brown trout	13	Elliott 1975 a & b
Rainbow trout	17 constant 16 - 17 fluctuation	Hokanson et al. 1977
Rainbow trout	16.7	Present study
Arctic charr	10 - 13	Present study
Brook trout	13 - 16	Present study

natal and postnatal nutritional influence, a mother had upon her young. In fish as in other domestic animals, maternal effect is included as one of the environmental factors. For example, Gall (1974) found a positive correlation between age of female and egg size and growth of rainbow trout. Kanis et al (1976) also found a maternal effect for uneyed egg and eyed egg survival of salmon, sea trout and rainbow trout. Similarly, maternal effects were higher for the uneyed and eyed stage survival than the alevin stage of splake hybrids (Salvelinus fontinalis X S. namaycush) (Ayles 1974). Maternal effects have not been separated from the environmental factors in this study. Generally, however, maternal effects decrease as the age of progeny increases. Chevassus (1976) in Refstie (1980) found the maternal effect on early growth of rainbow trout disappeared after 2 months. Experiments D.1. and D.2. were started when the fish were 60 and 120 days old respectively. In D.3. and F.3. fish were started at ages of 250 and 196 days respectively. Therefore, in D.1. the maternal effect could have caused some of the observed variation.

The genetic differences in growth rates between and within species of salmonids in the field experiments were clearly evident in the laboratory experiments. Preliminary laboratory experiments showed genetic differences in maximum specific growth rate and maximum and optimum ration. In experiment P.5., differences in maximum specific growth rates were found between Arctic charr, brook trout and rainbow trout. These differences in growth were also found between Arctic charr and rainbow trout under Norwegian cage farming conditions (Gjedrem and Gunnes 1978). Similarly, the differences in growth between Idaho and Tunkwa fish in experiment P. 4. are consistent with genetic differences between these strains when they were grown in central Canadian aquaculture lakes (Ayles 1975). In the definitive experiment, the influences of environmental factors (temperature and initial size) accounted for the majority of the variability in growth at maximum and optimum ration levels, specific growth rates and net and gross efficiences at maximum and optimum rations of the rainbow trout strains Manx, Nisqually and their hybrid (MN) (Appendix A; Table 15). Genetic differences accounted for between 4 and 16% of the total variability.

Although the environment and genotype - environment interactions were high for all characters, the genetic differences in maximum specific growth rates are large enough to allow for strain selection. Averaged for all temperatures and initial sizes, the Nisqually fish grew 2.0% day^{-1}, the Manx grew 1.7% day^{-1} while the hybrid (MN) grew 1.9% day^{-1}. The additive genetic effect on maximum growth for Nisqually and Manx was 9% of mid-parent values, while the non-additive genetic effect for the hybrid was 5% of mid-parent values. Additive differences between Nisqually and Manx remained constant over fish size, but the heterosis or non-additive genetic differences between Nisqually, Manx and their hybrid increased as the fish grew (Figure 2). This also appeared in the field experiment F. 3. when at harvest, the hybrid had the highest mean weight (156 g.) followed by Nisqually (150 g.) and Manx (133 g.). In addition, average net and gross efficiences for Nisqually, Manx and their hybrid in F. 3. showed heterosis in conversion efficiencies. The hybrid fish had the highest average net and gross efficiencies (23.9% and 17.5% respectively) followed by the Nisqually fish (23.3% and 17.2% respectively) with the Manx fish being the lowest (18.1% and 14.1% respectively). Therefore, the cross-bred strain is perhaps more desirable for selective breeding for maximum specific growth rate then either pure strain.

As described above, the optimum temperature for maximum specific growth rates was 16.7^{o} C. for all strains. However, the temperature effect was not the same for both purebred strains. Additive genetic differences in maximum specific growth rate between Nisqually and Manx were least at the optimum temperature, 4% of mid-parent values. The additive differences at temperatures outside the optimum temperature were 10% of mid-parent values at 12 and 19^{o} C. and 11% of mid-parent values at 14.3^{o} C. (Figures 2. I). In other words the Manx fish not only had lower maximum growth rates than the Nisqually fish, but the range of temperatures over which this maximum was achieved was much narrower than for the Nisqually strain. As temperature is one of the most important factors affecting fish growth (Haskell 1959 and Stauffer 1973), differences between strains in the range of temperatures over which maximum growth rate is achieved could cause large differences in growth in the field. When strains were reared in ponds or lakes in which the temperatures varied widely from the 16.7^{o} C. optimum, the Nisqually fish would continue to grow at near maximum growth rates while the growth rates of the Manx strain would decline. The hybrid fish were also less susceptible to changes in temperatures. Hybrids were similar to the Nisqually fish in maximum specific growth rates except at 19^{o} C. Heterosis was high at temperatures between 12 and 14.3^{o} C. and then declined as temperatures rose from 14.3^{o} C. to 19^{o} C. (Figure 21). This illustrates that the heterosis effect on maximum growth was high at temperatures between 12^{o} C. and 14.3^{o} C. Laboratory observations demonstrate that the heterosis effect is greater with larger size fish and at low temperatures. This is consistent with the findings from experiment F. 3., in that heterosis was present for fish greater than 67 g. and temperatures of 12.5^{o} C.

In general the pattern observed for genetic differences in growth rates at optimum ration at different temperatures was similar to that for maximum ration. The differences, however, were much less marked (Table 11).

At maximum rations average gross efficiencies for all temperatures and initial sizes of Nisqually, the hybrid and Manx were 14, 13 and 12% respectively. Similarly, net efficiencies were 15 , 15 and 14% respectively.

The effect of genotype on gross and net efficiencies at maximum ration was statistically significant but the variance component due to the genetic differences was small when compared to environment and genotype - environment interactions. This is because the observed values in gross and net efficiencies were estimated from an estimation of specific growth rate and ration. Consequently, error caused by the estimation of growth and ration as read from the graph is compounded with the error resulting from calculating gross and net efficiencies in wet and dry weights. These results do not necessarily show what the absolute efficiencies of these strains are but do illustrate how the environment (temperature and initial size) affects the conversion efficiencies of different strains.

The additive genetic effect on gross and net efficiencies at maximum ration for all temperatures and fish sizes, respectively averaged 6% and 5% of the mid-parent values. The non-additive genetic effect were respectively 4% and 3% of the mid-parent values.

At optimum rations, even though the genetic differences in effiencies were not significant, the additive genetic effects on gross and net efficiencies respectively 4% and 2%. The non-additive genetic effects were 6% of mid-parent values in both gross and net efficiencies. The presence of additive and non-additive genetic effects in efficiencies at maximum and optimum rations between Manx, Nisqually and their hybrid illustrates the importance of genetic differences between strains, even though the estimates of efficiencies are not precise. It can be concluded therefore, that additive and non-additive genetic effects in efficiencies do occur between strains of rainbow trout.

Generally, additive and non-additive or dominance genetic effects in gross and net efficiencies of Manx, Nisqually and their hybrid varies with temperature and fish size, although these observations are not able to explain any trend of these genetic effects over changes of temperature and size.

The present results have considerable implications for genetic improvement of rainbow trout production. Falconer (1960) outlines two basic methods of improving animal production. The first method is selection within a population which is the process by which superior individuals are selected to be parents. The second method is a selection between populations which is known as crossbreeding. Both intra and inter population selection and mating systems are used for improving production of domestic animals.

Large genetic gains can be obtained by selectively breeding for desirable economic traits of salmonids (Gjedrem 1976 and McKay and Friars 1979). This is because salmonids have very high fertility, a moderate generation interval (shorter than cattle but longer than pigs and poultry) and relatively high heritabilities of such economic traits as growth, survival, smolt % reproductive traits and resistance to disease (see Aulstad et al. 1972, Gjedrem et al. 1974, Ayles 1974, Kanis et al, 1976, Gall and Gross 1978 b and Gunnes and Gjedrem 1981). Selection has resulted in genetic improvement in rainbow trout (Donaldson and Olson 1955, Donaldson 1970 and Kincaid et al. 1977), chinook salmon (Donaldson and Menasveta 1961 and Hines 1976) and Atlantic salmon (Refstie et al. 1977).

The present experimental results relate primarily to interpopulation (strain) selection and hybridization of rainbow trout and not intrapopulation selection. Differences in growth between strains of rainbow trout have been found by numerous workers including the present study (Table 16). The Nisqually strain grew faster and more efficiently than the Manx strain under both field and laboratory conditions. Significant improvement in commercial production could be made simply by using this best performing strain. Interpopulation hybridization is also a distinct possibility. The hybrid (Manx X Nisqually) exhibited significant heterosis by growing better than the parents when the fish grew larger than 67 g. and at low temperatures (experiment F. 3.).

The results of the definitive experiments strongly implied that strain selection should concentrate on maximum specific growth rate, efficiencies at maximum ration and genotype - temperature interactions and indicate that it would not be worthwhile to select strain based on differences maintenance ration.

Weatherley (1976) suggested that there may be genetic differences in S. M. R.; however, in this study significant differences in maintenance ration requirements were not evident between the strains and their hybrid. Although genetic differences may indeed exist, they are too subtle and our tests are to imprecise to detect significant differences. There is certainly no proof that such genetic differences do exist, and there is no point in trying to select a strain for lower maintenance ration requirements.

The maximum specific growth rates (Table 10) and specific growth rate of optimum rations (Table 11) can be examined in economic terms. As an example the growth, in one month, of fish of an initial size of 50 g. was estimated. These figures show what improvement in performance a fish culturist might expect by choosing a different strain.

Expected weight of fish (g.) after growing one month

(fish initial size 50 g.)

Maximum growth

	12.0°C.	14.3°C.	16.7°C	19.0°C.
Nisqually	90	92	92	93
Manx	82	81	87	83
Hybrid	89	89	92	88

Growth at optimum ration

	12.0°C.	14.3°C.	16.7°C.	19.0°C.
Nisqually	70	70	74	72
Manx	65	67	72	67
Hybrid	71	69	69	71

Depending on the temperature, after one month, the Nisqually fish would be 5-11 g. larger than Manx when growing at maximum rates and 2-5 g. bigger when fed optimum rations. These figures also exemplify the genotype-temperature interactions and show the importance of the broad temperature optima of Nisqually and hybrid fish. The differences would be high, 8-11 g. at temperatures of 12, 14.3 and 19°C., but low, 5 g., at the optimum temperature, 16.7°C. In a similar manner, the genetic differences and genotype-temperature interactions in the specific growth rate at optimum rations can be seen. However, effects would be smaller and for strain selection differences in maximum specific growth rates should be emphasized.

As mentioned before genetic differences in conversion efficiencies were also evident, but only gross efficiencies at maximum ration should be considered for genetic improvement. This is because there were no genetic differences in maintenance ration so that the genetic effects for gross and net efficiencies should be the same.

The results of growth and feed conversion in this study can be translated directly into terms that are meaningful for commercial fish farmers. Feed conversion ratio is defined as the dry weight of feed per unit wet weight gain (feed/gain) (Castell and Tiew 1980). Averaged over all temperatures and fish sizes in the definitive experiments, the Nisqually fish had the best feed conversion ratios at optimum and maximum rations (1.6 and 2.5 respectively) followed by the hybrid fish (1.7 and 2.8 respectively) with the Manx fish being the poorest (1.8 and 3.0 respectively). However, in F. 3. the hybrid and the Nisqually fish were equal (2.1) followed by the Manx fish (2.9).

When the genetic differences in growths and feed conversions are combined, it is clear that the Nisqually fish showed better growth and food utilization than the Manx fish or their hybrid. When fish from 50 g. to 100 g. at maximum growth rates, the Nisqually fish would consume less food and take a shorter time (127 g. of food in 36 days) followed by the hybrid fish (138 g. of food in 37 days) and the Manx fish (151 g. of food in 42 days). Even at the optimum rations, the Nisqually fish would require less food and less time (78 g. of food in 60 days) followed by the hybrid fish (85 g. of food in 61 days) and the Manx fish (89 g. of food in 70 days).

In summary, the above examples of growth and food utilization of rainbow trout clearly imply three recommendations for a selective breeding program for improving rainbow trout growth. First, interpopulation selection and hybridization should concentrate on maximum specific growth rates and gross efficiencies at maximum rations.

Second, the evaluation and selection should be at the temperature optima and on fish of the same size. Finally, genotype - environment interactions should be considered carefully.

E. CONCLUSIONS AND RECOMMENDATIONS

1. Conclusions

1. Differences in growth between strains of rainbow trout were evident in both field and laboratory studies.

2. There were differences between Manx, Nisqually and their hybrid in maximum and optimum rations, specific growth rates at maximum and optimum rations and net and gross efficiencies at maximum rations.

3. There were no genetic differences in Standard Metabolic Rate (S.M.R.)

4. Genotype-environment interactions in rainbow trout growth were found in field and laboratory experiments.

5. Additive genetic differences between Manx and Nisqually in specific growth rates at maximum and optimum ration were high (10-11% of mid-parent values) at temperatures of 12, 14.3 and 19^{o}C, but the values were low (4% of mid-parent values) at optimum temperature, 16.7^{o}C.

6. Non-additive genetic differences for the hybrid in specific growth rate at maximum and optimum rations decreased as temperature increased.

7. Changes in fish size seemed not to affect the additive genetic differences in specific growth rate at maximum and optimum rations, but the non-additive genetic differences increased as fish grew larger.

8. Additive and non-additive genetic differences between Manx, Nisqually and their hybrid in net and gross efficiencies at maximum and optimum rations were low (2-6% of mid-parent values) when compared to specific growth rates.

9. Both additive and non-additive genetic differences in efficiencies at maximum and optimum rations decreased as temperature increased.

10. Changes in fish size seemed not to alter additive genetic differences in efficiencies at maximum ration but non-additive genetic differences increased as fish size increased.

2. Recommendations

1. Strain selection should be considered as there are strain differences in growth.

2. The strain comparisons should concentrate on identifying differences in maximum growth rates. There were no differences in maintenance rations so selecting for differences in Standard Metabolic Rate would not be fruitful. Differences in growth rates at optimum rations are difficult to measure and at any rate they appeared to be strongly correlated with maximum growth rates.

3. The strain selection should also concentrate on gross efficiencies at maximum rations. This is because there are no differences in S.M.R., and growth rates at optimum and maximum rations are strongly correlated. The standard fish culturists' "conversion rates" (food fed/weight gain) could be used.

4. In assessment of strain differences, temperature should be standardized at the optimum and fish of the same size should be used.

5. Strain-environment interactions should also be considered.

6. Heterosis for growth was found, suggesting that hybridization between strains may be important for selective breeding programs when two or more desirable characters are found in different strains.

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APPENDIX A

LIST OF TABLES

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Appendix A. Table 1. Field experiment F.1; Sampling dates, Mean weight ($\overline{X}$) and Number of samples of Idaho, Nisqually, Sunndalsora and Manx rainbow trout strains.

Strain	Date	Pond No. 1 Mean wet weight (g)	Pond No. 1 No.	Pond No. 2 Mean wet weight (g)	Pond No. 2 No.	Pond No. 3 Mean wet weight (g)	Pond No. 3 No.	Pond No. 4 Mean wet weight (g)	Pond No. 4 No.
Idaho	8/06/79	3.9	50	3.9	50	3.9	50	3.9	50
	26/06/79	10.2	17	6.3	23	6.1	7	5.1	14
	9/07/79	9.5	35	8.6	20	8.2	11	8.6	19
	23/07/79	17.2	38	12.6	50	14.7	33	9.7	22
	7/08/79	15.9	24	19.2	20	21.9	32	17.0	16
	20/08/79	23.0	18	30.8	15	33.3	21	22.3	24
	4/09/79	29.6	22	44.3	15	50.3	21	38.4	15
	17/09/79	49.1	11	78.5	15	70.9	23	57.2	18
	1/10/79	87.7	17	91.4	24	96.0	38	95.9	15
	15/10/79	85.3	22	102.1	20	114.3	27	77.8	18
	29/10/79	105.9	20	113.7	20	108.0	20	97.4	7
Nisqually	8/06/79	3.5	50	3.5	50	3.5	50	3.5	50
	26/06/79	2.8	16	4.4	24	5.5	7	6.2	13
	9/07/79	8.2	34	7.3	20	10.4	10	6.4	14
	23/07/79	10.4	26	9.8	37	13.4	18	8.5	21
	7/08/79	15.1	37	14.6	32	22.5	15	17.0	24
	20/08/79	20.4	20	23.8	25	30.7	21	25.0	27
	4/09/79	29.3	17	45.1	32	47.5	14	38.9	20
	17/09/79	45.5	19	56.9	30	70.6	26	58.3	24
	1/10/79	83.3	16	85.6	30	92.5	29	86.7	23
	15/10/79	75.2	44	96.0	33	147.7	24	72.4	15
	29/10/79	85.4	20	92.4	20	118.0	20	68.0	6
Sunndalsora	8/06/79	3.6	50	3.6	50	3.6	50	3.6	50
	26/06/79	4.9	17	3.1	23	3.6	7	3.3	13
	9/07/79	7.2	32	8.0	23	9.5	16	8.8	15
	23/07/79	9.4	14	11.1	19	12.1	23	9.4	27
	7/08/79	14.6	20	15.0	23	21.6	14	18.1	31
	20/08/79	22.1	30	29.5	17	37.2	14	29.8	22
	4/09/79	38.0	30	49.9	15	53.4	17	46.6	30
	17/09/79	55.3	24	69.3	30	85.9	25	44.8	21
	1/10/79	90.1	16	87.5	27	99.9	14	100.8	21
	15/10/79	78.8	34	109.7	18	99.2	13	98.2	16
	29/10/79	101.2	20	113.0	20	104.4	20	85.3	4
Manx	8/06/79	3.9	50	3.9	50	3.9	50	3.9	50
	26/06/79	2.8	17	4.4	23	5.0	7	3.6	13
	9/07/79	6.7	22	6.1	14	7.6	13	6.2	21
	23/07/79	8.5	37	8.8	27	11.9	15	6.6	22
	7/08/79	10.9	31	11.2	20	18.2	15	11.5	13
	20/08/79	14.6	22	15.2	18	15.8	11	18.0	13
	4/09/79	19.5	29	33.7	14	27.7	21	32.8	16
	17/09/79	32.4	27	38.0	17	48.8	20	42.9	12
	1/10/79	45.5	32	53.6	28	62.7	18	52.3	13
	15/10/79	49.8	40	57.4	32	60.6	32	48.1	18
	29/10/79	53.4	20	68.1	20	65.1	20	69.0	1

Appendix A. Table 2. a. Mean weight, date and specific growth rate of rainbow trout strains Manx'and Nisqually in field experiment F.1

Strain	Manx		Nisqually	
Date	Mean weight (g)	Specific growth rate (%.day^{-1})	Mean weight (g)	Specific growth rate (%.day^{-1})
8/06/79	3.9		3.5	
		1.76		2.70
9/07/79	6.6		8.1	
		2.12		1.92
23/07/79	9.0		10.5	
		2.46		3.32
7/08/79	13.0		17.3	
		1.57		2.82
20/08/79	15.9		25.0	
		3.87		3.17
4/09/79	28.4		40.2	
		2.73		2.80
17/09/79	40.5		57.8	
		1.99		2.92
1/10/79	53.5		87.03	

b. Mean weight, date and specific growth rate of rainbow trout strains Manx and Nisqually in field experiment F.2

Strain	Manx		Nisqually	
Date	Mean weight (g)	Specific growth rate (%.day^{-1})	Mean weight (g)	Specific growth rate (%.day^{-1})
6/05/80	12.1		10.1	
		2.85		3.86
29/05/80	23.3		24.5	
		2.19		2.16
11/06/80	31.0		32.4	
		1.82		3.47
25/06/80	40.0		52.7	
		2.91		2.02
8/07/80	58.4		68.5	
		-1.07		1.34
21/07/80	50.8		81.54	
		3.77		2.83
5/08/80	89.5		124.7	
		0.25		1.07
18/08/80	92.5		143.3	
		3.21		3.40
5/09/80	159.64		255.5	
		0.89		-0.49
30/09/80	189.11		232.9	

Appendix A. Table 3. Water chemistry average (range) for 4 ponds in field experiment F.1

Date	Ammonia ($\mu g.1^{-1}$)	Nitrite ($\mu g.1^{-1}$)	Nitrate ($\mu g.1^{-1}$)	Phosphorous ($\mu g.1^{-1}$)	Chlorophyl-a ($\mu g.1^{-1}$)	Secchi (m)	pH	Dissolved Oxygen (ppm)	Temperature (^{o}C)
13/06/79	1.0 (0-3)	2.0 (1-5)	-	4.2 (3-6)	1.1	1.4	8.4	10.3 (9-10)	20.8 (20.5-21)
18/06/79	0.7 (0-2)	1.7 (0-4)	4.0 (2-6)	4.3 (1-10)	1.0 (0.9-1.3)	1.5	8.5	10.3 (10-11)	17.4 (21-23)
26/06/79	4.2 (0-13)	0.8 (0-3)	6.8 (3-13)	1.8 (1-5)	2.3 (0.9-4)	1.5	8.7	9.5 (9-10)	19.5 (16-22)
5/07/79	4.0 (0-9)	-	51.3 (3-177)	4.8 (2-6)	1.8 (0.9-3)	1.5	8.0	10.3 (10-11)	22.2 (21-28)
18/07/79	47.5 (40-60)	4.5 (3-6)	9.5 (2-24)	3.0 (1-7)	2.3 (2-4)	1.4	8.3 (8-9)	10.7 (9-13)	25.4 (22-28)
2/08/79	47.5 (40-50)	1.8 (1-3)	71.0 (40-130)	5.3 (2-9)	2.1 (0.9-3)	1.4	8.6 (8-9)	-	24.2 (20-27)
9/08/79	0.5 (0-2)	2.0 (0-3)	60.3 (5-175)	6.3 (0-17)	2.3 (1-4)	1.5	8.9 (8-10)	11.5 (11-13)	22.2 (22-23)
15/08/79	-	1.8 (1-4)	9.7 (4-21)	8.0 (1-15)	3.3 (0.9-5)	1.5	8.9	12.3 (12-13)	19.5 (17-21)
23/08/79	1.8 (1-3)	0.5 (0-21)	10.5 (2-26)	4.3 (0-8)	6.5 (3.2-12)	1.5	9.1 (8-10)	10.3 (10-11)	20.8 (18-24)
30/08/79	3.0 (0-12)	5.5 (4-7)	11.5 (4-32)	5.3 (1-9)	11.1 (8-17)	1.5	-	6.0	18.9 (18-20)
11/09/79	47.5 (30-60)	0.3 (0-1)	3.0 (1-4)	5.8 (4-9)	-	1.5	-	8.5 (7-9)	17.5 (16-20)
19/09/79	-	-	-	11.3 (4-16)	6.73 (5-11)	1.5	8.8	9.6 (9-10)	16.2 (16-17)
27/09/79	1.2 (0-5)	-	-	6.0 (0-16)	9.3 (7-13)	1.5	8.7	13.0 (12-14)	15.3 (15-16)
11/10/79	12.0 (7-26)	0.3 (0-1)	71.5 (4-134)	16.0 (14-18)	11.8 (10-13)	1.5	8.8	13.0 (12-14)	11.2 (9-15)
19/10/79	-	-	-	-	-	-	-		8.5 (6-11)
27/10/79	-	-	-	-	-	-	-		8.7 (7-8)

Appendix A. Table 4. Field experiment F.2; Sampling dates, Mean weight ($\overline{X}$) and Number of samples of rainbow trout strains Nisqually and Manx.

Strain	Date	Pond No. 1 Mean wet weight (g)	No.	Pond No. 2 Mean wet weight (g)	No.	Pond No. 3 Mean wet weight (g)	No.	Pond No. 4 Mean wet weight (g)	No.
Nisqually	6/05/80	10.0	100	10.0	100	10.0	100	10.0	100
	14/05/80	10.3	10	12.1	10	18.0	10	15.3	10
	29/05/80	20.6	25	31.3	21	24.6	35	21.8	25
	11/06/80	25.7	16	42.6	25	36.1	50	25.2	66
	25/06/80	44.3	23	63.4	35	57.4	51	45.6	60
	8/07/80	62.1	21	79.3	31	80.0	25	52.5	33
	21/07/80	77.8	5	77.3	19	91.2	6	79.9	14
	5/08/80	-	-	137.1	7	132.3	13	104.6	13
	18/08/80	97.5	2	193.8	4	162.0	10	120.0	10
	5/09/80	-	-	280.0	2	286.6	6	200.0	10
	30/09/80	180.0	4	279.5	20	262.2	20	210.1	20
Manx	6/05/80	12.0	100	12.0	100	12.0	100	12.0	100
	14/05/80	12.3	10	10.4	10	12.5	10	12.5	10
	29/05/80	19.0	26	31.9	21	21.3	24	21.1	9
	11/06/80	27.8	11	37.2	20	33.2	38	25.8	41
	25/06/80	27.9	42	51.7	32	37.6	44	42.8	67
	8/07/80	48.9	11	71.5	28	59.6	17	53.5	16
	21/07/80	35.7	3	63.4	25	61.2	15	43.0	20
	5/08/80	58.3	6	100.0	2	128.8	8	70.9	22
	18/08/80	62.5	2	97.5	4	114.3	7	95.6	18
	5/09/80	160.0	1	-	-	151.2	5	167.9	14
	30/09/80	177.1	7	180.8	20	229.1	20	169.5	20

Appendix A. Table 5. Water chemistry average (range) for 4 ponds in field experiment F.2

Date	Ammonia (μg.l^{-1})	Phosphorous (μg.l^{-1})	Chlorophyl-a (μg.l^{-1})	Secchi (m)	pH	Dissolved Oxygen (ppm)	Temperature (^{o}C)
27/05/80	24 (10-47)	-	2.8(1.5-4.3)	1.5	8.6	-	-
29/05/80	-	-	-	-	-	15.7(13-18)	14.8 (9-23)
5/06/80	34 (0-64)	6.6 (5-10)	3.4 (2-5.6)	1.5	8.6 (8-9)	-	18.5 (15-22)
11/06/80	11.3(4-12)	4.5 (2-10)	3.4 (2-5)	1.5	9.2 (9-9.4)	11.3(12-11)	18.3 (16-20)
18/06/80	-	-	-	-	-	11.1(9-17)	19.5 (18-21)
19/06/80	6.5 (0-7)	4.6 (0-9)	3.7 (1-9)	1.5	8.7 (8-9)	-	-
25/06/80	-	-	-	-	-	11.9(10-14)	21.9 (18-26)
26/06/80	115 (0-346)	-	1.9 (1-3)	1.5	8.9(8.7-9.1)	-	-
2/07/80	-	-		-	-	13.8(10-17)	16.9 (10-20)
4/07/80	97.8(18-190)	9.3 (3-22)	5.6 (1-17)	1.5	8.8(8.5-9.3)	-	-
8/07/80	-	-	-	-	-	11.9(10-14)	-
9/07/80	30.0 (9-59)	3.8 (1-7)	5.1 (1-9)	1.5	8.8(8.4-9.1)	-	22.3 (20-25)
15/07/80	-	-	-	-	-	10.7 (7-12)	22.9 (22-23)
25/07/80	7.0 (0-28)	8.0 (1-16)	28.3 (4-65)	1.5	8.9(8.7-9.0)	-	21.9 (19-25)
28/07/80	-	-	-	-	-	13.8 (9-17)	-
11/08/80	-	-	10.3 (2-18)	1.5	9.4(9.1-10)	-	20.5 (17-23)
12/07/80	-	-	-	-	-	15.0(12-18)	-
14/08/80	127 (56-261)	-	6.7(2.8-17)	1.5	-	-	-
18/08/80	-	-	-	-	-	12.1(7-16)	20.2 (17-22)
21/08/80	26.9 (3-80)	-	6.7 (2-20)	1.5	8.8 (8-9)	-	-
25/08/80	-	-	-	-	-	13.1(12-14)	19.6 (18-21)
28/08/80	52.8(0-142)	-	1.4 (1-2)	-	-	-	-
5/09/80	-	-	-	-	-	16.1(12-18)	17 (15-19)
14/09/80	-	-	-	-	-	-	16.4 (15-19)
24/09/80	-	-	-	-	-	-	9.7 (8-15)
28/09/80	5.0(2-10)	-	-	-	-	-	-

Appendix A. Table 6. Field experiment F.3, mean weights, date and specific. growth rate of rainbow trout strains Manx, Nisqually and the Hybrid (MN).

Strain	Manx		Nisqually		Hybrid (MN)	
Date	Mean weight (g.)	Specific growth rate (%.day^{-1})	Mean weight (g.)	Specific growth rate (%.day^{-1})	Mean weight (g.)	Specific growth rate (%.day^{-1})
5/12/80	37.8		37.3		37.4	
		0.74		0.85		0.90
29/01/81	56.6		59.6		61.5	
		0.35		0.37		0.38
18/02/81	60.8		64.2		66.3	
		1.58		1.86		1.80
5/03/81	77.1		84.9		86.8	
		1.18		1.06		1.21
7/04/81	113.7		120.4		129.5	
		0.7		1.01		0.84
29/04/81	132.6		150.3		155.9	

Appendix A. Table 7. Field experiment F.4, stocking size, harvest weight and corrected harvest weight of rainbow trout strains Manx and Nisqually in lakes 316 and 321.

Lake	Strain	Stocking size	Harvested* weight	Corrected Harvest weight
316	Manx	3.59	137.00	159.15
	Nisqually	5.97	271.00	271.39
321	Manx	3.69	105.00	121.00
	Nisqually	6.03	214.00	213.65

* Initial data were from Ayles (Personal Communication).

Appendix A. Table 8. Preliminary experiment P.1; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of rainbow trout strains, Nisqually and Idaho at 12 ration levels.

Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
Nisqually	0	29.5	27.4	24.9	23.8	-0.52 ± 0.21	0
	0.5	29.7	29.4	29.3	30.7	0.08 ± 0.26	0.50 ± 0.01
	1.0	29.9	33.9	35.2	38.3	0.59 ± 0.36	1.01 ± 0.14
	1.5	26.7	29.2	33.4	38.1	0.84 ± 0.20	1.40 ± 0.02
	2.0	28.4	33.6	38.1	45.4	1.11 ± 0.23	1.84 ± 0.04
	2.5	28.5	32.9	39.2	49.2	1.31 ± 0.35	2.26 ± 0.04
	3.0	29.9	35.9	42.9	53.0	1.37 ± 0.14	2.56 ± 0.31
	3.5	28.9	36.8	44.8	55.0	1.53 ± 0.20	3.13 ± 0.09
	4.0	32.3	42.6	52.6	66.3	1.71 ± 0.28	3.51 ± 0.10
	4.5	33.9	44.5	57.9	72.7	1.82 ± 0.19	3.91 ± 0.09
	5.0	27.0	33.1	40.1	50.9	1.51 ± 0.19	4.46 ± 0.06
	5.5	30.3	36.3	43.2	53.3	1.35 ± 0.16	4.96 ± 0.06
Idaho	0	9.9	8.7	8.1	7.7	-0.59 ± 0.34	0
	0.5	12.2	12.2	14.1	13.3	0.21 ± 0.88	0.50 ± 0.03
	1.0	11.6	12.6	14.6	15.8	0.73 ± 0.31	0.96 ± 0.02
	1.5	12.0	14.5	16.8	20.3	1.25 ± 0.19	1.37 ± 0.04
	2.0	10.1	13.1	15.8	19.9	1.61 ± 0.31	1.77 ± 0.05
	2.5	10.4	14.0	17.3	22.8	1.87 ± 0.37	2.20 ± 0.07
	3.0	10.0	14.9	17.6	23.7	2.05 ± 0.97	2.57 ± 0.21
	3.5	9.5	12.4	15.8	19.8	1.76 ± 0.16	3.09 ± 0.07
	4.0	10.3	14.8	19.2	24.7	2.08 ± 0.52	3.44 ± 0.11
	4.5	10.9	14.3	18.7	23.8	1.87 ± 0.14	3.88 ± 0.15
	5.0	12.2	15.1	17.7	22.8	1.49 ± 0.39	4.47 ± 0.14
	5.5	10.1	15.0	18.4	24.8	2.14 ± 0.79	4.69 ± 0.28

Appendix A. Table 9. Preliminary experiment P.2; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of rainbow trout strain Mt. Lassen at 2 initial sizes and 12 ration levels.

Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd - mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
Mt. Lassen	0	5.4	5.6	4.7	4.1	-0.66 ± 0.88	0
	0.5	4.9	5.5	5.9	5.9	0.56 ± 0.65	0.52 ± 0.01
	1.0	5.8	7.2	8.2	8.8	0.99 ± 0.60	0.99 ± 0.03
	1.5	5.7	7.5	9.5	11.2	1.62 ± 0.47	1.43 ± 0.07
	2.0	5.6	7.9	10.8	13.0	2.01 ± 0.70	1.87 ± 0.13
	2.5	5.6	8.3	11.9	14.8	2.37 ± 0.76	2.27 ± 0.13
	3.0	5.8	8.4	12.3	16.8	2.53 ± 0.33	2.63 ± 0.07
	3.5	5.5	8.8	13.5	17.7	2.78 ± 0.87	3.07 ± 0.24
	4.0	5.6	9.0	14.5	18.9	2.90 ± 1.00	3.43 ± 0.27
	4.5	5.5	8.8	13.7	18.0	2.83 ± 0.91	3.90 ± 0.31
	5.0	5.2	8.7	14.1	19.3	3.10 ± 0.87	4.25 ± 0.35
	5.5	5.7	9.4	14.7	18.9	2.84 ± 1.09	4.77 ± 0.44
Mt. Lassen	0	15.2	15.2	14.2	12.7	-0.43 ± 0.47	0
	0.5	15.2	15.9	17.1	16.5	0.19 ± 0.47	0.53 ± 0.07
	1.0	16.7	19.5	22.7	25.1	1.27 ± 0.76	1.00 ± 0.00
	1.5	15.2	18.8	24.6	27.3	1.39 ± 0.69	1.43 ± 0.07
	2.0	14.8	19.5	25.7	31.3	1.79 ± 0.38	1.93 ± 0.07
	2.5	16.1	22.3	30.8	37.7	2.02 ± 0.58	2.33 ± 0.07
	3.0	16.0	22.4	32.3	42.2	2.32 ± 0.41	2.70 ± 0.12
	3.5	14.3	21.6	32.6	44.9	2.72 ± 0.44	3.23 ± 0.07
	4.0	15.8	25.1	37.8	48.7	2.68 ± 0.89	3.50 ± 0.31
	4.5	15.8	22.0	33.8	43.9	2.44 ± 0.70	4.00 ± 0.23
	5.0	14.6	22.8	34.4	43.4	2.60 ± 0.96	4.43 ± 0.37
	5.5	14.7	22.1	33.6	42.4	2.53 ± 0.87	4.93 ± 0.29

Appendix A. Table 10. Preliminary experiment P.3; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of rainbow trout strain, Mt. Lassen, at 2 initial sizes and 10-11 ration levels.

Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight. day^{-1})
Mt. Lassen	0	14.80	15.4	12.4	11.5	-0.60 ± 1.06	0
	1.0	16.30	19.1	22.4	27.3	1.23 ± 0.18	1.00 ± 0.00
	1.5	14.80	19.0	22.9	27.6	1.48 ± 0.30	1.47 ± 0.07
	2.0	15.10	19.8	26.2	31.5	1.75 ± 0.44	1.90 ± 0.00
	2.5	15.90	21.7	27.3	34.2	1.82 ± 0.40	2.37 ± 0.07
	3.0	14.80	20.2	25.4	32.3	1.86 ± 0.37	2.80 ± 0.12
	3.5	15.70	21.4	29.0	35.2	1.92 ± 0.54	3.27 ± 0.13
	4.0	14.40	22.3	29.2	38.3	2.33 ± 0.80	3.70 ± 0.12
	4.5	13.90	21.8	25.4	30.6	1.88 ± 1.34	4.23 ± 0.44
	5.0	15.20	22.8	30.2	41.7	2.40 ± 0.52	4.47 ± 0.18
Mt. Lassen	0	30.8	30.6	29.4	27.1	-0.30 ± 0.31	0
	0.5	28.2	30.9	31.2	30.0	0.33 ± 0.62	0.57 ± 0.07
	1.0	29.7	33.5	36.4	39.5	0.67 ± 0.18	1.03 ± 0.00
	1.5	28.9	37.0	43.5	49.2	1.27 ± 0.52	1.49 ± 0.02
	2.0	30.6	41.3	47.1	60.1	1.61 ± 0.72	1.94 ± 0.11
	2.5	30.6	41.7	55.2	63.2	1.73 ± 0.77	2.40 ± 0.13
	3.0	32.2	42.8	52.8	59.6	1.56 ± 0.70	3.04 ± 0.31
	3.5	29.4	41.5	53.1	66.6	1.85 ± 0.60	3.33 ± 0.06
	4.0	32.0	42.4	55.8	66.8	1.76 ± 0.47	3.83 ± 0.13
	4.5	30.4	41.5	53.1	67.3	1.89 ± 0.33	4.35 ± 0.29
	5.0	31.2	43.6	61.7	71.6	1.97 ± 0.91	5.22 ± 0.58

Appendix A. Table 11 Preliminary experiment P.4; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of rainbow trout strains, Idaho, Tunkwa and their hybrids (IT and TI) at 3-8 ration levels.

Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
I x I	0	4.9	4.7	4.1	3.3	-0.93 ± 0.65	0
	0.5	4.9	5.5	5.6	5.2	0.15 ± 0.72	0.52 ± 0.06
	1.0	5.0	5.8	6.7	6.8	0.66 ± 0.74	0.99 ± 0.10
	2.5	5.0	7.2	9.6	12.2	2.13 ± 0.54	2.24 ± 0.22
	4.5	5.2	8.6	12.4	13.8	2.33 ± 1.66	3.93 ± 0.60
	5.5	5.1	8.3	11.4	13.3	2.27 ± 1.36	4.85 ± 0.74
T x T	0	4.2	3.7	3.6	3.1	-0.72 ± 0.54	0
	1.5	5.2	6.4	8.3	9.4	1.39 ± 0.61	1.48 ± 0.15
	3.5	4.6	5.8	8.2	9.8	1.78 ± 0.70	3.26 ± 0.23
I x T	0	4.9	4.5	4.3	3.7	-0.64 ± 0.48	0
	0.25	5.0	4.8	4.9	4.4	-0.29 ± 0.55	0.27 ± 0.31
	0.75	4.9	5.5	5.7	5.7	0.35 ± 0.49	0.77 ± 0.08
	1.0	4.8	5.5	6.5	6.3	0.65 ± 0.91	1.01 ± 0.09
	2.0	4.6	6.0	7.5	9.2	1.62 ± 0.27	1.87 ± 0.13
	3.0	4.9	7.1	10.0	11.4	2.03 ± 1.09	2.71 ± 0.34
	4.5	4.8	7.5	8.8	10.5	1.88 ± 1.32	4.13 ± 0.62
	5.5	4.9	7.4	9.8	11.4	2.03 ± 1.07	4.98 ± 0.65
T x I	0	4.9	4.4	4.4	3.5	-0.792 ± 0.95	0
	0.25	4.6	4.8	4.8	4.1	-0.25 ± 0.85	0.26 ± 0.01
	0.75	4.7	5.2	6.2	5.8	0.54 ± 0.95	0.76 ± 0.78
	1.0	4.7	5.4	6.7	6.6	0.85 ± 0.98	0.99 ± 0.10
	2.0	4.7	6.1	8.0	9.3	1.62 ± 0.54	1.86 ± 0.15
	3.0	4.8	6.9	9.9	12.2	2.21 ± 0.77	2.67 ± 0.26
	4.5	4.6	7.1	9.8	12.1	2.31 ± 0.88	3.99 ± 0.44
	5.5	4.7	7.2	11.0	12.1	2.27 ± 1.56	4.90 ± 0.76

Appendix A. Table 12. Preliminary experiment P.5; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of Arctic charr, brook trout and rainbow trout at 8 ration levels and 4 temperatures.

Temperature (°C)	Species	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Week 8th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
10	Arctic charr	0	9.1	8.5	8.1	7.8	7.7	-0.32 ± 0.18	0
		0	9.0	8.3	7.8	7.8	7.5	-0.32 ± 0.22	0
		1.5	8.8	10.6	12.8	15.7	19.4	1.39 ± 0.07	1.43 ± 0.06
		3.0	8.7	10.9	14.3	19.0	25.6	1.95 ± 0.18	2.81 ± 0.23
		4.5	8.9	11.1	14.5	18.9	24.7	1.81 ± 0.13	4.22 ± 0.32
		6.0	8.7	11.3	15.0	20.3	26.7	1.98 ± 0.15	5.45 ± 0.18
		7.0	7.8	10.7	13.9	18.9	24.9	2.03 ± 0.22	6.31 ± 0.22
		7.0	9.5	12.3	16.4	22.3	29.1	2.00 ± 0.18	6.48 ± 0.59
10	Brook trout	0	7.1	7.2	6.4	6.2	5.9	-0.34 ± 0.35	0
		0	7.5	6.8	6.2	6.2	6.2	-0.33 ± 0.35	0
		1.5	6.9	7.7	8.5	10.0	11.8	0.89 ± 0.25	1.48 ± 0.07
		3.0	6.9	8.2	10.1	12.2	16.6	1.59 ± 0.41	2.58 ± 0.77
		4.5	7.7	8.8	10.7	14.0	19.0	1.63 ± 0.53	4.42 ± 0.41
		6	7.1	8.3	9.9	12.7	15.6	1.39 ± 0.25	5.74 ± 0.26
		7	7.1	7.9	9.4	11.3	13.8	1.32 ± 0.40	6.79 ± 0.35
		7	7.0	8.4	10.1	13.1	18.9	1.74 ± 0.53	6.62 ± 0.62
10	Rainbow trout	0	9.3	8.1	7.7	7.2	6.5	-0.64 ± 0.26	0
		0	8.0	7.3	7.0	6.8	6.7	-0.31 ± 0.28	0
		1.5	8.6	10.0	11.8	14.2	16.9	1.18 ± 0.12	1.37 ± 0.17
		3.0	8.9	10.7	14.4	18.4	23.0	1.67 ± 0.13	2.83 ± 0.26
		4.5	8.8	11.2	13.7	17.6	22.7	1.66 ± 0.13	4.16 ± 0.32
		6	8.9	10.3	13.2	17.6	21.8	1.57 ± 0.46	5.61 ± 0.31
		7	8.2	11.0	14.2	19.0	23.6	1.95 ± 0.19	6.39 ± 0.13
		7	7.7	10.0	13.0	17.4	22.8	1.93 ± 0.13	6.47 ± 0.54
13	Arctic charr	0	8.8	8.1	7.8	7.4	7.0	-0.40 ± 0.13	0
		0	8.4	7.8	7.4	7.4	6.8	-0.35 ± 0.24	0
		1.5	8.7	10.5	12.3	15.1	18.0	1.28 ± 0.15	1.41 ± 0.14
		3.0	8.0	10.2	13.2	17.5	24.5	1.96 ± 0.23	2.76 ± 0.13
		4.5	8.5	11.8	14.8	19.6	27.5	2.05 ± 0.33	4.05 ± 0.09
		6.0	8.8	12.2	16.3	21.8	27.5	2.01 ± 0.34	5.43 ± 0.10
		7.0	8.8	12.3	16.5	22.3	28.8	2.10 ± 0.29	6.27 ± 0.13
		7.0	7.9	10.6	14.4	19.2	25.1	2.24 ± 0.47	6.35 ± 0.16
13	Brook trout	0	7.7	7.1	6.6	7.2	6.0	-0.42 ± 0.76	0
		0	8.0	7.3	6.9	6.4	6.2	-0.46 ± 0.17	0
		1.5	7.2	8.6	10.3	12.1	14.7	1.25 ± 0.06	1.45 ± 0.07
		3.0	7.9	10.6	12.9	16.4	22.5	1.98 ± 0.19	2.79 ± 0.09
		4.5	8.0	11.3	14.2	18.3	24.4	1.95 ± 0.36	4.13 ± 0.12
		6.0	8.1	10.5	12.7	16.8	20.8	1.66 ± 0.29	5.57 ± 0.17
		7.0	7.6	9.8	11.3	16.2	21.1	1.84 ± 0.66	6.48 ± 0.38
		7.0	8.7	10.6	11.9	16.1	22.5	1.65 ± 0.66	6.52 ± 0.32
13	Rainbow trout	0	9.3	8.2	7.4	6.9	6.7	-0.59 ± 0.30	0
		0	8.5	7.8	7.6	7.5	6.4	-0.50 ± 0.43	0
		1.5	8.4	9.6	11.9	13.8	15.5	1.08 ± 0.32	1.48 ± 0.05
		3.0	8.0	11.0	15.0	19.7	26.3	2.09 ± 0.18	2.74 ± 0.05
		4.5	8.0	11.9	15.3	19.7	25.7	2.05 ± 0.51	4.05 ± 0.13
		6.0	8.5	13.2	16.9	22.7	27.8	2.08 ± 0.74	5.41 ± 0.24
		7.0	8.5	13.3	16.9	22.2	27.6	2.07 ± 0.76	6.24 ± 0.24
		7.0	8.4	12.9	17.9	23.8	30.3	2.26 ± 0.61	6.17 ± 0.38
16	Arctic charr	0	8.0	7.5	7.2	6.9	6.4	-0.40 ± 0.13	0
		0	8.2	8.0	7.5	7.1	6.5	-0.41 ± 0.15	0
		1.5	7.7	8.8	10.3	12.0	14.2	1.09 ± 0.06	1.49 ± 0.10
		3.0	8.1	9.5	12.2	15.6	20.2	1.60 ± 0.33	2.84 ± 0.09
		4.5	7.7	9.3	12.3	16.3	20.5	1.67 ± 0.24	4.29 ± 0.35
		6.0	8.2	11.3	14.9	19.3	23.4	1.88 ± 0.45	5.80 ± 0.72
		7.0	8.1	11.1	14.9	19.7	24.2	1.97 ± 0.43	6.49 ± 0.31
		7.0	7.5	9.7	11.8	16.2	21.9	1.87 ± 0.37	6.49 ± 0.63
16	Brook trout	0	7.4	6.9	6.6	6.1	5.7	-0.48 ± 0.09	0
		0	7.5	6.8	6.2	5.9	5.7	-0.51 ± 0.22	0
		1.5	7.2	8.6	10.0	12.3	14.4	1.23 ± 0.19	1.48 ± 0.09
		3.0	7.5	9.9	12.8	17.4	21.5	1.89 ± 0.33	2.84 ± 0.15
		4.5	7.5	10.0	13.4	17.0	21.7	1.92 ± 0.29	4.21 ± 0.25
		6.0	7.5	10.2	13.9	17.6	21.4	1.89 ± 0.49	5.63 ± 0.25
		7.0	7.6	10.5	14.0	15.3	21.3	1.83 ± 0.81	6.59 ± 0.45
		7.0	7.5	10.3	13.8	18.2	22.3	1.96 ± 0.44	6.62 ± 0.25

Appendix A. Table 12. (continued)

Temperature (°C)	Species	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Week 8th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
16	Rainbow trout	0	8.2	7.0	6.3	6.2	6.1	-0.54 ± 0.56	0
		0	8.5	7.4	6.8	6.4	6.4	-0.52 ± 0.44	0
		1.5	9.3	10.3	10.9	12.2	13.1	0.61 ± 0.18	1.54 ± 0.10
		3.0	8.3	11.4	14.9	19.7	27.4	2.10 ± 0.16	2.73 ± 0.24
		4.5	7.2	10.3	15.0	19.9	26.3	2.32 ± 0.45	3.97 ± 0.32
		6.0	9.1	13.3	18.3	22.9	27.2	1.99 ± 0.77	5.66 ± 0.22
		7.0	9.6	14.2	19.9	24.6	29.5	2.03 ± 0.83	6.59 ± 0.39
		7.0	8.2	12.5	16.8	21.0	25.1	2.02 ± 0.88	6.29 ± 0.24
19	Arctic charr	0	7.0	6.5	6.2	5.6	5.2	-0.54 ± 0.14	0
		0	7.7	7.0	6.6	6.1	5.7	-0.53 ± 0.11	0
		1.5	7.9	8.2	8.9	9.1	9.6	0.37 ± 0.19	1.59 ± 0.10
		3.0	7.2	7.8	8.8	9.5	9.9	0.56 ± 0.24	3.01 ± 0.32
		4.5	7.3	7.8	8.7	9.4	10.2	0.60 ± 0.15	4.74 ± 0.26
		6.0	7.9	8.9	10.1	11.5	12.2	0.79 ± 0.26	6.08 ± 0.38
		7.0	8.0	9.5	11.2	12.7	12.8	0.76 ± 0.58	7.10 ± 0.38
		7.0	7.6	8.3	9.6	10.7	11.4	0.74 ± 0.23	7.22 ± 0.44
19	Brook trout	0	7.3	6.5	6.0	5.5	5.2	-0.62 ± 0.22	0
		0	7.0	6.4	6.2	5.6	5.4	-0.48 ± 0.31	0
		1.5	7.2	8.3	9.2	10.5	12.0	0.92 ± 0.13	1.52 ± 0.09
		3.0	7.7	9.4	11.5	13.2	15.1	1.21 ± 0.30	3.17 ± 0.40
		4.5	7.6	8.4	10.2	11.7	13.8	1.05 ± 0.24	4.45 ± 0.19
		6.0	6.8	8.1	10.1	12.0	13.2	1.20 ± 0.42	5.94 ± 0.33
		7.0	6.4	7.9	9.9	11.4	12.8	1.24 ± 0.45	6.89 ± 0.29
		7.0	8.4	10.0	11.7	12.6	13.1	1.02 ± 0.83	7.14 ± 0.43
19	Rainbow trout	0	8.3	6.8	6.3	6.2	6.0	-0.59 ± 0.60	0
		0	7.6	6.3	5.5	4.6	4.1	-1.11 ± 0.28	0
		1.5	7.6	8.1	8.6	9.3	10.3	0.55 ± 0.11	1.60 ± 0.19
		3.0	6.7	8.8	11.2	14.6	19.1	1.88 ± 0.14	2.88 ± 0.15
		4.5	7.8	11.4	16.5	19.4	21.2	1.84 ± 1.14	4.19 ± 0.34
		6.0	8.7	11.5	15.4	18.6	20.6	1.57 ± 0.70	5.77 ± 0.20
		7.0	7.6	11.4	14.8	18.4	21.6	1.90 ± 0.88	6.43 ± 0.25
		7.0	7.6	10.5	14.5	16.9	21.2	1.84 ± 0.65	6.62 ± 0.52

Appendix A. Table 13. Preliminary experiment P.5; analysis of variance and percentage of variance components in maximum, optimum and maintenance rations and specific growth rate at maximum and optimum ration for Arctic charr, brook trout and rainbow trout in 4 temperatures.

Source	d.f.	Ration maximum M.S.	Ration maximum % Variance Component	Ration optimum M.S.	Ration optimum % Variance Component	Ration maintenance M.S.	Ration maintenance % Variance Component	Specific growth rate maximum M.S.	Specific growth rate maximum % Variance Component	Specific growth rate optimum M.S.	Specific growth rate optimum % Variance Component
Species	2	1.05	37	0.24*	16	0.02	4	0.15	6	0.20*	33
Temperature	3	0.17	29	0.71**	71	0.13**	77	0.15	44	0.23**	52
Error	6	0.37	34	0.04	13	0.01	19	0.10	49	0.02	15

Note:

1)

Source	Expected Mean Square
Species	$\sigma^2 + nbK^2A$
Temperature	$\sigma^2 + naK^2B$
Error	$\sigma^2 + nK^2AB$

2) * indicates significant at $P < 0.05$
** indicates significant at $P < 0.01$

Appendix A. Table 14.

Terms used for correction of measured ration level (food fed per fish weight as %) to actual dry weight values for calculating net and gross efficiencies.

Temperature (°C)	Corrected Term [*a] At maximum ration	At optimum ration
12.0	3.58	3.88
14.3	3.44	3.88
16.7	3.44	3.58
19.0	3.32	3.72

*a corrected term = Food dry weight as a % of measure weight (93%) divided by Fish dry weight as a % of wet weight (26% to 36%).

Appendix A. Table 15. Definitive experiments; analysis of variance and percentage of various components in maximum, optimum and maintenance rations and specific growth rate, net efficiency and gross efficiency at maximum and optimum rations of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 3 initial sizes.

		Ration (% wet weight.day^{-1})						Specific growth rate (%.day^{-1})				Net efficiency (%)				Gross efficiency (%)			
		Maximum		Optimum		Maintenance		Maximum ration		Optimum ration		Maximum ration		Optimum ration		Maximum ration		Optimum ration	
Source	df.	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component
Strains	2	0.23*	6	0.10*	4	0.00	①	0.32*	16	0.10**	12	7.60**	11	9.23	4	6.79**	14	7.39	5
Temperature	3	0.77**	30	0.66**	35	0.09**	29	0.03	1	0.07**	10	0.58	1	11.89*	8	1.07	2	15.71*	16
Initial Sizes	2	0.77**	23	0.83**	33	0.15**	35	1.28**	63	0.49**	60	41.68**	61	92.38**	54	29.92**	63	56.30**	46
Strains x Temperatures	6	0.03	①	0.01	①	0.00	1	0.01	①	0.01*	3	0.33	①	2.07	①	0.31	①	1.64	1
Strains x Initial Sizes	4	0.04	1	0.05*	5	0.01	6	0.02	2	0.00	2	0.71	2	2.92	1	0.67	2	1.2	①
Temperatures x Initial Sizes	6	0.18*	18	0.09**	14	0.02**	23	0.07**	12	0.02**	10	3.08**	16	3.72	4	1.67*	11	4.78	12
Error	12	0.06	22	0.02	10	0.00	6	0.01	6	0.00	3	0.54	10	4.08	29	0.32	8	2.00	20
Total	35	2.08	100	1.76	100	0.27	100	1.74	100	0.69	100	54.52	100	126.29	100	40.75	100	89.02	100

Note: A.

Source	Expected Mean Squares
Strains	$\sigma^2 + nbcK^2A$
Temperatures	$\sigma^2 + nacK^2B$
Initial Sizes	$\sigma^2 + nabK^2C$
Strains x Temperatures	$\sigma^2 + ncK^2AB$
Strains x Initial Sizes	$\sigma^2 + nbK^2AC$
Temperatures x Initial Sizes	$\sigma^2 + naK^2BC$
Error	$\sigma^2 + nK^2ABC$

B. ① These components were ≤ 0 and not included when calculating %

Appendix A. Table 16 Definitive experiments; analysis of variance and percentage of variance components in maximum, optimum and maintenance rations and specific growth rate, net efficiency and gross efficiency at maximum and optimum rations of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures at each initial size.

		Ration (% wet weight.day^{-1})						Specific growth rate (%.day^{-1})				Net efficiency (%)				Gross efficiency (%)			
		Maximum		Optimum		Maintenance		Maximum ration		Optimum ration		Maximum ration		Optimum ration		Maximum ration		Optimum ration	
Source	df.	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component	M.S.	% Variance Component
<u>Initial Size 7 g.</u>																			
Strains	2	0.15	7	0.03	2	0.00	①	0.22**	66	0.05*	26	4.55*	54	11.30	26	3.95**	77	4.35	6
Temperatures	3	0.33	41	0.58**	93	0.09*	91	0.05	13	0.07**	58	1.20	11	3.87	①	0.27	①	4.23	7
Error	6	0.10	53	0.01	5	0.00	9	0.02	21	0.01	16	0.63	35	5.25	74	0.28	23	3.42	87
Total	11	0.58	100	0.62	100	0.10	100	0.29	100	0.13	100	6.38	100	20.42	100	4.50	100	12.00	100
<u>Initial Size 17 g.</u>																			
Strains	2	0.00	①	0.00	①	0.01	①	0.06**	24	0.02*	24	1.9	20	2.4	8	2.25*	26	4.7	15
Temperatures	3	0.68**	95	0.17**	85	0.04**	86	0.11**	68	0.03**	58	3.6**	58	14.93**	82	3.47**	56	19.77**	83
Error	6	0.01	5	0.01	15	0.00	14	0.00	8	0.00	18	0.40	22	0.57	10	0.33	18	0.18	2
Total	11	0.69	100	0.18	100	0.04	100	0.17	100	0.05	100	5.9	100	17.9	100	6.05	100	24.65	100
<u>Initial Size 67 g.</u>																			
Strains	2	0.15	32	0.17	37	0.01	14	0.09**	76	0.05*	69	2.55*	38	1.35	5	1.90*	47	0.75	①
Temperatures	3	0.13	35	0.09	19	0.01	43	0.01	①	0.01	13	1.93*	36	0.53	①	0.70	15	1.27	8
Error	6	0.03	32	0.04	44	0.00	43	0.01	24	0.00	19	0.37	26	4.40	95	0.32	38	2.03	92
Total	11	0.31	100	0.30	100	0.02	100	0.11	100	0.06	100	4.85	100	6.28	100	2.92	100	4.05	100

Note:

Source	Expected Mean Squares
Strains	$\sigma^2 + nbK^2A$
Temperatures	$\sigma^2 + naK^2B$
Error	$\sigma^2 + nK^2AB$

① These components ≤ 0 and were not included in calculating %

Appendix A. Table 17. Definitive experiment D.1; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of rainbow trout strains Manx and Nisqually and their hybrid (MN) in 4 temperatures and 8 ration levels.

Temperature (°C)	Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
12.0	Manx	0	7.1	6.4	6.0	5.6	-0.58 ± 0.30	0
		0	7.2	6.5	6.0	5.8	-0.54 ± 0.31	0
		1.5	8.0	8.7	9.9	11.4	0.87 ± 0.26	1.45 ± 0.07
		3.0	8.0	9.7	12.6	15.9	1.69 ± 0.33	2.73 ± 0.10
		4.5	7.4	9.5	12.1	14.5	1.50 ± 0.58	4.14 ± 0.23
		6.0	7.0	9.1	11.2	13.9	1.66 ± 0.20	5.43 ± 0.38
		7.0	8.1	10.5	12.7	16.4	1.71 ± 0.20	6.37 ± 0.43
		7.0	7.7	10.1	13.0	15.3	1.67 ± 0.52	6.12 ± 0.52
12.0	Nisqually	0	6.5	5.6	5.4	5.1	-0.60 ± 0.49	0
		0	7.8	6.5	6.1	5.9	-0.67 ± 0.59	0
		1.5	7.1	7.8	8.8	10.5	0.95 ± 0.31	1.45 ± 0.67
		3.0	7.3	9.1	11.9	15.7	1.87 ± 0.42	2.70 ± 0.10
		4.5	7.4	9.7	12.6	15.6	1.79 ± 0.36	4.00 ± 0.29
		6.0	7.5	10.2	12.7	15.0	1.70 ± 0.57	5.40 ± 0.49
		7.0	7.6	11.0	13.6	16.5	1.88 ± 1.59	5.84 ± 1.00
		7.0	7.2	10.1	12.9	15.7	1.91 ± 0.60	6.06 ± 0.54
12.0	Manx x Nisqually	0	7.9	7.0	6.3	6.0	-0.71 ± 0.27	0
		0	7.8	6.7	6.3	6.2	-0.55 ± 0.60	0
		1.5	7.0	8.1	9.4	11.8	1.27 ± 0.31	1.43 ± 0.09
		3.0	7.5	9.1	11.6	14.7	1.64 ± 0.27	2.75 ± 0.12
		4.5	7.6	9.7	12.2	14.9	1.65 ± 0.20	3.97 ± 0.13
		6.0	7.1	9.7	12.6	16.3	2.02 ± 0.26	5.19 ± 0.46
		7.0	8.0	10.5	13.1	15.2	1.57 ± 0.49	6.28 ± 0.44
		7.0	6.9	9.4	12.5	15.7	2.02 ± 0.40	5.91 ± 0.31
14.3	Manx	0	7.6	7.5	6.9	6.2	-0.50 ± 0.46	0
		0	8.2	7.2	6.6	6.2	-0.68 ± 0.33	0
		1.5	7.3	7.9	8.9	10.5	0.89 ± 0.33	1.46 ± 0.05
		3.0	6.4	7.7	9.3	12.3	1.60 ± 0.49	2.77 ± 0.19
		4.6	8.7	11.4	13.6	16.3	1.52 ± 0.30	4.01 ± 0.44
		6.0	6.7	8.7	11.4	14.3	1.87 ± 0.28	5.32 ± 0.28
		7.0	7.7	9.0	12.2	15.1	1.67 ± 0.69	6.10 ± 0.51
		7.0	8.3	11.3	14.0	16.7	1.71 ± 0.58	6.42 ± 0.37
14.3	Nisqually	0	6.9	6.5	6.0	5.8	-0.35 ± 0.37	0
		0	7.1	5.8	5.3	5.3	-0.73 ± 0.81	0
		1.5	7.1	8.0	8.8	11.1	1.07 ± 0.53	1.41 ± 0.12
		3.0	7.0	8.4	10.7	13.9	1.68 ± 0.46	2.73 ± 0.13
		4.5	6.4	9.1	12.4	16.2	2.28 ± 0.30	3.90 ± 0.20
		6.0	6.8	9.6	12.7	18.9	2.48 ± 0.42	5.04 ± 0.56
		7.0	7.0	10.4	13.5	17.5	2.22 ± 0.57	5.89 ± 0.66
		7.0	7.7	10.4	13.7	17.2	1.95 ± 0.36	5.96 ± 0.63
14.3	Manx x Nisqually	0	7.4	6.4	5.8	5.4	-0.77 ± 0.35	0
		0	7.6	6.5	6.0	5.6	-0.67 ± 0.49	0
		1.5	6.9	8.6	9.8	11.2	1.16 ± 0.41	1.47 ± 0.07
		3.0	7.3	8.5	10.8	13.8	1.54 ± 0.48	2.76 ± 0.12
		4.5	7.2	9.5	12.6	15.9	1.93 ± 0.31	4.02 ± 0.18
		6.0	7.5	10.4	13.5	17.0	1.99 ± 0.38	5.08 ± 0.60
		7.0	7.6	10.5	13.9	17.2	1.99 ± 0.46	5.89 ± 0.73
		7.0	7.2	10.1	13.3	17.6	2.19 ± 0.30	6.03 ± 0.48
16.7	Manx	0	7.3	6.7	5.8	5.2	-0.83 ± 0.31	0
		0	7.8	6.6	6.1	5.7	-0.77 ± 0.40	0
		1.5	7.9	8.5	9.4	10.1	0.59 ± 0.24	1.49 ± 0.06
		3.0	8.1	9.6	11.9	14.9	1.50 ± 0.21	2.70 ± 0.24
		4.5	6.9	9.1	11.5	13.8	1.69 ± 0.41	4.10 ± 0.19
		6.0	7.4	10.4	13.2	16.1	1.89 ± 0.55	5.27 ± 0.26
		7.0	8.4	11.1	13.7	15.9	1.59 ± 0.54	6.02 ± 0.17
		7.0	7.3	10.7	13.4	16.2	1.92 ± 0.78	5.94 ± 0.28
16.7	Nisqually	0	7.4	5.9	5.4	5.0	-0.95 ± 0.64	0
		0	6.1	5.1	4.7	4.4	-0.78 ± 0.58	0
		1.5	8.0	8.3	9.0	9.9	0.52 ± 0.29	1.48 ± 0.07
		3.0	6.0	7.1	8.9	11.8	1.65 ± 0.44	2.64 ± 0.38
		4.5	6.8	9.0	12.5	16.8	2.21 ± 0.29	3.85 ± 0.27
		6.0	6.7	9.5	12.6	16.3	2.17 ± 0.38	5.13 ± 0.17
		7.0	7.3	10.5	13.8	17.0	2.07 ± 0.62	6.22 ± 0.38
		7.0	7.1	10.3	13.2	17.1	2.14 ± 0.53	6.07 ± 0.82

Appendix A. Table 17. (continued)

Temperature (°C)	Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean Specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
16.7	Manx x Nisqually	0	8.3	6.9	6.3	5.7	-0.92 ± 0.40	0
		0	7.4	6.4	5.8	5.2	-0.89 ± 0.28	0
		1.5	6.7	7.3	8.0	8.9	0.71 ± 0.12	1.45 ± 0.13
		3.0	7.5	9.1	11.4	14.7	1.64 ± 0.24	2.75 ± 0.17
		4.5	7.1	9.4	12.5	15.8	1.96 ± 0.35	3.95 ± 0.22
		6.0	7.1	10.8	13.6	17.3	2.17 ± 0.85	5.35 ± 0.43
		7.0	7.6	11.5	14.5	18.0	2.10 ± 0.90	6.24 ± 0.53
		7.0	7.3	10.2	13.4	17.1	2.07 ± 0.38	6.02 ± 0.53
19.0	Manx	0	7.8	6.4	6.0	5.5	-0.86 ± 0.52	0
		0	7.7	6.5	5.9	5.0	-1.03 ± 0.25	0
		1.5	6.6	7.8	8.5	9.3	0.82 ± 0.35	1.48 ± 0.11
		3.0	8.3	9.9	12.0	14.7	1.41 ± 0.15	2.78 ± 0.14
		4.5	6.6	9.0	11.6	14.1	1.85 ± 0.49	4.12 ± 0.11
		6.0	7.7	10.5	13.0	15.9	1.77 ± 0.48	5.01 ± 0.78
		7.0	7.8	10.1	12.8	14.6	1.56 ± 0.58	6.12 ± 0.09
		7.0	8.2	11.5	14.3	17.0	1.79 ± 0.70	5.88 ± 0.66
19.0	Nisqually	0	5.9	4.7	4.5	3.8	-1.06 ± 0.84	0
		0	6.7	5.4	5.0	4.5	-0.94 ± 0.57	0
		1.5	6.8	7.7	8.9	9.8	0.89 ± 0.21	1.45 ± 0.05
		3.0	7.0	8.2	10.1	13.4	1.59 ± 0.49	2.77 ± 0.10
		4.5	6.6	9.3	12.6	16.7	2.25 ± 0.25	3.83 ± 0.29
		6.0	5.5	8.4	11.5	15.1	2.45 ± 0.63	5.06 ± 0.37
		7.0	5.1	8.8	12.2	15.6	2.72 ± 1.24	5.73 ± 0.63
		7.0	6.5	9.9	12.8	15.7	2.14 ± 0.92	6.03 ± 0.67
19.0	Manx x Nisqually	0	6.4	5.3	4.9	4.4	-0.93 ± 0.43	0
		0	7.2	6.4	5.8	5.4	-0.72 ± 0.20	0
		1.5	7.1	6.9	7.8	8.6	-0.48 ± 0.66	1.50 ± 0.03
		3.0	7.4	8.9	11.3	14.1	1.57 ± 0.37	2.74 ± 0.08
		4.5	6.9	9.7	12.5	14.2	1.77 ± 0.90	4.14 ± 0.31
		6.0	7.3	10.7	13.6	17.2	2.08 ± 0.66	5.06 ± 0.49
		7.0	7.6	12.0	14.2	17.4	2.01 ± 1.27	6.11 ± 0.86
		7.0	7.0	10.3	13.5	16.2	2.03 ± 0.83	6.00 ± 0.41

Appendix A. Table 18. Definitive experiment D.2; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of rainbow trout strains Manx and Nisqually and their hybrid (MN) in 4 temperatures and 8 ration levels.

Temperature (°C)	Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
12.0	Manx	0	16.6	15.5	16.7	16.7	-0.004 ± 0.60	0
		0	15.7	15.2	13.9	13.2	-0.40 ± 0.22	0
		1.5	16.5	19.8	23.7	28.8	1.32 ± 0.06	1.36 ± 0.01
		3.0	17.5	23.9	30.9	39.0	1.91 ± 0.34	2.60 ± 0.07
		4.5	18.4	26.0	34.2	45.7	2.17 ± 0.32	3.82 ± 0.10
		6.0	16.0	21.9	29.7	36.4	1.96 ± 0.52	5.23 ± 0.31
		7.0	17.3	24.4	32.1	41.8	2.11 ± 0.36	5.97 ± 0.18
		7.0	16.8	22.9	32.1	39.8	2.06 ± 0.52	6.00 ± 0.25
12.0	Nisqually	0	16.5	15.3	14.7	14.4	-0.32 ± 0.26	0
		0	16.3	14.2	13.9	13.7	-0.43 ± 0.56	0
		1.5	18.1	22.2	26.2	32.1	1.33 ± 0.21	1.36 ± 0.02
		3.0	18.2	24.6	32.7	42.9	2.04 ± 0.14	2.57 ± 0.03
		4.5	19.3	26.9	34.6	48.4	2.20 ± 0.39	3.81 ± 0.12
		6.0	16.8	23.5	34.2	43.0	2.34 ± 0.74	5.17 ± 0.22
		7.0	17.1	25.4	34.8	47.0	2.40 ± 0.42	5.83 ± 0.20
		7.0	15.5	22.6	33.2	43.9	2.48 ± 0.48	5.80 ± 0.23
12.0	Manx x Nisqually	0	16.3	14.0	13.9	13.5	-0.44 ± 0.63	0
		0	16.4	14.4	14.5	13.8	-0.40 ± 0.56	0
		1.5	15.8	19.4	23.8	28.9	1.45 ± 0.06	1.35 ± 0.01
		3.0	15.7	21.8	29.6	40.5	2.24 ± 0.12	2.54 ± 0.03
		4.5	17.4	23.3	31.0	43.1	2.17 ± 0.20	3.82 ± 0.06
		6.0	15.8	23.1	32.9	44.8	2.50 ± 0.29	4.96 ± 0.12
		7.0	15.3	22.8	30.8	41.6	2.39 ± 0.48	5.85 ± 0.20
		7.0	17.8	25.2	35.1	46.0	2.25 ± 0.33	5.90 ± 0.16
14.3	Manx	0	17.0	14.8	14.4	12.9	-0.73 ± 0.55	0
		0	17.8	15.6	16.4	14.5	-0.49 ± 0.86	0
		1.5	17.0	19.7	23.7	27.8	0.77 ± 0.64	1.39 ± 0.01
		3.0	16.0	21.9	28.0	35.6	1.90 ± 0.34	2.60 ± 0.07
		4.5	16.1	22.8	29.2	33.9	1.77 ± 0.82	3.95 ± 0.25
		6.0	16.5	22.6	29.3	35.0	1.79 ± 0.55	5.25 ± 0.23
		7.0	15.8	22.3	28.4	33.2	1.77 ± 0.78	6.14 ± 0.37
		7.0	17.9	23.7	32.2	38.1	1.80 ± 0.61	5.86 ± 0.69
14.3	Nisqually	0	17.0	15.0	13.7	13.0	-0.63 ± 0.31	0
		0	18.0	15.8	15.1	14.4	-0.54 ± 0.42	0
		1.5	15.0	17.6	20.4	24.6	1.18 ± 0.17	1.38 ± 0.02
		3.0	15.6	21.8	28.2	36.7	2.04 ± 0.36	2.58 ± 0.05
		4.5	14.5	20.8	27.3	32.7	1.94 ± 0.73	3.90 ± 0.22
		6.0	14.5	20.4	28.7	35.5	2.13 ± 0.60	5.11 ± 0.25
		7.0	16.0	23.3	31.1	36.4	1.96 ± 0.90	6.05 ± 0.43
		7.0	16.0	23.4	33.7	39.2	2.13 ± 1.06	5.96 ± 0.51
14.3	Manx x Nisqually	0	17.8	16.3	15.2	14.4	-0.50 ± 0.14	0
		0	17.4	15.2	14.7	13.3	-0.64 ± 0.40	0
		1.5	14.2	17.1	19.5	22.6	1.09 ± 0.19	1.36 ± 0.06
		3.0	18.4	25.0	32.1	40.7	1.89 ± 0.30	2.60 ± 0.07
		4.5	16.5	23.8	31.4	37.1	1.93 ± 0.82	3.90 ± 0.25
		6.0	17.3	24.8	36.2	43.4	2.20 ± 0.89	5.09 ± 0.37
		7.0	16.0	22.4	31.8	36.0	1.93 ± 1.04	5.93 ± 0.24
		7.0	16.9	24.1	35.2	41.2	2.12 ± 1.01	5.96 ± 0.46
16.7	Manx	0	17.0	14.8	13.7	12.6	-0.71 ± 0.30	0
		0	15.3	13.5	13.1	12.5	-0.47 ± 0.45	0
		1.5	18.3	20.2	22.2	25.6	0.81 ± 0.22	1.42 ± 0.02
		3.0	19.0	25.7	32.9	42.8	1.99 ± 0.18	2.92 ± 0.66
		4.5	18.4	25.1	33.1	40.3	1.89 ± 0.46	3.91 ± 0.15
		6.0	15.5	22.6	31.1	42.7	2.42 ± 0.30	5.00 ± 0.12
		7.0	16.8	24.1	32.9	40.6	2.10 ± 0.63	5.98 ± 0.30
		7.0	15.2	22.1	29.4	37.5	2.16 ± 0.56	5.95 ± 0.27
16.7	Nisqually	0	16.8	15.0	14.1	13.1	-0.59 ± 0.22	0
		0	15.1	13.5	12.3	11.9	-0.56 ± 0.35	0
		1.5	16.3	17.8	20.4	24.2	0.95 ± 0.33	1.40 ± 0.04
		3.0	16.2	21.3	26.8	34.8	1.82 ± 0.17	2.62 ± 0.03
		4.5	15.3	21.2	29.2	37.8	2.15 ± 0.31	3.83 ± 0.10
		6.0	17.8	28.2	36.6	46.1	2.33 ± 1.00	5.05 ± 0.37
		7.0	17.1	26.1	35.0	42.8	2.18 ± 0.91	5.94 ± 0.44
		7.0	17.4	27.3	35.8	46.3	2.40 ± 0.84	5.84 ± 0.39

Appendix A. Table 18. (continued)

Temperature (°C)	Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
16.7	Manx x Nisqually	0	15.3	13.9	12.5	11.7	-0.62 ± 0.21	0
		0	16.3	14.5	14.3	13.4	-0.45 ± 0.42	0
		1.5	17.8	20.3	23.1	26.1	0.92 ± 0.04	1.40 ± 0.01
		3.0	16.9	20.4	28.8	36.5	1.83 ± 0.68	2.61 ± 0.12
		4.5	15.3	21.8	29.6	38.1	2.18 ± 0.43	3.82 ± 0.14
		6.0	17.8	26.9	36.9	46.1	2.27 ± 0.78	5.04 ± 0.29
		7.0	15.8	23.6	33.3	42.2	2.35 ± 0.70	5.83 ± 0.35
		7.0	18.2	28.3	39.0	50.3	2.49 ± 0.91	5.80 ± 0.43
19.0	Manx	0	16.4	14.2	13.7	13.2	-0.52 ± 0.52	0
		0	16.9	14.9	14.3	13.6	-0.52 ± 0.39	0
		1.5	19.2	20.6	22.7	25.9	0.72 ± 0.25	1.58 ± 0.30
		3.0	15.3	19.1	24.5	29.6	1.56 ± 0.23	2.64 ± 0.02
		4.5	17.7	25.4	30.5	36.4	1.72 ± 0.87	3.96 ± 0.27
		6.0	16.4	22.8	29.9	36.0	1.88 ± 0.60	5.23 ± 0.22
		7.0	16.9	21.6	26.8	32.6	1.57 ± 0.19	6.24 ± 0.10
		7.0	16.2	23.5	29.2	35.4	1.86 ± 0.80	6.07 ± 0.28
19.0	Nisqually	0	16.4	13.7	12.8	12.4	-0.63 ± 0.64	0
		0	16.1	14.3	13.2	12.9	-0.42 ± 0.61	0
		1.5	16.5	17.9	20.2	23.7	0.86 ± 0.33	1.42 ± 0.02
		3.0	18.1	22.9	29.7	37.7	1.75 ± 0.11	2.65 ± 0.04
		4.5	18.8	26.1	34.3	41.4	1.89 ± 0.58	3.91 ± 0.18
		6.0	18.6	26.6	34.4	41.6	1.92 ± 0.70	5.22 ± 0.25
		7.0	16.6	24.6	32.7	39.8	2.08 ± 0.81	5.99 ± 0.39
		7.0	20.2	30.1	39.0	47.9	2.09 ± 0.82	6.02 ± 0.43
19.0	Manx x Nisqually	0	17.7	15.6	14.5	13.6	-0.64 ± 0.30	0
		0	15.3	12.9	12.9	11.7	-0.65 ± 0.73	0
		1.5	16.1	18.0	20.5	23.4	0.89 ± 0.11	1.41 ± 0.01
		3.0	15.2	19.6	25.5	31.9	1.77 ± 0.17	2.63 ± 0.03
		4.5	15.9	20.2	27.6	34.6	1.86 ± 0.37	3.92 ± 0.12
		6.0	17.1	23.1	29.6	36.0	1.77 ± 0.43	5.29 ± 0.22
		7.0	15.8	22.9	28.0	35.2	1.91 ± 0.77	6.07 ± 0.36
		7.0	17.8	26.1	35.8	43.2	2.12 ± 0.83	5.97 ± 0.40

Appendix A. Table 19. Definitive experiment D.3; nominal ration, beginning mean weight, biweekly mean weight, mean specific growth rate and mean ration of rainbow trout strains Manx and Nisqually and their hybrid (MN) in 4 temperatures and 8 ration levels.

Temperature (°C)	Strain	Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2nd mean weight (g)	Week 4th mean weight (g)	Week 6th mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
12.0	Manx	0	64.5	59.5	56.4	54.5	-0.40 ± 0.19	0
		0	67.6	62.8	63.0	60.3	-0.27 ± 0.32	0
		1.5	64.3	74.7	75.4	84.5	0.86 ± 0.22	1.41 ± 0.08
		3.0	68.8	84.5	96.7	117.0	1.27 ± 0.31	3.14 ± 0.78
		4.5	67.0	81.3	93.2	104.6	1.13 ± 0.47	4.17 ± 0.10
		6.0	69.2	84.3	102.0	114.7	1.20 ± 0.37	5.45 ± 0.09
		7.0	65.0	80.3	91.0	107.3	1.19 ± 0.38	6.42 ± 0.17
		7.0	65.0	72.0	84.5	98.2	0.98 ± 0.26	6.49 ± 0.17
12.0	Nisqually	0	68.5	62.1	60.0	57.2	-0.43 ± 0.28	0
		0	69.2	62.1	60.5	57.0	-0.46 ± 0.34	0
		1.5	67.0	79.8	101.1	102.2	1.01 ± 0.96	1.34 ± 0.03
		3.0	71.9	88.4	109.5	135.7	1.51 ± 0.04	2.61 ± 0.14
		4.5	62.9	71.8	89.8	104.7	1.21 ± 0.40	4.25 ± 0.81
		6.0	68.2	79.0	97.3	114.2	1.23 ± 0.27	5.45 ± 0.17
		7.0	68.4	94.9	122.8	155.4	1.95 ± 0.40	6.17 ± 0.93
		7.0	67.4	86.9	106.8	131.3	1.59 ± 0.23	6.11 ± 0.12
12.0	Manx x Nisqually	0	66.4	61.6	61.5	57.8	-0.33 ± 0.32	0
		0	65.0	56.8	54.6	52.0	-0.53 ± 0.43	0
		1.5	69.4	76.0	85.8	100.2	0.88 ± 0.27	1.48 ± 0.19
		3.0	66.0	84.1	104.3	126.0	1.52 ± 0.18	2.68 ± 0.47
		4.5	67.0	89.6	108.2	129.8	1.57 ± 0.50	4.01 ± 0.16
		6.0	67.3	86.5	103.5	126.6	1.50 ± 0.30	5.32 ± 0.15
		7.0	65.0	80.0	101.0	121.4	1.49 ± 0.20	6.27 ± 0.10
		7.0	68.4	90.5	109.3	128.2	1.50 ± 0.52	6.13 ± 0.12
14.3	Manx	0	67.7	66.7	63.1	61.7	-0.22 ± 0.17	0
		0	63.1	55.6	52.5	49.6	-0.57 ± 0.33	0
		1.5	60.9	66.0	75.5	88.2	0.88 ± 0.32	1.41 ± 0.04
		3.0	68.3	77.9	90.0	104.7	1.02 ± 0.08	2.79 ± 0.01
		4.5	63.3	74.7	89.7	116.3	1.45 ± 0.41	4.12 ± 0.04
		6.0	65.4	80.1	98.8	116.8	1.28 ± 0.23	5.40 ± 0.03
		7.0	66.4	80.3	96.3	114.7	1.30 ± 0.65	6.34 ± 0.03
		7.0	68.4	80.4	99.0	112.3	1.18 ± 0.39	6.33 ± 0.10
14.3	Nisqually	0	67.6	63.8	60.2	57.5	-0.39 ± 0.06	0
		0	68.4	60.0	59.2	55.9	-0.42 ± 0.60	0
		1.5	67.3	75.3	86.0	101.3	0.97 ± 0.22	1.40 ± 0.02
		3.0	66.7	88.2	101.3	118.8	1.38 ± 0.63	2.65 ± 0.11
		4.5	62.8	82.0	102.9	125.0	1.64 ± 0.30	3.99 ± 0.10
		6.0	68.5	81.2	101.0	126.8	1.47 ± 0.26	5.29 ± 0.20
		7.0	63.0	78.0	96.0	115.2	1.44 ± 0.14	6.10 ± 0.06
		7.0	68.2	87.8	106.5	122.9	1.40 ± 0.45	6.22 ± 0.12
14.3	Manx x Nisqually	0	64.4	52.2	53.3	49.2	-0.64 ± 0.96	0
		0	67.2	61.2	61.5	58.0	-0.35 ± 0.41	0
		1.5	65.8	80.6	92.9	103.6	1.08 ± 0.39	1.38 ± 0.05
		3.0	68.6	80.2	95.4	119.3	1.32 ± 0.29	2.67 ± 0.17
		4.5	60.2	71.0	90.7	114.9	1.54 ± 0.36	4.02 ± 0.11
		6.0	66.0	84.4	107.3	127.0	1.56 ± 0.36	5.27 ± 0.03
		7.0	64.1	81.3	103.8	134.0	1.76 ± 0.73	6.14 ± 0.04
		7.0	61.1	76.0	94.5	116.4	1.53 ± 0.05	5.06 ± 0.20
16.7	Manx	0	68.6	66.2	60.5	56.2	-0.48 ± 0.23	0
		0	65.0	62.5	58.5	58.3	-0.27 ± 0.26	0
		1.5	63.8	69.3	85.0	100.0	1.07 ± 0.52	1.41 ± 0.03
		3.0	64.3	77.7	92.5	111.2	1.34 ± 0.12	2.53 ± 0.30
		4.5	66.4	80.0	95.6	111.6	1.24 ± 0.14	4.11 ± 0.04
		6.0	69.3	88.8	99.1	120.6	1.36 ± 0.65	4.92 ± 0.53
		7.0	66.0	75.2	92.6	115.0	1.32 ± 0.39	6.22 ± 0.60
		7.0	66.8	88.2	109.5	137.7	1.77 ± 0.37	6.08 ± 0.43
16.7	Nisqually	0	66.2	61.6	60.0	56.4	-0.38 ± 0.20	0
		0	60.0	53.9	52.5	50.7	-0.42 ± 0.40	0
		1.5	66.6	71.1	81.2	92.8	0.48 ± 0.95	1.37 ± 0.11
		3.0	64.1	80.0	97.5	110.9	1.35 ± 0.46	2.62 ± 0.23
		4.5	62.2	76.2	92.9	110.8	1.38 ± 0.12	3.80 ± 0.25
		6.0	62.0	79.0	100.5	118.4	1.59 ± 0.42	5.25 ± 0.48
		7.0	65.1	80.8	100.8	126.6	1.58 ± 0.05	6.16 ± 0.08
		7.0	60.0	77.1	92.2	124.8	1.79 ± 0.53	6.05 ± 0.13

Appendix A. Table 19. (continued)

Temperature (°C)		Nominal ration (% weight. day^{-1})	Beginning mean weight (g)	Week 2 mean weight (g)	Week 4 mean weight (g)	Week 6 mean weight (g)	Mean specific growth rate ± 2.S.E. (%.day^{-1})	Mean ration ± 2.S.E. (% weight.day^{-1})
16.7	Manx x Nisqually	0	65.8	62.3	59.2	56.2	-0.38 ± 0.02	0
		0	66.3	63.1	62.3	60.2	-0.24 ± 0.17	0
		1.5	57.0	66.5	77.2	88.8	1.06 ± 0.06	1.38 ± 0.01
		3.0	69.5	81.3	99.0	124.5	1.42 ± 0.25	2.70 ± 0.31
		4.5	70.8	85.1	99.3	117.0	1.18 ± 0.14	4.09 ± 0.10
		6.0	64.8	78.7	99.6	118.0	1.46 ± 0.27	5.34 ± 0.93
		7.0	63.8	74.4	101.6	125.2	1.61 ± 0.66	6.33 ± 0.06
		7.0	62.2	75.4	95.2	121.3	1.63 ± 0.15	6.32 ± 0.50
19.0	Manx	0	64.8	58.8	55.6	52.1	-0.52 ± 0.18	0
		0	64.5	57.5	54.2	50.0	-0.61 ± 0.24	0
		1.5	63.6	74.5	83.7	-	0.98 ± 0.24	1.30 ± 0.18
		3.0	67.4	84.6	101.3	115.6	1.29 ± 0.39	2.77 ± 0.28
		4.5	60.0	72.5	90.6	110.4	1.45 ± 0.15	3.99 ± 0.07
		6.0	64.9	76.4	92.3	101.2	1.06 ± 0.41	5.16 ± 0.70
		7.0	66.2	76.5	88.0	105.7	1.11 ± 0.20	6.22 ± 0.45
		7.0	66.5	84.4	107.0	129.2	1.62 ± 0.29	6.03 ± 0.33
19.0	Nisqually	0	67.7	62.6	59.0	57.9	-0.33 ± 0.33	0
		0	69.7	63.8	60.0	56.8	-0.50 ± 0.18	0
		1.5	56.4	60.0	65.2	68.7	0.47 ± 0.13	1.57 ± 0.23
		3.0	70.3	89.0	104.0	121.2	1.34 ± 0.47	2.65 ± 0.33
		4.5	66.0	83.7	104.7	124.1	1.50 ± 0.30	3.94 ± 0.23
		6.0	66.7	85.0	103.5	124.2	1.48 ± 0.27	4.64 ± 0.93
		7.0	67.8	94.3	121.6	146.2	1.99 ± 0.37	6.02 ± 0.44
		7.0	69.2	90.4	113.7	141.9	1.76 ± 0.30	6.00 ± 0.38
19.0	Manx x Nisqually	0	62.4	54.8	50.8	46.4	-0.71 ± 0.23	0
		0	64.5	58.0	54.6	53.2	-0.46 ± 0.33	0
		1.5	66.1	75.7	84.4	94.2	0.84 ± 0.13	1.38 ± 0.08
		3.0	63.9	73.5	91.1	107.3	1.23 ± 0.32	2.44 ± 0.45
		4.5	63.0	79.3	102.5	127.3	1.68 ± 0.17	3.92 ± 0.12
		6.0	67.1	94.1	105.6	130.6	1.59 ± 0.92	5.13 ± 0.59
		7.0	67.0	88.0	116.7	138.1	1.72 ± 0.52	6.09 ± 0.21
		7.0	69.0	88.5	107.1	125.2	1.46 ± 0.47	6.00 ± 0.61

Appendix A. Table 20. Definitive experiments, D.1, D.2 and D.3; initial mean length-weight, standard deviations, constants for the equation $\log_{10}$ weight = a + b $\log_{10}$ length and correlation coefficients (r) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures.

Experiment Number	Temperature (°C)	Strain	Sample size no.	Mean weight (g)	Mean Fork length (cm)	Constants a	b	r
D.1	12.0	MM	10	7.8 (1.7)*	8.1 (1.4)	-1.77	2.86	0.97
		NN	10	7.8 (2.7)	8.4 (1.3)	-1.92	3.01	0.98
		MN	10	7.1 (1.7)	8.1 (0.7)	-1.44	2.52	0.84
	14.33	MM	30	6.7 (2.0)	7.9 (0.9)	-1.71	2.80	0.94
		NN	30	6.8 (2.4)	7.9 (1.0)	-1.77	2.88	0.97
		MN	29	6.7 (2.3)	7.8 (1.1)	-1.70	2.81	0.98
	16.7	MM	30	7.8 (3.1)	8.1 (1.3)	-1.34	2.43	0.81
		NN	30	5.9 (2.9)	7.4 (1.3)	-1.87	2.99	0.96
		MN	30	7.3 (2.8)	8.1 (1.1)	-1.98	3.11	0.99
	19.0	MM	30	7.6 (2.5)	8.1 (1.1)	-1.39	2.48	0.84
		NN	30	6.4 (2.4)	7.8 (1.0)	-1.71	2.80	0.95
		MN	30	7.0 (2.2)	8.0 (0.8)	-1.67	2.78	0.90
D.2	12.0	MM	36	14.8 (4.8)	10.2 (1.1)	-1.91	3.04	0.93
		NN	40	17.8 (6.7)	10.6 (1.2)	-1.63	2.79	0.84
		MN	40	19.0 (7.3)	10.8 (1.4)	-1.84	2.99	0.91
	14.3	MM	40	17.0 (6.4)	10.5 (1.3)	-1.92	3.06	0.98
		NN	40	15.6 (6.8)	10.1 (1.4)	-1.75	2.90	0.89
		MN	40	15.4 (5.2)	10.4 (1.7)	-1.95	3.09	0.97
	16.7	MM	40	16.6 (5.3)	10.4 (1.1)	-1.95	3.10	0.94
		NN	40	18.5 (7.0)	11.1 (2.2)	-1.70	2.85	0.92
		MN	40	16.9 (5.5)	10.5 (1.1)	-1.88	3.03	0.96
	19.0	MM	40	17.7 (5.9)	10.6 (1.1)	-1.79	2.95	0.93
		NN	40	16.3 (6.9)	10.2 (1.3)	-1.85	3.01	0.97
		MN	40	15.5 (6.7)	10.1 (1.3)	-2.04	3.19	0.96
D.3	12.0	MM	80	67.4(19.2)	16.7 (1.7)	-1.64	2.83	0.92
		NN	80	71.8(21.8)	17.1 (1.8)	-1.72	2.89	0.94
		MN	80	70.0(19.2)	17.0 (1.4)	-2.04	3.14	0.92
	14.3	MM	79	65.2(17.1)	16.6 (1.5)	-1.39	2.62	0.86
		NN	80	73.5(22.0)	17.2 (1.7)	-1.93	3.06	0.96
		MN	80	69.0(19.5)	17.1 (1.7)	-1.59	2.77	0.92
	16.7	MM	80	61.0(17.7)	16.4 (1.5)	-1.90	3.03	0.92
		NN	80	68.0(17.7)	16.9 (1.4)	-2.02	3.12	0.92
		MN	80	66.9(21.6)	16.8 (1.7)	-1.95	3.07	0.94
	19.0	MM	80	64.7(20.5)	16.6 (1.8)	-1.83	2.97	0.94
		NN	78	63.3(19.3)	16.5 (1.6)	-1.91	3.03	0.95
		MN	79	62.6(20.2)	16.6 (1.7)	-2.00	3.11	0.96

* figures in brackets are standard deviations

Appendix A. Table 21. Definitive experiment D.1; final length-weight, standard deviation constants for the equation $\log_{10}$ weight = a + b $\log_{10}$ length and correlation coefficients (r) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 6 ration levels.

Temperature (°C)	Ration (% wet weight day^{-1})	Strain	Sample size no.	Mean weight (g)	Mean Fork length (cm)	Constants a	b	r
12.0	0	MM	10	4.8 (1.6)	7.7 (1.0)	-1.58	2.53	0.97
		NN	10	5.7 (2.1)	8.2 (1.0)	-2.11	3.21	0.98
		MN	10	6.1 (2.8)	8.2 (1.3)	-2.03	3.04	0.98
	1.5	MM	5	11.4 (2.1)	9.6 (0.6)	-1.75	2.85	0.98
		NN	5	9.6 (3.5)	9.0 (0.9)	-2.11	3.22	0.99
		MN	5	8.6 (3.3)	8.5 (1.0)	-1.46	2.56	0.82
	3.0	MM	5	17.5 (2.3)	10.8 (0.7)	-0.81	1.98	0.91
		NN	5	15.9 (4.0)	10.4 (1.1)	-1.59	2.74	1.00
		MN	5	14.8 (6.4)	10.3 (1.5)	-1.91	3.02	0.98
	4.5	MM	5	17.5 (2.3)	10.8 (0.7)	-1.83	2.94	0.99
		NN	5	10.3 (2.8)	9.0 (1.1)	-1.49	2.60	0.99
		MN	5	13.4 (3.8)	10.1 (0.9)	-2.00	3.10	0.94
	6.0	MM	5	11.8 (5.2)	9.5 (1.3)	-1.69	2.80	1.00
		NN	5	11.7 (4.2)	9.5 (1.2)	-1.75	2.87	0.97
		MN	5	16.2 (6.1)	10.7 (1.2)	-1.94	3.05	0.98
	7.0	MM	10	13.7 (4.4)	10.2 (1.3)	-1.84	2.94	0.99
		NN	10	13.8 (6.6)	10.0 (1.5)	-2.10	3.21	0.99
		MN	10	12.0 (4.2)	9.5 (1.4)	-1.16	2.28	0.94
14.3	0	MM	10	6.2 (1.8)	8.3 (1.0)	-1.87	2.88	0.98
		NN	10	5.5 (1.5)	8.1 (0.7)	-2.05	3.05	0.91
		MN	10	5.8 (2.1)	8.3 (1.0)	-2.02	3.00	0.98
	1.5	MM	5	10.8 (3.4)	9.3 (1.1)	-1.79	2.91	1.00
		NN	5	10.5 (2.5)	9.4 (0.6)	-2.34	3.44	0.97
		MN	5	10.6 (2.1)	9.5 (0.7)	-1.62	2.70	0.91
	3.0	MM	5	8.4 (5.2)	8.1 (1.5)	-1.78	2.94	1.00
		NN	5	10.7 (3.5)	9.2 (0.9)	-2.16	3.29	0.98
		MN	5	10.1 (4.9)	8.8 (1.5)	-1.76	2.90	0.95
	4.5	MM	5	17.7 (6.3)	11.2 (1.2)	-1.78	2.88	0.87
		NN	5	14.9 (8.5)	10.0 (2.1)	-1.80	2.93	0.99
		MN	5	19.2 (6.3)	11.2 (1.3)	-1.86	2.99	0.97
	6.0	MM	5	12.5 (6.2)	9.4 (1.5)	-2.06	3.21	0.98
		NN	5	17.6(12.0)	10.2 (2.0)	-1.92	3.10	0.98
		MN	5	13.1 (5.5)	9.7 (1.3)	-2.03	3.16	0.98
	7.0	MM	10	14.5 (4.7)	10.1 (1.0)	-1.59	2.73	0.88
		NN	10	16.0 (6.3)	10.3 (1.2)	-1.98	3.12	0.97
		MN	10	16.6 (7.0)	10.5 (1.7)	-1.69	2.83	0.99
16.7	0	MM	10	5.4 (1.0)	8.2 (0.6)	-1.68	2.63	0.95
		NN	10	4.6 (1.7)	7.6 (1.0)	-1.93	2.92	0.99
		MN	10	5.4 (1.6)	8.1 (0.8)	-2.02	3.02	0.93
	1.5	MM	5	9.8 (1.1)	9.1 (0.2)	-2.88	4.04	0.71
		NN	5	10.9 (3.3)	9.4 (0.9)	-1.86	2.97	0.98
		MN	5	7.6 (2.4)	8.3 (0.8)	-2.49	3.65	0.98
	3.0	MM	5	15.6 (5.1)	10.3 (1.3)	-1.42	2.58	0.96
		NN	5	12.1 (4.2)	9.4 (1.2)	-1.40	2.54	0.98
		MN	5	16.3 (4.9)	10.6 (1.2)	-1.54	2.67	0.94
	4.5	MM	5	16.2 (4.7)	10.4 (1.1)	-1.64	2.79	0.99
		NN	5	18.2 (4.0)	10.8 (1.0)	-1.30	2.48	0.97
		MN	5	15.0 (5.4)	10.3 (1.0)	-2.24	3.37	0.97
	6.0	MM	5	14.2 (3.8)	10.1 (0.8)	-2.23	3.36	0.99
		NN	5	12.3 (6.8)	9.4 (2.2)	-1.99	3.11	1.00
		MN	5	15.8 (4.0)	10.4 (1.3)	-2.06	3.19	0.98
	7.0	MM	10	18.5 (5.5)	10.8 (1.0)	-2.01	3.15	0.99
		NN	10	18.8 (2.9)	11.1 (0.4)	-2.49	3.61	0.87
		MN	10	15.5 (4.0)	10.3 (0.8)	-2.11	3.24	0.96

Appendix A. Table 21. (continued)

Temperature (°C)	Ration (% wet weight day^{-1})	Strain	Sample size no.	Mean weight (g)	Mean Fork length (cm)	Constants a	b	r
19.0	0	MM	10	3.8 (1.2)	7.3 (0.8)	-1.92	2.89	0.93
		NN	10	4.1 (1.3)	7.2 (0.9)	-1.77	2.75	0.91
		MN	10	4.3 (1.8)	7.6 (1.2)	-1.86	2.82	0.97
	1.5	MM	5	9.5 (3.4)	8.8 (1.2)	-1.57	2.68	0.98
		NN	5	10.6 (4.8)	9.1 (1.5)	-1.54	2.66	0.99
		MN	5	9.3 (4.4)	8.6 (1.3)	-2.02	3.16	0.96
	3.0	MM	5	15.9 (2.0)	10.5 (0.5)	-1.28	2.44	0.65
		NN	5	11.7 (5.3)	9.3 (1.4)	-1.56	2.70	0.97
		MN	5	9.2 (4.7)	8.5 (1.7)	-1.89	3.02	0.98
	4.5	MM	5	9.6 (5.4)	8.2 (1.7)	-1.54	2.72	0.97
		NN	5	21.7 (6.6)	11.4 (1.3)	-1.77	2.93	0.99
		MN	5	13.9 (5.2)	9.9 (1.2)	-2.27	3.41	1.00
	6.0	MM	5	17.6 (6.9)	10.7 (1.4)	-2.18	3.30	0.99
		NN	5	15.5 (9.7)	9.8 (2.0)	-1.56	2.74	0.98
		MN	5	15.1 (7.9)	9.6 (2.1)	-1.43	2.61	0.98
	7.0	MM	10	16.2 (5.4)	10.2 (1.2)	-1.88	3.05	0.90
		NN	10	13.5 (7.3)	9.4 (1.9)	-1.78	2.94	1.00
		MN	10	16.7 (4.7)	10.5 (1.1)	-1.68	2.83	1.00

Appendix A. Table 22. Definitive experiment, D.2; final length-weight, standard deviations, constants for the equation $\log_{10}$ weight = a + b $\log_{10}$ length and correlation coefficients (r) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 6 ration levels.

Temperature (°C)	Ration (% wet weight day^{-1})	Strain	Sample size no.	Mean weight (g)	Mean Fork length (cm)	Constants a	b	r
12.0	0	MM	20	14.3 (4.4)	10.6 (1.1)	-1.90	2.96	0.89
		NN	20	11.5 (5.6)	10.1 (1.5)	-1.97	2.99	0.87
		MN	20	12.5 (6.1)	10.2 (1.6)	-2.27	3.30	0.96
	1.5	MM	10	29.6 (7.1)	13.0 (1.2)	-1.46	2.63	0.99
		NN	10	33.3 (8.3)	13.5 (1.3)	-1.46	2.64	0.97
		MN	10	30.7(10.6)	13.1 (1.6)	-2.10	3.19	0.99
	3.0	MM	10	38.6(18.8)	13.9 (2.0)	-1.83	2.97	0.98
		NN	10	35.8(12.6)	13.7 (1.5)	-1.96	3.08	0.98
		MN	10	35.7 (7.4)	13.8 (0.8)	-1.85	2.98	0.88
	4.5	MM	10	50.7(12.5)	15.1 (1.6)	-1.95	3.09	0.99
		NN	10	44.1(11.0)	14.5 (1.2)	-1.91	3.05	0.98
		MN	10	39.1(11.8)	14.0 (1.5)	-1.65	2.82	0.97
	6.0	MM	10	37.9(15.1)	14.0 (2.2)	-1.75	2.88	0.97
		NN	10	44.0(20.0)	14.7 (2.2)	-1.76	2.89	0.97
		MN	10	43.6(10.0)	14.4 (1.2)	-1.49	2.69	0.91
	7.0	MM	20	45.7(14.2)	14.8 (1.5)	-1.79	2.93	0.76
		NN	20	45.69(17.0)	14.6 (1.9)	-2.06	3.18	0.97
		MN	20	45.8(13.3)	14.6 (1.4)	-1.99	3.11	0.91
14.3	0	MM	20	13.8 (6.6)	10.5 (1.8)	-1.92	2.96	0.95
		NN	20	13.6 (5.5)	10.6 (1.5)	-1.99	3.02	0.99
		MN	20	12.8 (5.8)	10.5 (1.4)	-2.09	3.12	0.91
	1.5	MM	10	28.1 (9.5)	12.5 (1.7)	-1.12	2.34	0.95
		NN	10	23.4 (9.5)	11.9 (1.8)	-1.71	2.84	0.98
		MN	10	21.2 (7.1)	11.4 (1.7)	-1.04	2.22	0.94
	3.0	MM	10	46.2(15.0)	14.8 (1.5)	-1.68	2.85	0.90
		NN	10	46.6(10.5)	15.1 (1.1)	-1.63	2.79	0.87
		MN	10	35.6(11.9)	13.6 (1.5)	-2.07	3.18	0.94
	4.5	MM	10	32.1(14.7)	12.8 (2.4)	-1.93	3.07	1.00
		NN	10	32.4(12.9)	12.8 (2.3)	-1.79	2.95	0.99
		MN	10	35.9(16.7)	13.4 (2.3)	-2.00	3.12	0.99
	6.0	MM	10	35.9(10.9)	14.0 (1.4)	-1.73	2.85	0.97
		NN	10	35.0(12.6)	13.5 (1.7)	-1.76	2.91	0.94
		MN	10	48.9(16.3)	14.6 (1.9)	-2.00	3.12	0.99
	7.0	MM	20	36.3(19.0)	13.6 (2.4)	-2.07	3.16	0.95
		NN	20	32.3(22.5)	13.0 (2.6)	-1.82	2.94	0.92
		MN	20	40.2(15.5)	14.1 (1.9)	-2.03	3.14	0.96
16.7	0	MM	20	12.5 (6.5)	10.2 (1.4)	-2.23	3.26	0.92
		NN	20	12.0 (6.5)	10.2 (1.8)	-2.16	3.17	0.96
		MN	20	12.4 (5.8)	10.2 (1.6)	-2.31	3.33	0.99
	1.5	MM	10	25.2 (5.5)	12.2 (1.1)	-1.67	2.82	0.95
		NN	10	23.2 (8.1)	11.8 (1.5)	-1.63	2.78	0.98
		MN	10	25.6 (6.4)	12.1 (1.2)	-1.27	2.74	0.93
	3.0	MM	10	44.1(14.7)	14.5 (1.6)	-1.74	2.90	0.97
		NN	10	31.8(14.2)	13.5 (1.8)	-2.01	3.08	0.85
		MN	10	35.4(11.3)	13.7 (1.4)	-1.64	2.79	0.86
	4.5	MM	10	43.1(12.4)	14.3 (1.3)	-1.76	2.93	0.95
		NN	10	34.7(16.9)	13.0 (2.1)	-1.39	2.59	0.70
		MN	10	25.9 (7.3)	12.0 (1.2)	-1.73	2.90	0.98
	6.0	MM	10	46.4(15.6)	14.9 (1.4)	-2.18	3.27	0.94
		NN	10	48.6(15.2)	15.0 (1.5)	-1.88	3.02	0.97
		MN	10	43.0(11.4)	14.4 (1.2)	-1.75	2.92	0.95
	7.0	MM	20	34.6(12.0)	13.2 (1.5)	-1.87	3.02	0.95
		NN	20	46.0(18.0)	14.5 (1.8)	-1.64	2.82	0.96
		MN	20	42.1(15.0)	14.1 (1.8)	-1.67	2.85	0.99

Appendix A. Table 22. (continued)

Temperature (°C)	Ration (% wet weight day-1)	Strain	Sample size no.	Mean weight (g)	Mean Fork length (cm)	Constants a	b	r
19.0	0	MM	20	11.5 (4.4)	9.9 (1.2)	-1.79	2.84	0.92
		NN	20	12.8 (5.6)	10.3 (1.5)	-1.95	2.98	0.96
		MN	20	12.7 (6.2)	10.2 (1.5)	-2.28	3.32	0.98
	1.5	MM	10	30.3 (6.9)	12.8 (1.0)	-1.53	2.71	0.94
		NN	10	21.6 (6.1)	11.5 (1.1)	-1.50	2.66	0.95
		MN	10	24.9 (5.2)	12.3 (0.9)	-1.55	2.70	0.97
	3.0	MM	10	34.4 (9.3)	13.4 (1.3)	-1.74	2.90	0.94
		NN	10	43.2(15.7)	13.9 (1.8)	-1.72	2.91	0.96
		MN	10	32.5(13.5)	12.9 (1.9)	-2.06	3.19	0.98
	4.5	MM	10	37.5(14.2)	13.3 (1.8)	-1.78	2.97	0.97
		NN	10	46.5(12.3)	14.9 (1.9)	-0.49	1.83	0.75
		MN	10	36.6 (9.5)	13.3 (1.3)	-1.34	2.57	0.96
	6.0	MM	10	39.5(19.6)	13.4 (2.2)	-1.97	3.13	0.97
		NN	10	36.6(17.2)	13.1 (2.3)	-1.75	2.94	0.99
		MN	10	30.22(11.9)	12.9 (1.8)	-1.56	2.72	0.94
	7.0	MM	10	35.0(12.7)	13.1 (1.6)	-2.57	3.66	0.81
		NN	10	43.8(14.8)	14.4 (2.1)	-0.92	2.20	0.77
		MN	10	38.6(10.6)	13.6 (1.3)	-1.52	2.73	0.79

Appendix A. Table 23. Definitive experiment, D.3; final length-weight, standard deviations, constants for the equation $\log_{10}$ weight = a + b $\log_{10}$ length and correlation coefficients (r) of rainbow trout strains Manx (MM), Nisqually (NN) and their hybrid (MN) in 4 temperatures and 6 ration levels.

Temperature (°C)	Ration wet weight day^{-1})	Strain	Sample size no.	Mean weight (g)	Mean Fork length (cm)	Constants a	b	r
12.0	0	MM	20	57.4(10.7)	17.1 (1.0)	-2.15	3.16	0.92
		NN	20	57.1(14.4)	17.2 (1.4)	-1.85	2.91	0.94
		MN	20	54.9(11.4)	16.9 (1.2)	-1.81	2.88	0.87
	1.5	MM	10	84.5(14.2)	18.3 (0.8)	-2.32	3.36	0.78
		NN	10	102.2(16.2)	19.3 (1.1)	-1.13	2.44	0.81
		MN	8	100.2(15.7)	19.4 (1.2)	-1.15	2.44	0.84
	3.0	MM	10	117.0(24.3)	20.1 (1.2)	-1.61	2.82	0.76
		NN	10	135.7(23.9)	21.0 (1.1)	-2.09	3.19	0.78
		MN	10	126.0(11.7)	20.5 (0.6)	-1.45	2.70	0.84
	4.5	MM	10	104.6(16.7)	19.6 (0.9)	-2.27	3.32	0.87
		NN	9	104.7(18.3)	19.4 (1.2)	-1.73	2.90	0.92
		MN	10	129.8(26.3)	20.5 (1.2)	-2.14	3.24	0.87
	6.0	MM	10	114.7(15.0)	20.3 (1.3)	0.10	1.50	0.52
		NN	10	114.2(17.5)	19.9 (0.6)	-3.37	4.18	0.64
		MN	10	126.6(25.6)	20.5 (1.4)	-1.56	2.79	0.90
	7.0	MM	20	102.7(23.8)	19.2 (1.3)	-2.08	3.19	0.89
		NN	19	142.7(26.0)	21.0 (1.1)	-1.24	2.57	0.57
		MN	20	124.8(19.4)	20.5 (0.8)	-2.79	3.72	0.88
14.3	0	MM	20	55.3(12.4)	17.0 (1.1)	-2.17	3.18	0.95
		NN	20	56.7(11.5)	17.1 (1.1)	-1.90	2.96	0.94
		MN	19	53.8(10.0)	17.0 (0.9)	-2.22	3.21	0.91
	1.5	MM	10	88.2(14.5)	18.8 (1.3)	-1.16	2.44	0.96
		NN	8	101.3(12.5)	19.5 (0.7)	-2.10	3.18	0.78
		MN	10	103.6(10.5)	19.3 (0.8)	-1.04	2.37	0.84
	3.0	MN	10	104.7(26.4)	19.6 (1.5)	-2.29	3.33	0.98
		NN	10	118.8(19.1)	20.4 (1.1)	-1.70	2.88	0.93
		MN	10	119.3(29.7)	20.3 (1.6)	-2.40	3.43	0.94
	4.5	MM	10	104.6(19.4)	19.6 (1.4)	-1.00	2.33	0.82
		NN	10	125.0(22.3)	20.6 (1.0)	-2.38	3.40	0.85
		MN	10	114.9(21.3)	19.8 (1.3)	-1.44	2.70	0.91
	6.0	MM	10	116.8(17.6)	20.1 (1.0)	-1.75	2.93	0.85
		NN	10	126.8(19.0)	20.5 (1.2)	-0.82	2.23	0.75
		MN	10	127.0(19.1)	20.4 (1.2)	-1.18	2.50	0.91
	7.0	MM	20	113.5(21.4)	20.1 (1.4)	-1.19	2.49	0.86
		NN	20	119.0(20.5)	20.3 (1.1)	-1.76	2.93	0.89
		MN	20	125.2(32.4)	20.3 (1.5)	-1.94	3.08	0.92
16.7	0	MM	20	57.2(11.9)	16.9 (1.1)	-1.92	2.99	0.84
		NN	20	53.5(11.7)	16.6 (1.0)	-2.28	3.28	0.93
		MN	19	58.1(14.2)	17.2 (1.2)	-1.86	2.92	0.90
	1.5	MM	9	100.0(14.6)	19.1 (1.0)	-1.55	2.77	0.96
		NN	10	92.8(31.7)	18.6 (2.1)	-1.56	2.77	0.97
		MN	10	88.8(13.2)	18.7 (0.9)	-1.72	2.88	0.88
	3.0	MM	10	111.2(21.9)	19.8 (1.1)	-2.03	3.14	0.81
		NN	10	110.9(24.1)	19.8 (1.3)	-1.97	3.09	0.86
		MN	10	124.5(14.5)	20.5 (0.8)	-1.45	2.71	0.87
	4.5	MM	10	111.6(32.6)	19.4 (1.6)	-2.48	3.50	0.98
		NN	9	110.8(23.9)	19.6 (1.2)	-2.39	3.43	0.89
		MN	10	117.0(41.4)	19.7 (1.8)	-2.61	3.60	0.96
	6.0	MM	10	118.8(21.5)	20.3 (1.1)	-2.06	3.16	0.89
		NN	10	118.4(28.0)	19.6 (1.3)	-2.44	3.49	0.89
		MN	10	118.0(17.0)	20.1 (0.9)	-2.12	3.21	0.91
	7.0	MM	20	128.4(38.2)	20.1 (1.4)	-2.75	3.72	0.75
		NN	20	125.7(30.6)	20.0 (1.5)	-1.60	2.83	0.92
		MN	17	122.9(34.1)	20.0 (1.5)	-2.71	3.68	0.93

Appendix A. Table 23. (continued)

Temperature (°C)	Ration (% wet weight day^{-1})	Strain	Sample size no.	Mean weight (g)	Mean Fork length (cm)	Constants a	b	r
19.0	0	MM	20	51.1 (9.1)	16.5 (1.0)	-1.00	2.20	0.23
		NN	19	57.3(12.0)	17.1 (1.1)	-2.00	3.04	0.93
		MN	19	49.8 (7.5)	16.4 (0.8)	-1.44	2.58	0.70
	1.5	MM	10	102.8(33.1)	19.0 (1.9)	-2.16	3.25	0.96
		NN	6	68.7(25.5)	17.3 (1.8)	-2.44	3.44	0.94
		MN	9	94.1(19.6)	18.9 (0.8)	-3.41	4.22	0.75
	3.0	MM	10	116.8(31.8)	19.5 (1.7)	-2.10	3.22	0.97
		NN	10	121.2(15.7)	20.0 (1.0)	-1.06	2.42	0.77
		MN	10	107.3(21.8)	19.4 (1.1)	-2.55	3.56	0.94
	4.5	MM	10	110.4(23.6)	19.4 (1.3)	-2.32	3.38	0.98
		NN	10	124.1(30.8)	19.7 (1.1)	-3.51	4.32	0.95
		MN	10	125.5(28.9)	20.2 (1.1)	-2.19	3.29	0.89
	6.0	MM	10	101.2(28.8)	18.7 (1.6)	-2.04	3.17	0.94
		NN	10	124.2(20.4)	20.0 (1.1)	-1.68	2.90	0.87
		MN	10	130.7(23.7)	20.3 (1.1)	-1.97	3.12	0.89
	7.0	MM	20	117.4(26.1)	19.6 (1.4)	-2.00	3.14	0.88
		NN	20	144.0(33.3)	20.7 (1.4)	-1.97	3.13	0.87
		MN	20	131.7(26.5)	20.6 (1.3)	-1.99	3.12	0.94

APPENDIX B

A MODEL FOR ESTIMATING THE GROWTH of CULTURED RAINBOW TROUT (*Salmo gairdneri* RICHARDSON)

by

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ABSTRACT

Papst, M.H., G.B. Ayles and S. Uraiwan. 1980. A model to determine maximum growth of cultured rainbow trout (*Salmo gairdneri* Richardson).

A maximum growth rate model for rainbow trout is developed which incorporates a polynomial function to describe the growth temperature relationship, allowing the model to be used over a wide range of water temperatures (5° C. to 24° C.). Model simulations of the growth of trout in pond, cage, lake and raceway culture systems compared favourably with the actual observed growth. The model reasonably simulated the growth of the rainbow trout strains Idaho, Nisqually and Sundalsora, but failed to describe the growth of the Manx strain. The model proved to be a better estimator of trout growth than existing models.

A series of curves were developed so the model can be of use to fish culturists.

Key Words: Rainbow trout, cultured, model, maximum growth, pond, cage, lake culture.

INTRODUCTION

Mathematical models describing fish growth are potentially important. Such models enable the fish culturist to estimate fish growth while allowing for the planning of production, as well as feeding and marketing schedules. To be of use to the fish culturist the models must accurately estimate growth over a wide range of culture conditions and should be flexible enough so that the model can be adapted to specific culture systems.

It has been shown that the relationship between specific growth and temperature for salmonids is best described by a dome shaped curve (Brett et al. 1969, Elliott 1975, and Hokanson 1977). Yet existing models of trout growth assume linear or exponential growth temperature curves (Haskell 1955, 1959, Piper 1970, Jorgensen 1976, Speece 1973, Sparre 1976, Sperber et al. 1976). This means that these models are inappropriate for estimation of growth rates above 15^{o} C. This is an important limitation, since many types of trout culture are conducted at temperatures higher than 15^{o} C.

Stauffer (1973) described a growth model for hatchery-reared salmonids which incorporated a dome shaped growth temperature curve. McLean (1979) developed a pond rearing model using the curve developed by Stauffer (1973). The growth rate temperature curve developed by Stauffer (1973) was based on the work presented by Banks et al. (1971) and Brett et al. (1969) for Chinook salmon (*Oncorhynchus tshawytscha*) and Sockeye salmon (*Oncorhynchus nerka*).

In this paper, we develop a deterministic growth model for rainbow trout using Stauffers' (1973) approach. The model is developed using rainbow trout growth experiments and is evaluated against the growth of rainbow trout in pond, cage, extensive lake and waste heat (raceway) culture systems, where temperatures exceed 15^{o} C.

This model considers only growth at maximum ration (ration level at which maximum growth occurs). As yet there appears to be no proven way of expressing the growth ration relationship (Ricker 1979). However this is not a limitation to the use of this model in practical fish farming as most fish culturists feed from standard tables which provide for maximum or near maximum ration.

The ability of the model to estimate the growth of different strains of rainbow trout is assessed.

The basic model is reduced to graphic format to facilitate its use by fish culturists.

METHOD

GROWTH MODEL

Stauffer (1973) expressed the maximum specific growth rate as the product of a temperature function and weight function.

$$GM = f_5(T) \cdot f_6(W) \qquad EQ(1)$$

or

$$GM = (a_1 + a_2T + a_3T^2 + a_4T^3 + a_5T^4) \cdot (a_6 W^{-a_7}) \qquad EQ(2)$$

Where GM is the maximum specific growth rate, T is the water temperature °C. W is the weight of the fish in gm., $f_5(T)$ is a temperature growth function and $f_6(W)$ is a weight growth function.

The temperature function $f_5(T)$ was described as a fourth degree polynomial by Stauffer (1973) (Fig. 1). Growth rates from a 1978 pond culture experiment (Uraiwan 1980 unpublished results) and the results from experiments described by Sperber et al. (1976) were transformed to $f_5(T)$ values using EQ. 3 and 4 as described by Stauffer (1973).

$$GM = a(T) \cdot W^{-0.333} \qquad EQ(3)$$

$$f_5(T) = (a(T)/a_6) \qquad EQ(4)$$

Where a (T) is interpreted as the maximum growth rate of a 1 gm. fish at temperature 'T'.

The temperature growth function $f_5(T)$ is then calculated using equation 4.

The $f_5(T)$ curve (temperature growth) was fitted with a fourth degree polynomial over the temperature range of 2°C. to 24°C. (Fig. 1).

The fitted polynomial was then substituted into the equation for $f_5(T)$.

$$f_5(T) = (0.6087-0.127T+0.054T^2-0.0035T^3+0.000062T^4) \qquad \text{EQ(5)}$$

Stauffer (1973) interpreted the coefficient a_6 as representing the maximum instantaneous growth rate of a 1 gram fish at 10°C. However, since a_6 is used to adjust the growth equation for different culture conditions, we do not assign any biological interpretation to the coefficient and therefore it is treated as a scaling factor. Stauffer estimated from the work of Kond and Nore (1971) that a_6 for rainbow trout was approximately 0.055. We have used this as a first estimate of a_6 for our model. The coefficient a_7 was estimated to equal -0.333 assuming that growth is isometric and that weight is the cube of the length (Haskell 1959 reviewed in Ricker 1979).

Substituting in equation 2:

$$GM = (0.6087-0.127T+0.054T^2-0.0035T^3+0.000062T^4)\ (0.055W^{-0.333}) \qquad \text{EQ(6)}$$

The solution of the growth equation is:

$$W = (W_0^{0.333}+0.055f_5(T).(t/3.0))^3 \qquad \text{EQ(7)}$$

Where W_0 is the starting fish weight and W is the final weight of the fish in gm. after time (T) in days.

Assuming that the growth temperature relationship described by $f_5(T)$ describes the growth of trout in all culture systems the model can be adjusted to a specific system by estimating a value for a_6 from past growth temperature records, using equations 8 and 9.

$$GM = (\ln W - \ln W_0)/t \qquad \text{EQ(8)}$$

$$a_6 = GM/(f_5(T) \cdot W^{-0.333}) \qquad \text{EQ(9)}$$

MODEL VALIDATION TRIALS

Pond studies

Experimental pond culture results were used to develop the temperature growth function (1978)* and to verify the model and assess the effect different strains of trout would have on the accuracy of the model predictions (1979)*. The ponds were earthen, still water ponds, .06 hectares in area with mean depths of 1 m. Fish were acclimatized in the ponds for 14 days in floating cages. Fish were fed commercial trout food three times per day at standard feeding table rates (Deuel et al 1952). The rates were adjusted bi-weekly for changes in water temperature and fish weight (Uraiwan 1980).

In the 1978 experiments four ponds were stocked with 25g. fingerlings of Tunkwa (Summerland, B.C., Can.)** rainbow trout, in the 1979 experiments each of the same four ponds was stocked with equal numbers of 4g. Idaho (Soda Springs, Idaho, U.S.A.)**, Nisqually (Olympia, Washington, U.S.A.)** Sundalsora, (Norway)**, and Manx (Isle of Man, U.K.)** rainbow trout forming a mixed population.

Cage Culture

Observation from two cage culture experiments conducted by Whitaker

* indicates year of experiments.

** names indicate the source of the genetic strains.

and Martin (1974) at Heming Lake in northern Manitoba, Canada were used to test the model. Daily temperatures and starting fish weights were used with the model to estimate fish growth. Estimated fish weights were compared with the weights observed by Whitaker and Martin (1974).

In these cage culture experiments fish were held in 5.8 m^3 floating cages and were fed with automatic feeders. The feeding rate was initially obtained from the standardized feeding tables (Deuel et al 1952) but on June 13th was increased by 50%.

Pothole Lake Culture

A comparison was made between the weights estimated by the model$_{1m}$ and weights observed by Tavarutmaneegul(1978), for rainbow trout stocked in two small lakes in Manitoba Canada. The trout were given no supplemental feeding after stocking. Daily records of temperature reported by Tavarutmaneegul(1978) were used to model the growth of the fish. Model estimates of fish growth were compared with weights observed by Tavarutmanegul (1978).

The lakes were stocked with a domestic strain of rainbow trout from an Idaho commercial hatchery. Lakes were sampled weekly with trap nets to obtain average fish weights.

Raceway Culture

Observations from the 1976 raceway culture experiments reported by Eble *et al*. (1979) were used to test the model for use in raceway culture systems (intensive aquaculture) and to test the method for adjusting the a_6 constant. Observations of water temperatures and fish weights for the growth intervals came from figure 10.10 and table 10.3 of Eble et al. (1979).

In this experiment 40g. trout were stocked in a raceway 21.3m x 39.62m x 0.9m deep. Water flow was 1,893 1/min. and the trout were fed commercial trout food at standard feeding table rates.

RESULTS AND DISCUSSION

MODEL VALIDATION

Pond Culture

Predicted weekly mean fish weights for the mixed populations of trout from the four experimental ponds were compared with the actual observed weights (Fig. 2). The projected fish growth curve compared favourably with the observed weights. Figure 2 shows the observed weights for each pond as a function of the predicted fish weights. Both the slope and the intercept are significantly different than 1 and 0 respectively, suggesting that agreement between the model and observations was not perfect (at the 5% level). Growth of the Manx strain in the mixed populations was poor and the model estimates of Manx were higher than the observed growth (Fig. 2C). Agreement between the model and the observed fish weights improved when the Manx strain was excluded (Fig. 2).

The results indicated that the accuracy of the model in predicting growth is affected by the strain of trout used, however the model appears to give reasonable estimates of the growth of the trout strains Nisqually, Idaho and Sundalsora in pond culture.

Pond water temperatures ranged from 12^{o}C. to greater than 24^{o}C. during the pond experiments (Uraiwan 1980). Model predictions of growth were not affected by the fact that water temperatures exceeded 15^{o}C.

Cage Culture

Weekly fish weights were projected for the cage culture experiments of Whitaker and Martin (1974) (Fig. 3).

Agreement between the model and the observed weights for the 1973A experiment was acceptable. However, the model overestimated fish weights during the latter part of the 1973B experiment. Growth of fish in the cages in the 1973B experiment during the weeks 3, 5 and 7, 9 were observed to be poor. These periods of poor growth correspond to the time of an outbreak of bacterial gill disease and changes in the trout feeding schedule (Whitaker and Martin 1974). Restarting the model on week nine to the observed weight lessened the discrepancy between the model and the observed fish weights (Fig. 3B).

The model can be used for the estimation of trout growth in cage culture. However the results of the 1973B experiment highlight the fact that changes in fish health or culture strategies can affect growth and when such changes occur the fish culturist will have to adjust the model predictions to account for the change in growth that results.

Pothole Lake Culture

Fish weights estimated by the model compared favourably with the observed weights for the first 130 days following the stocking of the two lakes (Fig. 4). After 130 days model estimated weights were higher than observed weights and restarting the model on the observed weight at day 142 did not improve the agreement between the model and the observations. Water temperatures declined markedly after 130 days and were less than 5°C. on day 160 in both the lakes (Fig. 4A). It appears that the model cannot accurately estimate trout growth for water temperatures of 5°C. or less.

The initial estimations of fish weights in lake 255 tended to be lower than the weights that were observed (Fig. 4C). When the model was restarted on day 60 at the observed weights, subsequent observed weights agreed with model estimations. The lack of initial agreement may reflect a problem with the estimation of the water temperatures, Tavarutmaneegul (1978) reported a significant difference between surface and bottom water temperatures during this period.

The highest proportion of the fish growth occurred during the first 130 days, when model estimation agreed with the observed fish growth. The model has considerable potential as a method of estimating trout growth in these types of lake culture systems, but the fish culturist must consider the method of taking water temperatures so that the temperatures used in the model actually represent the culture temperature.

Raceway Culture and Model Adjustments

Three instantaneous growth rates were randomly selected from the results reported by Eble et al. (1979), and were used to calculate a value for the a_6 constant. The value for a_6 was estimated to be 0.0243. Fish weights were projected for all of the temperature growth periods reported by Eble et al. (1979) using this value of a_6. Estimated weights compared well with the observed weights (Fig. 5).

In contrast other trout growth models failed to correctly simulate trout growth (Fig. 5). The exponential model markedly overestimated growth at temperatures above 17^{o}C., resulting in an overall overestimate of the trout growth, even when the conservative 0.5 feeding level was assumed. The Haskell (1959) and Speece (1973) linear model significantly underestimated growth.

Graphic Growth Model

The growth model developed in this paper requires the user to do more calculations than did the linear or "Haskell" model. However the present model can be reduced to a graphic format which allows for the direct interpretation of the model with a minimum of calculations.

PROCEDURE:	EXAMPLE:
Using Fig. 6	
STEP 1 Determine $f_5(T)$ by entering the water temperature on curve 1 and reading the value of $f_5(T)$ from scale B.	for 18°C., $f_5(T) = 1.92$
STEP 2 now determine the value of $f_6(W)$ by reading the D scale value from the weight growth curve 2 that corresponds to the starting weight on scale C.	for a starting weight = 60g. the $f_6(W)$ value is = .0141
STEP 3 Daily growth rate (g/g/day) is determined by multiplying $f_5(T)$ by $f_6(W)$	$1.92 \times .0141$ = .027 g/g/day.

STEP 4 Determine weight gain of fish for one week (7 days) by multiplying the daily growth rate by the starting weight, then by the number of days (7 days)	.027 x 60 = 1.26 g/day 1.26 x 7 11.34 g.
STEP 5 Determine fish weight after one week by adding the starting weight and the weekly weight gain.	11.34 + 60 71.34 g.

Solution of the model in this way will introduce a systematic error. Therefore the user should not use growth periods greater than two weeks (14 days) and ideally the one week period as used in the above example should be used when possible. The user estimates the growth of his fish over time by repeating the above procedure using the estimated weight as the starting weight of the next week. This enables the user to adjust the model for changes in water temperature. The procedure can then be repeated for as long of a culture period as is needed or if the water temperatures are known the culturist can project ahead and determine the length of time needed to bring the trout to marketable size.

An adjusted or culture specific model can also be interpreted graphically by plotting a weight growth curve using the culture specific (adjusted) value for a_6 (Fig. 6 curve 3).

CONCLUSIONS

On the basis of the results, the growth model described by equation four reasonably estimates the growth of rainbow trout in pond, cage, lake and raceway culture systems when the trout are fed at maximum ration. The model can be used over a water temperature range of grom $5^{o}C$. to $24^{o}C$. This is an important advancement over existing models. The model can be adjusted to a specific cultural system, by estimating the value of the a_6 constant using past growth records. The model may be inappropriate for some trout strains as was observed to be the case with the Manx strain. On the basis of this study the model was appropriate for use with three of the four strains tested and there appeared to be no problems with a genetic strain effect in the cases where the strain of trout used was from a domestic hatchery and the genetic strain of the trout was not specified.

The present model better simulated the maximum growth of trout than did existing models.

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FD-6

FIGURES

Fig. 1. The curve of $f_5(T)$, the relation between temperature and maximum specific growth rate for the viable temperature range standardized at 10^{o} C. Curve #1 from Stauffer (1973) curve #2 from rainbow trout experiments. Solid dots results from Sperber (1976), open dots from 1978 pond study.

Fig. 2. Comparison of predicted and mean observed fish weights in the 1979 pond studies, for the mixed and Manx populations; observed pond fish weights as a function of the predicted weights, for the mixed and Manx populations. Solid dots and curves represent predicted weights, open circles represent mean weight of trout in four ponds, vertical bars indicate the range of weights observed. Straight line was fitted by least-squares method.

1- solid dot represents four observations of equal fish weights.

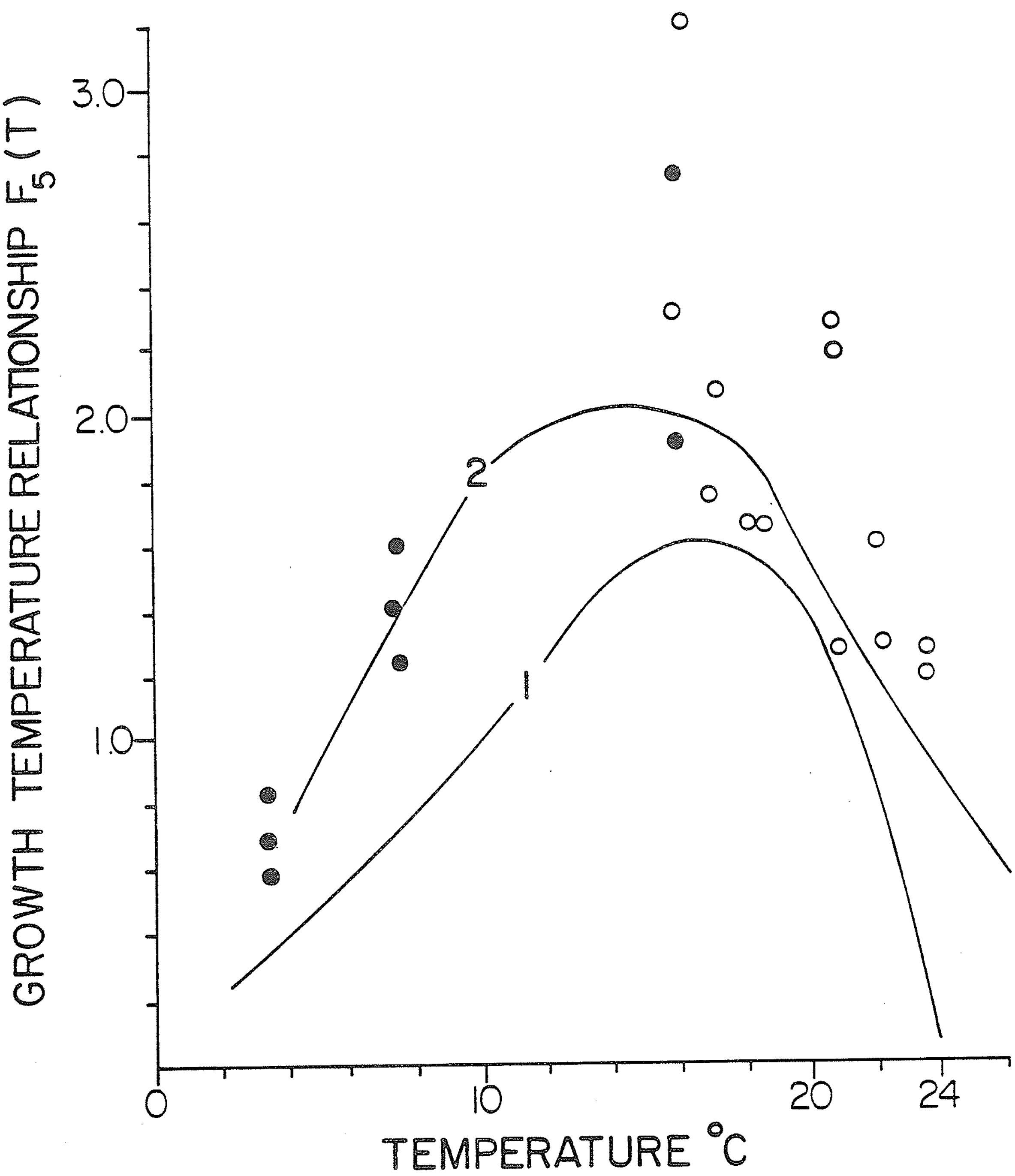
Fig. 3A.B. Comparison of predicted (solid dots) and observed fish weights from 1973 cage experiments Whitaker & Martin (1974). X - represented model prediction after week nine restart (see text).

Fig. 4A. Lake 200 and 255 ten day period mean water temperatures from Tavarutmaneegul (1978).

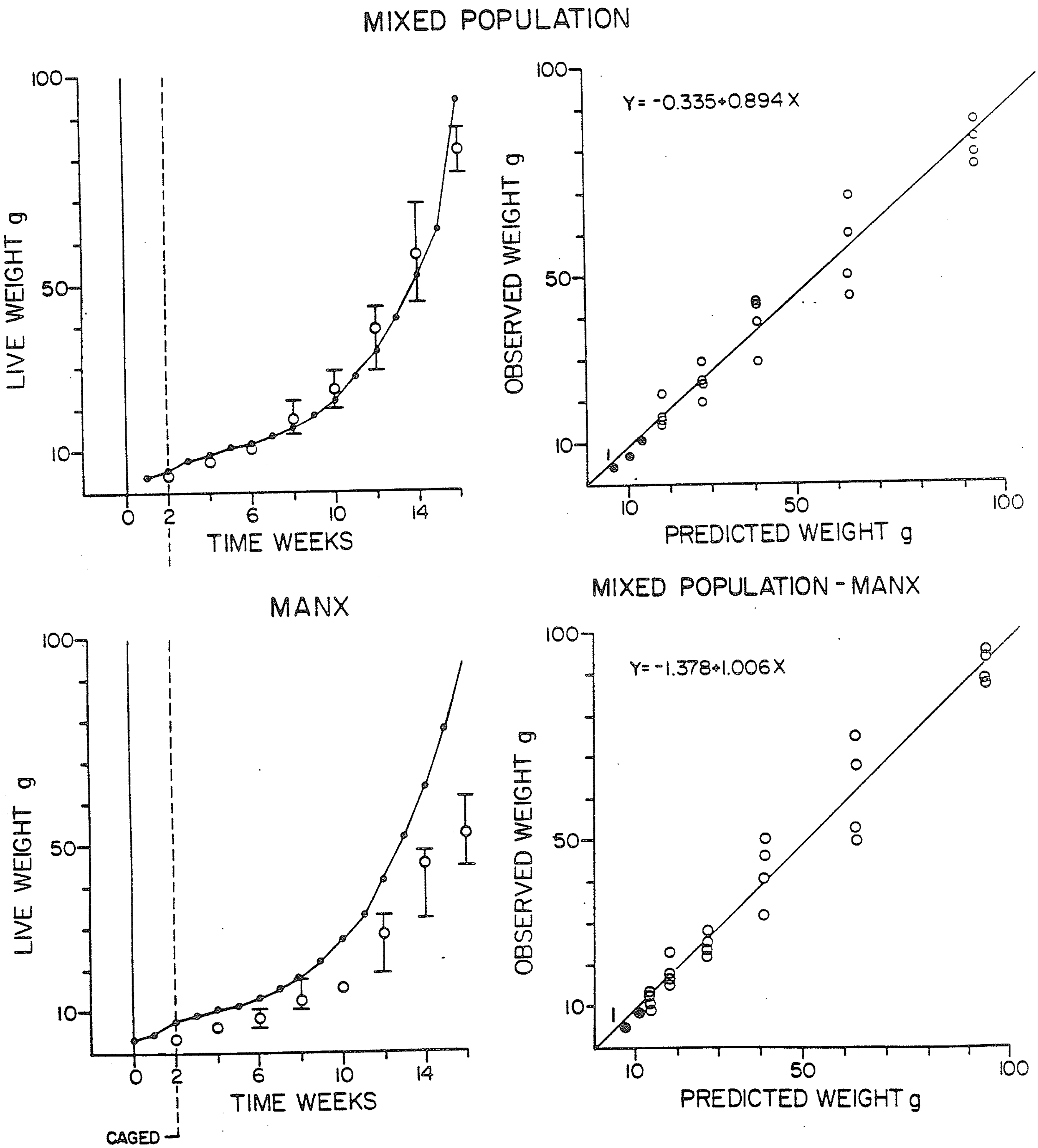
Fig. 4B.C. Comparison of observed (open dots) and predicted (solid & dash lines) fish weights for lake 200 & 255. 1 & 2, restart of model on observed weights (see text). Vertical bars equal IS.D.

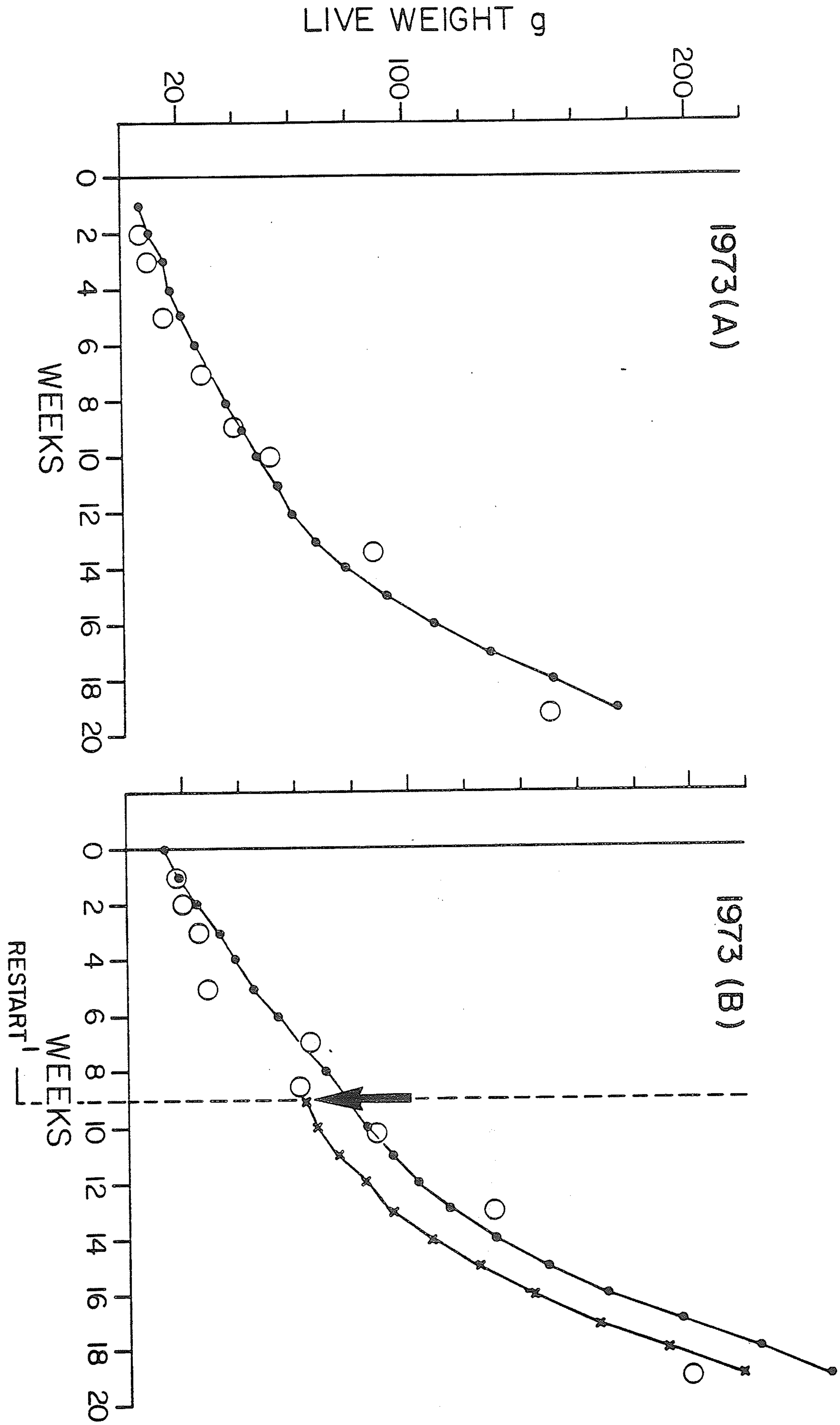
Fig. 5. Comparison of predicted and observed fish weights for the 1976 raceway experiment reported by Eble _et al_. (1979).

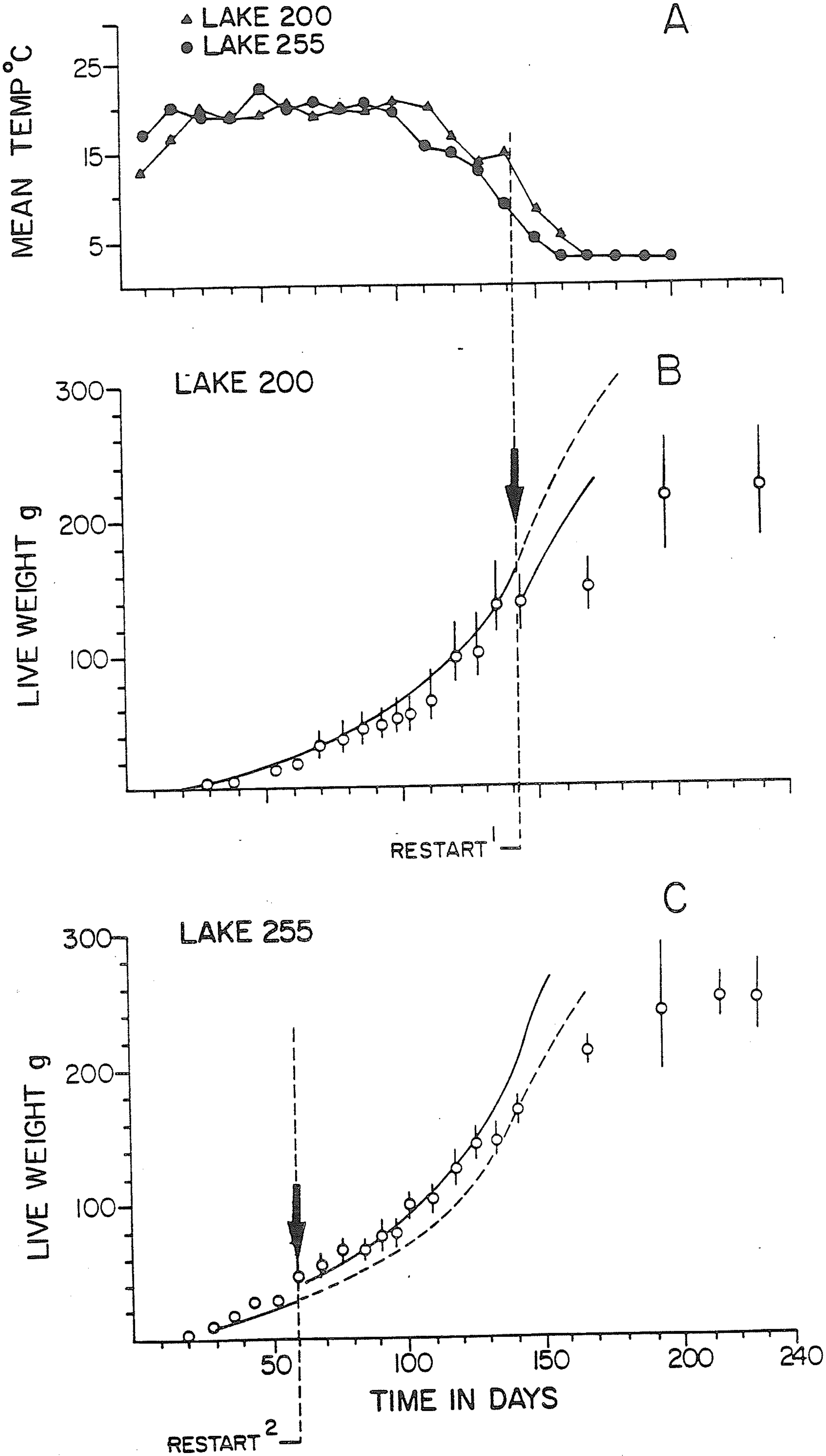
Fig. 6. Graphic format of the growth model; see text for sample calculation.



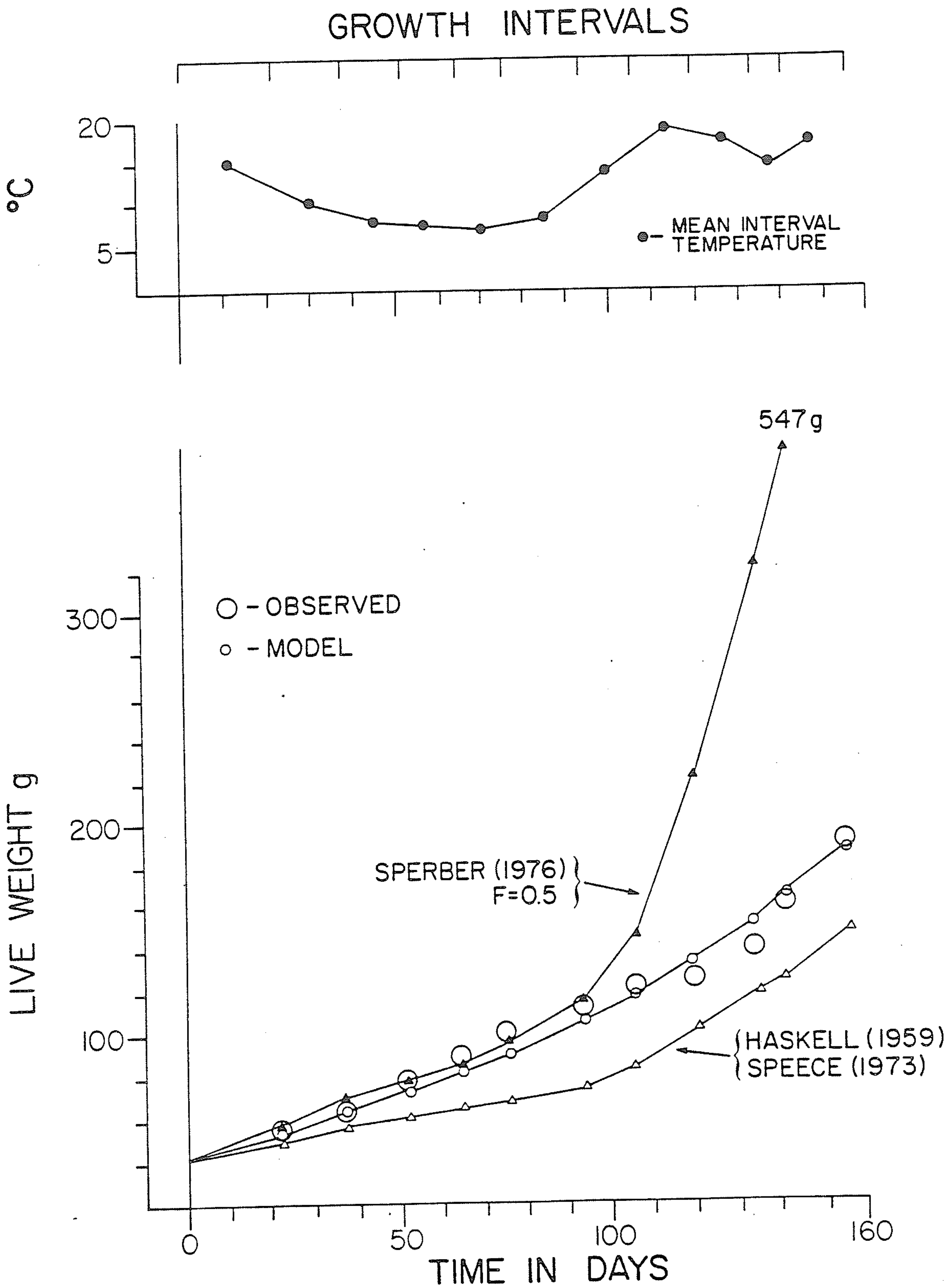
GROWTH TEMPERATURE RELATIONSHIP $F_5(T)$
3.0
2.0
1.0
2
1
0
10
20
24
TEMPERATURE °C

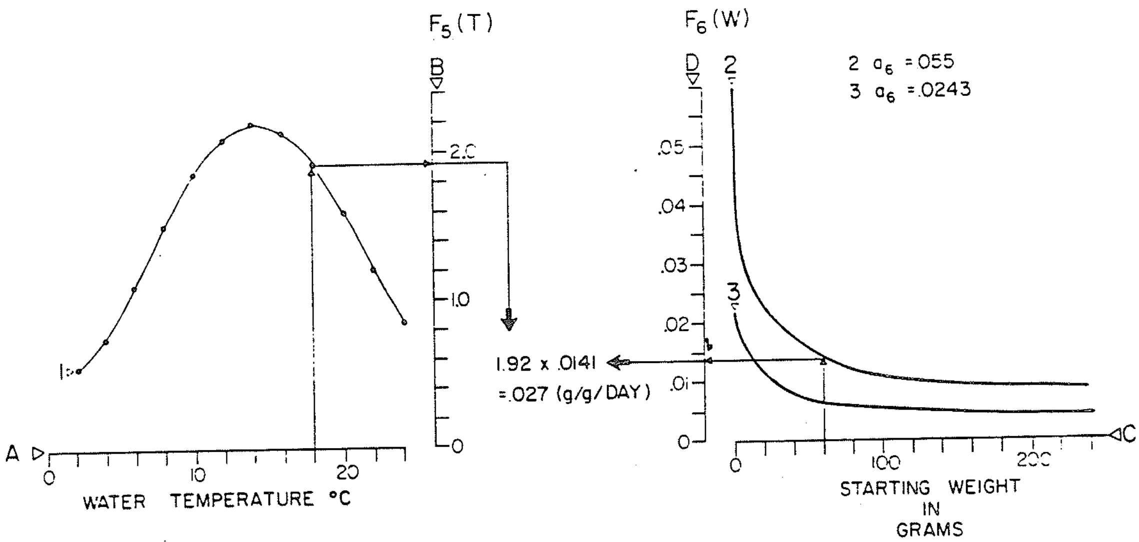

MIXED POPULATION
LIVE WEIGHT g
TIME WEEKS
Y= -0.335+0.894 X
OBSERVED WEIGHT g
PREDICTED WEIGHT g
MIXED POPULATION - MANX
MANX
Y= -1.378+1.006 X
CAGED


LIVE WEIGHT g
20
100
200
1973(A)
1973 (B)
WEEKS
0 2 4 6 8 10 12 14 16 18 20
RESTART



LAKE 200
LAKE 255
A
MEAN TEMP °C
25
15
5
B
LAKE 200
300
200
100
LIVE WEIGHT g
RESTART 1
C
LAKE 255
300
200
100
LIVE WEIGHT g
50
100
150
200
240
TIME IN DAYS
RESTART 2


GROWTH INTERVALS
°C
20
5
MEAN INTERVAL TEMPERATURE
547g
○ - OBSERVED
○ - MODEL
LIVE WEIGHT g
300
200
100
SPERBER (1976) F=0.5
HASKELL (1959) SPEECE (1973)
0
50
100
160
TIME IN DAYS



F5 (T)
B
2.0
1.0
0
A
0
10
20
WATER TEMPERATURE °C
1.92 x .0141
=.027 (g/g/DAY)
F6 (W)
D
2
3
2 a6 =.055
3 a6 =.0243
.05
.04
.03
.02
.01
0
C
0
100
200
STARTING WEIGHT
IN
GRAMS