COMBINED EFFECTS OF TEMPERATURE, BODY SIZE AND FOOD DENSITY ON SWIMMING BEHAVIOUR AND GROWTH OF JUVENILE BROOK TROUT (Salvelinus fontinalis)

LIDONG LIU

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COMBINED EFFECTS OF TEMPERATURE, BODY SIZE AND FOOD DENSITY ON SWIMMING BEHAVIOUR AND GROWTH OF JUVENILE BROOK TROUT (*Salvelinus fontinalis*)

BY

LIDONG LIU, B.Sc., M.Sc.

A thesis submitted to the School of Graduate
Studies in partial fulfilment of the
requirements for the degree of
Doctor of Philosophy

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November 1998

St. John's Newfoundland Canada

ABSTRACT

This study is an attempt to quantify experimentally the body size allometry and thermal dependence of foraging rate (swimming velocity) in juvenile brook trout (*Salvelinus fontinalis*) under different food densities. The results of behavioural experiments on swimming velocity were used in conjunction with additional experimental data on maximum feeding rate and growth rate to carry out a theoretical analysis of the potential effects of changes in body size, temperature, and food density on growth, habitat use, and adult size.

This study differs from previous studies of salmonid feeding in that the foraging movements of individual fish were tracked in real time through a computerized monitoring and control system that provided an accurate quantitative measure of the distance swum vs. time. The monitoring and control system automatically dispensed a food item each time an experimental fish had swum a prescribed distance. The distance swum per food item consumed, a measure of food density, could thus be held constant for any combination of temperature and body mass treatments, allowing for the investigation of the effects of temperature, body mass and food density on feeding behaviour under conditions close to those encountered in a natural foraging environment.

The results of the foraging activity experiments show that the total distance swum, the proportion of time spent actively foraging, and swimming speed are all positively affected by both body mass and temperature, but not by food delivery schedule. The data are clearly not consistent with an optimal foraging model in which foraging velocity is predicted to decrease with increasing body mass and increase with increasing food density.

The body mass allometric scaling factors for total distance swum (0.33-0.56), foraging time (0.21-0.46), and swimming speed (0.10-0.12) at 5, 12, and 18 °C are all markedly lower than the scalings for maximum feeding rate and both standard and active metabolic rates of fish. The allometric scalings for instantaneous and daily swimming costs, however, are close to the scalings for metabolic rates at all three temperatures, suggesting that swimming speeds are regulated by the instantaneous costs of swimming rather than its energy benefits. Because the rate of energy intake is directly proportional to the distance swum, the scaling for energy intake is expected to be well below that for energy requirements .

In contrast to the situation for body mass, the values of the Van't Hoff thermal parameter for distance swum of experimental fish are close to those for sustained swimming speeds and the frequency of muscle contraction and tail beat of most fish, and also comparable to those for the standard and active metabolic rates of fish. This

suggests that distance swum may respond to temperature changes in a way that parallels metabolic rate. If energy intake is a linear function of distance swum, then equivalent temperature scalings of distance swum and metabolic rate would mean that food intake should parallel temperature related changes in metabolic requirements.

The growth rate data is consistent with previous studies and shows that there is a positive relationship between ration and the temperature for maximum growth at any body mass. Daily growth rate increases with increasing temperature at high ration level but decreases at low ration level. As a result, the temperature for maximum growth decreases as food density is decreased.

The analyses of growth rate in actively foraging fish indicated that growth rate should increase with both body mass and temperature at high food densities, and decrease with both body mass and temperature at low food densities. At intermediate densities the situation was more complex as the effect of body mass and temperature on growth rate depended on food density, body size, and temperature. In the low food density simulation, $\mathbf{W}_{\mathbf{max}}$, the body mass at which absolute growth rate is zero, is sensitive to both food density and temperature. $\mathbf{W}_{\mathbf{max}}$ is predicted to increase with increasing food density but decrease with increasing water temperature.

The analyses of growth in actively foraging fish suggested that the temperature at which growth rate is maximized decreases with decreasing food density and

increasing body mass. These results are consistent with previous studies of the effects of temperature on habitat use in fishes. It was not possible to draw any conclusions regarding the effect of temperature on adult size from the results presented in the thesis.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. Robert L. Dunbrack, my supervisor, for his invaluable advice, interest and constant support during the course of my studies at Memorial University of Newfoundland, and during my experimental work and the writing of this dissertation. I would also like to thank my supervisor committee members, Dr. Joseph A. Brown and John M. Green, for their helpful supports, suggestions and their critical evaluations of the dissertation.

I do appreciate Dr. Donald H. Steele for his providing me the backpack electroshocker for fish capture and his invaluable help during the experimental work. Special thanks are also due to Xiaoxiong Li, Xiaolong Yang and Zuxu Yao for their assistance during the laboratory and field work. My gratitude is extended to my wife, Shujun Lin, for her contributing to the typing of the thesis, showing great patience and providing much assistance and encouragement throughout this program, to my parents for their encouragement, and to all my friends at Memorial University for their invaluable help and suggestions during my research.

Financial support was provided by a Natural Sciences and Engineering Research Council grant to Dr. R. L. Dunbrack and a Fellowship to L. Liu from the School of Graduate Studies, Memorial University of Newfoundland.

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Chapter 1

INTRODUCTION

1.1. Introduction

Temperature, body size, and food density are the three most important variables affecting the growth of fishes (Webb 1978; Brett & Groves 1979; Weatherley & Gill 1987). Their influence on growth is mediated through both behavioural (foraging) and physiological (growth and metabolism) mechanisms and these effects have been widely investigated (e.g. Pentelow 1939; Donaldson & Foster 1940; Brown 1946a, b, c; 1957; Baldwin 1956; Taylor 1958; Kinne 1960; Menzel 1960; Strawn 1961; Davies 1964; Paloheimo & Dickie 1966a, b; Brett et al. 1969; Pandian 1970; McCormick et al.1972; Niimi & Beamish 1974; Elliott 1975a, b, c; 1976; Gerald 1976; Hokanson et al. 1977; Davies & Massey 1977; Wurtsbaugh & Davis 1977; Spigarelli et al. 1982; Jobling 1983; Sadler et al. 1986; Hidalgo et al. 1987; Cui & Wootton 1988a, b; Wieser et al. 1988; Vondracek et al. 1989; Jensen 1990; Siemien & Carline 1991; Smith et al 1991; Woiwode & Adelman 1991; Xie & Sun 1992; Borghetti & Canzi 1993; Salam & Davies 1994). However, most works have focused on applied physiological problems such as the identification of temperature optima for food consumption and conversion efficiency at fixed ration levels, or the effect of body mass on feeding processes under fixed or replete rations. There has been little experimental work on the influence of temperature, body mass, or food density on feeding and growth when rations are below these maxima and are not fixed by the experimental design but rather are determined by a fish's food search activity as well as food density; conditions typical of the foraging of wild fishes.

In wild populations, the feeding and growth rates of individuals are generally limited by the availability of food and not by physiological constraints on the rate at which food can be processed (Ware 1972). Feeding rates are usually well below physiological maxima and should be proportional to the density of food in the environment and the rate at which a fish moves through its environment searching for food. Consequently, the effect of changes in temperature and body size on feeding and growth rates under natural conditions cannot necessarily be inferred from the general allometric and thermal equations that apply to the physiological processes of metabolism, digestion, and food conversion. What is instead required are allometric and thermal equations of behaviour that describe how foraging behaviour, specifically the rate of search, changes with body mass and temperature. When this is known, it should be possible to relate changes in body mass and temperature to the feeding and growth of wild fishes.

Physiological parameters, such as rates of metabolism or digestion, generally vary allometrically with body mass, that is, **(physiological rate) = k(body mass)**^{n}, where **k** and **n** are constants and **n** is typically less than 1.0 (Winberg 1956; Jobling 1985). Similarly, these physiological rates change in a predictable and proportional way for a given change in temperature (Fry 1967; Reynolds & Casterlin 1980; Cossins & Bowler 1987). This proportional change is often expressed as a "$\mathbf{Q_{10}}$" ratio (rate at temperature T)/(rate at temperature T-10) or by using the Van't Hoff thermal parameter, **b** (the effect of temperature is expressed as $\mathbf{b^T}$, where **b** is a constant and **T** is the temperature in degrees centigrade; Cossins & Bowler 1987). Although behaviour is inherently more variable than the physiological processes described by these allometric and thermal parameters (Cossins & Bowler 1987), relationships should also exist between behavioural phenomena and temperature and body size that are the behavioural analogs of these physiological scalings. Of specific interest for studies of feeding and growth in wild fishes are body size allometries and thermal scalings that link a fish's rate of movement while searching for food (swimming velocity or distance swum) to body size and temperature (Ware 1978; Malmqvist & Bronmark 1982; Dabrowski et al. 1988; Boisclair 1992).

The body size allometry of behavioral rates and their response to temperature change are generally not well known (Calder 1984; Schmidt-Nielsen 1984). This is partly because this area of behavioural ecology has received relatively little attention and also because behavioural processes are more difficult to measure than physiological rates and tend to show considerable variation among and within individuals (Tang & Boisclair 1993). There are few data for fish and no studies have quantified the behavioral effects of changes in both body mass and temperature for a single species.

The research reported in this thesis is an attempt to quantify experimentally the body size allometry and thermal dependence of swimming velocity and foraging activity in juvenile brook trout (*Salvelinus fontinalis*). To illustrate the utility of such data in behavioural and ecological studies of fish, this work is combined with analyses, based on ecological models and simulations, of the potential effect of changes in body size, temperature, and food availability on growth and certain aspects of habitat use and life history.

1.2. Cost-benefit Model of Feeding Behaviour and Growth in an Actively Foraging Juvenile Fish.

The qualitative response of foraging behaviour to changes in temperature and body mass, and how this may influence feeding, growth, habitat use, and life history will initially be explored using a series of simple graphical cost-benefit models.

The purpose of this theoretical exercise is to identify the relationships between body mass, temperature, food density, and foraging behaviour that are critical for predicting the growth response of fish to temperature and body mass changes, and also to clarify the type of experimental data required to quantify these relationships.

In these models juvenile fish encounter prey only by swimming through the environment and growth is food-limited (i.e. fish never reach satiation). Juvenile fish are specified initially because juveniles allocate all of their net gain from foraging to growth, whereas adults divide this between growth and reproduction.

The instantaneous growth rate of a juvenile fish is measured as the difference between its rate of ingestion of assimilable food biomass (benefit) and the rate at which assimilated biomass is catabolized to supply energy for standard metabolism and the locomotory costs of foraging (cost). The behaviour-dependence of these costs and benefits is illustrated in Fig 1.1. The rate at which fish encounter and eat prey as they move along a search trajectory through the environment varies linearly with their search velocity. Therefore, the rate of ingestion of assimilable biomass (benefit) is approximated as a linear function of swimming velocity passing through the origin (Fig. 1.1, line B; in reality this line would rise less steeply at higher velocities as the

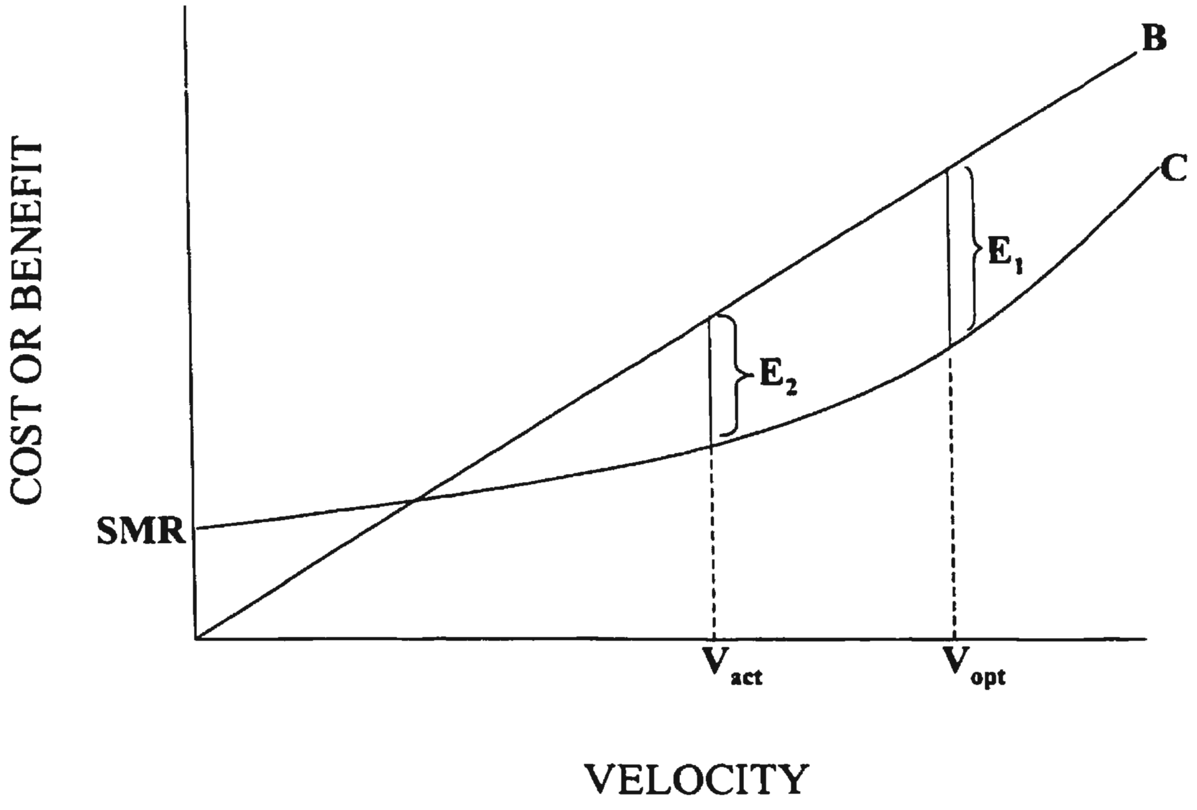

Fig. 1.1. A Cost-benefit Model of Feeding Behaviour and Growth in an Actively Foraging Juvenile Fish

Line B: Ingestion of assimilable food biomass or energy (benefit);
Curve C: The cost of foraging (cost); SMR: Standard metabolic rate;
V_{opt}: Theoretical optimal foraging velocity; V_{act}: Actual Foraging velocity;
E_1: Net energy gain or growth at V_{opt}; E_2: Net energy gain or growth at V_{act}.

earch for prey is interrupted more frequently by the handling of individual prey items (Holling 1966;Ware 1972). However, this linear approximation is reasonable at low food densities because the mean time between encounters would be large relative to prey handling time). The cost of foraging (line C) is shown as an accelerating function of velocity (Webb 1978; Ware 1978), with a Y-intercept equal to the standard metabolic rate (**SMR**) (the effect of prey handling time on the shape of this curve will also be negligible at low prey densities).

The vertical distance between the benefit (line B) and cost (line C) curves is the net rate of gain of assimilable biomass ($\mathbf{E}_{net}$, growth, or "surplus power"; Ware 1982) which clearly depends on swimming velocity. At zero velocity $\mathbf{E}_{net}$ will be negative and equal in magnitude to the **SMR**. $\mathbf{E}_{net}$ increases with velocity and reaches zero where the benefit and cost curves intersect. As velocity increases beyond this point, $\mathbf{E}_{net}$ will remain positive until the cost curve again intersects the benefit curve at some higher velocity. Within the range of velocities that give a positive $\mathbf{E}_{net}$ there will be a theoretical optimal velocity, $\mathbf{V}_{opt}$, where the slopes of the cost and benefit curves are equal, and at which $\mathbf{E}_{net}$ is maximized (line E1). An optimal foraging treatment of this model would assume that the actual velocity, $\mathbf{V}_{act}$, should approximate $\mathbf{V}_{opt}$ (Norberg 1977; Weihs 1977; Ware 1978; Pyke 1984; Wildhaber &

Crowder 1990). However, $\mathbf{V_{opt}}$ may well fall outside the aerobic range of the fish, in which case actual velocity, $\mathbf{V_{act}}$, would be less than $\mathbf{V_{opt}}$ with a correspondingly smaller $\mathbf{E_{net}}$ (line E2) (Sogard 1994). Regardless of the value of $\mathbf{V_{act}}$, it is clear that growth rate ($\mathbf{E_{net}}$) depends directly on behaviour (swimming velocity).

In the model, growth rate is expressed as an instantaneous rate (e.g. g/sec) at some time **t**. To interpret this as a daily growth rate, the X axis would be rescaled as the total distance swum over the daily foraging period and the Y axis as total daily cost or benefit. The Y intercept of the cost curve would be the total standard metabolic costs over 24 hours. None of these changes would alter the qualitative arguments presented above.

The possible effects of a change in environmental temperature on behaviour, feeding, and growth are examined in Fig. 1.2. The lines are labeled as in Fig. 1.1 with the exception that cost curves are shown for two temperatures ($\mathbf{T_1}$ and $\mathbf{T_2}$; $\mathbf{T_2 > T_1}$). The two cost curves ($\mathbf{C_1}$ and $\mathbf{C_2}$) are parallel (i.e. the rate of energy expenditure over and above **SMR**, when swimming at any velocity, is assumed to be independent of temperature) and only differ in their Y intercept ($\mathbf{SMR_2 > SMR_1}$). $\mathbf{V_{opt}}$ will not change with temperature because $\mathbf{C_1}$ and $\mathbf{C_2}$ are parallel, so that $\mathbf{E_{net}}$ (growth) at $\mathbf{V_{opt}}$ must

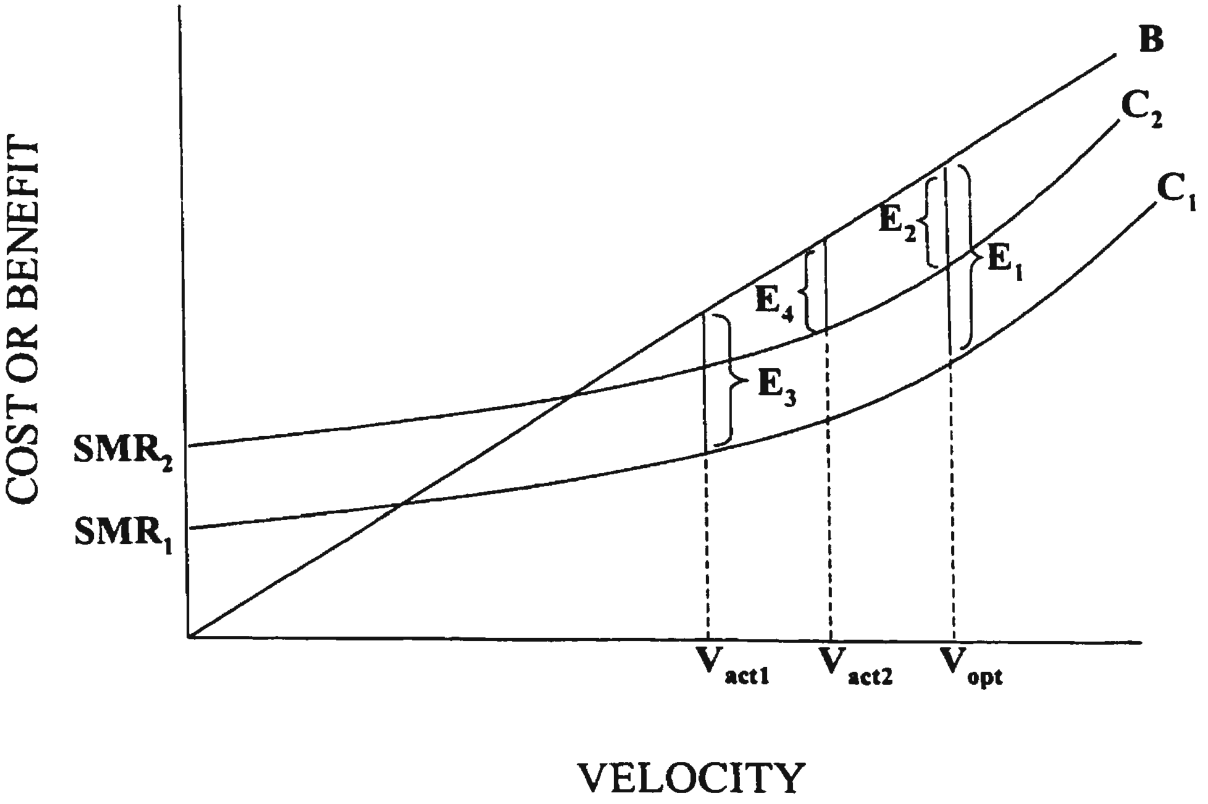

Fig. 1.2. A Cost-benefit Model of Feeding Behaviour and Growth for a Juvenile Fish Foraging at Two Different Temperatures

Line B: Ingestion of assimilable food biomass or energy (benefit);
Curve C_1, C_2: The cost of foraging (cost) at temperature T_1 and T_2 ($T_2 > T_1$) respectively;
SMR_1, SMR_2: Standard metabolic rate at T_1 and T_2 respectively;
V_{opt}: Theoretical optimal foraging velocity at both T_1 and T_2;
V_{act1}, V_{act2} : Actual Foraging velocity at T_1 and T_2 respectively;
E_1, E_2 : Net energy gain or growth for V_{opt} at T_1 and T_2 respectively;
E_3, E_4: Net energy gain or growth for V_{act} at T_1 and T_2 respectively.

clearly decrease with increasing temperature. However, if $\mathbf{V_{act}}<\mathbf{V_{opt}}$, and $\mathbf{V_{act}}$ is temperature dependent, the change in $\mathbf{E_{net}}$ with temperature will depend on how behaviour ($\mathbf{V_{act}}$) changes with temperature. As an example, $\mathbf{V_{act}}$ at $\mathbf{T_1}$ could give $\mathbf{E_{net}}=\mathbf{E_3}$ and $\mathbf{V_{act}}$ at $\mathbf{T_2}$ could give $\mathbf{E_{net}}=\mathbf{E_4}$ with $\mathbf{E_4}<\mathbf{E_3}$. However, a different behavioural response to temperature change (i.e. different $\mathbf{V_{act}}$s) could produce $\mathbf{E_4}=\mathbf{E_3}$ or $\mathbf{E_4}>\mathbf{E_3}$. It is not immediately clear which trend to expect. The potential qualitative effect on growth of small quantitative changes in the behavioural response (swimming velocity) to temperature highlights the importance of information on the temperature dependence of behaviour, particularly when making inferences regarding how temperature change may alter growth, and other ecological processes, in natural fish populations.

The effects of a change in fish size on behaviour, feeding, and growth could be examined in a similar fashion. However, in the general case, the graphical analysis is complicated by the potential expansion of the prey size range as fish grow so that larger fish consume items not available to smaller fish (Griffiths 1975; Ware 1972; Dunbrack & Ware 1987). For simplicity, only a special case of the above model will be considered in which prey size range and encounter rate (food mass encountered/distance swum) does not change with body mass.

This special case could arise because the increase in maximum prey size as fish grow will eventually be limited, either by the absence of larger prey in the environment (e.g. in stream environment, the primary foods are insects and other invertebrates that are generally small, (Allan 1978; Dunbrack 1992)), or by morphological and behavioural specialization on the part of the fish that prevents the exploitation of ever increasing prey sizes (Dunbrack & Ware 1987). In the vicinity of this fish size, the size composition of the diet would be independent of fish size. (This simplification does not alter the analysis of temperature effects (Fig. 1.2) because the prey assemblage was already assumed to be independent of temperature).

The effects of changes in fish size on behaviour, feeding, and growth (for the special case) are illustrated in Fig. 1.3. Two cost curves are shown for fish masses 1 and 2 (2>1). Both the Y intercepts (**SMRs**) and slopes at any velocity are greater for $\mathbf{C_2}$ than $\mathbf{C_1}$ (the slope increases because the cost of swimming at any particular velocity is proportional to body mass (Ware 1978; Webb 1978). Because the slope of $\mathbf{C_2}$ is higher at all velocities, both $\mathbf{V_{opt}}$ and $\mathbf{E_{net}}$ (at $\mathbf{V_{opt}}$) will decrease as body size increases. However, if $\mathbf{V_{act}}<\mathbf{V_{opt}}$ and $\mathbf{V_{act}}$ is body size dependent, the relationship between growth and body size will depend on how changes in body size affect behaviour. In the example shown, $\mathbf{V_{act}}$ increases with body size in such a way that $\mathbf{E_{net}}$

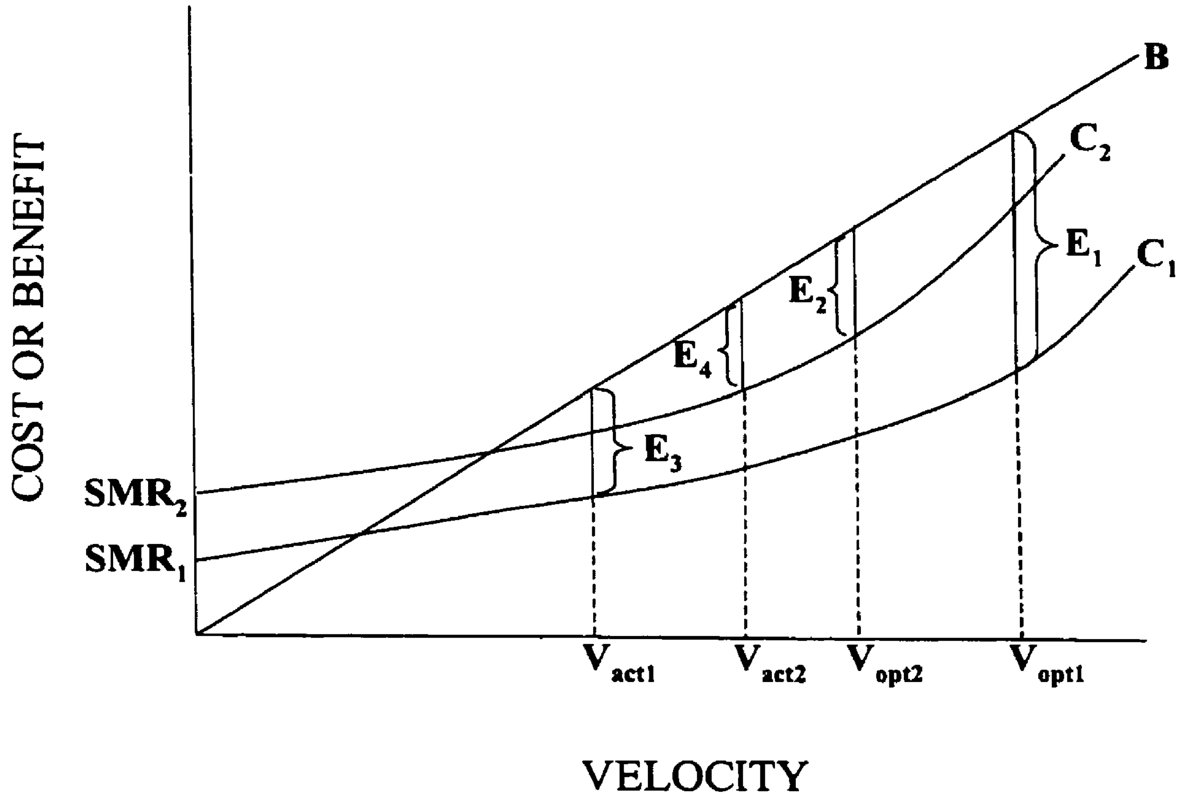

Fig. 1.3. A Cost-benefit Model of Feeding Behaviour and Growth for Juvenile Fish of Two Different Sizes

Line B: Ingestion of assimilable food biomass or energy (benefit); Curve C_1, C_2: The cost of foraging (cost) for body mass 1 and 2 (2 > 1) respectively; SMR_1, SMR_2: Standard metabolic rate for body mass 1 and 2 respectively; V_{opt1},V_{opt2}: Theoretical optimal foraging velocity for body mass 1 and 2 respectively; V_{act1}, V_{act2} : Actual Foraging velocity for body mass 1 and 2 respectively; E_1, E_2 : Net energy gain or growth at V_{opt} for body mass 1 and 2 respectively; E_3, E_4: Net energy gain or growth at V_{act} for body mass 1 and 2 respectively.

decreases with increasing body size. However, as was the case for temperature, a different behavioural response to changes in body mass could produce an increase or decrease in growth rate as body size increases. It is not obvious which trend in growth is more likely. This once again highlights the importance of information on behavioural responses to changes in body mass when making inferences as to the effects of body mass on feeding and growth in fishes.

It has been shown how changes in behaviour with temperature and body mass could alter growth rate. It is also possible that the effect of either temperature or body mass on growth may be influenced by food availability. When body mass increases, say from size **x** to size y, this will lead to an increase in both the costs and benefits of foraging. The net effect on absolute growth rate will be positive if the increase in benefits exceeds the increase in costs. The increase in costs will be equal to

(cost of fish of mass y swimming at V_y) - (cost of fish of mass x swimming at V_x)

This will be more or less independent of food density and can be treated as a constant **K_1**. The increase in benefits will be approximately equal to

food density(V_x) - food density(V_y) = food density (V_x-V_y)

where food density is measured as the mass of food encountered per distance swum. Setting (V_x-V_y) to K_2, the condition for absolute growth rate to increase as a fish grows from **x** to y is

food density (K_2) > K_1

or

food density > K_1/K_2,

which identifies a food density threshold above which growth is positively related to body mass.

Similarly, an increase in temperature from **m** to **n** will increase the foraging costs by

(costs of swimming at V_n - cost of swimming at V_m) = K_3,

and increase benefits by

food density (V_n-V_m) = food density(K_4)

The condition for absolute growth rate to increase as temperature increases from **m** to **n** is

food density > K_3/K_4,

which identifies a food density threshold above which growth is positively related to temperature.

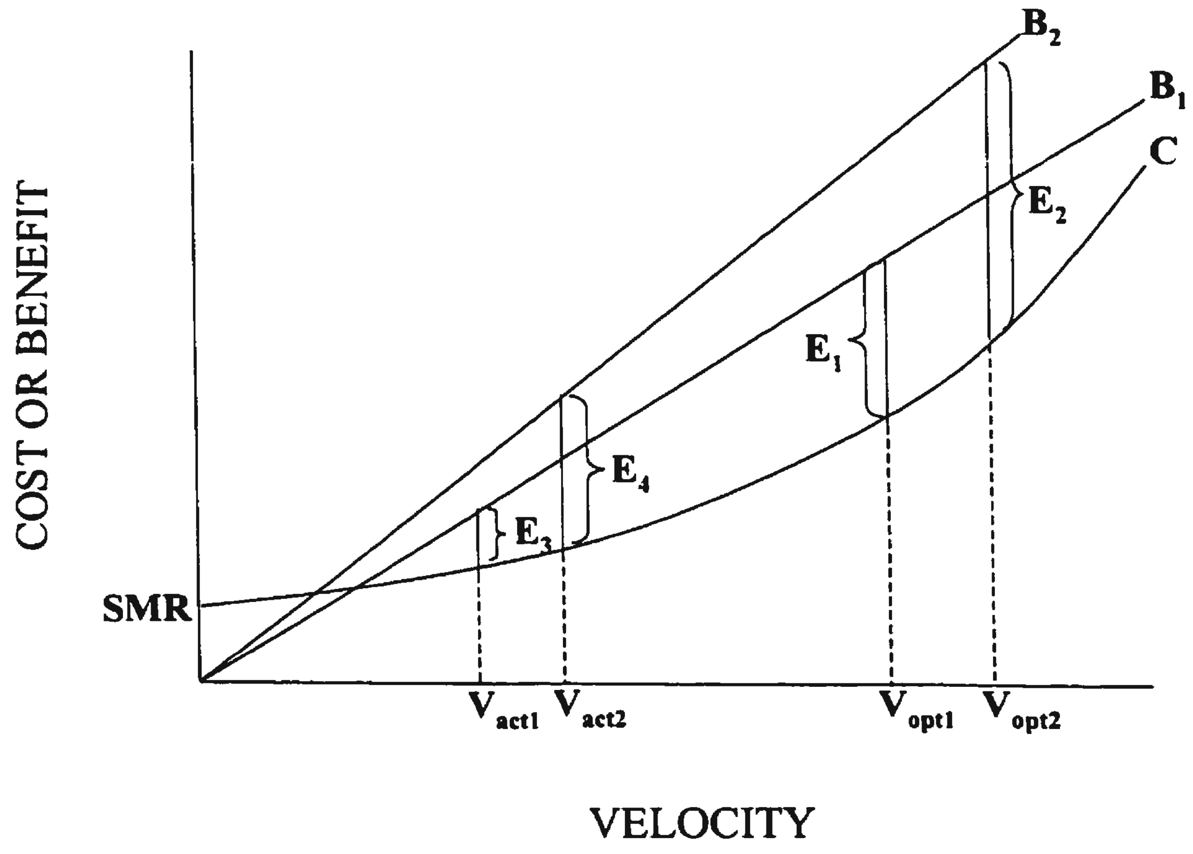

Fig. 1.4. A Cost-benefit Model of Feeding Behaviour and Growth for a Juvenile Fish Foraging at Two Different Food Densities

Line B_1, B_2: Ingestion of assimilable food biomass or energy (benefit) at food density 1 and 2 (2 > 1) respectively; Curve C: The cost of foraging (cost); SMR: Standard metabolic rate; V_{opt1}, V_{opt2}: Theoretical optimal foraging velocity at food density 1 and 2 respectively; V_{act1}, V_{act2} : Actual Foraging velocity at food density 1 and 2 respectively; E_1, E_2 : Net energy gain or growth for V_{opt} at food density 1 and 2 respectively; E_3, E_4 : Net energy gain or growth for V_{act} at food density 1 and 2 respectively.

Although food availability may thus qualitatively alter the relationships between body mass, temperature, and growth, it is not possible to know if these critical densities exist within the range of densities normally encountered by wild fish without information on the behavioural response of fish to changes in body mass and temperature.

In addition to its direct influence on feeding rate at any given swimming velocity, food density may also indirectly influence feeding through food density dependent changes in foraging behaviour. One possibility is illustrated in Fig. 1.4. Here a single cost curve (C) is shown with benefit curves for two different food densities (food density for $\mathbf{B_2}$> food density for $\mathbf{B_1}$). Because the slope of $\mathbf{B_2}$ is greater than the slope of $\mathbf{B_1}$, the model predicts an increase in foraging velocity as food density increases, if fish forage at $\mathbf{V_{opt}}$. This prediction may also hold for the case of $\mathbf{V_{act}}<\mathbf{V_{opt}}$. For example, if $\mathbf{V_{act}}$ (<$\mathbf{V_{opt}}$) maximizes $\mathbf{E_{net}}$ under some unknown set of constraints, then at that velocity, the benefit of increasing $\mathbf{V_{act}}$ by some increment should equal the incremental increase in cost. However, if food density increases, the benefit of an incremental increase in $\mathbf{V_{act}}$ would then exceed its cost and $\mathbf{V_{act}}$ should increase until the incremental costs and benefits are once again equal. Such increases in velocity with increasing food density have been predicted previously on theoretical grounds (Dunbrack & Giguere 1987), however this effect has not been observed in natural populations.

The analyses of these cost-benefit models has highlighted the difficulties of predicting the effect of body mass and temperature on growth rate in the absence of general expressions for allometric and thermal effects on behaviour. Therefore, the primary aims of this thesis are to (1) quantify experimentally these allometric and thermal effects on feeding behaviour, and (2) use these data to predict the consequent effects of food availability, body mass, and temperature on growth in natural populations.

Although the focus will be on the above relationships, the question of how thermal and allometric effects on behaviour may also influence habitat use and constraints on adult body size is briefly explored below and in Chapters 2 and 6.

1.3. E_{net} and Habitat Use

A fish's rate of net energy gain has been shown above to depend, in part, on two important habitat variables: food availability and temperature. When multiple habitats that differ only in the rate of net energy gain, or "surplus power", are accessible to a fish, the habitat that offers the highest surplus power should be "chosen" (Crowder & Magnuson 1983). Using this criterion, the above models suggest conditions under which the energetically optimal habitat (that giving the highest surplus power) might depend on body mass or temperature (Werner et al. 1983; Gilliam & Fraser 1987; Wildhaber & Crowder 1990; Luecke & Teuscher 1994).

When habitats do not differ in temperature, a body size dependent shift from a habitat, $\mathbf{h}_1$, to another habitat, $\mathbf{h}_2$, would be advantageous energetically if the energy density in $\mathbf{h}_1$ exceeded that in $\mathbf{h}_2$ over the size range of items available in $\mathbf{h}_1$, but $\mathbf{h}_2$ contained larger food items that were unavailable to smaller fish. When these items are included, $\mathbf{h}_2$ would have the higher energy density, but only for larger fish and, at some body size, the energetically optimal habitat would shift from $\mathbf{h}_1$ to $\mathbf{h}_2$. In the absence of such differences in the size frequency distribution of food between habitats, shifts would have to be based on something other than the rate of foraging gain, such as differences in size-specific mortality rates among habitats or some difference between habitats in the energy cost of maintenance.

Body size-dependent habitat shifts based on temperature differences among habitats could occur if, for example, a high temperature habitat provided higher surplus power to small fish but low or negative surplus power to larger fish. For these larger fish a lower temperature habitat could be more advantageous because of the lower maintenance costs despite a lower level of food availability. In other cases it may be possible that the additive effects of temperature and food availability could favour a size-dependent habitat shift although neither factor could do this in isolation (see Chapter 6).

Although temperature changes could influence habitat choice, the investigation of the energy basis of habitat use, particularly as it is affected by temperature, requires information on how surplus power changes with temperature, a relationship that in turn depends on the effect of temperature, body size, and food availability on feeding behaviour.

1.4. Adult Body Size

Fish as a group exhibit the greatest range in adult body size of any living class of organisms (Dunbrack & Ware 1987). The interactions between the factors that determine adult body size are perhaps best illustrated by the problems of energy acquisition and the allocation of this energy to maintenance, growth, and reproduction (Clarke 1987; Dunbrack & Ware 1987).

Once food has been captured, ingested, digested, and assimilated, at least part of the assimilated fraction must be used for maintenance (**SMR**, transport, food processing) (Tytler & Calow 1985). Any energy (or biomass) that is surplus to maintenance requirements is "surplus power" (surplus energy/time; Ware 1982) and is available for allocation to either growth or reproduction (e.g. gamete production). By definition, juveniles allocate all of their surplus power to growth while adults allocate surplus power between growth and reproduction.

In theory, the switch from investing in growth to investing in reproduction should be abrupt and occur at that body size where the fitness value of investments in current reproduction first exceeds that of investments in growth (future reproduction). (A qualitative change in the relative value of current vs. future reproduction would be expected in the vicinity of the body size where growth rate begins to decrease with increasing body mass). Although the switch from growth to reproduction is typically more gradual in most iteroparous species, it should, in general, be disadvantageous to grow larger than the size,"$\mathbf{W_r}$", at which the product of surplus power and expected time to death is maximized (Myers & Doyle 1983). This is because the above product measures the expected lifetime reproductive output (**ELRO**) of a fish of any given size if growth ceases at that size. At $\mathbf{W}_r$ any investment in growth would decrease fitness.

A difficulty encountered when attempting to directly model temperature and food density effects on adult size, is the requirement for information on size-dependent patterns of mortality and how these depend on temperature and food availability, topics that are beyond the scope of this thesis. However, if it is assumed that changes in food density or temperature are not accompanied by changes in mortality, it can be shown that the qualitative effects of changes in temperature or food availability on $\mathbf{W}_r$ would be identical to their effects on the peak position of the curve of surplus power. However, as noted above (1.2), the relationships between body mass, temperature, food availability, and surplus power will depend on the effects of temperature, body mass, and food availability on foraging behaviour, effects which have yet to be quantified. Adult body size is discussed further in Chapter 2 and 6.

1.5. W_{max}, the Maximum Body Size in a Habitat

As noted, in the absence of behavioural data it is not possible to predict the effect of changes in temperature or body mass on growth rate for any particular combination of temperature, body mass, and food density. However, the inequalities derived in (1.2) indicate that below certain food densities increases in temperature or body mass should have negative effects on growth rate. While these threshold densities cannot be quantified without behavioural data, it is possible to make inferences regarding their value in relation to certain body sizes by modeling the effects of food availability, body mass, and temperature on growth at the body size where the level of food availability is just sufficient to meet maintenance costs (i.e. surplus power = 0).

In terms of the cost-benefit models discussed above, when the range of prey sizes in the diet is independent of fish body size, increases in fish size will be accompanied by increases in the cost curve's Y-intercept (**SMR**), as well as its slope at any given velocity. Consequently, there should be a fish size at which the cost curve will just touch the benefit curve at $\mathbf{V_{opt}}$. This size, $\mathbf{W_{max}}$, would be the maximum size possible for a fish in that habitat (Fig. 1.5; line C_1). The cost curve for fish larger than this (Fig. 1.5; line C_2) will lie entirely above the benefit curve, and $\mathbf{E_{net}}$ would be

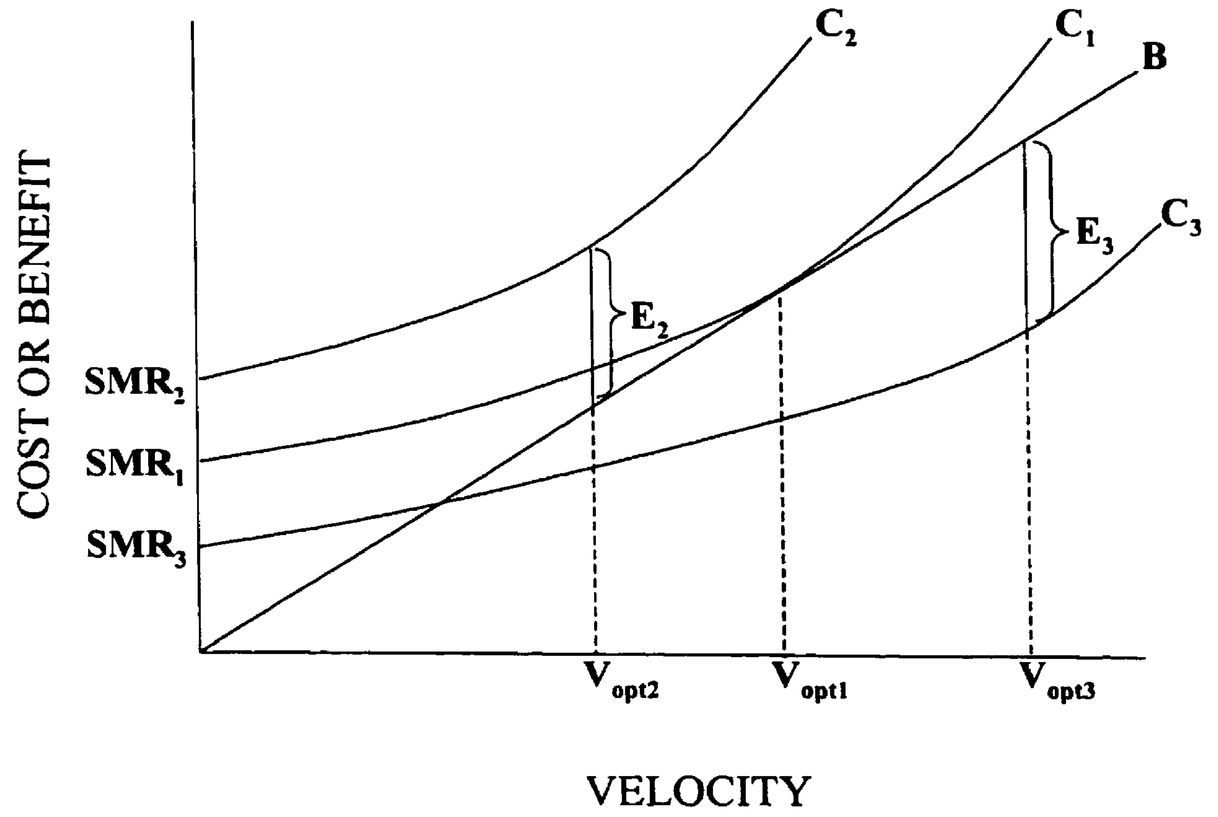

Fig. 1.5. A Cost-benefit Model of Feeding Behaviour and Growth for Juvenile Fish of Different Sizes Swimming at the "Optimal" Velocity

Line B: Ingestion of assimilable food biomass or energy (benefit); Curve C_1, C_2, C_3 : The cost of foraging (cost) for body mass 1, 2 and 3 (2 > 1 > 3) respectively; SMR_1, SMR_2, SMR_3: Standard metabolic rate for body mass 1, 2 and 3 respectively; V_{opt1},V_{opt2} ,V_{opt3}: Theoretical optimal foraging velocity for body mass 1, 2 and 3 respectively; E_1, E_2, E_3 : Net energy gain or growth at V_{opt} for body mass 1, 2 and 3 respectively.

negative regardless of swimming velocity. Cost curves for smaller fish (e.g. line C_3) will lie partly below the benefit curve, producing a positive $\mathbf{E}_{\mathbf{net}}$ for a range of velocities around $\mathbf{V}_{\mathbf{opt}}$.

By definition, $\mathbf{W}_{\mathbf{max}}$ is the body size at which the rate of net energy production, or surplus power, is zero. Consequently, a fish of size $\mathbf{W}_{\mathbf{max}}$ could neither grow nor reproduce and $\mathbf{W}_{\mathbf{max}}$ represents a constraint that no fish would be expected to reach. However, because the food density associated with a particular $\mathbf{W}_{\mathbf{max}}$ would be the lowest possible density allowing fish of size $\mathbf{W}_{\mathbf{max}}$ to meet their maintenance requirements, any increase in size beyond $\mathbf{W}_{\mathbf{max}}$ would, by definition, lead to a decrease in absolute growth rate, i.e. the food density must be below the threshold density for growth to decrease with increasing body mass. To show that this body size exists, it is sufficient to show that there is a size at which growth is zero. The potential effect of temperature on $\mathbf{W}_{\mathbf{max}}$ is discussed below.

1.5.1. Foraging at $\mathbf{V}_{\mathbf{opt}}$: Effects of food density and temperature on $\mathbf{W}_{\mathbf{max}}$

It is clear from Fig. 1.5 that when fish move at $\mathbf{V}_{\mathbf{opt}}$ the maximum body mass, $\mathbf{W}_{\mathbf{max}}$, is well defined and the effects of changes in food density and temperature on $\mathbf{W}_{\mathbf{max}}$ are easily obtained.

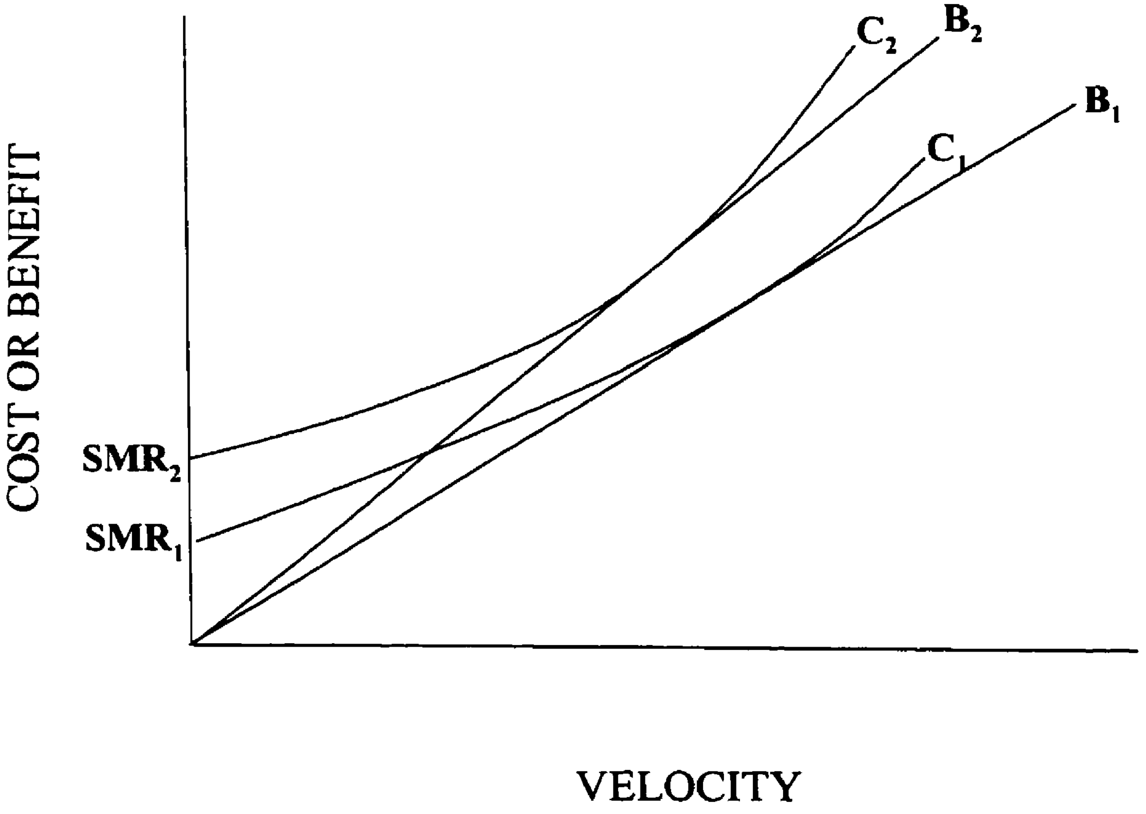

Fig. 1.6. A Cost-benefit Model of the Effect of Food Density on Maximum Body Mass for Fish Swimming at the "Optimal" Velocity

Line B_1, B_2: Ingestion of assimilable food biomass or energy (benefit) at food density 1 and 2 (2 > 1) respectively; Curve C_1, C_2 : The cost of foraging (cost) for body mass 1, and 2 (2 > 1) respectively; SMR_1, SMR_2 : Standard metabolic rate for body mass 1, and 2 respectively.

The effect of food density on $\mathbf{W_{max}}$ is straightforward: $\mathbf{W_{max}}$ increases with increasing food density (Fig. 1.6).

The effect of temperature changes on $\mathbf{W_{max}}$ are illustrated in Fig. 1.7. Curve C_1 (Fig. 1.7a) is the cost curve for fish of size 1. Size 1 is also $\mathbf{W_{max}}$ at the prevailing temperature ($\mathbf{T_1}$). Curve C_2 is for a fish of size 2 (2>1) and curve C_3 is for a fish of size 3 (3<1). The temperature is increased to $\mathbf{T_2}$ in Fig. 1.7b. At $\mathbf{T_2}$ the cost curves for all three fish sizes have moved upward because of the increase in **SMR** from $\mathbf{T_1}$to $\mathbf{T_2}$. $\mathbf{W_{max}}$ is now equal to size 3 and fish of sizes 1 and 2 cannot maintain a positive $\mathbf{E_{net}}$ in the habitat, that is $\mathbf{W_{max}}$ has decreased. Similarly the temperature is reduced to $\mathbf{T_3}$ ($\mathbf{T_3}$<$\mathbf{T_1}$) in Fig. 1.7c. At $\mathbf{T_3}$ the cost curves all move downward because of the decrease in **SMR** from $\mathbf{T_1}$ to $\mathbf{T_3}$ and $\mathbf{W_{max}}$ is now equal to fish size 2 and fish of size 1 and 3 have positive $\mathbf{E_{net}}$, that is $\mathbf{W_{max}}$ has increased. Therefore, for the case of foraging at $\mathbf{V_{opt}}$, food density would be below the threshold for growth to decrease with increasing temperature. The combined effects of temperature and body size on growth and $\mathbf{W_{max}}$ (for foraging at $\mathbf{V_{opt}}$) are shown in Fig. 1.8.

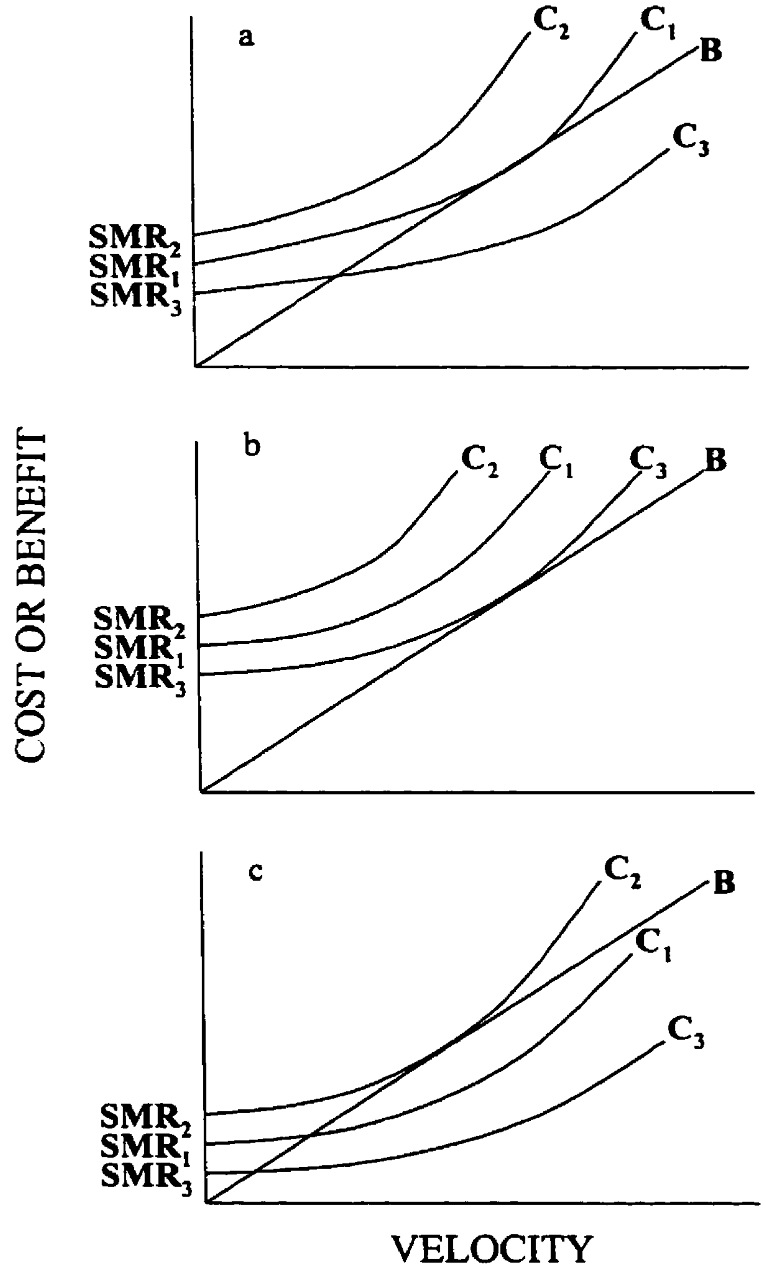

Fig. 1.7. A Cost-benefit Model of the Effect of Temperature on Maximum Body Mass for Fish Swimming at the "Optimal" Velocity

Line B: Ingestion of assimilable food biomass or energy (benefit); Curve C_1, C_2, C_3 : The cost of foraging (cost) for body mass 1, 2 and 3 respectively; SMR_1, SMR_2 , SMR_3: Standard metabolic rate for body mass 1, 2 and 3 respectively; a, b, c: at temperature T_1, T_2 and T_3 ($T_2 > T_1 > T_3$) respectively;

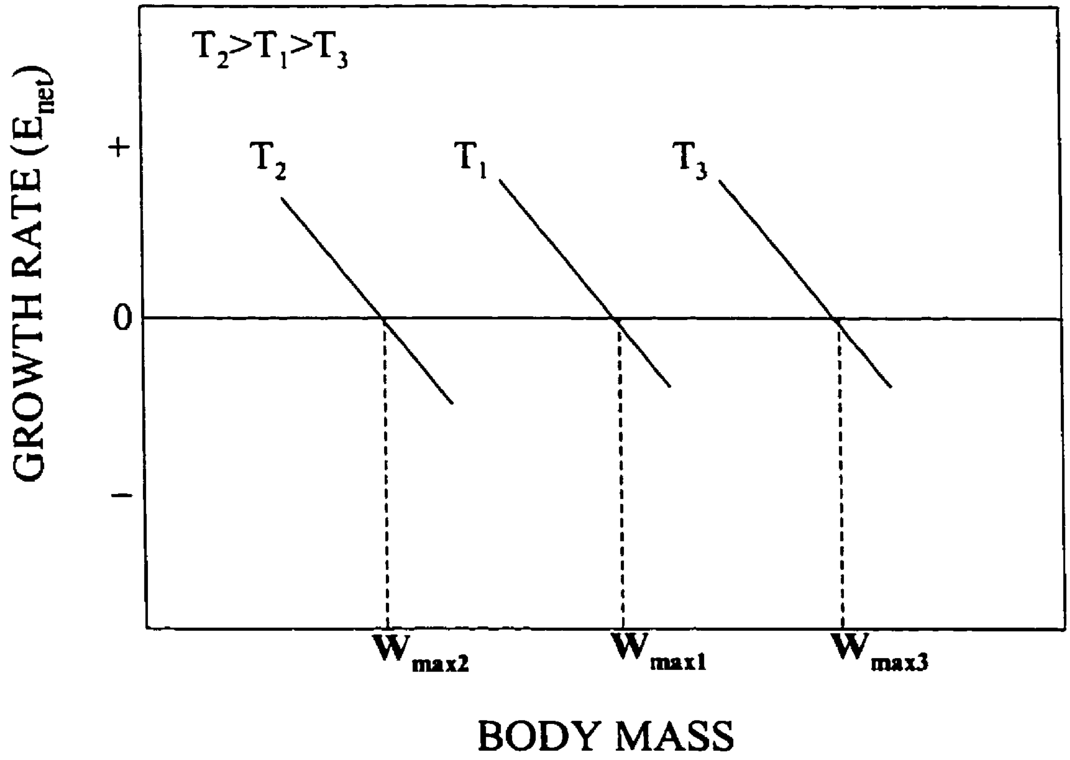

Fig. 1.8. A Diagram of the Combined Effects of Temperature and Body Size on Growth and Maximum Body Mass of Fish Swimming at the "Optimal" Velocity

W_{max1}, W_{max2}, W_{max3}: Maximum Body Mass at temperature T_1, T_2 and T_3 ($T_2 > T_1 > T_3$)

1.5.2. Foraging at $V_{act}<V_{opt}$

The above analyses apply to the case of foraging at V_{opt}, but, as pointed out, fish probably forage at some V_{act} less than V_{opt} (Sogard 1994).

For example, V_{opt} decreases as body size increases and is independent of temperature. But it is clear that the rate at which fish move increases with both body mass and temperature (Ware 1975, 1978; Wardle 1977, 1980; Wardle & Videler1980; Dabrowski et al 1988). Consequently, the case of $V_{act}<V_{opt}$ is considered below.

1.5.2.1. Existance of W_{max}

When $V_{act}<V_{opt}$, W_{max} would be defined as the body size at which V_{act} coincides with the intersection point of the cost and benefit curves (Fig. 1.9). In this figure, cost curves are shown for body sizes 1, 2, and 3 (2>1>3). V_{act} is assumed to increase with body size. For the assumed relationship between body size and velocity, W_{max} is equal to fish size 1 ($E_{net}=0$) while E_{net} is negative for fish size 2 and positive for fish size 3. W_{max} is less well defined (slope of E_{net} as a function of body mass has a flatter slope) than for foraging at V_{opt} because of the increase in foraging velocity with body mass. In theory, the increase in V_{act} with mass could be sufficient to cause E_{net} to actually increase with body mass, and W_{max} would not exist. However,

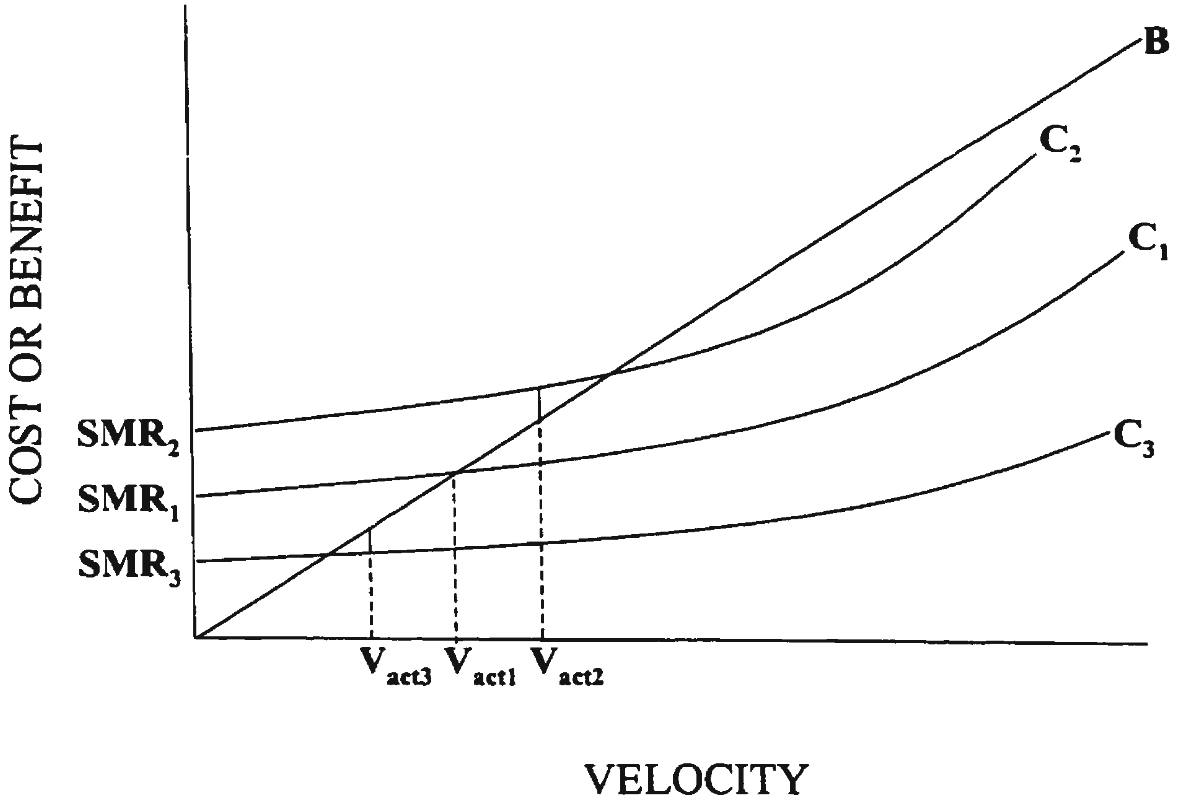

Fig. 1.9. A Cost-benefit Model of Feeding Behaviour and Growth for Juvenile Fish of Different Sizes Swimming at Their "Actual" Velocity($< V_{opt}$)

Line B: Ingestion of assimilable food biomass or energy (benefit); Curve C_1, C_2, C_3 : The cost of foraging (cost) for body mass 1, 2 and 3 ($2 > 1 > 3$) respectively; SMR_1, SMR_2 , SMR_3: Standard metabolic rate for body mass 1, 2 and 3 respectively; V_{act1},V_{act2} ,V_{act3}: Actual foraging velocity for body mass 1, 2 and 3 respectively.

this would require an increase in $\mathbf{V}_{act}$ with body mass that was proportionately greater than the increase in **SMR** with body mass, or equivalently, an increase in a fish's power output that far exceeded the increase in its **SMR**. Although this seems unlikely, there are few experimental data that can be used to address this point, and it is not clear that $\mathbf{W}_{max}$ or the threshold food density below which growth decreases with body mass, exist.

1.5.2.2. The effect of food density on $\mathbf{W}_{max}$

Assuming that $\mathbf{W}_{max}$ exists, the qualitative effect of food density on $\mathbf{W}_{max}$ is identical to its effect when swimming at $\mathbf{V}_{opt}$ (Fig. 1.10). Cost curves are shown for two fish sizes (mass 2>mass1) and two food densities (food density 2>food density 1). At food density1, $\mathbf{W}_{max}$ is equal to fish mass 1 and $\mathbf{E}_{net}$ for fish size 2 is negative ($\mathbf{E}_1$). At food density 2, $\mathbf{W}_{max}$ is now equal to fish mass 2 and $\mathbf{E}_{net}$ for fish mass 1 is positive ($\mathbf{E}_2$). Thus, $\mathbf{W}_{max}$ is predicted to increase as food density increases. Under these conditions, any increase in $\mathbf{V}_{act}$ with body mass would increase the slope of the relationship between $\mathbf{W}_{max}$ and food density.

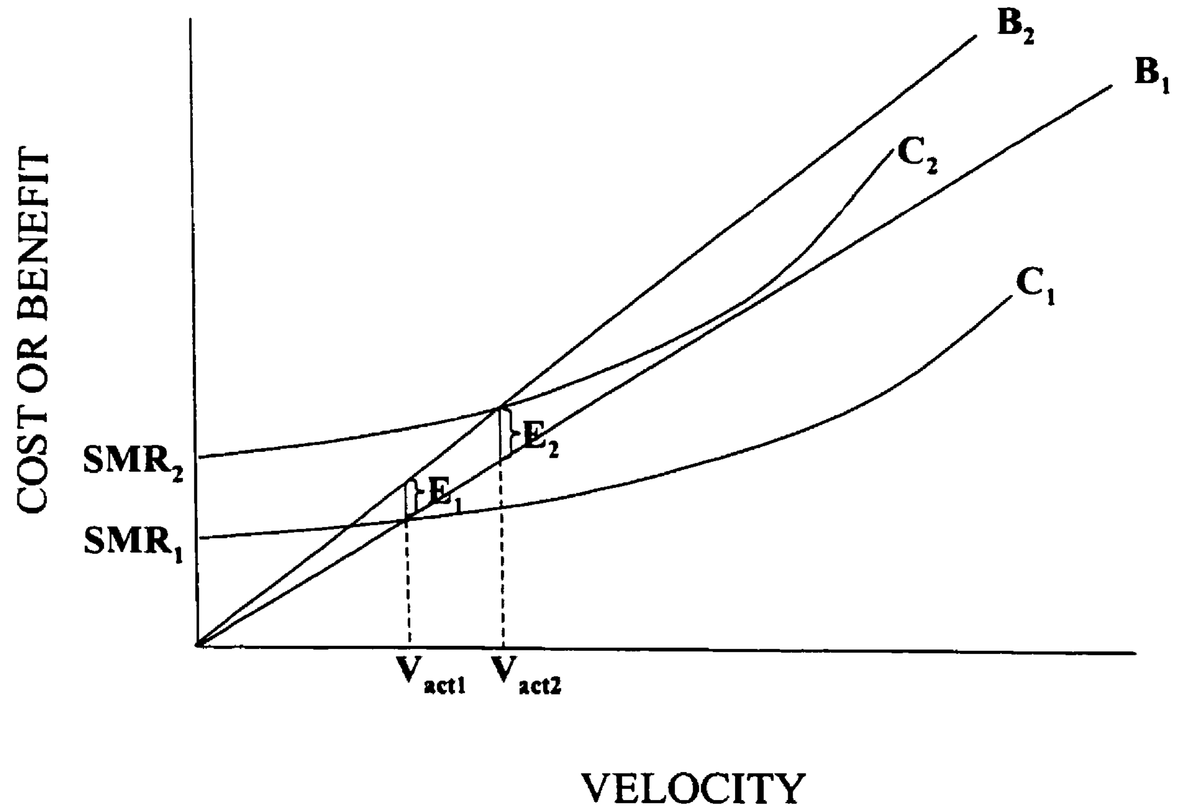

Fig. 1.10. A Cost-benefit Model of the Effect of Food Density on Maximum Body Mass for Fish Swimming at Their "Actual" Velocity

Line B_1, B_2: Ingestion of assimilable food biomass or energy (benefit) at food density 1 and 2 (2 > 1) respectively; Curve C_1, C_2 : The cost of foraging (cost) for body mass 1, and 2 (2 > 1) respectively; SMR_1, SMR_2 : Standard metabolic rate for body mass 1, and 2 respectively. V_{act1}, V_{act2} : Actual Foraging velocity which less than theoretical optimal velocity for body mass 1 and 2 respectively; E_1: Net energy gain or growth for body mass 1 at food density 2; E_2: Net energy gain or growth for body mass 2 at food density 1.

1.5.2.3. The effect of temperature on W_{max}

The potential effect of temperature on W_{max} is illustrated in Fig. 1.11. Cost curves for fish of mass 1 are shown for temperatures T_1 and T_2 ($T_2 > T_1$). At temperature T_1, velocity equals V_{act1} and W_{max} is equal to fish size 1. At temperature T_2, V_{act} has increased (V_{act2}) but E_{net} for fish of size 1 is now negative (E_2) and W_{max} would be smaller. That is, W_{max} decreases as temperature increases. Although this result is qualitatively similar to that obtained when fish forage at V_{opt}, it is given only for illustration because the way in which V_{act} increases with temperature is unknown. In theory, the increase in V_{act} with temperature could be sufficient to cause W_{max} to increase with temperature (E_3 at V_{opt2}'; Fig. 1.11). Although this would require a proportionate increase in V_{act} with temperature equal to or greater than the proportional change in SMR, there are, once again, few experimental data that can be used to determine the likelihood of such an increase, and the existence of a threshold food density below which growth rate decreases with temperature is therefore problematic.

The effects of temperature and body mass on E_{net} and W_{max} for the case of $V_{act} < V_{opt}$ are summarized in Fig. 1.12. This figure differs from Fig. 1.8 in that the slopes of the functions relating body mass and E_{net} are flatter and the lines for the

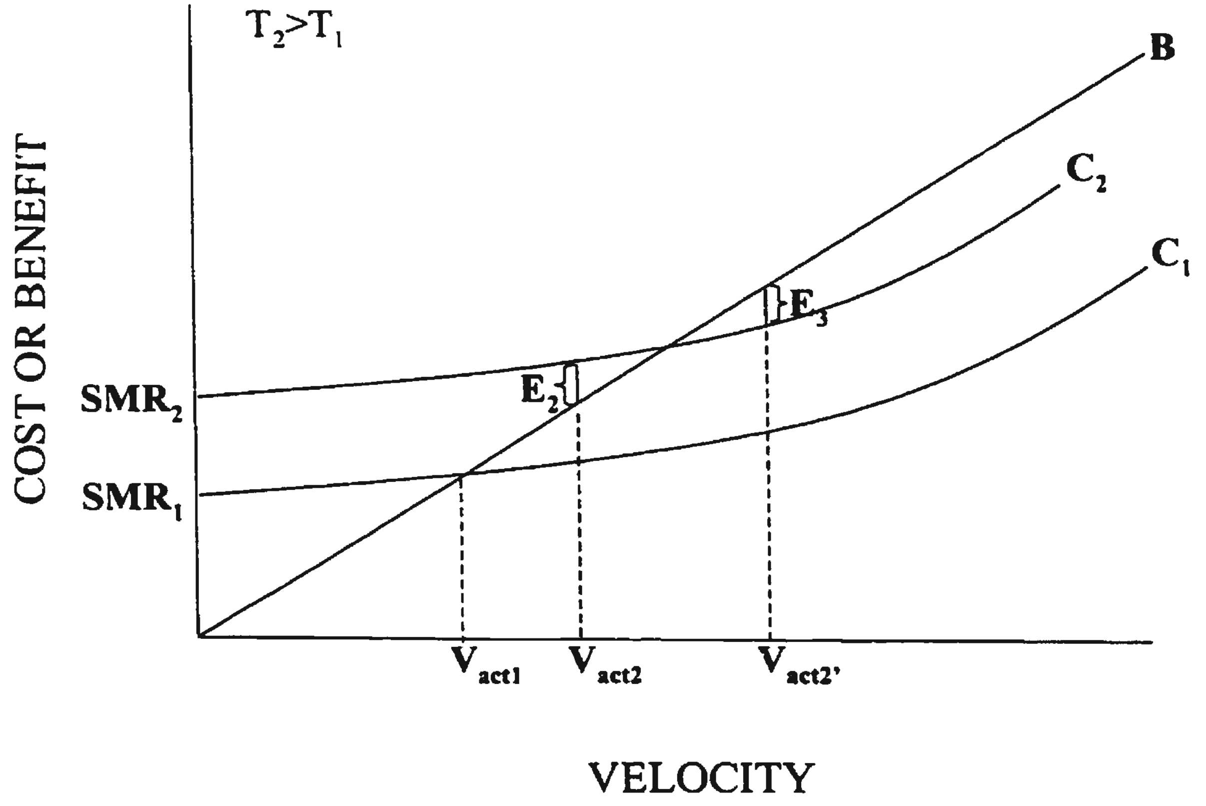

Fig. 1.11. A Cost-benefit Model of the Effect of Temperature on Maximum Body Mass for Fish Swimming at Their "Actual" Velocity ($<V_{opt}$)

Line B: Ingestion of assimilable food biomass or energy (benefit); Curve C_1, C_2 : The cost of foraging (cost) at temperature $T_1$and T_2 ($T_2 > T_1$) respectively; SMR_1, SMR_2 : Standard metabolic rate at T_1 and T_2 respectively; V_{act1}: Actual foraging velocity at T_1; V_{act2} ,$V_{act2'}$: Actual foraging velocity at T_2 ($V_{act2} < V_{act2'}$); E2, E3: Net energy gain or growth at T2 for V_{act2} ,$V_{act2'}$ respectively.

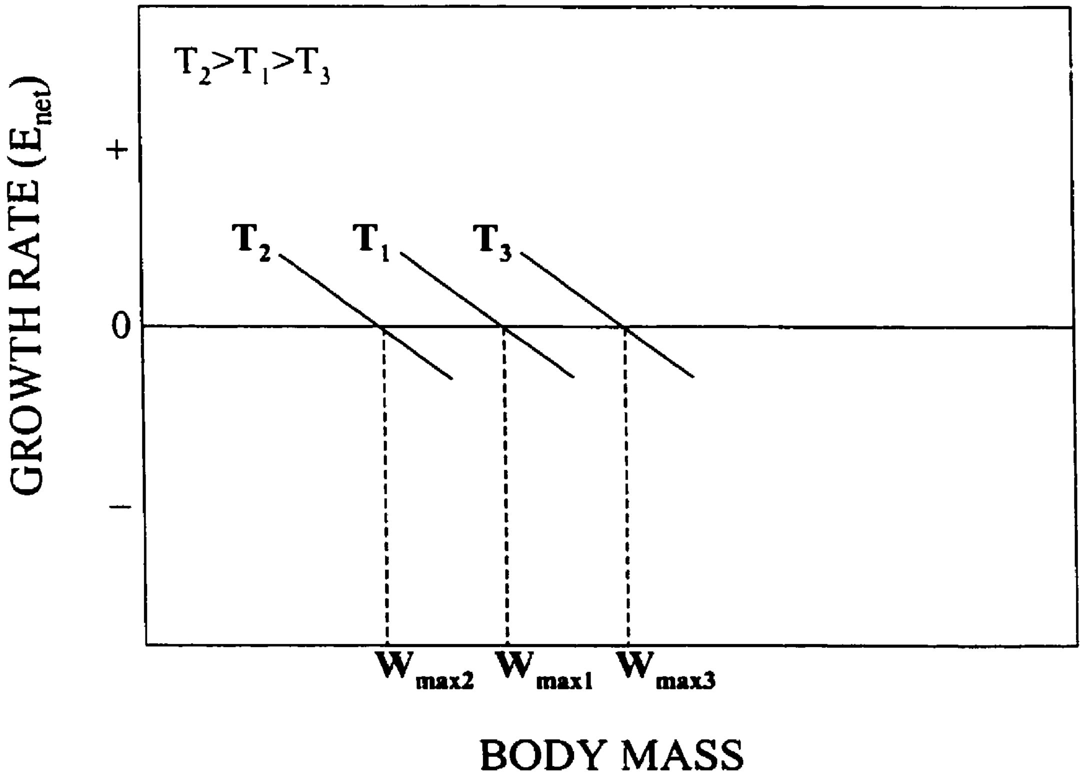

Fig. 1.12. Diagram Illustrating the Combined Effects of Temperature and Body Size on Growth and Maximum Body Mass of Fish Swimming at Their "Actual" Velocity ($<V_{opt}$)

W_{max1}, W_{max2}, W_{max3}: Maximum Body Mass at temperature T_1, T_2 and T_3 ($T_2 > T_1 > T_3$)

different temperatures are closer together. However, this figure is based on the assumption that W_{max} exists over the given body size range and that increased temperature has the effect of reducing W_{max}. As noted above, these assumptions have not been tested experimentally and could be incorrect, at least over some body size range. Therefore, any predictions regarding the existence of threshold food densities or W_{max} and how it may be influenced by temperature also require knowledge of how foraging behaviour is influenced by temperature, body size, and food availability.

1.6. Summary of the Outcome of the Cost-benefit Analyses

The relationships between temperature, body mass, food density, and swimming velocity in wild fish are of intrinsic interest because of their wide applicability to questions in fish ecology related to body size, growth, and habitat use. The cost-benefit analyses have been used to highlight the variety of theoretical models that can be applied to these questions as well as to the problem of relating changes in foraging velocity, food density, body mass, and temperature to growth, habitat use, and adult body mass. In the absence of good experimental data, any general conclusions regarding these relationships are problematic.

However, the models also indicate that information on the effect of food density, temperature, and body mass on swimming velocity is critical for exploring these relationships. In the remainder of this thesis I will present the results of experiments designed to measure the response of foraging velocity to these variables under conditions intended to resemble those in a natural foraging environment.

1.7. Structure of the Thesis

The thesis is divided into seven chapters as follows:

Chapter 1

Introduction, discussion of models of allometric and temperature effects on behaviour and growth, models of the effect of behaviour on $\mathbf{W}_{max}$, outline of thesis.

Chapter 2

Chapter 2 contains a review of previous work on the effects of temperature, body mass, and food availability on the metabolism, growth, and feeding behaviour of fish; a review of habitat use in relation to temperature, body size, and food density; and a review of the effects of temperature and food density on adult size.

Chapter 3

This chapter describes an initial set of experiments which quantify the effects of temperature on the relationships between body mass and both maximum meal size and maximum feeding rate in juvenile brook trout (*Salvelinus fontinalis*). These results contribute to the comparative study of feeding and gut evacuation processes in fishes and are necessary to identify appropriate feeding levels for the behavioural experiments described in Chapter 5 and the growth experiments described in Chapter 6.

Chapter 4

Chapter 4 describes an automated system that was constructed specifically to carry out the experimental examination of feeding behaviour described in Chapter 5. The approach taken in these experiments differs from previous work on fish feeding because the daily ration is not fixed by the experimental design but is instead determined by food density and the food search activity of the fish. This protocol required the use of a novel technique in which the foraging movements of individual fish were tracked in realtime through a computerized monitoring and control system. This system automatically dispensed a food item each time an experimental fish had swum a prescribed distance. The distance swum per food item consumed, a measure of food density, could thus be held constant (or varied systematically over time) for any combination of temperature and body mass treatments, allowing for the investigation of the effects of temperature, body mass and food density, on feeding behaviour, in particular foraging velocity, under conditions intended to resemble those encountered in a natural foraging environment.

Chapter 5

Chapter 5 presents the results of a series of experiments designed to measure the effects of food density, temperature, and fish body mass on foraging behaviour. Each experiment, which involved an individual fish fed at a single food density, yielded data on feeding rate, swimming velocity, total distance swum, and the proportion of time spent actively swimming for that combination of fish mass, temperature, and food delivery schedule. These data allowed the effects of food density, temperature, and body mass on swimming velocity to be quantified. These relationships were then compared to allometries and thermal scalings for the physiological processes associated with food processing and metabolism.

Chapter 6

Chapter 6 describes a series of experiments used to determine the effects of ration level, body mass, and temperature on growth rate of *Salvelinus fontinalis*. The data add to existing knowledge on salmonid growth and were also combined with the relationships between distance swum and temperature and body mass, described in Chapter 5, to predict the way in which rates of feeding and growth vary with temperature, body mass, and food density. This, in turn, allowed for the investigation of how temperature and food density may affect adult body size and $\mathbf{W}_{\mathbf{max}}$ for comparison with the results of the models described in Chapter1.

Chapter 7

Chapter 7 contains a brief review and summary of the results of the thesis.

Chapter 2

GENERAL REVIEW

2.1. The Effects of Temperature on the Metabolism, Feeding and Growth of Fish

Temperature is the most pervasive and critical environmental variable in the lives of fish (Prosser 1987; Cossins & Bowler 1987; Hazel 1993). It acts as a controlling and lethal factor (Fry 1967, 1971) and influences almost every aspect of their behaviour and physiology (Reynolds & Casterlin 1980; Prosser 1987; Cossins & Bowler 1987; Hazel 1993). This is because most fish, as poikilotherms, are largely unable to prevent variation in their body temperature with changes in the temperature of their immediate surroundings (Fry 1967; Jankowsky 1973). Hence, changes in environmental temperatures can have profound effects on their temperature-dependent metabolic processes. Although these effects are initially expressed at the molecular and cellular levels, they also have physiological and ecological consequences with the most obvious effects being on the food consumption and growth of individual fish. As a controlling factor (controlling factors govern the metabolic rate by their influence on the state of molecular activation of the components of the metabolic chain, see Fry 1967; 1971), temperature affects biochemical reaction rates and hence influences the energy requirements for repair and maintenance, costs which in turn determine the appetite, feeding activity, food consumption, conversion efficiency and growth rates of fishes. Consequently, temperature will also have ecological implications at the level of individuals, populations, and species.

A number of workers have investigated the effects of temperature on fish metabolic rates (e.g. Beamish 1964; Beamish & Mookherjii 1964; Brett 1964; Kutty 1968; Hettler 1976; Davies & Massey 1977; Marais 1978; Caulton 1978; Robinson et al 1983; Walsh et al 1983; Preez 1987; Wells 1987; Cui & Wootton 1988c; Paul et al. 1988; Xie & Sun 1990; Johnston & Battram 1993). Most results showed that, within a certain range, metabolic rate is related to temperature according to the Van't Hoff rule,

Metabolic Rate $\mathbf{R} = \boldsymbol{a}\boldsymbol{b}^{\mathrm{T}}$,

where **R** is metabolic rate, ***a*** and **b** are constants, and **T** is the temperature in degrees centigrade. However, the temperature range for which this expression is valid depends on a number of factors including habitat, behaviour, and preconditioning to temperature (acclimation or acclimatization) (Cossins & Bowler 1987). The values of the Van't Hoff thermal parameter, **b**, for various physiological and behaviourial rates in fish are summarized in Table 2.1.

Table 2.1. Values of the Van't Hoff Thermal Parameter, b, for Various Physiological and Behavioural Rates in Fish, from the Indicated Sources.

Variable	Species	Temperature Range (°C)	b	Source
Standard Metabolic Rate	**Atlantic salmon** (*Salmo salar*)	3-12	1.037	Smith et al, 1978
		12-18	1.025	
	brook trout (*Salvelinus fontinalis*)	6-12	1.075	Smith et al, 1978
		12-18	1.052	
		5-10	1.129	Macan, 1974
		10-15	1.104	
		15-20	1.108	
	brown trout (*Salmo trutta*)	3.8-7.1	1.212	Elliott, 1976
		7.1-19.5	1.098	
	cyprinid (*Phoxinus phoxinus*)	5-9	1.105	Cui & Wootton 1988c
		9-12	1.105	
		12-15	1.105	
	(*Rutilus rutilus*)	15-20	1.062	Wieser & Medgyesy, 1990
	European eel (*Anguilla anguilla*)	20-24	1.216	Degani et al, 1989
		24-27	1.062	
	lake trout (*Salvelinus namaycush*)	6-10	1.059	Smith et al, 1978
		10-18	1.055	
	rainbow trout (*Oncorhynchus mykiss*)	3-12	1.069	Smith et al, 1978
		12-18	1.024	

Table 2.1. Values of the Van't Hoff Thermal Parameter, b, for Various Physiological and Behavioural Rates in Fish, from the Indicated Sources (cont. 1).

Variable	Species	Temperature Range (°C)	b	Source
Standard Metabolic Rate	**sockeye salmon** (*Oncorhynchus nerka*)	5-10	1.077	Brett, 1964
		10-15	1.036	
		15-20	1.112	
	southern catfish (*Silurus meridionalis*)	10-15	1.040	Xie & Sun, 1990
		15-20	1.006	
		20-25	1.013	
		25-30	1.011	
Active Metabolic Rate	**brook trout** (*Salvelinus fontinalis*)	5-10	1.141	Macan 1974
		10-15	1.050	
		15-20	1.011	
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.041	Brett, 1964
		10-15	1.427	
		15-20	1.077	
Maximum Meal Size	**brown trout** (*Salmo trutta*)	3.8-6.6	1.370	Elliott, 1975a
		6.6-13.3	1.142	
		13.3-18.4	1.007	
		18.4-21.6	0.456	
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.115	Brett, 1971b
		10-15	1.026	
		15-20	0.979	

Table 2.1. Values of the Van't Hoff Thermal Parameter, b, for Various Physiological and Behavioural Rates in Fish, from the Indicated Sources (cont. 2).

Variable	Species	Temperature Range (°C)	b	Source
Sustained Feeding Rate	**brook trout** (*Salvelinus fontinalis*)	3.5-7.6	1.203	Baldwin, 1956
		9-13	1.082	
		13-17	0.931	
		17-21	0.537	
	brown trout (*Salmo trutta*)	3.8-6.6	1.519	Elliott, 1975a
		6.6-13.3	1.187	
		13.3-18.4	1.134	
	cyprinid (*Phoxinus phoxinus*)	5-9	1.196	Cui & Wooton 1988a
		9-12	1.124	
		12-15	1.095	
	Ophiocephalus punctatus	20-28	1.157	Gerald, 1976
		28-33	0.898	
	pike (*Esox lucius*)	10-15	1.066	Salam & Davis 1994
		15-20	1.058	
	sea bass (*Dicentrarchus labrax*)	15-20	1.099	Hidalgo et al, 1987
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.104	Brett, 1971a
		10-15	1.033	
		15-20	0.993	

Table 2.1. Values of the Van't Hoff Thermal Parameter, b, for Various Physiological and Behavioural Rates in fish, from the Indicated Sources (cont. 3).

Variable	Species	Temperature Range (°C)	b	Source
Sustained Feeding Rate	**tilapia** (*Tilapia zillii*)	20.8-25.5	1.344	Platt & Hauser 1978
		25.5-31.4	1.118	
		31.4-34	0.857	
Gastric Evacuation Rate	**brown trout** (*Salmo trutta*)	5.2-9.8	0.893	Elliott, 1972
		9.8-15	0.896	
----Time taken for 50% Evacuation	**rainbow trout** (*Oncorhynchus mykiss*)	5-10	0.909	Windell et al, 1976
		10-15	0.908	
		15-20	0.909	
Swimming Speed	**coho salmon** (*Oncorhynchus kisutch*)	10-15	1.0082	Davis et al, 1963
		15-20	1.0155	
	cod (*Gadus callarias*)	5-10	1.089	Wardle, 1980
		10-15	1.055	
	lemon sole (*Microstomus kitt*)	5-10	1.065	Wardle, 1980
		10-15	1.049	
	pacific mackerel (*Scomber japonicus*)	5-10	1.133	Wardle, 1980
		10-15	1.063	
	plaice (*Pleuronectes platessa*)	5-10	1.080	Wardle, 1980
		10-15	1.051	
	skipjack tuna (*Katsuwonus pelamis*)	20-25	1.054	Wardle, 1980
		25-30	1.076	

Table 2.1. Values of the Van't Hoff Thermal Parameter, b, for Various Physiological and Behavioural Rates in Fish, from the Indicated Sources (cont. 4).

Variable	Species	Temperature Range (°C)	b	Source
Swimming Speed	**sockeye salmon** (*Oncorhynchus nerka*)	5-10	1.104	Brett, 1964
		10-15	1.033	
		15-20	0.993	
Growth Rate (at maximum ration)	**arctic char** (*Salvelinus alpinus*)	4-8	1.189	Jobling, 1983
		8-12	1.107	
	Atlantic salmon (*Salmo salar*)	10-14	1.543	Siemien & Carline, 1991
		14-18	1.133	
		18-22	0.856	
	black rockfish (*Sebastes melanops*)	7-12	1.214	Boehlert & Yoklavich, 1983
		12-18	1.071	
	brook trout (*Salvelinus fontinalis*)	3.5-7.6	1.380	Baldwin, 1956
		9-13	1.125	
		13-17	0.889	
		17-21	0.473	
		7.1-9.8	1.184	McCormick et al, 1972
		9.8-12.4	1.063	
		12.4-15.4	1.004	
		15.4-17.9	0.952	
		17.9-19.5	0.834	

Table 2.1. Values of the Van't Hoff Thermal Parameter, b, for Various Physiological and Behavioural Rates in Fish, from the Indicated Sources (cont. 5).

Variable	Species	Temperature Range (°C)	b	Source
Growth Rate (at maximum ration)	**brook trout** (*Salvelinus fontinalis*)	10-16 strainD	1.122	Sadler et al. 1986
		10-16strainN	1.099	
	brown trout (*Salmo trutta*)	5-8	1.504	Brown, 1946c
		8-12	0.876	
		12-15	0.928	
		15-18	1.205	
		18-20	0.627	
		3.8-7.1	2.058	Elliott, 1975c
		7.1-19.5	1.142	
		12.8-17.8	0.780	
	cyprinid (*Phoxinus phoxinus*)	5-9	1.362	Cui & Wootton, 1988b
		9-12	1.029	
		12-15	1.068	
	Rutilus rutilus	15-20	1.155	Wieser et al, 1988
		20-25	1.028	
	Leuciscus cephalus	20-25	1.056	
	Aiburnus alburnus	20-25	1.043	
	lake trout (*Salvelinus namaycush*)	10-16 strainM	1.015	Sadler et al. 1986
		10-16 strainP	1.022	

Table 2.1. Values of the Van't Hoff Thermal Parameter, b, for Various Physiological and Behavioural Rates in Fish, from the Indicated Sources (cont. 6).

Variable	Species	Temperature Range (°C)	b	Source
Growth Rate (at maximum ration)	**rainbow trout** (*Oncorhynchus mykiss*)	10-16 strainN	1.041	Sadler et al. 1986
		10-16 strainS	1.067	
		fall 10-13.3	1.049	Wurtsbaugh & Davis, 1977
		fall 13.3-16.4	1.009	
		winter 6.9-10.1	0.933	
		winter 10.1-13	1.041	
		spring 9.4-12.6	1.052	
		spring 12.6-15	1.037	
		summer 16 -19.5	0.976	
		summer 19.5-22	0.891	
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.146	Brett et al, 1969
		10-15	1.058	
		15-20	0.930	
	southern catfish (*Silurus meridionalis*)	15-20	1.237	Xie & Sun, 1992
		20-25	1.113	
		25-30	1.013	
	tilapia (*Tilapia zillii*)	20.8-25.5	1.775	Platt & Hauser 1978
		25.5-31.4	1.137	

Changes in temperature usually induce concomitant short-term adjustments in metabolic rate, but, if the temperature change persists, gradual compensation or acclimation generally occurs, that may shift the metabolic rate closer to that preceding the temperature change (Cossins & Bowler 1987; Prosser 1987). Metabolic compensation may also take place as a result of long-term evolutionary adaptation to an environmental temperature regime (Cossins & Bowler 1987). Despite this, animals living in warm areas generally have higher metabolic rates than those from cold areas (Wohlschlag 1960; Holeton 1974; Clarke 1983; Johnston et al. 1991). Clarke (1983, 1987) has argued that the lower standard metabolic rates in high latitude groups means that for any given amount of food consumed, a relatively greater proportion can be directed to growth, less being lost to maintenance. As a result, growth efficiency should be higher at high latitudes. However, this ignores the fact that the food capture rate, a behavioural variable, would also decrease with temperature and in an unknown fashion, so that the effect of temperature on the metabolic rate per unit food ingested, the critical parameter in determining growth efficiency, would also be unknown. At present there are insufficient data to test Clarke's hypothesis (Conover 1990).

In contrast to Clarke's (1987) argument, there is one component of standard metabolism, the cost of osmoregulation, that may not decrease appreciably with decreasing temperature. Kroger & Remmer (1984) have suggested that the cost of osmoregulation in marine fishes, relative to the rate of energy consumption, will increase at low temperatures. They have argued that this would decrease the influence of temperature on standard metabolism and, as a result, decrease the energy available for growth and reproduction at low temperatures. This may explain the anomalously low biomass of fish in polar marine waters relative to the abundance of invertebrates (osmoconformers), particularly in the Antarctic (Everson 1984).

The level of behavioural activity is also influenced by temperature. Swimming velocity and spontaneous activity of fish are lower at colder temperatures, both within and among species (Holeton 1974; Montgomery & Macdonald 1984; Johnston 1990). There may also be a reduction in burst-swimming velocity and endurance, as well as an increase in recovery time, with decreasing temperature (McVean and Montgomery 1987; Macdonald et al 1987; Dunn and Johnston 1986). Generally, animals living in warm areas have relatively higher active metabolic rates than those from cold areas. However, the cost of transport (i.e. the energy cost per unit distance swum) appears to be comparable in cold and warm water fishes (Forster et al. 1987). Metabolic scope (maximum active metabolism minus standard metabolism) either increases continuously with temperature or may be related to temperature by a peaked curve with a maximum at some intermediate temperature (Brett & Groves 1979).

The relationship between temperature and feeding processes has been well documented. For example, in planktivorous fishes (e.g. *Coregonus pollan* and *Thymallus arcticus*), the swimming speed for food capture and the time required to consume a unit of food energy are greatly affected by temperature (Schmidt & O'Brien 1982; Dabrowski et al. 1988). Digestion and assimilation are also influenced by temperature and, as a result, gastric evacuation rate, appetite and food consumption are temperature dependent. In rainbow trout, *Oncorhynchus mykiss*, assimilation efficiency increased slightly from 72 to 78% as the temperature increased from 5 to 20 °C (Brocksen & Bugge 1974). However, assimilation efficiency in fish appears to vary little among species (Webb 1978), suggesting that temperature has a minimal effect on this parameter when comparisons are made among species at their ambient environmental temperatures.

Within species, gastric evacuation rate tends to increase with rising temperature, reaching a maximum as the limit of a species' temperature tolerance is approached (Molnar & Tolg 1962; Smit 1967; Brett & Higgs 1970; Tyler 1970; Elliott 1972; Windell et al. 1976; Ryer & Boehlert 1983). Several studies have shown that the maximum rate of food consumption and the rate of stomach evacuation change in similar ways with temperature, although evacuation rates often increase more rapidly than does appetite over higher temperature ranges (Magnuson 1969; Brett & Higgs 1970; Brett 1971b; Beamish 1972; Elliott 1972; Niimi & Beamish 1974; Steigenberger & Larkin 1974; Salvatore et al. 1987). Under natural conditions, food consumption decreases rapidly with decreasing temperature, both within and among species, and hence feeding activity must do so as well. Field studies have shown a reduction in feeding activity during the winter even though prey items remain abundant throughout the year (Johnston & Battram 1993), suggesting that slow winter growth in polar and temperate fish is not simply due to food limitation, but rather reflects a marked reduction in appetite. However, there is little information on feeding activity as a function of temperature in natural populations.

Several studies show that the response of growth to temperature is a result of interactions with food consumption and metabolic expenditure (Brown 1957; Brett 1971a; Elliott 1976; Gerking & Lee 1983; Dutta 1994). Brown (1946b) found growth maxima at two different temperatures (7-9; 16-19 °C) in laboratory reared brown trout

(*Salmo trutta*) fed to satiation. These two maxima occurred because temperature had different effects on metabolism, appetite and activity. The low-temperature maximum (7-9 °C) occurred because basal metabolism and activity were low but appetite was relatively high. allowing surplus energy to be channelled into growth. The trough occurred because of the dramatic rise in activity at 10-12 °C which took proportionally more of the energy intake. The high-temperature maximum (16-19 °C) was the result of sustained high food intake even though activity had fallen, making more energy available for growth. The decline in growth at higher temperatures occured because of a suppression of appetite and activity combined with a continued increase in standard metabolism. Since feeding rate is directly linked to activity level in wild fish, similar results would not be expected under natual conditions.

The most comprehensive study of the interaction between temperature and growth in fish was carried out by Brett (1971a) on the sockeye salmon (*Oncorhynchus nerka*). A variety of physiological variables related to growth were studied in fish acclimated to different temperatures between 4 and 24 °C. Standard metabolism increased continuously with temperature, whereas active metabolism and metabolic scope showed a marked peak at 15 °C. The 15 °C group also showed the highest growth rates. However, the temperature giving the maximum growth rate decreased as ration decreased. The dramatic increase in standard metabolism at higher acclimation temperatures results in correspondingly less energy being available for growth leading to a reduction in specific growth rates at higher acclimation temperatures when ration is limited. When several parameters such as metabolic rate, maximum meal size, and digestion rate are considered together, it is possible to determine the conditions under which fish convert food energy into flesh with the highest efficiency (percentage gross conversion efficiency). Brett (1971a) related these results to the known thermal ecology of this species and interpreted the diurnal vertical migration of juvenile sockeye as a dynamic response to temperature gradients that maximizes growth rate and efficiency. Similar comprehensive studies have been carried out on brown trout, *Salmo trutta* (Elliott 1982) and *Cyprinodon nevadensis* (Gerking & Lee 1983). It seems likely that the model developed for sockeye salmon by Brett (1971a) will provide a reasonable description of the effect of temperature on growth in a wide range of fish species held under laboratory or hatchery rearing conditions.

Field studies also show that temperature is an important factor in the growth of fishes (Holt 1959; Cossins & Bowler 1987; Jensen 1990). In general, growth appears to be limited to a relatively narrow species-specific temperature range. Within that range, almost all species in the young stages show a rapid acceleration in growth rate as temperature rises, passing through a peak (optimum temperature), and then falling precipitously at temperatures above the optimum (Elliott 1975c; Brett 1979; Weatherley & Gill 1987). Both low and high temperatures may inhibit growth, so that temperature may act as a signal to induce growth activity (Cossins & Bowler 1987; Karas 1990).

The consequences of the rate-controlling effects of temperature on growth are directly reflected in seasonal variation in growth rates within species, and latitudinal clines in growth rates among geographic fish faunas. Most fish are subjected to major changes in growth rates in different seasons (Jones 1976). Although seasonal changes are attributed to several factors (e.g. photoperiod, food availability), temperature, undoubtedly, is the most important.

Staples (1975) has provided evidence of marked seasonal changes in gross growth efficiency of *Philypnodon breviceps* that are correlated with changes in water temperature. Elliott (1975d) reported that the optimum temperature for growth of brown trout decreased progressively from about 13 °C at maximum rations to about 4 °C at a ration size just above the maintenance ration. A similar relationship was found in sockeye salmon (Brett et al. 1969) and hybrid bass (Woiwode & Adelman 1991).

Previous studies have shown that tropical fish grow faster than temperate fish, which in turn tend to grow faster than polar fish (Pauly 1980). These comparisons are complicated by the effects of size and the various corrections for temperature that are often applied. However, when a more detailed examination of the data is undertaken, the basic trend remains: fish growth rates tend to increase in the order polar-temperate-tropical (Clarke & North 1991). At any temperature there are, of course, wide variations in growth rate associated with size, ecological niche, and activity pattern. Nevertheless, there appears to be an underlying positive relationship between growth rate and temperature across faunas. Clarke and North (1991) have argued that, besides temperature, there might be other critical factors (e.g. food) that limit the growth of cold water species since, over the course of evolutionary time, fish should adapt to the ambient temperature regime and evolve compensatory physiological mechanisms to minimize the direct thermodynamic effects of low temperature. Unfortunately, little is know of the relative importance of evolutionary and environmental effects in determining the relationship between growth and temperature although there are likely to be limits on the ability of evolution to overcome thermodynamic constraints. However, the effect of temperature on growth efficiency is not merely a straightforward thermodynamic effect of temperature on biochemical synthesis but is often a complex result of a number of temperature-dependent processes (Hepher et al. 1983; Malloy & Targett 1991). Therefore, if these separate processes have different thermal optima or dependence on temperature , the resulting effect of temperature on growth is likely to be complex. Although the qualitative temperature response of the various parameters which influence growth performance are known, it is not clear what the net quantitative effect of temperature on growth of fish is likely to be under natural feeding conditions.

2.2. Appetite, Feeding Rate and Growth Rate as Functions of Body Mass

Body mass is an important factor influencing the rates of feeding and growth in fish. Winberg (1956) proposed a model for the relationship between metabolic rate (**R**) and body mass (**W**), $\mathbf{R} = \mathbf{cW^d}$, that has been widely used and modified by many investigators. According to Winberg's equation, as a fish increases in size, its metabolic activities decrease relative to its body mass, although the absolute metabolic costs increase with size. The value of the weight exponent (**d**), which ranges from 0.65 to 0.90 for most fish (Jobling 1985), has received wide attention, but the physiological basis for the effects of body mass on metabolic rate have as yet not been adequately explained (Xie & Sun 1990).

The influence of body mass on the maximum rate of food consumption parallels the effect of mass on metabolic rate. Maximum appetite and sustained feeding rate increase allometrically with body size so that smaller fish usually consume more food, in proportion to their body weight, than larger fish (Pandian 1967; 1970; Kato 1970; Brett 1971b; Elliott 1975b; Dunbrack 1988; Salam & Davies 1994). The fact that absolute food consumption increases with body size means that there is an increase in the workload necessary to obtain food as fish grow, because of the increase in body mass, search velocity, and the distance swum. In general, there are three possible ways for fish to meet the increased food requirements that accompany increasing body mass: (1) shift to larger food items; (2) increase only the distance, hence the total time, traveled; or (3) increase only the swimming speed. In reality, fish are likely to increase their food intake through a combination of these methods. In any case, if the metabolic costs of feeding are a significant portion of total metabolism at any weight, this may impose a rather severe restriction on growth when larger food items are not available to larger fish.

Although both metabolic rate and appetite increase with increasing size, the increase in respiratory metabolism may be greater than that in appetite (Paloheimo & Dickie 1966a; Pandian 1970). That is, the increase in energy input (food intake) with increasing body mass is not proportionate to the increase in energy output through metabolism. For example, in dab (*Limanda limanda*), food intake increases with body mass by a weight exponent of 0.54 at 13 °C while metabolic expenditures increase by 0.61 (Pandian 1970). Bioenergetic analyses also suggest that metabolism in wild pelagic fish increases at a faster rate with body size than does the energy gained from the ration at the optimal swimming speeds (Ware 1975; 1978). Therefore, as fish grow, the maximum rate of food consumption, relative to body weight, decreases more rapidly than does the maintenance ration (Brett 1979). As a result, with increasing fish size, smaller and smaller proportions of the total energy intake are channelled into growth, and larger fish will usually have a lower growth efficiency (proportion of ration allocated to growth) than smaller fish (Brett 1979; Dunbrack & Ware 1987). The slope of the relationship between growth rate and body weight is species-specific and both the slope and the intercept vary among species and with environmental factors (Brett & Shelbourn 1975).

The equation $\mathbf{R} = \mathbf{a}\mathbf{T}^{b1}\mathbf{W}^{b2}$ or $\mathbf{R} = \mathbf{a}\mathbf{e}^{b1T}\mathbf{W}^{b2}$ has often been used to describe the relationship between metabolic rate (**R**), body mass (**W**) and Temperature (**T**) (Caulton 1978; Pierce et al. 1981; Cui & Wootton 1988c). However, Xie and Sun (1990) suggest that there should be an interaction term in this equation because the relationship between metabolic rate and body mass varies with temperature and the relationship between metabolic rate and temperature varies with body mass. That is, the mass exponent (b_2) is a function of temperature, and the temperature exponent (b_1) is a function of body mass. An interaction between these two factors was found in most species studied (Xie & Sun 1990). Temperature and body mass may also interact in their joint effect on growth as, in some species, the temperature optima for maximum food consumption and growth shifts downward with increasing body weight (Kinne 1960; Pandian 1970; Jobling 1981; Boehlert 1982; Boehlert & Yoklavich 1983).

Many fish species also show ontogenetic changes in preferred temperatures, with younger stages generally occupying higher temperatures (McCauley & Huggins 1979, Brandt 1980). These preferred temperatures are closely related to the optimal temperatures for growth (McCauley & Casselman 1981, Jobling 1981), suggesting that ontogenetic changes in preferred temperatures may be relatively common, although there is little information on this question.

2.3. The Effects of Food Availability on the Feeding and Growth of Fish

There is general agreement that the food consumption rate of fish is closely correlated with food density, and food availability has often been regarded as a crucial limiting factor affecting the survival and growth of fishes, particularly at low food densities.

The functional response is defined as the change in feeding rate with food density. Holling (1959; 1965) distinguished three basic forms of the functional response: type I, in which feeding rate increases linearly to a maximum as prey density increases; type II, in which feeding rate increases asymptotically at a continuously decreasing rate; and type III, in which feeding rate increases sigmoidally to an asymptote. Type I and type II responses do not have a regulatory influence on the dynamics of predator-prey interactions. In contrast, a type III response, in which an animal is stimulated to increase its rate of prey search as prey become more abundant, is potentially regulatory in nature as it will tend to stabilize the size of the prey population (Oaten & Murdoch 1975a; b; Houck & Strauss 1985). Most fishes investigated have demonstrated type II or type III functional responses (Anderson et al. 1978).

In addition to food density, feeding rates of fishes are determined by the interaction between the state of hunger and experience of fish, as well as their movements in relation to the available food supply (Ware 1972; Dunbrack & Giguere 1987). There is evidence that fish move at different speeds when presented with different prey concentrations (Munk & Kierboe 1985; Dabrowski et al. 1988). Herring larvae respond to low food densities by searching an increasing water volume for food particles. This is done in two ways: by increasing swimming activity and, to some degree, by increasing reactive distance at low food densities (Munk & Kierboe 1985). However, as food density decreases, a fish has to spend progressively more time searching for food, and it will eventually have difficulty meeting its energy requirements.

It was believed that the quantity of energy allocated to foraging has a strong influence on the quantity of energy available for fish growth and reproduction (Ivlev 1961; Kerr 1971, 1982; Cho et al. 1982; Sharp 1982; Koch & Wieser 1983; Hart &

Connellan 1984; Boisclair & Leggett 1989; Gerking 1994). However, no direct test of this hypothesis has been performed, mainly because of the difficulty of estimating fish activity costs. The most common strategy for estimating fish foraging cost involves the estimation of swimming speed which is then used to calculate energy expenditures (Feldmeth & Jenkins 1973; Ware 1975, 1978; Puckett & Dill 1985; Boisclair 1992). The transformation of swimming speed into energetic cost is often based on laboratory-derived relationships between oxygen consumption and speed for fish swimming against a unidirectional current of known velocity (see Beamish 1978 for a review). However, experimental and empirical studies indicate that oxygen consumption--speed relationships derived using the forced swimming approach may underestimate true costs associated with swimming at a given speed under natural conditions (Puckett &Dill 1984; Weatherley & Gill 1987; Forstner & Wieser 1990; Webb 1991; Boisclair & Tang 1993). In addition, the estimation of fish foraging cost might be more difficult since fish frequently change velocity under natural condition to search and capture food or respond to variation in food density.

Food density (along with food search activity) determines ration level (James & Findlay 1989), and ration level, expressed generally as a percentage of the body weight of the fish, is a key variable that strongly influences growth rate (Webb 1978).

Relationships between specific growth rate and ration level have been documented for several species. In some cases these variables were linearly correlated (Boehlert & Yoklavich 1983; Klaodatos & Apostopoulos 1986), but in general a plot of growth vs. ration produces a decelerating curve (Brett 1979; Xie & Sun 1992). In a typical growth-ration curve, growth rises steeply from a minimum negative value at zero ration to cross the point of zero growth rate at the maintenance ration. This steep rise in growth flexes downward so that a tangent from the origin touches the curve at the point where the ratio of growth to ration is maximal, defining the optimum ration for growth efficiency. The growth curve then flexes further, reaching a plateau of maximum growth rate at the point of maximum ration.

Many researchers have attempted to model growth using the results of feeding and growth experiments to describe the relationship between specific growth rate and ration level. Allen & Wootton (1982), Cui & Wootton (1988a, b) and Xie & Sun (1992) found that a linear regression with specific growth rate (**SGR**) as the dependent variable and log (ration level, **RL**; **RL**>0) as the independent variable fit their experimental data well. However, they did not explain the biological implications of their model. Most authors have focused their attention on the effects of ration level on the specific growth rate and conversion efficiency (**K**), highlighting the critical points, i.e. maintenance, optimum and maximum ration levels (Brett et al. 1969; Hidalgo et al. 1987; Krishnan & Reddy, 1989; Woiwode & Adelman 1991).

Paloheimo & Dickie (1965; 1966b) used conversion efficiency (i.e. gross growth efficiency----growth rate/ingestion rate) as an index to discuss the effect of ration level on growth. They suggested that the relationship between **K** and **RL** could be described by a linear semi-logarithmic relationship, the so-called 'K-line' equation: **lnK = a - bRL**. Several authors subsequently argued that the correlation in the 'K-line' equation required a high ration level (Warren & Davis 1967; Gerking 1971; Staples & Nomura 1976; Davies & Massey 1977; Elliott 1979). Brett et al. (1969), Rafail (1968), Elliott (1975b) and Davies & Massey (1977) have found the existence of a positive phase of the K-line in young sockeye salmon, plaice (*Pleuronectes platessa*), brown trout, and goldfish (*Carassius auratus*). For these species the gross conversion efficiency increased with ration level to a maximum value at the optimum ration and then decreased with increasing ration at higher ration levels. Therefore, these authors suggested that an inflected, biphasic K-line is a more appropriate model for food utilization than the simple negative relationship originally proposed by Paloheimo and Dickie (1966b).

Paloheimo and Dickie (1965) concluded that their K-line was independent of the size of the fish, applicable to a wide range of rations, and remained constant over a wide range of temperature. The results of most studies do not support any of these conclusions. In fact, conversion efficiencies are dependent on both ration level and temperature. As food consumption rate increases, conversion efficiency increases. In most cases, the efficiency reaches a maximum level and declines slightly at repletion ration levels. However, when high temperatures inhibit consumption, conversion efficiencies continue to increase up to the highest food consumption levels (Wurtsbaugh & Davis 1977). Within the normal temperature range, and at high ration levels, temperature appears to have little effect on growth efficiency, but at low consumption rates, elevated temperatures result in reduced conversion efficiencies. Consequently, if food is abundant, fish growth should be enhanced by increasing temperature up to the optimal temperature for food consumption, but, if food is limited, any substantial temperature increase would result in decreased growth (Wurtsbaugh & Davis 1977; Xie & Sun 1992; Letcher & Bengtson 1993). Although little attention appears to have been paid to the interaction between ration level and body mass on growth performance, as appetite and feeding rate vary with the weight of fish, a corresponding variation in the relationship between growth and ration with fish size is expected.

It must be pointed that rations for wild individuals are usually well below physiological maxima and largely depend on the density of food in the environment and the rate at which a fish moves through its environment searching for food. Consequently, the effects of changes in temperature and body size on feeding and growth rates under natural conditions cannot be inferred using only the general allometric and thermal equations that apply to the physiological processes of metabolism, digestion, and food conversion. What is instead required are allometric and thermal equations ofbehaviour that describe how foraging behaviour, specifically the rate of search, changes with body mass and temperature. However, the allometry of behaviourial rates and their response to temperature change are generally not well known.

2.4. Habitat Use in Fish Relation to Temperature, Food Availability and Body Size.

The above review has shown that both food and temperature have major effects on the growth and activity of fishes. Although little is known of the joint effects of temperature and food availability on habitat use, a number of bioenergetics models of habitat choice that include food and temperature effects, have been proposed (Crowder & Magnuson 1983; Wildhaber & Crowder 1990).

Most models that explore the influence of food availability on habitat choice are based on optimal foraging theory (Pyke 1984). A common assumption of this theory is that animals will choose habitats that allow fish to maximize their net rate of energy intake, a metric that is thought to be correlated with fitness (Pyke 1984). Many studies of foraging behaviour have shown that fish appear to make adaptive habitat choices when faced with variation in the availability of food (Murdoch et al. 1975; Mittelbach 1981, 1984; Dill 1983; Werner et al. 1983; Crowder 1985). Although optimal habitat use requires that individuals occupy habitats that maximize their rate of net energy gain, fish often appear to use suboptimal foraging habitats. Reasons for this could include incomplete information on the temporal and spatial distribution of food resources, physical limitations, competitive interactions, predator avoidance, and habitat degradation (Sogard 1994). Few studies have considered the implications of the use of suboptimal habitats by fish.

Temperature preferences in fish have been well documented (Neill & Magnuson 1974; Coutant & Carroll 1980). In laboratory studies, fish spend about 2/3 of their time within 2 °C of a final preferred temperature (Magnuson et al. 1979; Mathur et al. 1981) that tends to match the optimal temperature for physiological activity and growth maximization (Fry & Hochacka 1970; Brett 1971a; Crawshaw

1977; Beitinger & Fitzpatrick 1979; Magnuson et al. 1979; Neill 1979; McCauley & Casselman 1981; Coutant 1987; Wildhaber & Crowder 1990; Clark & Green 1990; Bevelhimer & Adams 1993). Under natural conditions, the effects of temperature on habitat choice are often complex as fish must generally respond to both food and temperature, as well as other factors, in making habitat choices (Neill & Magnuson 1974; Ware 1982; Crowder & Magnuson 1983; Wildhaber & Crowder 1990; Bevelhimer & Adams 1993; Luecke & Teuscher 1994). A number of studies have suggested that when food abundance is high, fish seem to choose the habitat whose temperature produces the maximum surplus power, but the results are equivocal (Javaid & Anderson 1967; Stuntz & Magnuson 1976; Reynolds & Casterlin 1979; Mac 1985). Field studies have also suggested that the combined effects of food and temperature may be a major influence on the distribution of fish in thermally stratified lakes (Caulton 1978; Rudstam & Magnuson 1985; Hamrin 1986; Wurtsbaugh & Neverman 1988; Bevelhimer & Adams 1993). The preliminary evidence that fish may integrate the effects of food and temperature led Crowder and Magnuson (1983) to propose the "behavior energetic hypothesis", which proposes that fish should choose the habitat with the highest rate of net energy gain. The energy value of a habitat can be determined using the fish bioenergetics model (Kitchell et al. 1977), which integrates the effects of food and temperature on growth rate. The Crowder-Magnuson hypothesis also suggests that dynamic energy conservation measures, such as moving to cooler temperatures during non-feeding periods, may be energetically advantageous (Ware 1982; Bevelhimer & Adams 1993; Wildhaber &Crowder 1990; Woiwode & Adelman 1991). It has also been suggested that when food supply varies with fish size, fish of different sizes may achieve optimum growth by using water of different temperatures (Hamrin 1986), that is, habitats that vary in temperature could also vary in the size distribution of fish using the habitats.

2.5. The Effect of Food Density and Temperature on Adult Body Mass.

Although a large number of studies (Webb 1978; Brett 1979; Allen & Wootton1982; Reznik 1983; Jensen 1985; Hidalgo et al. 1987; Cui & Wootton 1988a, b; Krishnan & Reddy 1989; Boehlert & Yoklavich 1983; Klaodatos & Apostopoulos 1986; Woiwode & Adelman1991; Xie & Sun 1992) suggest a relationship between food availability and adult body mass, there seems to be little direct evidence for such effects from field studies. Consequently, it is difficult to assess the effect of food availability on adult size using existing data. One difficulty is that measurements of size at maturity, among populations, are generally not accompanied by detailed measurements of food availability. In cases where this has been done, food availability and size at sexual maturity are positively correlated (Hutchings 1993).

Changes in temperature could also alter the relative value of investments in current vs. future reproduction, leading to temperature-dependent changes in the average size at maturity, observed across populations. However, as noted in Chapter 1, in the absence of quantitative information on the effect of temperature on behaviour it is unclear in which direction selection would shift the size at maturity in response to long term changes in temperature. It is also difficult to interpret any of the trends noted below, as changes in temperature may be accompanied by changes in food availability or mortality.

It has been reported that the adult body size of freshwater fishes increases with latitude both within and between species (Lindsey 1966; Jonsson et al. 1991). However, the relationship is not well defined in marine faunas and, with the notable exception of a small number of very large shark species, large fishes are seldom found in cold, high latitude marine waters (Wimpenny 1941; Lindsey 1966; Everson 1984; Dunbrack & Ware 1987). Although it is plausible that geographic trends in adult body size could ultimately be related to the effects of temperature on the balance between current and future reproduction, as outlined above (Precht et al. 1973; Clarke 1987; Dunbrack & Ware 1987), this is by no means certain.

The increase in adult body size with latitude has been attributed to delayed age at sexual maturity due to reductions in metabolic rate, growth rate, and mortality at low temperatures (Alm 1959; Jonsson 1977; Pauly 1980; Thorpe 1986). However, it is unclear why delays in the age of sexual maturity should be associated necessarily with increased adult size when growth rates are also reduced. In addition, this hypothesis cannot explain the negative correlation between latitude and body sizes in polar pelagic teleosts because they also have relatively lower metabolic rates and grow more slowly than warmer water species (Clarke 1983, 1987, 1991; Clarke & North 1991). When adult body size is found to be smaller at higher temperatures this has been attributed to higher metabolic rate, rapid development, early maturity (Precht et al.1973), and relatively higher fecundity (Levinton 1983), all consequences of higher temperatures. Unfortunately, many of these interpretations are ad hoc, circular, and deal only with proximal explanations rather than addressing evolutionary questions. One reason for this may be the often equivocal nature of temperature related trends in body size both within and among fish faunas.

The discussion of adult body size in Chapter 1 is primarily an evolutionary one and does not necessarily apply to the responses of individual fish to short term changes in food availability. In salmonid husbandry, for example, it is often observed that high feeding and growth rates lead to reductions in the average size at maturity of males (Thorpe 1986). This does not imply that high feeding rates lead to a reduction in $\mathbf{W}_{\mathbf{max}}$, only that, under natural conditions, maturity at a small size (and early age) may be favoured in males experiencing unusually high growth rates relative to long term population means. In wild populations the adaptive nature of this developmental response is probably related to unknown competitive advantages of early maturity for males at the extreme upper end of the body size distribution for their cohort. Early maturity in male salmonids is only common under the feeding regimes used in artificial rearing when a large proportion of males can reach a size threshold that triggers maturation (Thorpe 1986). Interestingly, high feeding rates do not induce early maturity in female salmonids.

Chapter 3

MAXIMUM MEAL SIZE AND SUSTAINED FEEDING RATE

3.1. Introduction

The experiments described in this chapter provide a quantification of the body size allometry and temperature dependence of feeding and digestion in juvenile brook trout (*Salvelinus fontinalis*). These results contribute to the comparative study of feeding and gut evacuation processes in fishes and are also used to establish an appropriate range of ration levels necessary for the behavioural experiments described in Chapter 5, which examine the relationship between behavioural and physiological responses to changes in temperature and body mass. The results of the feeding and digestion experiments also provide data on feeding rates that are necessary for the design of the growth experiments described in Chapter 6.

3.2. Materials and Methods

3.2.1. Experimental Fish

The fish used in these experiments were captured by backpack electroshocker from the Pouch Cove River near Pouch Cove, St. John's, Newfoundland, in seven collections made in July, September, and November 1994, and April, May, July, and August 1995. Water temperature in the river at the time of capture varied from 3 to 17 °C. Following capture the fish were placed in individual 22 L aquaria in the laboratory. The ranges in body mass and length of experimental fish are given in Table 3.1.

Table 3.1. The Numbers of Fish Used, and Their Range in Mass and Length, in Feeding Experiments

Experiment	Temp. (°C)	Number	Body Weight (g)	Body Length (cm)
Sustained	5±0.4	16(x4*)	4.0-17.7	6.1-10.4
Feeding	12±0.4	16(x4*)	3.8-17.2	6.4-10.4
Rate	18±0.4	16(x4*)	3.9-16.1	6.4-10.1
Maximum	5±0.4	16(x2*)	4.0-17.7	6.1-10.4
Meal	12±0.4	16(x2*)	3.8-17.2	6.4-10.4
Size	18±0.4	16(x2*)	3.9-16.1	6.4-10.1

* number of replicates per fish

Fish were allowed to acclimate to changes in water temperature for at least 10 days prior to their use in experiments. A continuous flow of partially recirculated stream water was supplied to all tanks. Lighting was provided on a 12 h light : 12 h dark cycle by two 40 W fluorescent ceiling tubes covered with blue plastic film. Fish were fed to satiation twice daily with live beetle larvae and most fish began feeding within 3-10 days of capture.

3.2.2. Food Organisms

Fish were fed live beetle larvae (*Tribolium castaneum*) (average length, weight, energy content and proximate composition are given in Table 3.2). The moisture content of the larvae was determined by drying 2 g of larvae at 105 °C to constant weight (AOAC 1990). Ash content was measured using the AOAC (1990) method, total nitrogen was determined using the Kjeldahl method (AOAC 1990), and total lipids were extracted according to the method of Bligh and Dyer (1959) using a chloroform-methanol-water system. Energy content was calculated by using protein, lipid and carbohydrate composition according to Brett & Groves (1979). To facilitate comparison with other studies, the amount of food consumed by fish was expressed as dry weight using a wet to dry conversion factor of 0.40.

Table 3.2. The Average Length, Weight, and Composition of Beetle Larvae (±SD) Used as Trout Food.

Length (mm)	5.6 ± 1.2
Live Weight (mg)	2.1 ± 0.2
Dry Weight (mg)	0.84 ± 0.07
Protein (%)	26.9 ± 1.3
Lipid (%)	11.2 ± 0.5
Carbohydrate (%)*	1.3 ± 0.08
Water (%)	60.0 ± 1.4
Ash (%)	0.56 ± 0.12
Energy Content (cal./mg)**	2.03

*calculated by difference.

** metabolizable energy calculated according to Brett & Groves (1979).

3.2.3. Experimental Tanks and Water Temperature Control System

Experiments were conducted in 16 22-L glass aquaria supplied with a continuous flow of partially recirculated stream water. Temperature was controlled by pumping water through a heat exchange water cooler that allowed precise regulation throughout the 5 to 20 °C range. Water temperature remained constant during each series of experiments.

3.2.4. Maximum Sustainable Feeding Rate and Maximum Meal Size

These experiments were carried out between August and October, 1994. For each series of experiments, single fish were placed in each of the 16 tanks and acclimated to the experimental water temperature for 10 days. Fish were fed to satiation twice daily during this pre-experimental period and were assumed to have reached an equilibrium between their daily rates of intake and gut evacuation by the end of this period. Fish not feeding actively during the pre-experimental period were not used in the experiments.

To determine maximum sustainable feeding rate, fish were provided with two daily meals at approximately 9:00 am and 5:00 PM, beginning on day 11. A measured quantity of beetle larvae, in excess of the amount finally consumed, was introduced to each tank and the fish allowed to feed for 30 minutes. Preliminary trials indicated that this time was sufficient for fish to reach satiation (most fish ceased feeding within 15 minutes). All remaining larvae were then removed by siphon, weighed, and this value subtracted from the total weight of larvae introduced to give ration size. Assuming that intake and evacuation rates were at approximate equilibrium at the end of the pre-experimental period, the total mass of the two daily meals during the experimental period would estimate the maximum sustainable daily feeding rate. Experimental feeding continued for four days to give four estimates of the sustainable feeding rate for each fish.

Following the four days of experimental feeding, fish were starved for 48 hours to clear previously ingested food from their stomachs. Maximum meal size was then determined by providing an excess amount of food in a single meal as in the feeding rate experiments described above. The total mass of larvae ingested by the fish within 30 minutes gave the maximum meal size. Following this meal, fish were again starved for 48 hours and another determination of maximum meal size made. After this second feeding, fish were weighed immediately and the weight of food consumed in the last meal subtracted from the fish weight to give the weight of fish after 48 hours of fasting. This weight was taken as the weight of fish in both the sustainable feeding rate and the maximum meal size experiments.

The procedure described above (determination of maximum sustainable feeding rate followed by determination of maximum meal size) was repeated for the two remaining temperatures. The order of presentation of temperatures was 12, 5, 18 °C. Four fish used in the 12 °C experiments were also used in the 5 °C experiments. Ten fish used in the 5 °C experiments were also used in the 18 °C experiments.

3.3. Results

At each experimental temperature, both maximum sustainable feeding rate and maximum meal size increased with body mass (Figs. 3.1, 3.2) according to the allometric equation

$$C_{max} = cW^{d}$$

where C_{max} is the maximum daily ration or meal size, **W** is fish mass, and c and d are constants. All values of the intercept c and slope d are given in Table 3.3. The regressions of feeding rate and meal size on body mass were significant ($p<0.001$) at all temperatures. Values of c and d increased slightly with increasing temperature for both maximum meal size and sustainable feeding rate.

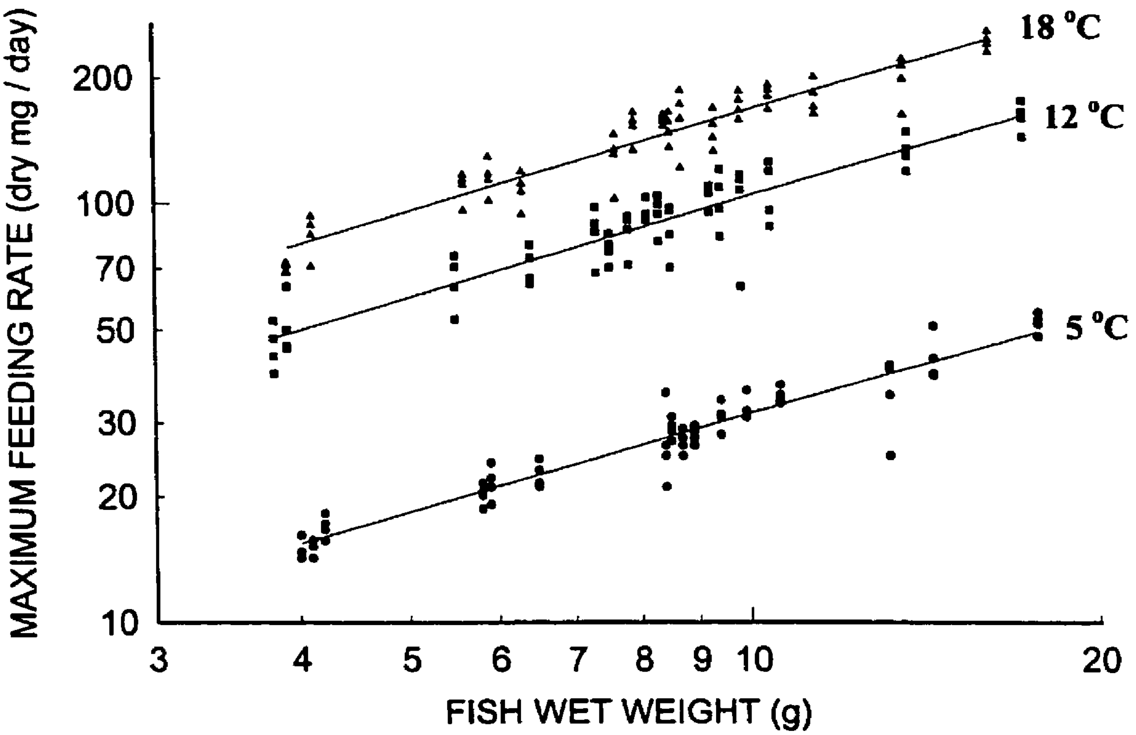

Fig. 3.1. Sustained Feeding Rate of Brook Trout as A Function of Body Mass and Temperature

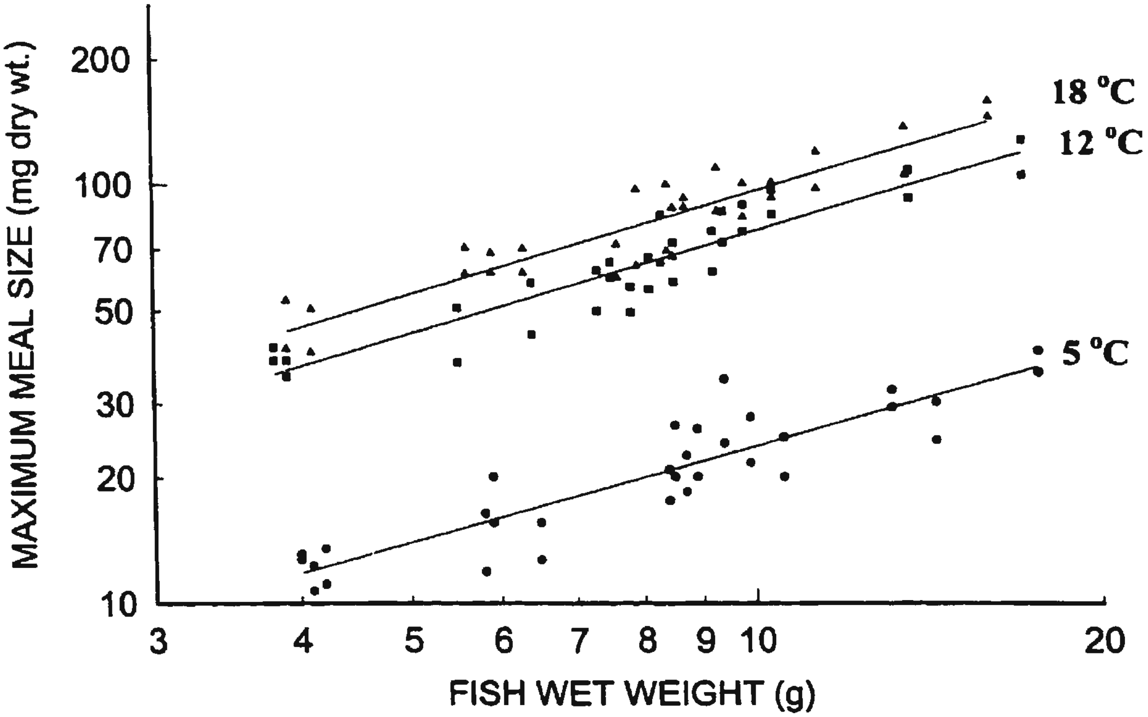

Fig. 3.2. Maximum Meal Size of Brook Trout as A Function of Body Mass and Temperature

Table 3.3. The Intercept (*c*) and Coefficient (*d*) of the Regression Equations for the Relationships between Maximum Meal Size or Sustainable Feeding Rate and Body Mass.

Dependent Variable	Body Mass (g)	Temp (°C)	n	c	d	P value
Maximum	4.0-17.7	5	32	4.076	0.7656	$p<0.001$
Meal	3.8-17.2	12	32	11.97	0.8094	$p<0.001$
Size	3.9-16.1	18	32	14.716	0.8146	$p<0.001$
Sustain.	4.0-17.7	5	64	4.3652	0.7809	$p<0.001$
Feeding	3.8-17.2	12	64	13.5425	0.8090	$p<0.001$
Rate	3.9-16.1	18	64	25.8941	0.8131	$P<0.001$

The Van't Hoff thermal parameter, b, was used to quantify the effects of temperature on maximum meal size and maximum sustained feeding rate. The Van't Hoff equation expresses temperature effects on metabolic rate as

$$\textbf{Metabolic rate} = ab^{T},$$

where a and b are constants and T is the temperature in degrees Celsius. The parameter b is the proportionate change in the rate of the process per degree change in temperature. If maximum meal size, for example, is expressed in the form of the Van't Hoff equation then, at any given body mass, the ratio of meal sizes at temperatures T and $T+n$ will be

$$ab^{T+n}/ab^{T} = b^{n}$$

The parameter **b** will therefore equal the **n**th root of the ratio of the maximum meal sizes. A general expression for b can be obtained by taking the ratios of the equations that describe maximum meal size as a function of body mass at two temperatures. In theory this ratio would vary with body mass since the weight exponents change somewhat with temperature. However, in practice, the effect of ignoring weight will be negligible because the weight exponent will be close to zero. For example, the ratio of the expressions for maximum meal size at 12 and 5°C gives a ***b*** value of $1.166W^{0.0063}$. Even at the largest size of fish used (~20 g), $W^{0.0063}$ is only 1.02 and has only a small effect on the estimated value of ***b***. A similar procedure is used to obtain ***b*** for the maximum sustained feeding rate. These results are summarized in Table 3.4. To facilitate comparisons, the b value for metabolic rate, maximum meal size and sustained feeding rate of salmonids from previous studies are listed in Table 3.5.

Table 3.4. Values of the Van't Hoff Thermal Parameter, b, for Maximum Meal Size and Sustained Feeding Rate.

Variable	Temperature Range (°C)	b
Maximum Meal Size	5-12	$1.166W^{0.0063}$
	12-18	$1.035W^{0.0009}$
Sustained Feeding Rate	5-12	$1.176W^{0.0040}$
	12-18	$1.114W^{0.0007}$

3.4. Discussion

In this study, the maximum sustainable feeding rate of trout increased continuously from 5 to 18 °C. Although higher temperatures were not used in this study, preliminary experiments indicated a decrease in feeding rate above 20 °C, suggesting a peak in maximum feeding rate between 18 and 20 °C. In contrast, Baldwin (1956) identified 13 °C as the temperature that maximized food consumption in 31 to 91 g brook trout. The different results of this study and Baldwin's (1956) are problematic but may be due to Baldwin's (1956) use of larger fish. Such a decrease in the temperature that maximizes feeding rate with increasing fish size has been reported for dab (*Limanda limanda*) (Pandian 1970). A feeding peak between 18 and 20 °C is, however, consistent with works on other salmonids. For example, the temperature for maximum ration in brown trout was found to be 19 °C over the body mass range of 5 to 300 g (Elliott 1975b; 1975c), while appetite in juvenile sockeye salmon (*Oncorhynchus nerka*) was reported to peak at 20 °C (Brett et al. 1969).

The nearly parallel regression lines of Fig. 3.2 indicate that the proportional increase with temperature in maximum food consumption is size-independent, at least over the body size range of 2 to 20 g. Similar results have been reported for brown trout (Elliott 1975b) and pike (*Esox lucius*) (Salam & Davies 1994). However, other studies have shown a size-dependent effect of temperature on food consumption (Hatanaka et al. 1956; Menzel 1960; Pandian 1970) with smaller individuals generally being more sensitive to temperature.

The increases in maximum meal size and maximum sustainable feeding rate with body weight fit the allometric model

$$C_{max} = cW^d,$$

which describes increases in food consumption with body weight in several other fish species (e.g. Elliott 1975b; Wootton et al. 1980; Cui & Wootton 1988a; Dunbrack 1988; Salam & Davies 1994). Although reported values of the weight exponent, ***d***, vary between 0.54 to 0.88, the weight exponents given in Table 3.3 are comparable to those reported for other salmonids, including brown trout (Elliott 1975b) and coho salmon (Dunbrack 1988). There is less agreement over the value of the coefficient, *c*, for salmonids. In particular, the values in Table 3.3. are very similar to those obtained by Dunbrack (1988) for juvenile coho salmon, but are substantially lower than the coefficients Elliott (1975a) reported for brown trout. The equilibrium method of measuring sustainable feeding rate used in this study is very similar to Dunbrack's (1988), and lends support to his argument that studies that do not use equilibrium measurements (e.g. Elliott 1975a) are likely to overestimate maximum feeding rate.

Table 3.5. Values of the Van't Hoff Thermal Parameter, b, for Metabolic Rate, Meal Size and Feeding Rate of Salmonids.

Variable	Species	Temperature Range (°C)	b	Source
Standard Metabolic Rate	**Atlantic salmon** (*Salmo salar*)	3-12	1.037	Smith et al, 1978
		12-18	1.025	
	brook trout (*Salvelinus fontinalis*)	6-12	1.075	Smith et al, 1978
		12-18	1.052	
		5-10	1.129	Macan, 1974
		10-15	1.104	
		15-20	1.108	
	brown trout (*Salmo trutta*)	3.8-7.1	1.212	Elliott, 1976
		7.1-19.5	1.098	
	lake trout (*Salvelinus namaycush*)	6-10	1.059	Smith et al, 1978
		10-18	1.055	
	rainbow trout (*Oncorhynchus mykiss*)	3-12	1.069	Smith et al, 1978
		12-18	1.024	
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.077	Brett, 1964
		10-15	1.036	
		15-20	1.112	
Active Metabolic Rate	**brook trout** (*Salvelinus fontinalis*)	5-10	1.141	Macan, 1974
		10-15	1.050	
		15-20	1.011	
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.041	Brett, 1964
		10-15	1.427	
		15-20	1.077	

Table 3.5. Values of the Van't Hoff Thermal Parameter, b, for Metabolic Rate, Meal Size and Feeding Rate of Salmonids (Cont).

Variable	Species	Temperature Range (°C)	b	Source
Maximum Meal Size	**brook trout** (*Salvelinus frontinalis*)	5-12	1.166	present study
		12-18	1.035	
	brown trout (*Salmo trutta*)	3.8-6.6	1.370	Elliott, 1975a
		6.6-13.3	1.142	
		13.3-18.4	1.007	
		18.4-21.6	0.456	
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.115	Brett, 1971b
		10-15	1.026	
		15-20	0.979	
Sustained Feeding Rate	**brook trout** (*Salvelinus frontinalis*)	5-12	1.176	present study
		12-18	1.114	
		3.5-7.6	1.203	Baldwin, 1956
		9-13	1.082	
		13-17	0.931	
		17-21	0.537	
	brown trout (*Salmo trutta*)	3.8-6.6	1.519	Elliott, 1975a
		6.6-13.3	1.187	
		13.3-18.4	1.134	
	sockeye salmon (*Oncorhynchus nerka*)	5-10	1.104	Brett, 1971a
		10-15	1.033	
		15-20	0.993	

Chapter 4

DESIGN OF THE AUTOMATED EXPERIMENTAL SYSTEM

4.1. Introduction

Body mass, temperature, and the density and distribution of food are important determinants of the foraging behaviour of wild fish and their influence should be considered in any attempt to investigate the feeding and growth of fish under natural conditions. However, due to the methodological difficulties of controlling food density precisely throughout the course of an experiment, there is little detailed information on how these factors influence feeding behaviour, either singly or in combination. Such studies require a quick, easy, and accurate technique for the real-time measurement of fish activity, feeding rate, and the control of food density. This level of experimental control has only recently become feasible because of new developments in microcomputer interfaces and image analysis hardware. This chapter describes an experimental system that was applied to the study of fish feeding behaviour and which may prove to be useful in other animal movement studies.

The key to the experiments described in Chapter 5 is the ability to monitor, in real time, the distance swum by actively foraging fish and to simultaneously control food density through a system of feeders that dispense single food items when experimental fish have swum a prescribed distance. Food density is expressed as food items encountered per distance swum, an ecologically reasonable measure of the density of food. Both the real time monitoring and the dispensing of food were performed by a computerized monitor and control system that was designed and constructed by myself. A brief description of this automated system will be given in this chapter.

4.2. Automated system hardware

Fig. 4.1 is a schematic diagram of the components of the experimental system: a large shallow (2.0x1.8x0.3 m) plywood tank covered with white waterproof plastic film, a CCD black & white low illumination video camera SSC-M350 (Sony Corporation, Japan) with ultra wide angle lens, a plug-in image QuickCapture board DT2855 (Data Translation, Inc., Marlboro, MA, USA), an IBM PC 80486DX 50MHz compatible microcomputer, a plug-in 8-channel isolated relay I/O board (Omega Engineering, Inc., Stamford, CT, USA) and four automatic feeders of my own design. The real time video digitizer is the crucial hardware item that allowed the real time monitoring required for this experiment.

The DT2855 board can digitize video images individually or continuously at the same rate cameras produce them (30 video frames/sec). The board converts the video signal into a 480 lines by 640 square pixels per line matrix at 8 bits per pixel.

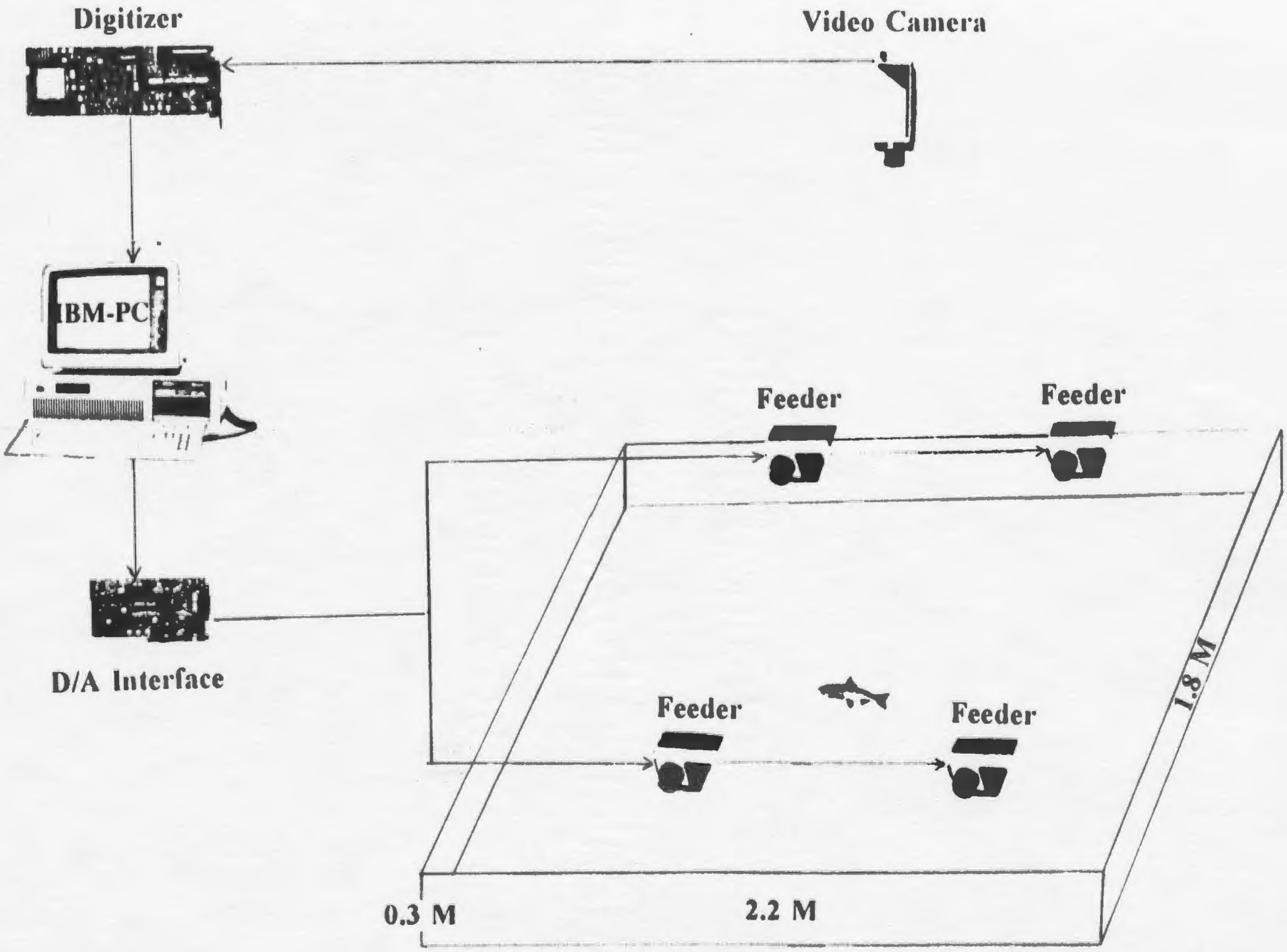

Fig. 4.1. Schematic Diagram of the Experimental Apparatus

This allows each pixel to be represented by one of 256 possible gray levels. As an image is acquired, the 8-bit input values are sent through one of four software-selectable input look-up tables stored in onboard RAM. The input look-up tables allow the board to perform real-time image processing on acquired data as it flows into the frame-store memory. Captured images are first stored in frame-store memory on the board. This board memory can then be accessed over the computer bus using standard I/O instructions. Frame memory operations are controlled by hardware timing circuits and arbitrators, which are fast enough so that video input, video output, and normal memory access can all be done simultaneously. The other advantage of this board is that images are displayed by square-pixels with a 1:1 pixel aspect ratio. Square pixels are free of geometric distortions so that the real distance between two points in an image can be measured precisely. The feeder control was accessed through an economical 8 channel isolated relay D/A interface board, PDISO-8. The eight electro-mechanical relay outputs are addressed as a single output I/O byte and can be programmed by using standard I/O instructions. Information flow within the monitor and control system is summarized in Fig. 4.2.

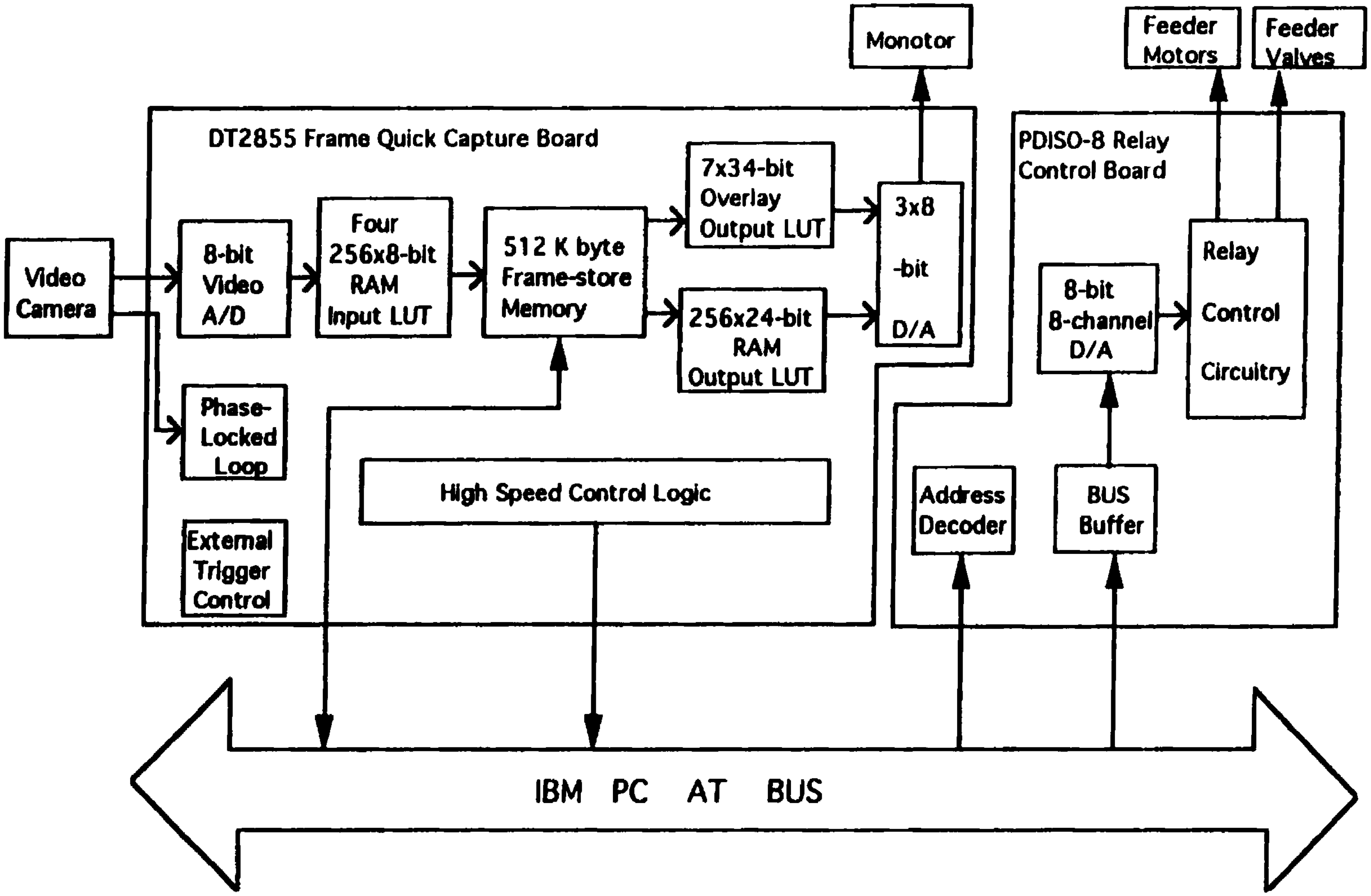

Fig. 4.2. Block Diagram of the Monitoring and Control System Hardware

4.3. Automated system software

An integral part of the automated control system is the control software. The computer program was based on the following principles.

During an experiment, fish movements were recorded by an overhead video camera. The analog image signal from the video camera was input to the video digitizer (DT2855) which transformed the analog signal into a digital image signal which was then stored in a frame-store memory buffer. The gray level of the digital image was then binarized (black or white) using a programmed Input Look-up Table stored in onboard RAM which allowed the gray level of each pixel in the frame to be compared with a prescribed threshold value. The pixel gray value was replaced by 00000000 (black) if the gray level was higher than the threshold, or by 11111111 (white) if the gray level was lower. This preliminary image processing enhanced the contrast of the image and removed background noise.

After an image was acquired and filtered, the position of the fish was determined by examining the gray level values of each pixel in the filtered image. The position of the fish was determined by searching for some fixed number of contiguous pixels that were all black (00000000). The actual position of the fish was then taken as the mean position of the pixel group (average X, average Y). These coordinates were stored in computer RAM and the computer then produced a signal to trigger the acquisition of the next image from the camera. The coordinates of the fish in the second frame were determined as above and then compared with the coordinates from the first frame. If the distance between these consecutive fixes was less than some threshold value, the fish would be assumed to have not moved and the second fix would be discarded. This process continued until the distance between the fish's coordinates in the first frame captured and those in the **n**th frame captured was greater than the threshold value. When this occurred the distance between these two fixes was added to the previous sum stored in computer RAM, the first position was replace by the **n**th position, and the process was repeated for the duration of the experiment.

When the total distance swum reached some prescribed value corresponding to a particular feeding schedule, one of the feeders was chosen using a random number generator, activated by the computer through the D/A isolated relay output board (PDISO-8), and a food item was dispensed. Individual food items were delivered by briefly turning on an air jet that blew them out of the feeder onto the water surface. The air line was controlled by a solenoid valve via a relay. After the food item was dispensed another relay activated a motor that advanced the feeder to the next item. At the same time, the distance swum by the fish and the time taken to cover the distance were automatically recorded in a data file. This allowed the total distance swum, the active swimming time, the average cruising velocity, and the amount of food dispensed to be calculated at the end of experiment.

The software was written in both FORTRAN and Assembly languages. The main program including calculation, analysis, judgment and data management was written in Fortran. However, because of the speed limitations of advanced languages in programming A/D and D/A interfaces, the image processing, including initializing the digitizer, binarizing the gray level and scanning for black pixels, and control of the feeder were handed over to several subroutines written in Assembly language. A flow chart for the controlling software is given in Fig. 3.3, while the critical subroutines are listed in Appendix A.

4.4. Remark

This system was completed in the spring of 1994 and operated as intended throughout the numerous foraging behaviour experiments. This success demonstrates that this is an economical and accurate technique for automating real-time measurements of animal activity and for controlling food consumption rates or taking other action in response to the measured activity. The present study could clearly not have been carried out without this automated system as the only alternative would involve continuous visual monitoring by several human observers for 12 hours/day, six days/week throughout most of two years. An additional advantage of the technique is that the experimental animal does not need to be unduly disturbed during the experimental period so that man-made stress to the trial fish is minimized.

Although designed for the particular problems of my research, this technical achievement is of wider interest as it could be adapted to a number of problems in animal behaviour that would otherwise be intractable.

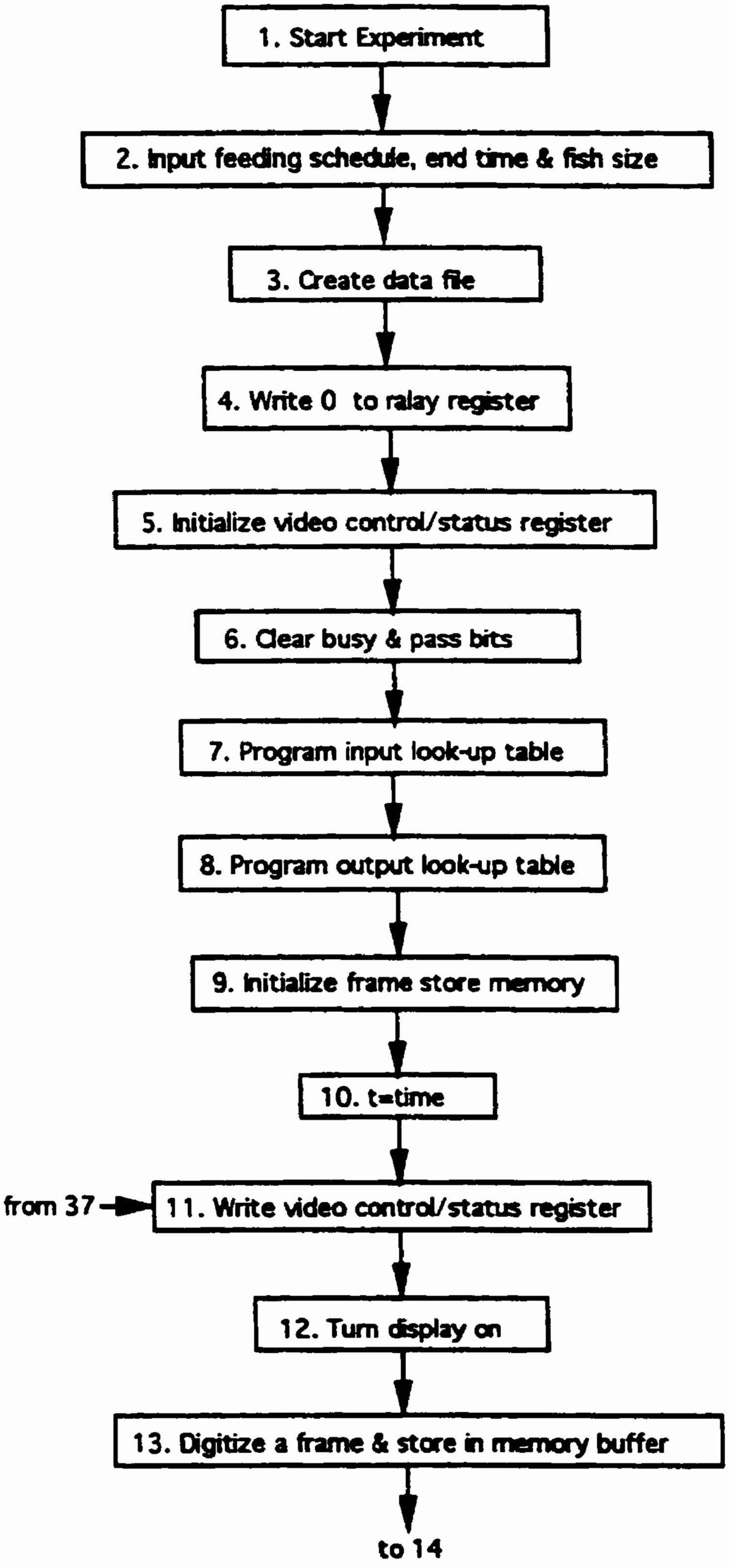

Fig. 4.3. Programming Flow Diagram of the Monitoring and Control Software (continued on next page)

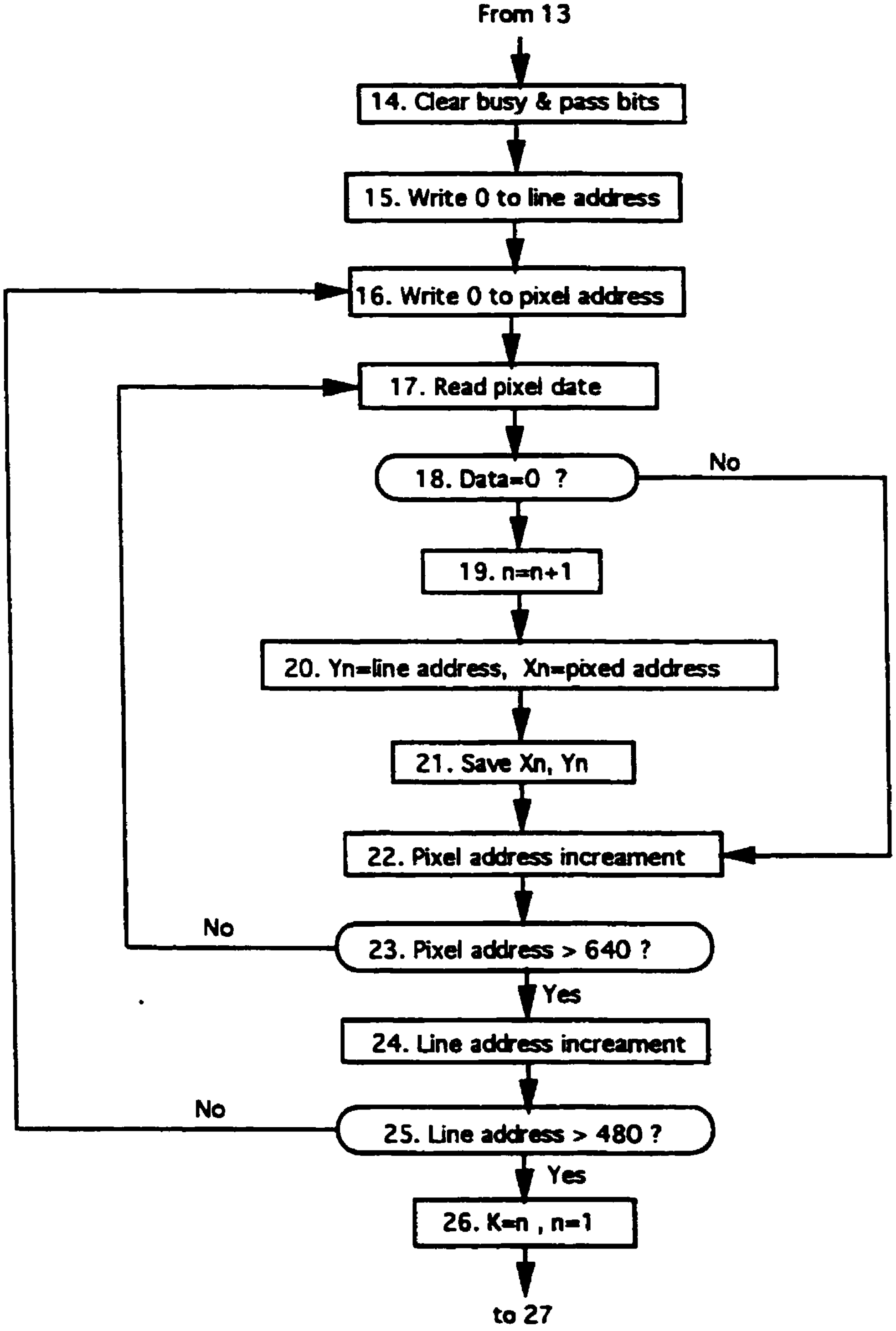

Fig. 4.3. Programming Flow Diagram of the Monitoring and Control Software (continued on next page)

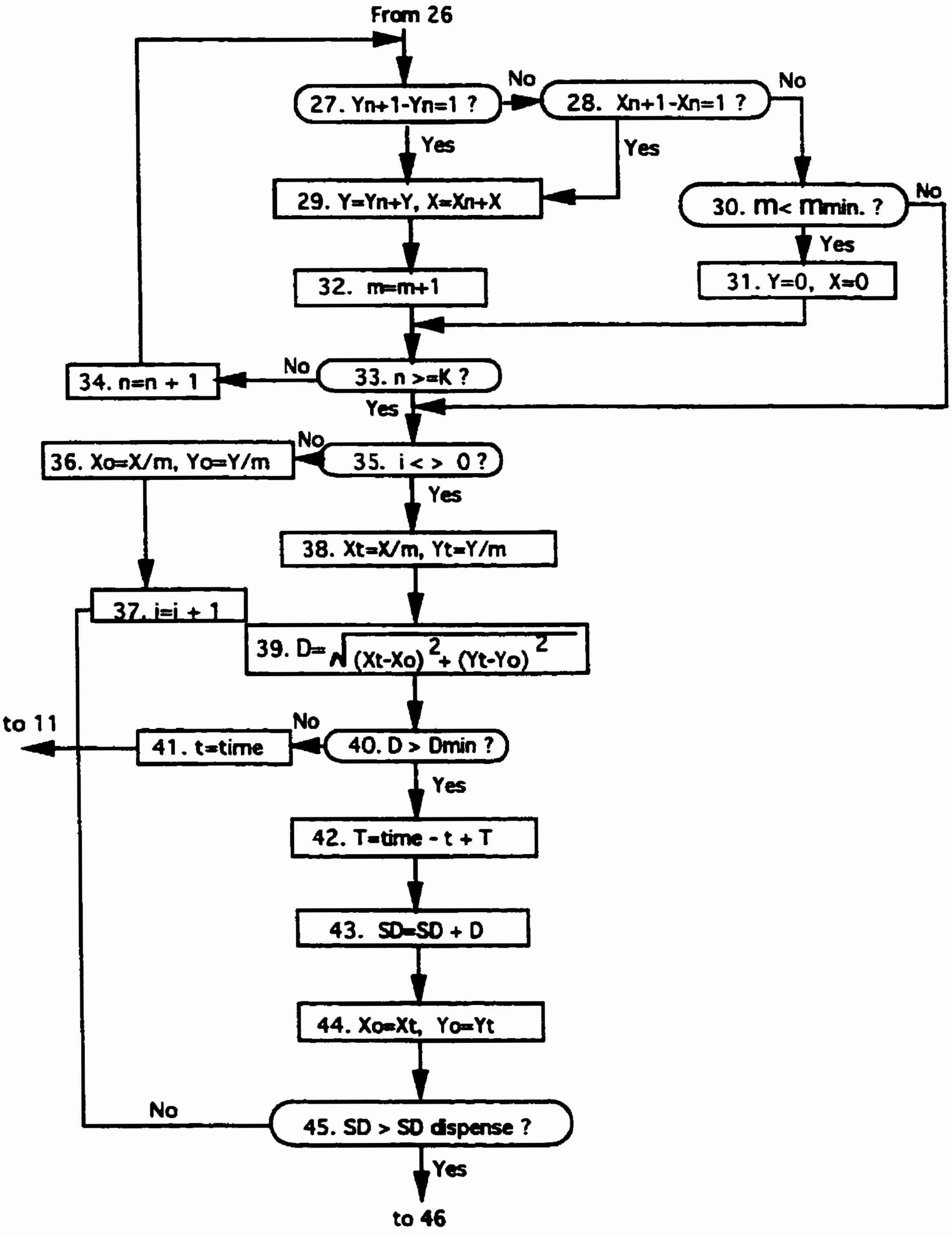

Fig. 4.3. Programming Flow Diagram of the Monitoring and Control Software (continued on next page)

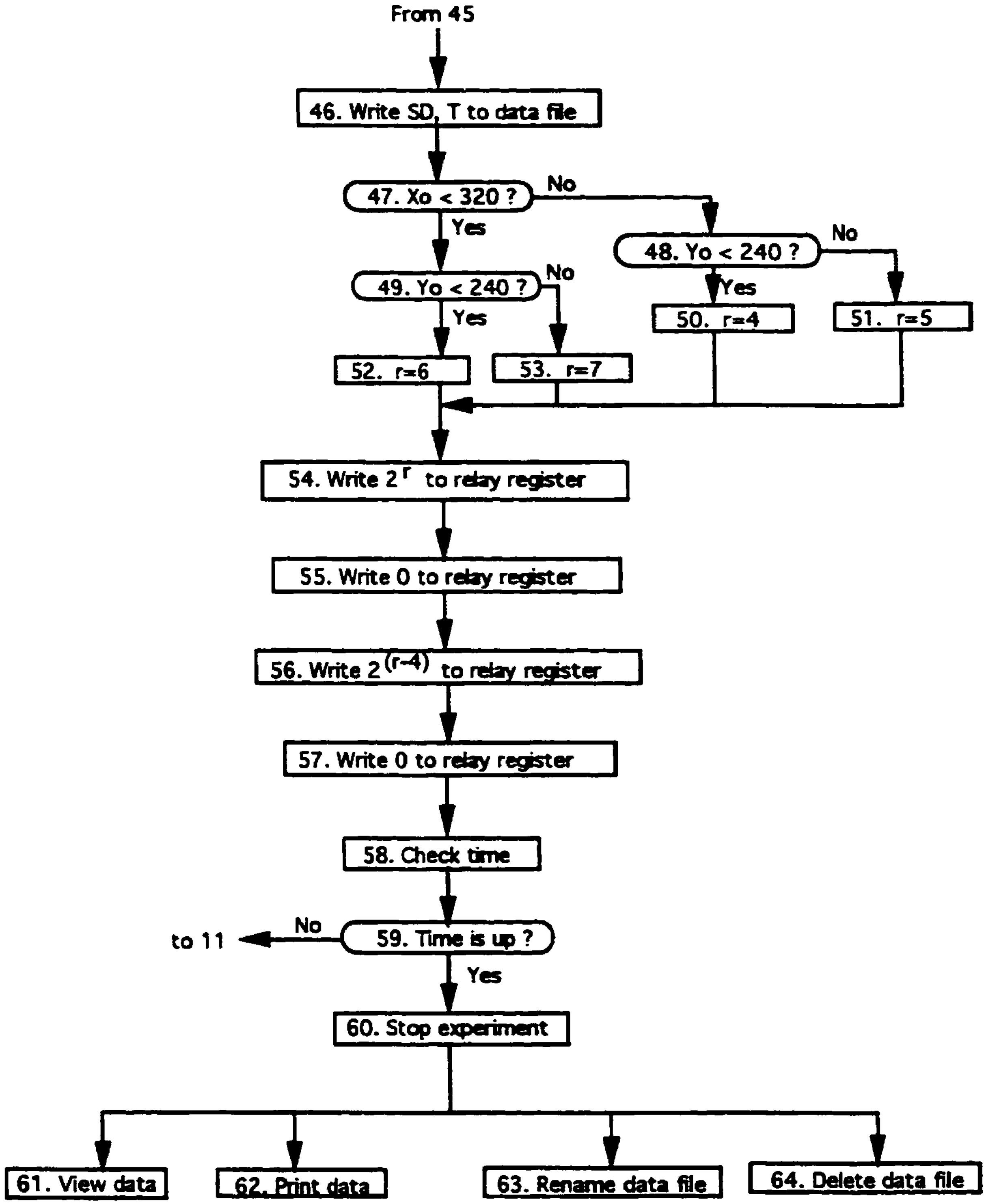

Fig. 4.3. Programming Flow Diagram of the Monitoring and Control Software

Chapter 5

FEEDING BEHAVIOUR

5.1. Introduction

The intent of the experiments described in this chapter is to determine the effects of food density, temperature, and body mass on the rate at which juvenile *S. fontinalis* search for food (see Chapter 1). The allometric and temperature relationships obtained from these experiments will be compared to the allometric and temperature effects found for maximum feeding rates and maximum meal size in Chapter 3, as well as to feeding and metabolic rates from studies carried out on other species. This comparison should provide some insight into (1) variation in foraging behaviour with food density, temperature, and body mass when daily feeding rates are below satiation levels and fish must actively search for prey, and (2) how this variation in behaviour may be related to variation in physiological rates.

5.2. Materials and Methods

5.2.1. Experimental fish

The fish used in these experiments were taken from the collections of wild fish described in 3.2.1. Only juveniles (age 1+) were used in these experiments as they appear to be less affected by experimental manipulations than larger fish. Fish were transferred to 22-L holding aquaria in the laboratory following capture and were allowed to acclimate to any changes of water temperature for at least one week prior to their use in experiments. Weights and lengths of the fish used in these experiments are given in Table 5.1.

Table 5.1 Body Weights and Lengths of the Fish Used in Feeding Behaviour Experiments

Experiment	Temperature (°C)	Weight (g)	Length (cm)
Feeding behaviour	5	4.5	6.2
		7.1	7.6
		8.7	8.5
		13.7	9.8
	12	5.2	6.8
		8.7	8.5
		11.5	9.5
		14.5	10.0
	18	6.3	7.4
		8.7	8.5
		10.6	8.7
		14.5	10.1

5.2.2. Experimental Protocol

Feeding behaviour experiments were conducted between September, 1994 and January, 1995 and between April and September, 1995. The experimental apparatus consisted of a large shallow plywood tank (2.0x1.8x0.3 m) lined with white plastic film. Temperature was controlled as described in Chapter 3. Lighting (12 h light : 12 h dark cycle) was provided by two 40 W fluorescent tubes covered with blue plastic film which provided a surface illumination of approximately 60 lux.

The automated system (Chapter 4) provided real-time tracking of the swimming activity of fish during experiments and dispensed food from the feeder closest to the fish on a predetermined "delivery schedule" (measured as food delivered per distance swum). Food consisted of beetle larvae (*Tribolium castaneum*) previously killed by freezing to prevent their escape from feeders. Details of the length, weight, and proximate composition of larvae are given in section 3.2.2..

Five food delivery schedules were used in these experiments (5±0.04 mg/80m, 5±0.04 mg/40m, 5±0.04 mg/20m, 10±0.05 mg/20m, 20±0.05 mg/20m) and these differed both in the amount of food dispensed to the water surface for a given distance swum by the fish and the distance swum between successive food deliveries. Thus, a delivery schedule of 5±0.04 mg/80m means that 5±0.04 (SE) mg of larvae (live weight) were dispensed each time the fish had swum 80 m following the last food delivery, whereas for a schedule of 20±0.05 mg/20m, 20±0.05 mg of larvae were dispensed each time the fish had swum 20 m since the last food delivery. The five delivery schedules, expressed as live weight of food dispensed (±SE) per meter, are 0.0625±0.005 mg/m, 0.125±0.01 mg/m, 0.25±0.02 mg/m, 0.5±0.025 mg/m, and 1.0±0.025 mg/m. (The uncertainty in the mass of food dispensed arises because of variation in the mass of final instar beetle larvae.) In preliminary experiments, the highest schedule used (1.0 mg/m) gave a feeding rate close to the maximum sustainable rate, obtained from the experiments described in Chapter 3.

Prior to their use in experiments, fish were placed individually in the large tank where they were fed on a delivery schedule of 0.5 mg/m for 3 to 10 days. Fish that did not feed actively during this period (less than 10%) were not used. Preliminary observations in the large tank showed that trout seldom moved and did not feed when the lights were off. Therefore, individual experimental trials were confined to the 12 hour light period.

An experimental "trial" consisted of monitoring the movements of a single fish during the 12 hour light period at a fixed combination of temperature and food delivery schedule. Between 16:30 and 17:00 on the day preceding a trial, the experimental fish was fed to satiation to standardize hunger at the beginning of the next day's trial. Monitoring of the fish's movements started automatically when the lights came on at 09:00 the next day. During the following 12 hour experimental period, the movement of the fish was tracked continuously by the monitoring and control system, which maintained a real time record of the distance swum and dispensed food items according to the chosen reward schedule. At the end of the 12 hour experimental period any larvae remaining in the tank were removed and weighed. The total weight of these larvae was subtracted from the total weight introduced to give the total weight of larvae consumed during the 12 hours.

The above experimental procedure (a trial) was repeated a number of times at the same temperature using the same fish and a randomly determined delivery schedule to produce a "set" of trials carried out at the same temperature. A set of trials consisted of a maximum of two trials per delivery schedule for up to five different delivery schedules. When a set of trials was finished, a new set was initiated that could involve the same fish at a different temperature, a different fish at the same temperature, or a different fish at a different temperature. Fish were given a 7 day acclimation period prior to their use in a set of trials at a different temperature. Four sets of trials were carried out at each of three temperatures (5, 12 and 18 °C). A listing of the order of presentation of delivery schedules and temperature treatments for each fish is provided in Table 5.2.

Table 5.2. The Order of Presentation of Experimental Treatments in the Swimming Rate Experiments.

Fish	Time Period	Temp. (°C)	Order of Delivery Schedules (mg/m)
1	July 21-Aug. 12, 1994	18	.5-.0625-.25-.125-.25-.125-.5-.0625
2	Sept. 6-26, 1994	5	1-1-.125-.25-.125-.5-.25-.5
3	Oct. 5-21, 1994	18	.5-.25-.25-.125-.5-.125
	Oct. 28-Nov. 16, 1994	12	1-.25-.5-.125-1-.5-.125-.5
4	Nov. 18-Dec. 6, 1994	12	.5-.25-.125-.0625-.125-.0625-.5-.25
	Dec. 14, 1994-Jan. 9, 1995	18	.5-.25-.125-.5-.25-1-.0625-.125
	Jan. 20-Feb. 11, 1995	5	.5-.5-.125-.25-.25-.125-.0625-.0625
5	Apr. 20-May 13, 1995	5	.5-.25-.125-.0625-.125-.25-.0625
6	May 14-June 1, 1995	5	.25-.125-.0625-.25-.125-.0625
7	June 4-29, 1995	12	.5-.125-.0625-.25-.5-.125-.25-.0625
8	July 4-24, 1995	12	.5-.0625-1-.0625-.25-.5-.125-1-.125-.25
9	Aug. 14-Sept. 14, 1995	18	.0625-.25-.125-.5-1-.5-.0625-1-.125-.25

5.2.3. Distance swum, foraging time, and swimming speed

As described in Chapter 4, the automated tracking system recorded a fish as having moved to a new position if the distance between the new position and the previous position was greater than a given threshold. If the calculated distance moved was less than this threshold, the fish was assumed not to have moved, the previous position was retained as the current position, and the process was repeated. This procedure should give an accurate measure of total distance swum so long as the threshold distance is sufficiently large that small artifactual changes in the centre of the dark area are not recorded as real movements. Such changes might occur, for example, due to lighting fluctuations or tail movements while the fish is stationary. However, this technique does not produce a record of variations in the activity level of the fish. For example, fish could be alternating between active swimming and resting in a stationary position. In order to quantify activity level, additional data were collected by the automated system. First, to minimize bias due to body size that could arise because larger fish swim more rapidly, the threshold for detecting movement was set at 1/3 body length rather than at an absolute distance. Thus, any movements that were calculated at less than 1/3 body length were ignored and the original position was retained. In addition, the time between successive position determinations was set to 2 seconds. This would ensure that only movements made in excess of 1/6 body length per sec (BL/s) were calculated as continuous swimming. This threshold speed is below normal cruising speeds calculated for small salmonids (Beamish 1978). At the beginning of each experiment a counter (in the software) was set to zero. Each time there was a movement recorded within a 2 second interval (i.e. distance calculated more than 1/3 body length) 2 seconds were added to the counter. At the end of the 12 hour experimental period the value of the counter divided by 12 hours was used as a measure of the proportion of time that fish spent actively swimming. Although fish swimming continually at less than 1/6 BL/s would thus have a proportion of time spent actively swimming calculated at less than 1, such slow swimming speeds are not observed in salmonids (Beamish 1978). Hence, this technique should not introduce additional errors to the data.

5.2.4. Delivery Schedule, Prey Density, and Feeding Rate

The intent of the experimental protocol, in dispensing a measured amount of food after fish had swum a prescribed distance, was to simulate foraging in an environment with a constant (non-depleting) density of food. A characteristic of such foraging would be the direct proportionality of the amount of food consumed to the distance swum. One way of conducting such an experiment would be to establish, at the outset of a feeding trial, the equilibrium food density corresponding to a particular delivery schedule (food eaten/distance swum). It would then be possible to maintain a more or less stable equilibrium between prey consumption and prey introduction by delivering prey at a rate (prey delivered/distance swum) equal to the estimated feeding rate (items eaten/distance swum). Unfortunately, determining the relationship between food density and feeding rate (items eaten/distance swum) would have involved carrying out a prohibitively large number of preliminary experiments using a range of fish sizes for each combination of food delivery schedule and temperature. In addition, this quantification would prove unnecessary if there were no behavioural response to changes in prey density.

Because of this, an experimental model was used in which the initial prey density was zero and the first prey were delivered only after the fish had swum the distance prescribed by the schedule for that trial. If prey items are detected and captured shortly after they are dispensed, the average feeding rate would approximate the delivery schedule throughout the experiment. Alternatively, if prey are sufficiently small that they may not be immediately detected when dispensed, the feeding rate at the beginning of a trial would be less than the delivery rate, and the density of prey would gradually increase. As prey density increased, the encounter rate with prey, and the feeding rate, would also increase and, eventually, prey density and feeding rate would become sufficiently high to produce a stable equilibrium between the rate at which prey are dispensed (delivery rate) and the rate at which they are encountered and eaten. Because of the small size and relatively low visibility of the beetle larvae (the reaction distance of the trout to the prey in this environment is less than 50 cm), feeding rate in these experiments was of this latter type in which prey density must build up before feeding rate approximates delivery schedule (it can be seen in Table

5.3. that fish only ate 40-80% food delivered and the food left in the tank is proportion to the distance swum).

A problem with this approach could arise if search velocity changes with food density, one of the predictions of the optimal foraging model described in Chapter 1. However, if this were the case it would be possible to use only the distance swum after an equilibrium had been reached between prey delivery and consumption, for example by using only the last 3 or 6 hours of an experimental trial.

5.3. Results

5.3.1. The effect of delivery schedule, temperature, and body mass on distance swum, active foraging time, and average swimming velocity.

The results of the experiments are shown in Table 5.3.

Total distance swum was the total distance fish moved during the 12 hours of the experiment. Active swimming time (%) was calculated as the 100((total time fish were recorded as moving)/12 hours). Average speed was calculated by dividing the total distance swum in 12 hours by the active swimming time (estimated as a time and not a percentage; i.e. (total distance swum)/(total time fish were recorded as moving)).

Table 5.3. Distance Swum in 12 Hours, % Time Active, the Average Swimming Speed, Total Food Dispensed, Total Food Eaten, and the % of Dispensed Food Eaten, for Each Combination of Fish, Temperature, and Food Delivery Schedule.

Fish	Mass (g)	Temp. (°C)	Delivery Schedule (mg/m)	Distance Swum (m)	Foraging Time (%)	Average Speed (m/min.)	Dispensed (mg live)	Eaten (mg live)	% Eaten
1	10.6	18	1	911.6	30.29	4.18	912	409	44.8
				635.9	29.79	2.96	636	343	53.9
			0.5	932.6	32.75	3.96	466	292	62.7
				869.9	31.22	3.87	435	297	68.3
			0.25	1197.6	41.58	4	299	154	51.5
				831.5	28.17	4.09	208	132	63.5
			0.125	1047.2	36.97	3.93	131	79	60.3
				966.5	34.01	3.95	121	72	59.5
			0.063	963.2	33.13	4.04	60	34	56.7
				1044.9	34.63	4.19	65	31	47.7
2	13.7	5	1	192.4	11.49	2.33	192	92	47.9
				243.4	15.92	2.12	243	94	38.7
			0.5	224.9	11.97	2.61	112	75	67.0
				219.6	12.89	2.37	110	77	70
			0.25	295.4	16.79	2.44	74	56	75.7
				238.1	15.18	2.18	60	49	81.7
			0.125	206.7	11.54	2.49	26	21	80.7
				322.6	18.04	2.48	40	25	62.5
3	14.5	18	0.5	1258.8	44.42	3.94	629	385	61.2
				1239.4	41.83	4.12	620	361	58.2
			0.25	1275.7	44.29	4	319	196	61.4
				975.1	36.46	3.72	244	172	70.5
			0.125	1209.2	43.28	3.88	151	86	57.0
				1025.9	37.17	3.83	128	76	59.4
		12	1	546	25.96	2.92	546	285	52.2
				425.1	17.38	3.4	425	260	61.2
			0.5	429.6	19.5	3.06	215	198	92.1
				648.2	28.97	3.11	324	216	66.7
			0.25	473.1	21.19	3.1	118	85	72.0
				715.2	33.32	2.98	179	124	69.3
			0.125	869.1	37.88	3.19	109	53	48.6
				653.3	30.22	3.01	82	44	53.7

Table 5.3. Distance Swum in 12 Hours, % Time Active, the Average Swimming Speed, Total Food Dispensed, Total Food Eaten, and the % of Dispensed Food Eaten, for Each Combination of Fish, Temperature, and Food Delivery Schedule (cont. 1).

Fish	Mass (g)	Temp. (°C)	Delivery Schedule (mg/m)	Distance Swum (m)	Foraging Time (%)	Average Speed (m/min.)	Dispensed (mg live)	Eaten (mg live)	% Eaten
4	8.7	12	0.5	509.2	24.18	2.92	255	170	66.7
				426.1	20.03	2.95	213	149	70
			0.25	385.9	17.64	3.04	96	75	78.1
				545.2	23.65	3.2	136	102	75
			0.125	402.8	18.07	3.1	50	44	88.0
				415.4	19.21	3.01	52	36	69.2
			0.063	643.5	29.43	3.04	40	23	57.5
				487.6	22.19	3.05	30	17	56.7
		18	1	910.5	35.76	3.54	911	360	39.5
				635.9	21.64	4.08	636	343	53.9
			0.5	852.1	31.44	3.76	426	271	63.6
				795.5	30.13	3.67	398	262	65.8
			0.25	969.9	33.67	4.01	242	166	68.6
				785.9	28.38	3.85	196	159	81.1
			0.125	892.6	33.78	3.67	112	78	69.6
				764.2	26.47	4.01	96	75	78.1
			0.063	723.6	33.13	3.03	45	28	62.2
				802.3	34.63	3.22	50	32	64
		5	0.5	205.3	11.33	2.52	103	57	55.3
				182.9	12.06	2.11	91	53	58.2
			0.25	210.9	15.88	1.85	50	41	82.0
				181.3	12.21	2.06	45	29	64.4
			0.125	202.5	12.51	2.25	25	20	80
				329	17.26	2.65	41	23	56.1
			0.063	243.1	13.69	2.47	15	9	60
				161.5	10.39	2.16	10	7	70
5	4.5	5	0.5	163.3	11.74	1.93	82	36	43.9
			0.25	204.2	13.4	2.12	51	29	56.9
				159.5	11.89	1.87	40	23	57.5
			0.125	123.2	9.6	1.78	15	11	73.3
				205.6	12.26	2.33	26	15	57.7
			0.063	150.4	9.07	2.3	9	5	55.6
				161	10.44	2.14	10	6	60

Table 5.3. Distance Swum in 12 Hours, % Time Active, the Average Swimming Speed, Total Food Dispensed, Total Food Eaten, and the % of Dispensed Food Eaten, for Each Combination of Fish, Temperature, and Food Delivery Schedule (cont. 2).

Fish	Mass (g)	Temp. (°C)	Delivery Schedule (mg/m)	Distance Swum (m)	Foraging Time (%)	Average Speed (m/min.)	Dispensed (mg live)	Eaten (mg live)	% Eaten
6	7.1	5	0.25	223.6	14.43	2.15	56	32	57.1
				244.3	14.76	2.3	61	36	59
			0.125	245.2	13.63	2.5	31	19	61.3
				163.7	9.75	2.33	20	17	85
			0.063	162.4	11.32	1.99	10	6	60.0
				206.5	11.96	2.4	13	8	61.5
7	5.2	12	0.5	399.6	20.17	2.76	200	119	59.5
				374.5	17.89	2.91	187	97	51.8
			0.25	344.4	17.82	2.68	86	52	60.5
				364.5	16.21	3.12	91	57	62.6
			0.125	403.1	19.11	2.93	50	40	80.0
				323.4	14.97	3	40	33	82.5
			0.063	402.9	20.92	2.67	25	16	64.0
				322.8	16.86	2.66	20	11	55
8	11.5	12	1	485.3	21.4	3.15	485	229	47.2
				586.9	28.57	2.86	587	235	40
			0.5	497.6	22.89	3.02	249	203	81.5
				486.9	21.03	3.22	243	194	79.8
			0.25	547.2	25.74	2.95	137	90	66.0
				763.2	33.13	3.2	191	104	54.5
			0.125	604.8	27.97	3	76	50	65.8
				621.8	30.35	2.85	78	43	55.1
			0.063	722.9	34.13	2.94	45	27	60.0
				643.5	30.82	2.9	40	19	47.5
9	6.3	18	0.5	770.8	28.68	3.73	385	218	56.6
				860.7	33.35	3.59	430	236	54.9
			0.25	649.7	23.1	3.91	162	104	64.2
				586.9	24.89	3.28	147	107	72.8
			0.125	725.3	27.61	3.65	91	71	18.0
				765.9	28.58	3.72	96	67	69.8
			0.063	804.5	28.46	3.92	50	29	58
				723.3	26.35	3.81	45	25	55.6

Table 5.4 Statistical Results for the Multiple Regression of Distance Swum, Active Foraging Time and Average Foraging Speed as Functions of Temperature, Body Mass and Delivery Schedule.

Dependent variable	Intercept **a**	Coefficient					
		Body mass		Temperature		Delivery Schedule	
		b	**P** Value	**c**	**P** Value	**d**	**P** Value
Distance swum (m)	-288.6	28.9	P<0.001	51.2	P<0.001	-145.1	P=0.058
Foraging time (%)	-2.52	1.06	P<0.001	1.47	P<0.001	-5.11	P=0.059
Foraging speed (m/min.)	1.4	0	P<0.001	0.12	P<0.001	0.082	P=0.31

The relationships between the variables in Table 5.3 were investigated by multiple regression of total distance swum, active swimming time (%), and average swimming speed vs. temperature, body size, and reward schedule (Table 5.4). All three variables were positively and significantly affected by temperature and body mass but not by delivery schedule. This allowed the data on total distance swum, active swimming time, and average swimming speed for all delivery schedules to be pooled for each combination of fish and temperature treatment (Table 5.5).

Table 5.5. Mean Distance Swum, Active Foraging Time and Swimming Speed of Experimental Fish at Different Temperatures.

Temp. (°C)	Fish mass (g)	Mean distance swum in 12 h (±SE)[1] (m)	Mean Active Foraging Time (±SE)[1] (%)	Mean Foraging Speed (±SE)[1] (m/min.)
5	4.5	166.7 ± 11.1	11.2 ± 0.6	2.07 ± 0.08
	7.1	207.6 ± 15.3	12.6 ± 0.8	2.28 ± 0.08
	8.7	214.6 ± 18.5	13.2 ± 0.8	2.27 ± 0.10
	13.7	242.9 ± 15.7	14.2 ± 0.9	2.38 ± 0.06
12	5.2	366.9 ± 12.0	18.0 ± 0.7	2.84 ± 0.06
	8.7	477.0 ± 31.0	21.8 ± 1.4	3.04 ± 0.03
	11.5	596.0 ± 30.4	27.6 ± 1.5	3.01 ± 0.04
	14.5	595.0 ± 55.0	26.8 ± 2.5	3.09 ± 0.05
18	6.3	735.9 ± 30.6	27.6 ± 1.1	3.68 ± 0.07
	8.7	813.3 ± 30.7	30.9 ± 1.4	3.70 ± 0.11
	10.6	953.5 ± 38.7	33.3 ± 1.2	3.91 ± 0.11
	14.5	1164.0 ± 52.9	41.2 ± 1.5	3.92 ± 0.06

[1] Standard Error

These pooled data were log transformed and regressions were carried out of total distance swum, active swimming time, and average swimming speed, all vs. body mass for each of the three temperatures. The purpose of this was to provide allometric body mass exponents that could be compared with published allometric exponents for physiological processes such as metabolic rate and maximal feeding rates. These regressions are shown in Fig. 5.1-3 and the regression statistics are given in Table 5.6. Table 5.6 also contains the parameter values for maximum ration and maximum feeding rate (Chapter 3) for comparison.

Table 5.6. The intercept (*c*) and Exponent Factor (*d*) of the Allometric Equations for the Relationship between Different Variables and Body Mass at Three Different Temperatures.

Variable	Temperature (°C)	Body Mass (g)	c	d	P value
Distance Swum (m)	5	4.4-13.7	102.5	0.3299	$p<0.001$
	12	5.2-14.5	163.8	0.4946	$p<0.001$
	18	6.3-14.5	252.5	0.559	$p<0.001$
Foraging Time (%)	5	4.4-13.7	8.207	0.2083	$p<0.01$
	12	5.2-14.5	9.034	0.4178	$p<0.01$
	18	6.3-14.5	11.38	0.4645	$p<0.001$
Foraging Speed (m/min.)	5	4.4-13.7	1.724	0.1237	$p<0.01$
	12	5.2-14.5	2.367	0.0991	$p<0.001$
	18	6.3-14.5	3.054	0.1044	$p<0.001$
Maximum meal size (mg)	5	4.0-17.7	4.076	0.7656	$p<0.001$
	12	3.8-17.2	11.97	0.8094	$p<0.001$
	18	3.9-16.1	14.72	0.8146	$p<0.001$
Sustained Feeding Rate (mg)	5	4.0-17.7	4.365	0.7809	$p<0.001$
	12	3.8-17.2	13.54	0.809	$p<0.001$
	18	3.9-16.1	25.89	0.8131	$p<0.001$

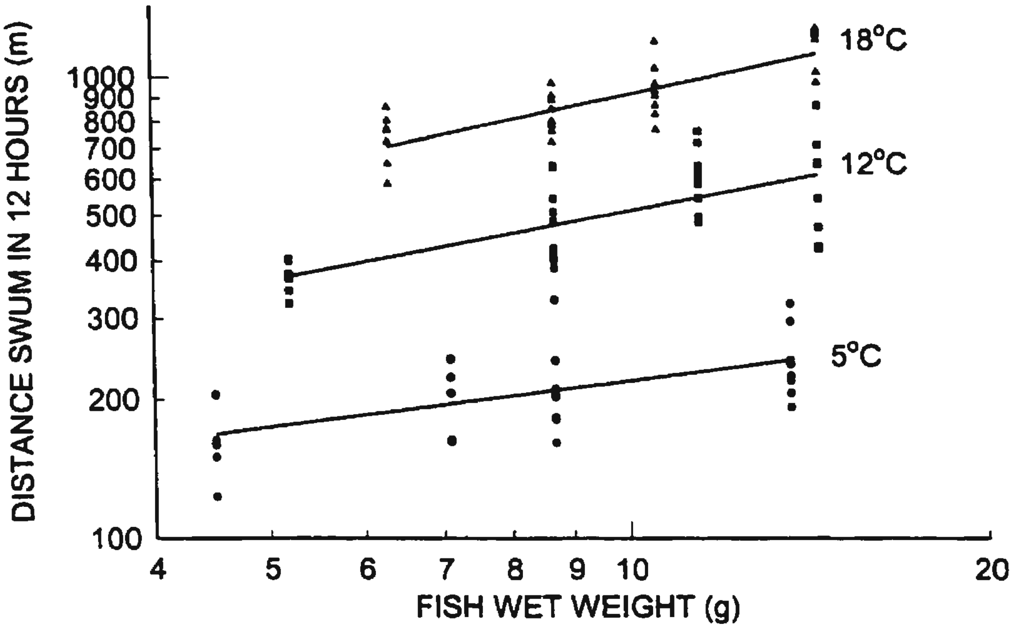

Fig 5.1 Total Distance Swum in 12 Hours as a Function of Body Mass and Temperature

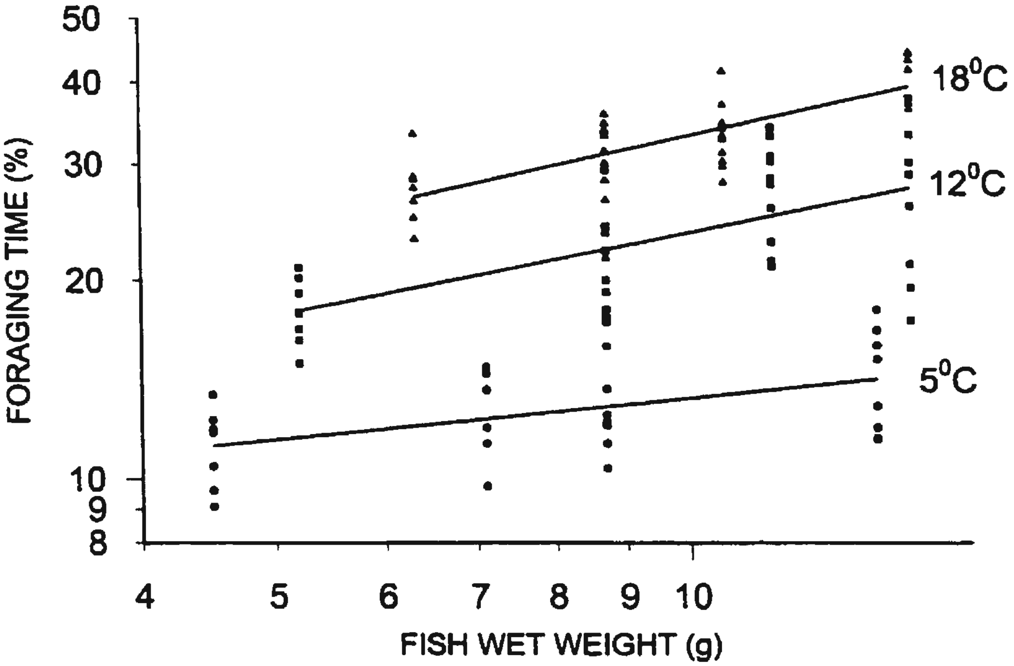

Fig. 5.2 Active Foraging Time (%) as a Function of Body Mass and Temperature

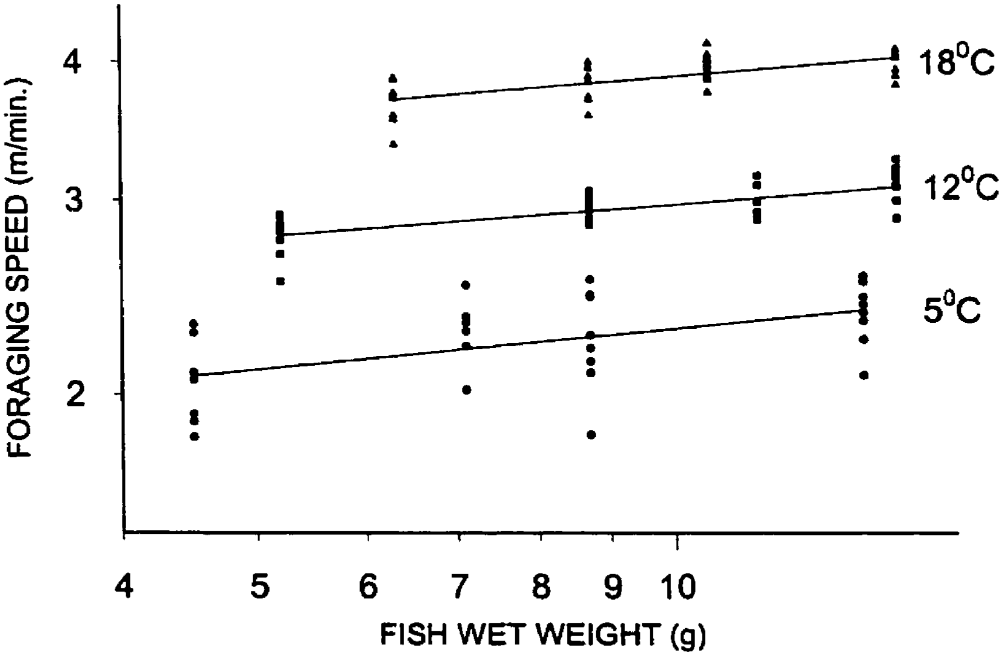

Fig. 5.3 Average Swimming Speed (m/min.) as a Function of Body Mass and Temperature

The effects of temperature on swimming were quantified using the Van't Hoff ***b*** parameter (Chapter 3). This was obtained by taking the seventh (temperature range 5 to 12 °C) or sixth (12 to 18 °C) root of the ratio of the allometric equations for distance swum, active swimming time, and average swimming speed at the extremes of each of the two temperature ranges. The expressions for ***b***, which are positive in all cases, are given in Table 5.7 along with those obtained in Chapter 3 for maximum meal size and maximum feeding rate.

Table 5.7. Values of the Van't Hoff Thermal Parameter, b, for Different Behaviourial and Physiological Rates of Brook Trout.

Variable	**Temperature Range (°C)**	**b**
Total Distance Swum	5-12	$1.069W^{0.0235}$
	12-18	$1.075W^{0.0107}$
Active Foraging Time	5-12	$1.014W^{0.0299}$
	12-18	$1.039W^{0.0078}$
Average Foraging Speed	5-12	$1.046W^{-0.0035}$
	12-18	$1.043W^{0.0008}$
Maximum Meal Size	5-12	$1.166W^{0.0063}$
	12-18	$1.035W^{0.0009}$
Sustained Feeding Rate	5-12	$1.176W^{0.0040}$
	12-18	$1.114W^{0.0007}$

Average swimming speeds, expressed in BL/s, ranged from 0.41 BL/s to 0.56 BL/s at 5 °C, from 0.52 BL/s to 0.7 BL/s at 12 °C, and from 0.65 BL/s to 0.83 BL/s at 18 °C. These values are all in the range of observed sustained swimming speeds for the same species (McLaughlin et. al. 1992 & 1994) or most fish including salmonids of 0.2 to 1.8 BL/s (Beamish 1978) and close to the theoretical optimal cruising speed (that maximizes feeding efficiency) for salmonids of 0.73 BL/s to 0.76 BL/s (Weihs 1977; Blake 1983). They are however somewhat lower than the speed calculated to maximize growth rate at 15 °C of 0.95 BL/s to 2.7 BL/s (Ware 1975; 1978).

5.3.2. Active foraging time

It is important to point out some difficulties in interpreting the data on active swimming time and average swimming speed.

At 5 °C, total distance swum scaled with body mass as $\mathbf{W^{0.33}}$, that is approximately as body length. If fish were swimming continually, or for a constant proportion of the time, then, regardless of body mass, the higher velocity of the larger fish would be offset by the fact that the threshold distance for active swimming was set at a fixed proportion of length. Under these conditions the probability of the distance swum in 2 seconds falling below the threshold value of 1/3 BL would be independent of body mass and the data collection technique should not produce the observed increase in swimming time for larger fish. That is, the behavioural allometry described by the data should be real. At 12 and 18 °C distance swum increases with body mass faster than does body length, so that the data collection technique could possibly indicate an increase in active swimming time with body mass when none existed. However, because swimming speeds below 1/6 BL/s are not typical of salmonid swimming and because a similar trend was observed at 5 °C where such a bias is unlikely, the trends at 12 and 18 °C probably reflect a real behavioural allometry in distance swum.

A similar potential problem exists with the data for the effects of temperature on active swimming time. There was no correction in the movement detection threshold for the increase in swimming speed with temperature. Consequently, an increase in average swimming speed (BL/s), with no accompanying increase in the proportion of time spent swimming, could, in theory, be recorded as an increase in active swimming time with temperature. However, for the reasons outlined above for the effect of body mass on active swimming time, the increase in active swimming time recorded by the data collection software is a real qualitative trend although there may be some quantitative inaccuracies in the calculated value.

5.4. Discussion

5.4.1. The effects of body mass

The results of the swimming activity experiments are clearly not consistent with the optimal foraging model discussed in Chapter 1. This model predicted a decrease in swimming speed with increased body mass; the opposite was observed. Although the experimental results are consistent with the special case model, this is because the special case model makes no predictions regarding the effect of body mass on swimming speed or distance swum. However, it is possible to test the assumption of the special case model that swimming speed is less than that predicted in the optimal foraging model.

The energy cost of transport in fish is approximately $\mathbf{3.2W^{-0.3}}$ **cal** $\mathbf{g^{-1}}$ $\mathbf{km^{-1}}$ (Beamish 1978). For a 10 g fish the mean distances swum in 12 h were 219 m (5 °C), 512 m (12 °C), and 915 m (18 °C). The above expression for the cost of transport gives total swimming costs over 12 hours of approximately of 3.5 (5 °C), 8.2 (12 °C), and 14.6 (18 °C) cal. The maximum daily feeding rates for a 10 g fish feeding on live beetle larvae at each of these temperatures, calculated using the expressions for sustained feeding rate given in Table 5.6 and the energy content of beetle larvae (Table 3.2), are 133.8 (5 °C), 442.6 (12 °C), and 854.4 (18 °C) cal. Thus, in all cases, the daily costs of movement represent less than 3% of the maximum daily feeding rate. Although it has been suggested that the above expression for the cost of transport, derived using forced swimming experiments, may underestimate the cost of transport by as much as a factor of 3 (Tang & Boisclair 1993), this would still give a daily cost of swimming that is less than 9 % of the maximum daily feeding rate. For fish feeding at an encounter rate that provides them with a daily ration of 1/3 the maximum, close to their maintenance requirement, the ratio of energy intake to swimming cost over any distance would still be approximately 6 (at 12 °C). By definition, a swimming speed that is optimal energetically has the property that any increase in speed would lead to a decrease in net energy gain. Because the ratio of the energy ingested to that expended while swimming any fixed distance is so high at any encounter rate giving positive growth, it seems clear that any increase in swimming speed, beyond the swimming speeds observed in these experiments, would result in an increase in daily net energy gain rather than a decrease, that is, the observed swimming speeds must be below theoretical optima for maximization of the rate of net energy gain. Although the special case model seems to apply, as noted it does not provide any direct insight into the observed trends.

The lack of agreement between the observed swimming behaviour and the predictions of the optimal foraging model is not necessarily surprising since theoretical "optimal" swimming speeds may far exceed physiological capabilities. However, because of the low cost of transport, relative to the gain from feeding activity (see above), the results also suggest that fish would increase their rate of net energy gain through even small increases in swimming velocity. The adaptive nature of the observed activity pattern is thus unclear.

It is important to note that both classes of models discussed in Chapter 1 assumed that there would be no variation in the proportion of time spend actively swimming. This is because, in terms of energy, it is always better to forage (gain energy) than to be inactive (lose energy). Consequently, the model provides no insight into this behaviour. Because fish would increase their rate of net energy gain if they increase the proportion of time spent swimming, the observed behaviour appears to produce unnecessarily low rates of net energy gain, and the adaptive nature of the swimming behaviour of these brook trout is once again unclear. An experimental approach that might shed light on the seemingly low swimming speeds and activity levels would be the measurement of growth responses to increases in swimming velocity and/or the time spent foraging, perhaps induced hormonally.

Although the possibility exists that the high rate of inactivity observed in these experiments is an artifact of the experimental procedure, if this were the case the clear trends for activity to increase with both temperature and body mass would not be expected.

To better understand the relationship of distance swimming behaviour to changes in body mass, it may be useful to compare the body size allometries of the behaviour (average swimming speed or distance swum) and the energy cost of the behaviour, to other body size allometries. The mass exponents of the allometric equations for average swimming speed are comparable, at all temperatures, to values reported for sustained swimming speed of sockeye salmon (Brett 1965) and other fish species (Wardle 1977; Beamish 1978), as well as for flight speed in birds (Calder 1984). However, these exponents are substantially lower than those for maximum feeding rate (Chapter 3; Table 5.5) and both standard and active metabolic rates of fish (Table 2.2). To compare the scaling of swimming costs to those for the metabolic processes noted above, it is first necessary to derive allometric expressions for the rate of energy expenditure during swimming.

The instantaneous rate of energy expenditure during swimming, over and above **SMR**, can be approximated by the expressions

power (energy/time) = $\mathbf{K_1W^{0.44}V^{2.42}}$ (5.1)

where $\mathbf{K_1}$ is a constant, **W** is expressed in wet weight, and **V** is swimming speed (Ware 1978; Dunbrack and Ware 1987).

At 5 °C, average swimming speed scales with body mass as

swimming speed (cm/sec) = $\mathbf{2.87W^{0.12}}$ (5.2)

(Table 5.6). Substituting the expression for average swimming speed (5.2) for **V** in (5.1) gives

power = $\mathbf{K_1W^{0.44}(2.87W^{0.12})^{2.42}}$

or

power = $\mathbf{K_1(2.87)^{2.42}W^{0.73}}$ (5.3).

Similarly, for 12 °C,

power = $\mathbf{K_1(3.95)^{2.42}W^{0.68}}$

and for 18 °C

power = $\mathbf{K_1(5.08)^{2.42}W^{0.69}}$

At all three temperatures, the body mass exponents for power expended while swimming at the average speed are very close to published exponents for the **SMR** (Table 2.1). The instantaneous energy cost of swimming therefore appears to be a more or less constant multiple of the **SMR** and the scaling of average swimming velocity may reflect some influence of standard metabolic rate on the rate at which energy can be made available for locomotion.

The mass exponent for total distance swum, at all temperatures, exceeds that for average swimming speed. These different body mass scalings for swimming speed and total distance swum arise because the proportion of time spent actively foraging increases with body mass (see above). Because total distance swum has a higher mass exponent than average swimming speed, it follows that the total daily energy cost of swimming will also have a higher mass exponent than the instantaneous cost of swimming. At 5 °C distance swum is described by

distance swum (m/12 h) = $102.5W^{0.33}$ (5.4)

The scaling for total daily cost of swimming is obtained by dividing power (5.3) by velocity (5.2) and multiplying by distance swum (5.4), thus

daily cost of swimming = $K_1 102.5(2.87)^{1.42}W^{0.94}$ (5.5)

Similarly at 12 °C

daily cost of swimming = $K_1 163.8(3.95)^{1.42}W^{1.07}$

and at 18 °C

daily cost of swimming = $K_1 252.5(5.08)^{1.42}W^{1.15}$

Daily energy expenditures for swimming thus scale considerably higher with body mass than either instantaneous energy expenditures while actively swimming or **SMR**.

An alternative scaling for the daily cost of swimming can be calculated directly using the expression for the cost of transport given above as

cost of transport = $K_2W^{-0.3}$cal g^{-1} km^{-1}

Converting this to a total cost per individual gives a cost per unit distance proportional to $W^{0.7}$. Multiplying this by the scalings for distance swum gives mass scalings for the daily cost of swimming of $W^{1.03}$, $W^{1.2}$, and $W^{1.26}$ at 5, 12 and 18 °C, respectively. Although these differ somewhat from the exponents calculated using the previous method (0.94, 1.07, and 1.15) they are comparable and still produce a scaling for total daily swimming cost that is well in excess of that for **SMR**.

As noted above, the adaptive nature of the increase with body mass in the proportion of available time spent foraging is unclear. However, this increase is not inconsistent with the relationship between the scaling of the instantaneous cost of swimming and SMR, as instantaneous costs are not influenced by the proportion of time spent actively foraging. When the proportion of time spent foraging is equal to

1, or is fixed at some other value, the total daily swimming costs would also scale as does SMR.

If the proportion of time spent swimming is a consequence of the amount of energy that is available for activity, then it is unclear what metabolic processes would lead to the observed increase in activity with both temperature and body mass. Certainly, the small increase in swimming speed with body mass means that for a fixed encounter rate (g/meter), a fish's ration, expressed as a proportion of its maximum ration, will decrease rapidly as its mass increases. While the increase in the proportion of time spent swimming substantially lessens the decrease in % ration with body mass, % ration will still decrease with body mass. However, this only highlights the advantages of high levels of activity for all fish and the reasons for the low activity levels at low temperature and small body sizes remains unclear.

Although the proportion of time spent swimming is treated as an allometric function of body mass, this can clearly only apply over a limited size range because eventually a size will be reached at which the equation will produce a value of 1 or 100%. Values calculated for this body mass from the allometric equations are 163,000 g, 316 g, and 108 g (at 5, 12, and18 °C). Although it is not known if this trend would continue to these sizes at 12 and 18 °C, the predicted sizes for 100% activity span much of the juvenile size range for this species.

In the models described above and in Chapter 1, it is assumed that feeding rate and distance swum are linearly related. To what extend is this likely to be the case for wild fish? At fixed body mass and food density, feeding rate should be a linear function of distance swum (Dunbrack and Giguere 1987). In a stream environment, changes in fish body mass may not alter the relationship between distance swum (or water velocity if feeding is from a fixed station) and feeding rate because the primary foods are insects and other invertebrates that are generally small and available to even the smallest fish (Dunbrack 1992). In contrast, pelagic environments may be characterized by an increase in the average mass of food particles consumed with increasing fish mass because larger prey may be available as fish grow. However, if the ratio of the masses of the largest and smallest food particles a fish consumes is more or less independent of fish size, then the encounter rate with food per distance swum (e.g. g/m) should also be independent of body mass because of the relatively constant total biomass density of particles within log equal mass ranges that seems to be characteristic of pelagic systems (Sheldon 1972). The constraint that feeding rate is a linear function of distance swum (volume searched) that existed in this experiment may thus apply widely in natural environments and, as a consequence, the body mass scaling for energy intake in stream and pelagic environments may in general be well below the scaling for energy requirements.

5.4.2. The effect of temperature

As noted in 5.3.2., the movement detection threshold could not be modified to take into account increases in swimming velocity with temperature. Consequently, the discussion of the effects of temperature will only focus on the results for total distance swum.

The values of the thermal parameter, ***b***, for distance swum are close to those for sustained swimming speeds obtained in studies of other species (Table 2.1), and comparable to those for the frequency of muscle contraction and tail beat of most fish (Wardle 1980) and standard and active metabolic rates in fish (Table 2.1). Distance swum thus appears to respond to temperature changes in a way that parallels metabolic rate. If energy intake is a linear function of distance swum (see above), then equivalent temperature scalings of distance swum and metabolic rate mean that food intake should also be linearly related to metabolic requirements, regardless of temperature. This is in contrast to the situation for body mass where the scaling of distance swum (food intake) was lower than the scaling of **SMR**, while the scaling for the daily cost of swimming exceeded that for **SMR**.

As was the case for the effect of body size, a significant component of the increase in the distance swum with temperature was an increase in the proportion of time spent foraging. Although in this case the increase was sufficient to maintain a feeding rate that was a more or less constant fraction of the maximum ration, it is once again unclear why a high and constant level of activity was not maintained at all temperatures.

If the thermal scaling of distance swum is similar to that for **SMR**, it follows that the thermal scaling of daily energy expenditures will exceed the scaling of **SMR**. Thermal parameters for the daily energy cost of swimming were obtained by taking the seventh (5 to 12 °C) or sixth (12 to 18 °C) root of the ratio of the allometric equations for daily foraging expenditures at the extremes of each of the two temperature ranges. The ***b*** values are $1.141W^{0.0017}$ (5-12 °C) and $1.141W^{0.0133}$ (12-18 °C). As expected, the thermal parameters for energy expenditure are larger than those for most reported measures of metabolic rates.

5.4.3. The effect of delivery schedule

Contrary to the predictions of the optimal foraging model, no relationship was found between food delivery schedule and foraging time, distance swum, or swimming speed, at any temperature. However, because the assumption that fish swim at the speed that maximizes their rate of net energy gain is not met (see above), these predictions do not apply to the results of these experiments, and may be generally invalid for most fishes. Clearly, considerations other than strict energy maximization determine swimming speeds and distance swum in these fish.

The lack of statistically significant effects of delivery schedule could also be due in part to the large variation of activity between individuals and the small number of fish tested. In addition, one way in which fish could detect changes in the food delivery schedule is through changes in hunger level (Ware 1972). The experimental procedure, in which fish were fed to satiation before preceding a next day's trial, and the initially slow feeding rate as food density increased may have produced a lag in the development of hunger differences between delivery schedule treatments that would reduce the ability of the experiment to resolve potential behavioural differences between food delivery treatments.

Although the relationship between delivery schedule and distance swum is not statistically significant, it borders on significance (Table 5.4.). Notably, however, the regression coefficients are negative, not positive. This reverse trend may be related to a decrease in swimming activity by some fish at the highest delivery schedules due to a reduction in their hunger level over the latter part of the 12 hour experimental period.

Chapter 6

GROWTH AND MAXIMUM BODY SIZE

6.1. Introduction

Previous chapters in this thesis have dealt with the effects of temperature and body mass on maximum feeding rate and foraging behaviour (swimming velocity and distance swum). The experiments described in this chapter quantify the effects of temperature and body mass on growth in *S. fontinalis* under controlled ration levels. The results of these experiments are used in conjunction with those of Chapter 5 to predict the way in which growth rate will vary with temperature, body mass and food density when fish are foraging in an environment in which foraging gain varies linearly with distance swum. These predictions are discussed with reference to habitat choice, adult size, and $\mathbf{W}_{max}$ (see Chapter 1).

6.2. Materials and Methods

6.2.1. Experimental fish

The fish used in these experiments were obtained from the collections described in section 3.2.1. Following capture the fish were placed in 200 L holding aquaria supplied with a continuous flow of partially recirculating stream water. Lighting was provided on a 12 h light : 12 h dark cycle by two 40 W fluorescent ceiling tubes covered with blue plastic film. Fish were fed to satiation twice daily with live beetle larvae and most fish began feeding within 3-10 days following capture. The ranges in body mass and length of experimental fish are given in Table 6.1.

Table 6.1. The size range (mass and length) of fish used in growth experiments

Experiment	Temperature (°C)	Number	Body Mass (g)	Body Length (cm)
Growth Rate	5±0.4	16(x2*)	2.0-18.3	5.0-10.3
	12±0.4	16(x2*)	2.4-19.5	5.5-10.3
	18±0.4	16(x2)	4.0-19.7	6.5-10.3

Note: * number of replicates per fish

6.2.2. Food Organisms

Fish were fed live beetle larvae (average length, weight, and proximate composition given in Table 3.2).

6.2.3. Experimental Tanks and Water Temperature Control System

Experiments were conducted in 16 22-L glass aquaria supplied with a continuous flow of partially recirculated stream water. Temperature was controlled by pumping water through a heat exchange water cooler that allowed precise regulation throughout the 5 to 20 °C range. Water temperature remained constant during each series of experiments.

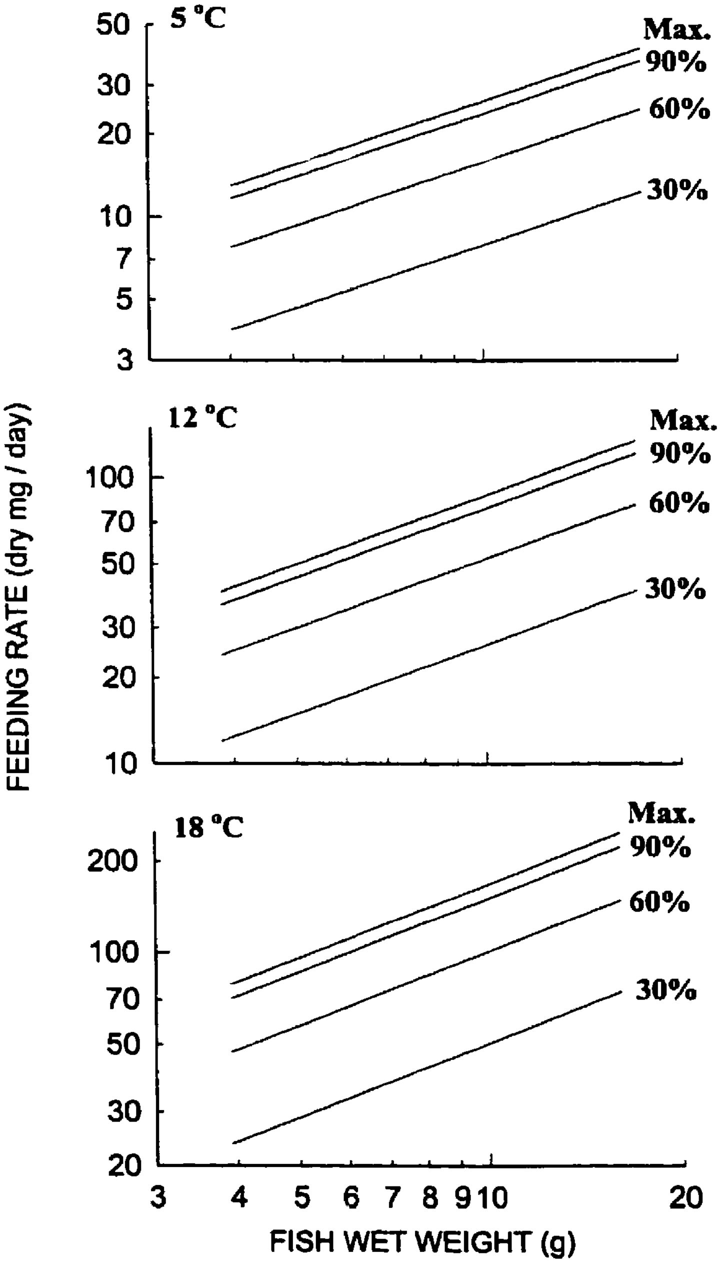

Fig. 6.1. Predicted Feeding Rate at the Given Ration Level (30, 60, 90 % of Maximum Ration) as a Function of Body Mass and Temperature

6.2.4. Growth Rate

Experiments were carried out from April to September,1995. For each series of experiments, 16 fish were placed individually in 22 L aquaria and acclimated to the water temperature (5, 12, or 18 °C) for 10 days. During this period fish were fed to satiation twice daily with live beetle larvae. Fish not feeding actively during this pre-experimental period were not used in the experiments.

On day 11, the 16 fish were randomly divided into three groups (5 or 6 fish per group) with each group fed at one of three ration levels:30%, 60% or 90% of their maximum sustainable feeding rate. The rations representing 30%, 60%, and 90% maximum ration, obtained from the maximum sustainable feeding rate experiments (3.2.4), are shown in Fig. 6.1. Individual fish were fed a twice daily ration of live beetle larvae equal to 1/2 the daily ration calculated for the fish's mass and ration group. If all larvae were not eaten during the two daily feedings, a third meal, equal to the total mass of larvae not eaten, was provided 2 hours after the second daily meal to ensure that the correct ration was consumed each day.

Growth experiments lasted 14 days. Fish were weighed (live weight to nearest 0.01 g) at the end of the pre-experimental period and at the end of each experiment, following a 12 hour period without food. Fish were anaesthetized by immersion in a 0.2 ml/L 2-phenoxyethanol bath for 5 minutes, then rolled in soft paper to remove surface moisture before weighing. Behavioural recovery from anesthesia, in a tank of fresh water, was complete within 1-5 minutes.

The above procedure was repeated with the same group of 16 fish at the same temperature. In this second experiment the fish fed at a 30% ration in the initial experiment were fed at a 90% ration, the fish fed at a 60% ration in the initial experiment were fed at a 30% ration, and the fish fed at a 90% ration in the initial experiment were fed at a 60% ration.

Following the completion of the two experiments, the entire procedure described above was repeated at the other experimental temperatures using 16 new fish. The order of presentation of temperatures was 5, 12, and 18 °C.

6.3. Results and Discussion

6.3.1. Daily growth rate as a function of feeding rate, body mass, and temperature

Daily growth rate (**DGR**) was assumed to be a constant proportion of body mass during the 14 day experimental period and was calculated as

$$\mathbf{DGR = 100[\{ln(W_f/W_i)\}/t]}$$

where $\mathbf{W_i}$ and $\mathbf{W_f}$ are the initial and final trout weights (dry mass in g), and t is experiment duration (days). **DGR** will be positive when weight increases and negative when weight decreases. Growth efficiency was calculated as the change in dry weight of fish during the experimental period divided by the total ingested dry ration and expressed as a percentage. Fish weights were converted to dry weights using a conversion factor (0.2615) obtained by drying 5 sample fish in an oven at 105 C for 24 hours.

DGR is shown as a function of body mass for (i) each of the three ration levels (Fig. 6.2), and (ii) each of the three temperatures (Fig. 6.3). Regression statistics are given in Table 6.2.

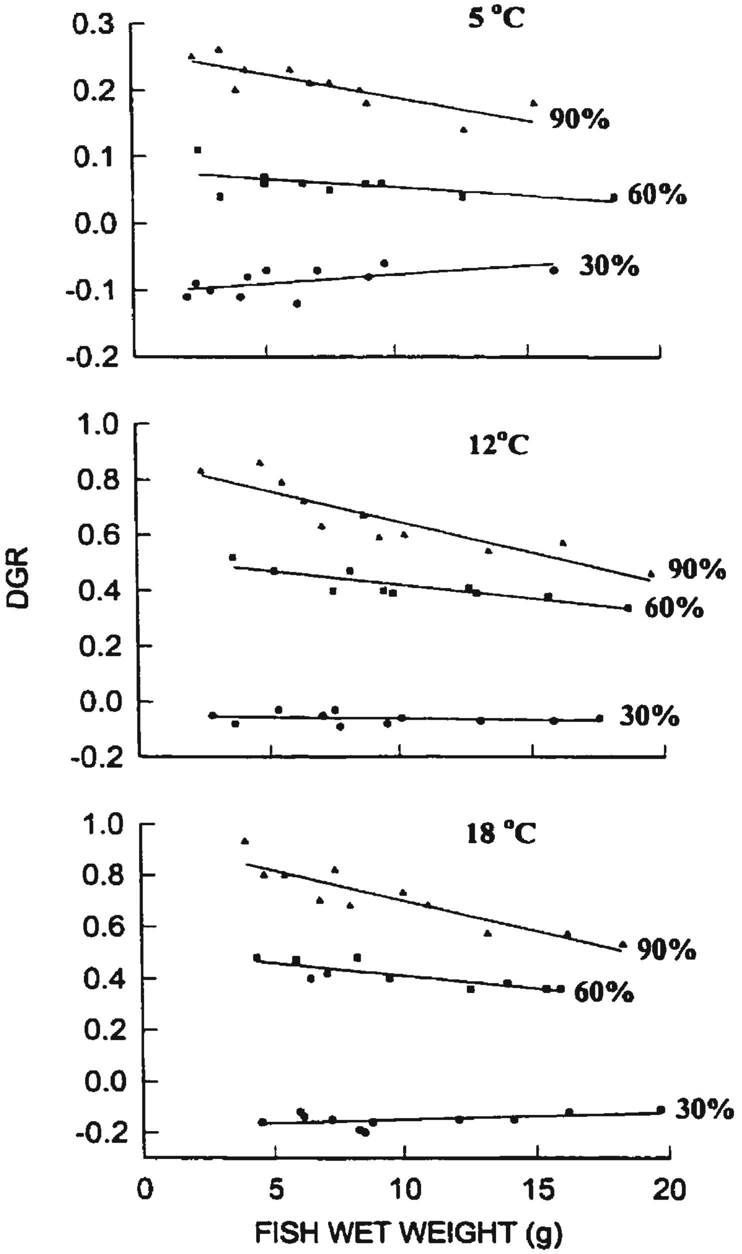

Fig. 6.2. Daily Growth Rate (DGR) as a Function of Body Mass, Ration (30, 60, 90 % of Maximum Ration), and Temperature

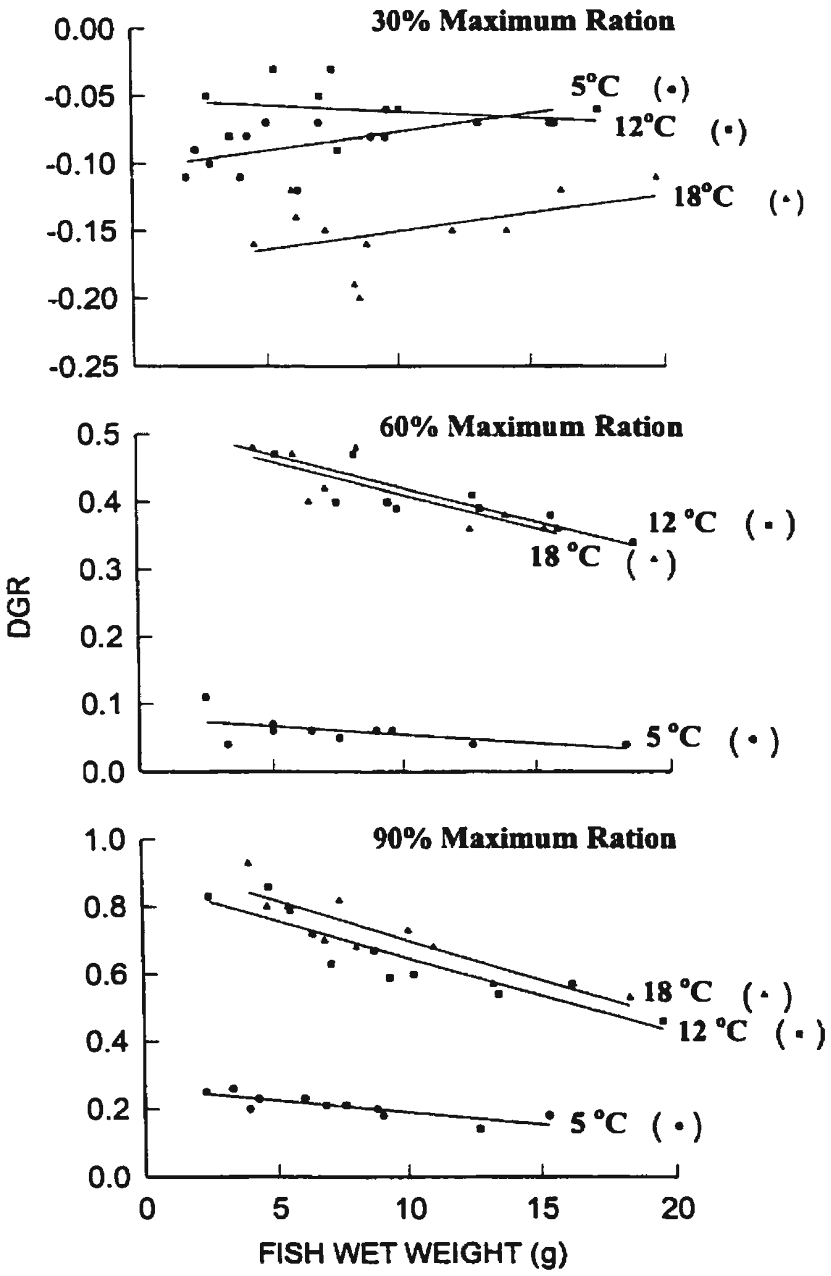

Fig. 6.3 Daily Growth Rate (DGR) as a Function of Body Mass, Temperature and Ration

Table 6.2 Statistics for the Linear Regressions of Daily Growth Rate vs. Body Mass at Different Temperature and Ration Treatments

Temp. (°C)	Ration (%max.)	Intercept **a**	Body Mass		
			Range	Coefficient **b**	**P** value
5	30	-0.104	2.0-18.3	0.0027	$p<0.05$
	60	0.079		0.0025	$p<0.01$
	90	0.259		0.0070	$p<0.001$
12	30	-0.053	2.4-19.5	0.0009	$p<0.05$
	60	0.519		0.0099	$p<0.001$
	90	0.868		0.0222	$p<0.001$
18	30	-0.177	4.0-19.7	0.0027	$p<0.05$
	60	0.508		0.0098	$p<0.01$
	90	0.935		0.0245	$p<0.001$

At 90% and 60% rations, **DGR** was positive and decreased with fish wet weight at all experimental temperatures. **DGR** at 5°C was considerably lower than at 12 or 18 °C, which had similar **DGRs**. **DGR** at 30% ration was negative at all temperatures and increased slightly with mass at 5 and 18 °C and decreased slightly with mass at 12 °C.

There was little variation in growth efficiency with fish mass. Growth efficiency increased with ration level at all temperatures, although there was little

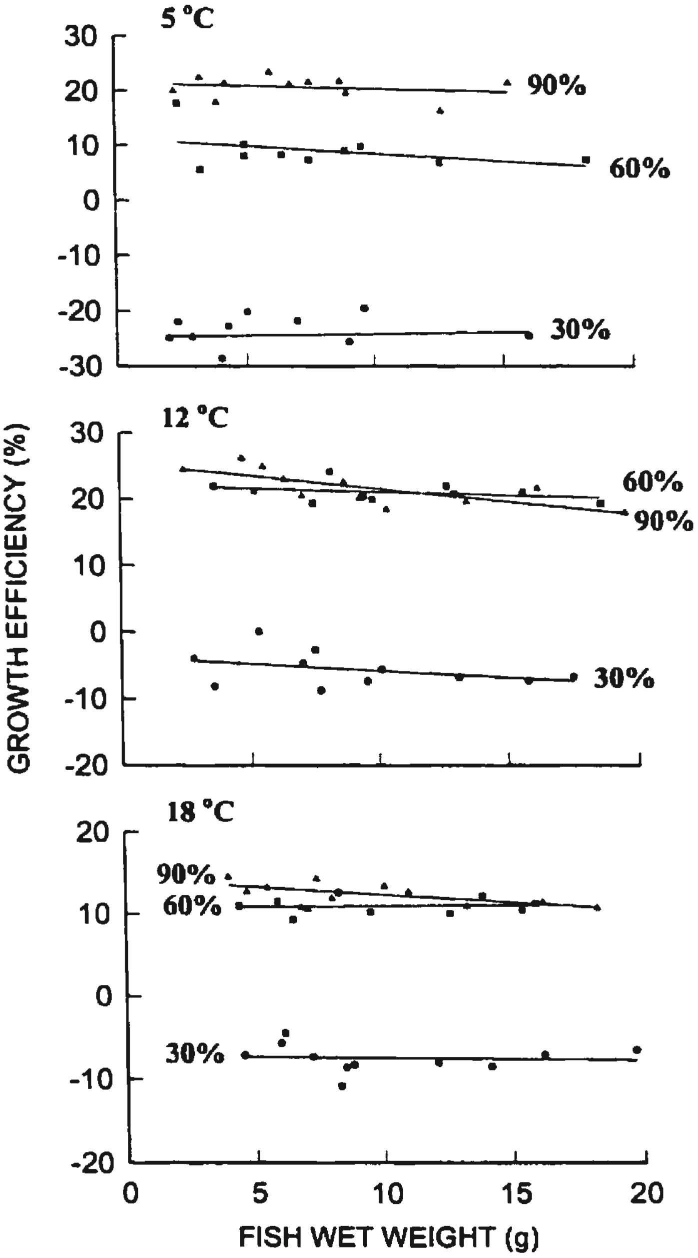

Fig. 6.4. Growth Efficiency as a Function of Body Mass, Ration (30, 60, 90 % of Maximum Ration), and Temperature

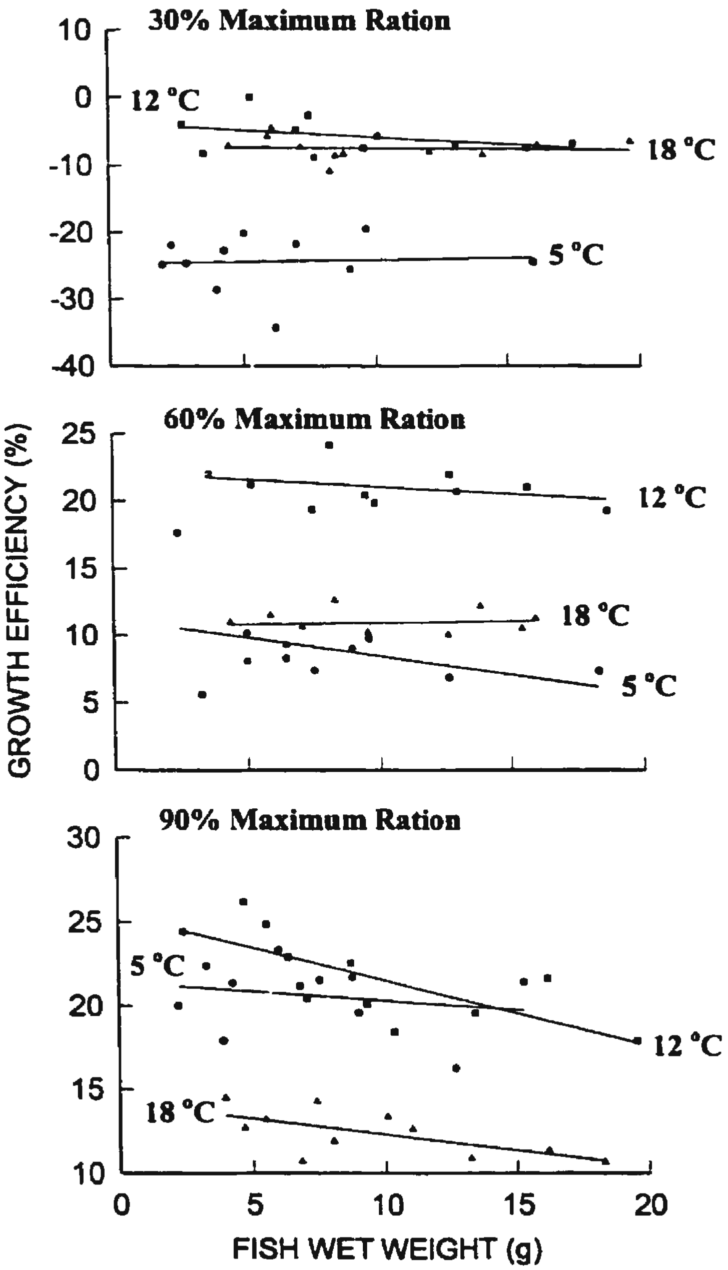

Fig. 6.5. Growth Efficiency as a Function of Body Size for Brook Trout at 5, 12 and 18 °C and Three Different Rations

difference in efficiency between the two highest ration levels for the 12 and 18 °C treatments (Figs. 6.4, 6.5).

The growth rate data (Figs. 6.2, 6.3) show that there is a positive relationship between % ration and the temperature for maximum growth at any body mass. Thus, at 90% ration, growth was lowest at 5, highest at 18 and somewhat lower at 12. At 30% ration, growth at 5 and 12 °C was considerably higher than at 18 °C (at 30% ration growth was negative at all temperatures and body masses). Although no data were collected for 0% ration (starvation), it is reasonable to assume that growth would have been negative and would have decreased in the order 5>12>18 °C. These results are consistent with previous experimental work (Brett et al. 1969; Elliott 1975d; Wurtsbaugh & Davis 1977; Woiwode & Adelman 1991; Brandt 1993) as well as with observations of fish selecting lower temperatures as food supply decreases (Brett 1979; Wildhaber & Crowder 1990; Woiwode & Adelman 1991).

Although **DGR** increases with increasing temperature at the highest ration level (90%), the difference in growth rate between 12 and 18 °C is minimal at any body size, despite the increase in absolute ration between the two temperatures. This implies either (1) a decrease in assimilation efficiency between 12 and 18 °C that approximately counteracts the increase in ration, or (2) a proportionate increase in the costs of maintenance between 12 and 18 °C that exceeds the proportionate increase in ration.

A decrease in assimilation efficiency at higher temperatures and ration levels could arise as an adaptation of the digestive physiology of trout to cool water and moderate levels of food abundance, conditions typical of stream salmonid habitats (Brett & Windell et al. 1976). This would not normally be disadvantageous because such high sustained feeding rates and high temperatures would rarely be encountered by wild fish. Confirmation of a decrease in assimilation efficiency would require analysis of fecal material from fish feeding at different rates and temperatures.

A proportional increase in **SMR** with temperature, larger than the increase in feeding rate, could be detected by comparing the thermal parameter, **b**, for the allometric equations of metabolism and maximum sustained feeding rate, for the temperature interval 12 to 18, and 5 to 12 °C. Although the thermal parameter for maximum sustained feeding rate was lower between 12 and 18 °C than between 5 and 12 °C, the thermal parameter for **SMR** also appears to decrease at higher temperature (Table 3.5). Thus it is unclear if different temperature responses of these variables could have been sufficient to equalize the growth rates at 12 and 18 °C. However, even if this were the case, the behaviour of the thermal parameter for maximum feeding rate could still reflect adaptions of the digestive system for high efficiency at intermediate temperatures and low rations.

6.3.2. The effect of food density, body mass, and temperature on absolute growth rate.

Two approaches are used to combine the results of the above experiments with those of Chapter 5 to examine the way in which absolute growth rate may vary with food density and temperature in actively foraging fish (i.e. when feeding rate is a linear function of distance swum). The first (6.3.2.1) uses the relationships between feeding rate and growth rate (Figs. 6.2, 6.3), to convert the feeding rates in the experiments described in Chapter 5, to predicted growth rates. In the resulting relationships, delivery schedule, the independent variable, is assumed to be correlated with food density.

The second approach (6.3.2.2) relies on the fact that when food density, temperature, and the feeding rate of a fish are know or assumed, the feeding rate for any other combination of fish body mass, food density, and temperature can be predicted using the relationships between distance swum, body mass, and temperature

(Fig. 5.1) and by assuming that (1) feeding rate varies directly with food density for any given distance swum, and (2) feeding rate varies directly with distance swum for any given food density.

Growth is expressed as absolute growth rather than **DGR** in the following analyses, to be consistent with the models outlined in Chapter 1.

6.3.2.1. Analysis of variation in growth rate based on feeding rates from Chapter 5

The above results (6.3.1) were used to carry out a multiple regression, at each temperature, of absolute growth rate (mg weight gain in dry weight per day) as a function of feeding rate and wet body mass (Table. 6.3) These equations were used to calculate predicted growth rates from the feeding rates obtained in the large tank feeding experiments (Chapter 5; Table 5.3). These predicted growth rates (Fig. 6.6) indicate that at food delivery schedules for which the associated feeding rate produced growth that was negative or close to zero (0.06-0.25 mg/m), predicted growth rate

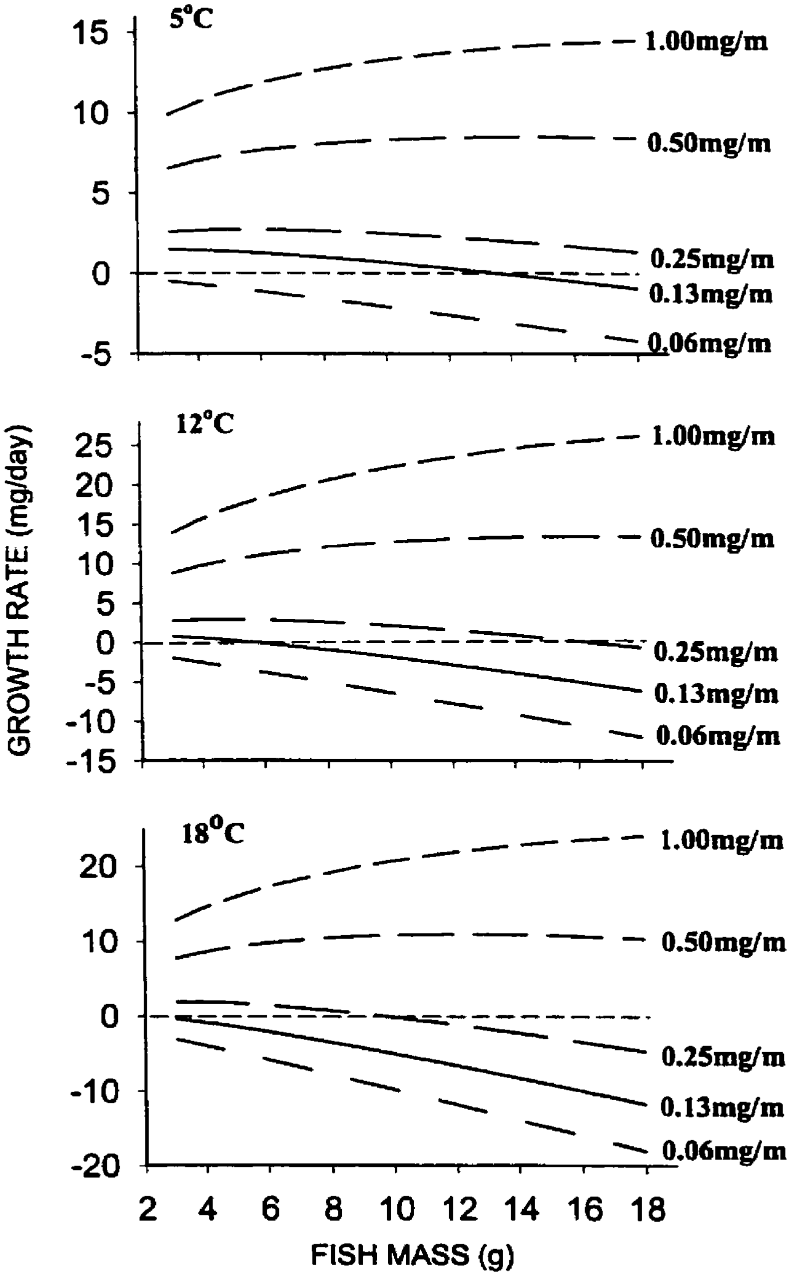

Fig. 6.6. Absolute Growth Rate (mg dry weight/day) as a Function of Body Mass, Delivery Schedule and Temperature

decreased with increasing fish mass, decreased with increasing temperature, and increased with increasing delivery schedule. Thus, the food densities that would correspond to these low delivery schedules would fall below the threshold food densities for growth to increase with increases in either temperature or body mass.

Table 6.3 Statistical Results for the Multiple Linear Regression[1] of Absolute Growth Rate (mg/day) as a Function of Feeding Rate and Body Mass

Temperature (°C)	Intercept **a**	Feeding Rate		Body Mass	
		a_1	**P value**	**a_2**	**P value**
5	-0.725	0.423	$p<0.001$	0.306	$p<0.001$
12	-1.208	0.339	$p<0.001$	0.816	$p<0.001$
18	-1.280	0.216	$p<0.001$	1.180	$p<0.001$

[1] (absolute growth rate) = a + a_1 (feeding rate) - a_2 (body mass)

In contrast, at higher delivery schedules (0.5-1 mg/m), absolute growth was positive and predicted to increase with both temperature and body mass. This is consistent with the predictions of the special case model, indicating that fish are swimming below the theoretical growth maximizing velocity (see Chapter 5 Discussion). Although predicted growth rates were generally below maximal values, these higher delivery schedules must correspond to food densities that would be above the threshold densities for growth to increase with temperature and body mass. Since growth rate decreased with both temperature and body mass at the lower food densities, these threshold densities must fall within the range of prey densities encountered by juvenile trout.

The above results are consistent with the results of several experimental studies that show that the optimum temperature for growth decreases with decreasing ration level (Brett et al. 1969; Elliott 1975d; Wurtsbaugh & Davis 1977; Woiwode & Adelman 1991; Brandt 1993). The results are also consistent with observation of fish selecting lower temperatures, usually by moving deeper in a thermally stratified water column, when food availability decreases (Brett 1979; Wildhaber & Crowder 1990; Woiwode & Adelman 1991). The results presented here also suggest that the energetically optimal temperature for growth may be body size dependent at intermediate levels of food density, a phenomenon that has been observed for a number of species (McCauley & Huggins 1979; Brandt 1980; McCauley & Casselman 1981; Jobling 1981).

Although this analysis is consistent with the special case model of Chapter 1, it may not be the best approach for quantifying the relationship between temperature, food density, and growth. This is because of the probable increase, with time, in feeding rates prior to the establishment of an equilibrium between food capture and food density (i.e. during the initial part of each trial; see Chapter 5). Therefore, an additional examination of the relationship between food density, temperature, and growth rate was carried out using observed distance swum rather than observed feeding rate.

6.3.2.2. Analysis of variation in growth rate based on distance swum from Chapter 5

Previous results (6.3.1) provide information on how the relationship between feeding rate and growth rate varies with temperature and body mass. These results are now used to examine variation in growth with temperature and food density, using a procedure that incorporates the information on distance swum as a function of temperature and body mass from Chapter 5. This analysis should be less affected by variation in food density than that presented in 6.3.2.1 because distance swum was found to be independent of delivery schedule and only varied with temperature and body mass.

These simulations are based on"standard" habitats with a temperature of 12°C and one of three food encounter rates: high, intermediate, and low.

High Food Density

The encounter rate for the high food density simulation was arbitrarily set to the value that would give an 8 g fish, foraging at 12 °C, a predicted feeding rate equal to 90% of its maximum ration. The 90% ration was obtained from Fig. 6.1. The encounter rate corresponding to this ration was calculated by dividing the ration by the total distance swum in a day (i.e. 12 hours) by an 8 g fish at 12 °C (Fig. 5.1).

This encounter rate (g encountered/m swum) was assumed to apply to all fish, regardless of body mass or temperature. This allowed the distance swum data (Fig. 5.1) to be used to calculate feeding rates as a function of fish mass and temperature. The multiple regression equations (Table 6.3) were then used to convert these feeding rates to growth rates (Fig. 6.7).

The results show that predicted growth rate increases with both temperature and body mass. Consequently, the density corresponding to this encounter rate must exceed the density thresholds for growth to increase with either body mass or temperature.

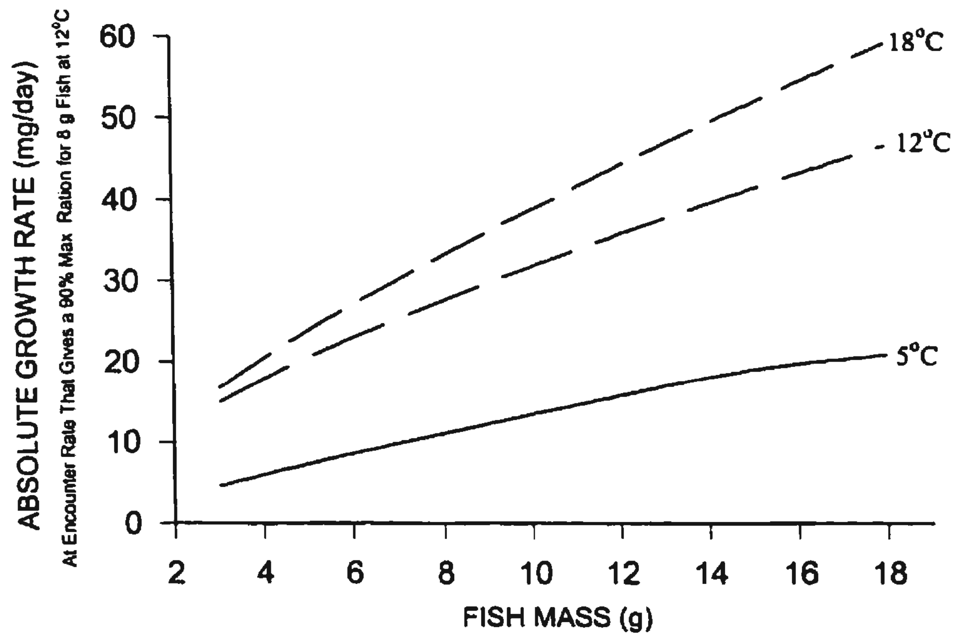

Fig. 6.7. The Absolute Growth Rate of Brook Trout when Foraging at the Encounter Rate That Gives a 90% Maximum Ration for an 8 g Fish at 12°C, as a Function of Body Size and Temperature

Intermediate density

The procedure for calculating growth rate as a function of body mass and temperature at the intermediate food density was identical to that described for the high food density simulation, with the exception that the intermediate food encounter rate was that giving an 8 g fish (at 12 °C), a feeding rate equal to 60% of its maximum ration.

These results (Fig. 6.8) are more complex than those for the high food density. At all temperatures, and for body sizes below about 10 g, growth rate increases with both temperature and body mass. Above 10 g, growth decreases with body mass at all temperatures. This indicates that the food density corresponding to this intermediate encounter equals the threshold density for fish of about 10 g. Above this body size, the threshold density would be higher, below this size it would be lower. In other words, the threshold food density (above which growth increases with body mass) increases with body mass. If this feeding rate is representative of feeding rates found in wild fish, then the qualitative effect of body mass on absolute growth rate would be difficult to predict and could be sensitive to small changes in food density.

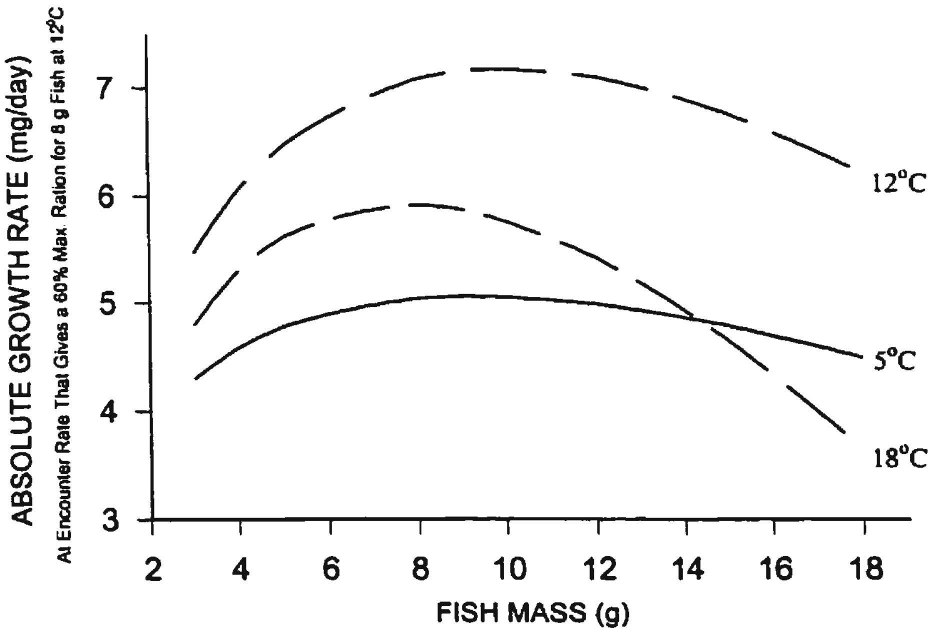

Fig. 6.8. The Absolute Growth Rate of Brook Trout when Foraging at the Encounter Rate That Gives a 60% Maximum Ration for an 8 g Fish at 12°C, as a Function of Body Size and Temperature

Between 5 and 12 °C, growth increases with temperature throughout the body size range. This suggests that the threshold density for temperature is lower than that for body mass over this range.

Between 12 and 18 °C, growth rate decreases with temperature. This suggests that the threshold density for growth to increase with temperature is itself an increasing function of temperature.

To further examine the effects of body mass and temperature on growth performance for this intermediate encounter rate, feeding rates were converted to % maximum ration as a function of fish mass and temperature (Fig. 6.9). It is important to note that in this figure the density of food in the environment does not change with temperature or body mass. The food density is fixed and the % ration varies with body mass and temperature due to the behavioural response of the fish to changes in body mass and temperature. These results show that there is a continuous decrease in the % ration as body size and temperature increase. Therefore, as fish grow, or the temperature increases, fish would experience a decrease in habitat quality, relative to a habitat that provided the maximum ration.

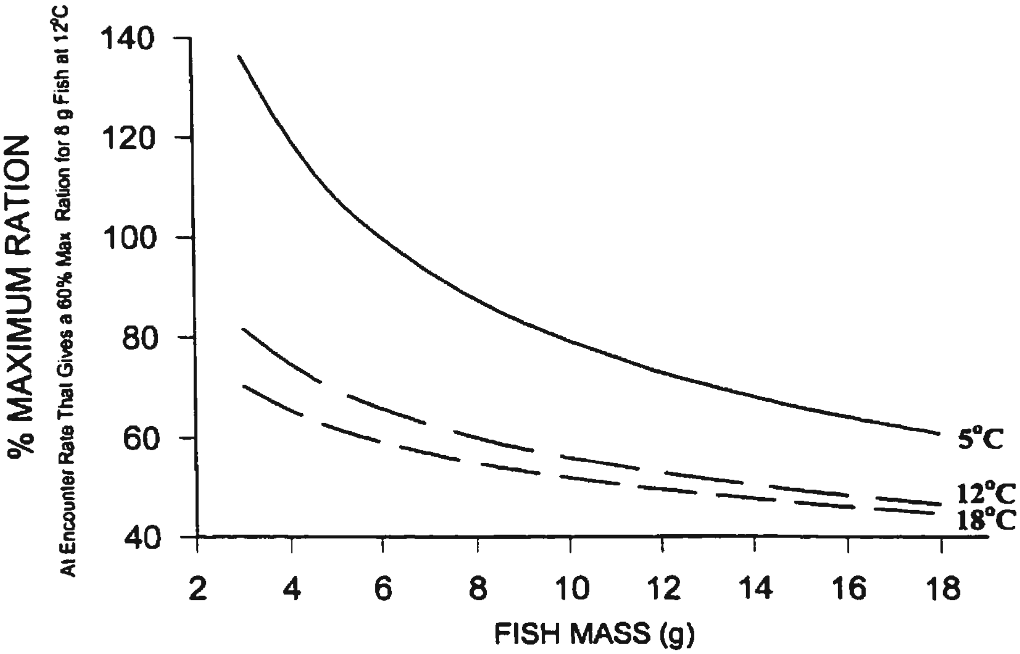

Fig. 6.9. The Ration (expressed as % of the maximum ration) for Fish Foraging at the Encounter Rate That Gives a 60% Maximum Ration for an 8 g Fish at 12 °C, as a Function of Body Size and Temperature

Low food density

The procedure for calculating growth rate as a function of body mass and temperature at low food density was identical to that described above for the high and intermediate food density simulations, with the exception that the food encounter rate was that which gave an 8g fish at 12 °C a growth rate of zero. That is, in this hypothetical "low food" habitat, $\mathbf{W_{max}}$ is 8 g. To obtain the required encounter rate, the daily ration giving an 8 g fish a growth rate of zero at 12 °C was estimated using the multiple regression of absolute growth rate vs. daily ration and body mass (Table 6.3; Fig. 6.10). The encounter rate (mg encountered/distance swum) in this theoretical habitat was then calculated by dividing the above daily ration by the total distance swum during the day (i.e. 12 hours) by an 8 g fish at 12°C (Fig. 5.1). This encounter rate was multiplied by the distance swum functions (Fig. 5.1) to construct predictive curves expressing feeding rate as a function of body mass (given this encounter rate) at the three experimental temperatures (Fig. 6.11). Finally, these feeding rate functions were used to calculate growth rate curves (Fig. 6.12), using the multiple regression equation (Table 6.3).

Fig. 6.12 shows that absolute growth rate is predicted to decrease with fish body mass at all three temperatures when growth rate is close to zero. As expected

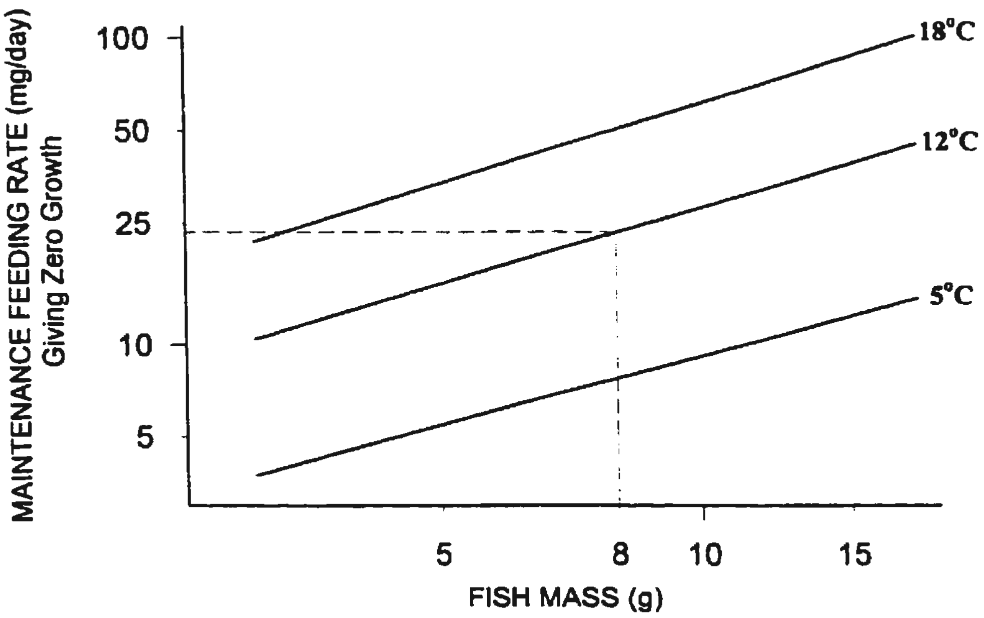

Fig. 6.10. Maintenance Feeding Rate (in dry weight) as a Function of Body Mass and Temperature

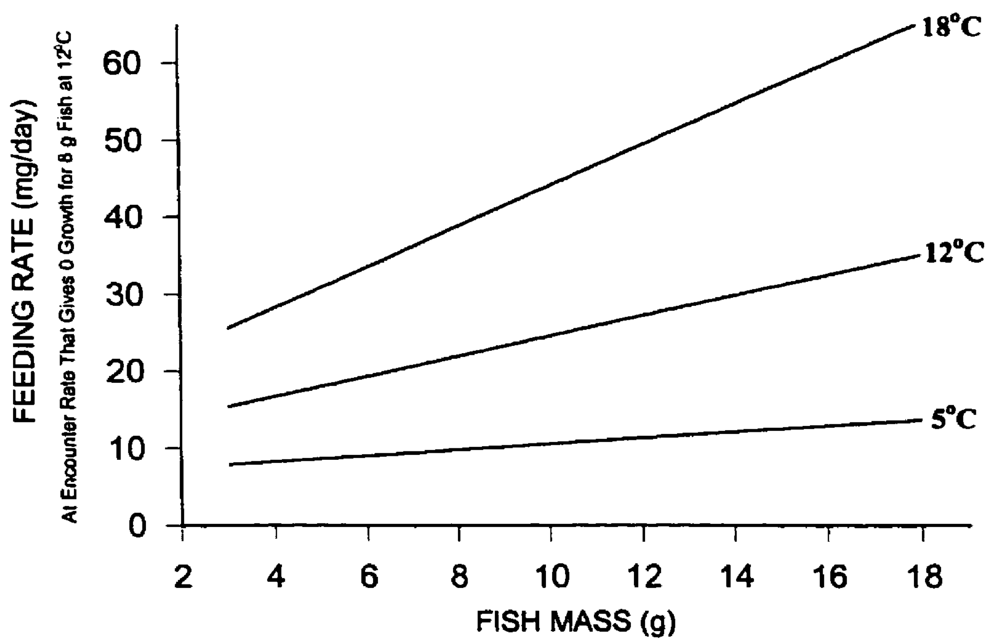

Fig. 6.11. Calculated Feeding Rate for Trout Feeding at the Encounter Rate That Gives Zero Growth for an 8 g Fish at 12 °C, as a Function of Body Mass and Temperature

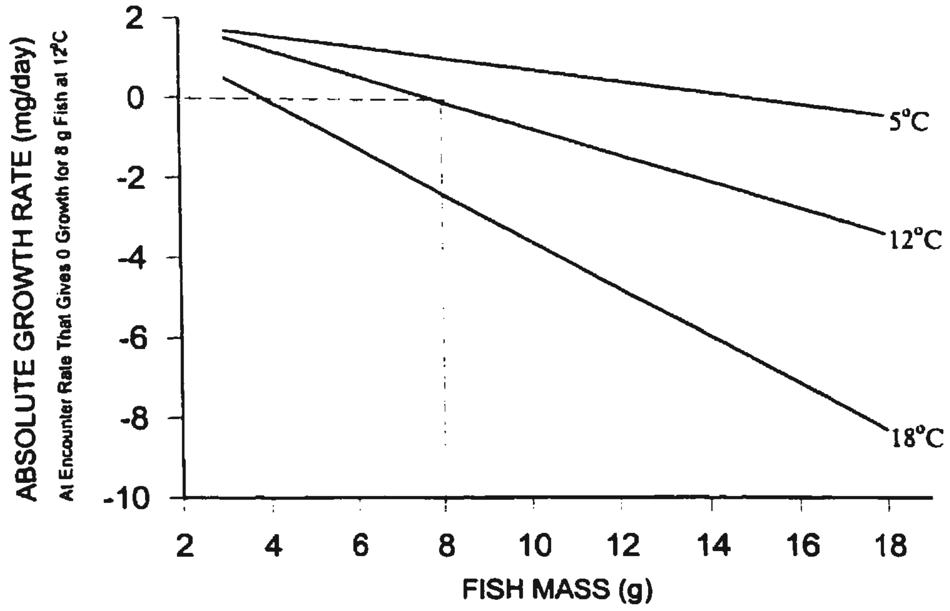

Fig. 6.12. Absolute Growth Rate for Trout Feeding at the Encounter Rate That Gives Zero Growth for an 8 g Fish at 12°C, as a Function of Body Mass and Temperature

from the results for intermediate density, the threshold food density for growth to increase with body mass is well above the density corresponding to the standard encounter rate at all temperatures. The downward slope of the growth curves increases from 5 to 18 °C, so that **W_{max}** (body size at which growth is zero) should decrease rapidly as temperature is increased. As a result, **W_{max}** is predicted to be less than 4 g at 18 °C.

In contrast to the results for the intermediate food density, growth rate decreased with increasing temperature over the entire temperature range from 5 to 18 °C. Therefore the food density corresponding to the standard encounter rate is clearly below the threshold density for growth to increase with temperature.

The results of the three simulations indicate that at high food densities there should be a positive growth response to increased temperature, while this effect would be reversed at low food densities. However, as was the case for body mass, the effect of temperature on growth will be difficult to predict at intermediate feeding levels.

The response of **W_{max}** to changes in temperature predicted in the simulation (Fig. 6.12) directly reflect the different thermal scalings of distance swum and maintenance ration. In particular, $\mathbf{W}_{max}$ will decrease with increasing temperature when maintenance ration has the higher scaling, and will be independent of temperature if distance swum and ration have similar scalings. To compare the thermal scalings of distance swum and ration to the results of the simulations, linear regressions of log (maintenance feeding rate) as a function of log (body mass) were carried out for each of the experimental temperatures (Table 6.4). Van't Hoff thermal parameters for maintenance ration were then obtained by taking the ratio of these allometric equations as adjacent temperatures. These values are given in Table 6.5 along with those for total distance swum, maximum sustained feeding rate, and **SMR**. As expected, the thermal parameters (**b**) for maintenance ration exceed those for distance swum over both temperature ranges.

Table 6.4. The Intercept and Exponent of the Allometric Equations for the Relationship between Maintenance Feeding Rate and Body Mass.

Temperature (oC)	Intercept (**c**)	Weight Exponent (**d**)
5	1.642	0.746
12	4.23	0.823
18	8.43	0.863

Table 6.5. Values of the Van't Hoff Thermal Parameter, b, for Maintenance Feeding Rate, Total Distance Swum, Maximum Sustained Feeding Rate and Standard Metabolic Rate.

Variable	Temperature Range (°C)	Thermal Parameter b
Maintenance Feeding Rate	5-12 12-18	$1.145W^{0.011}$ $1.122W^{0.0067}$
Total Distance Swum	5-12 12-18	$1.069W^{0.0235}$ $1.075W^{0.0107}$
Maximum Sustained Feeding Rate	5-12 12-18	$1.176W^{0.004}$ $1.114W^{0.0007}$
Standard Metabolic Rate	6-12 12-18 5-10 10-15 15-20	1.075(1) 1.052(1) 1.129(2) 1.104(2) 1.108(2)

(1) from Smith et al., 1978; (2) from Macan, 1974.

The cost-benefit models define growth rate as the difference between the feeding rate and the costs of locomotion plus the SMR. In the simulations the calculation of growth rate was instead based on feeding rate-growth rate conversion equations obtained from experiments in which fish were not required to actively search for their food. There is thus the possibility that predicted growth rate (in the simulations) could overestimate the actual growth rate of actively foraging fish. However, locomotion costs are likely to be small relative to energy intake (Chapter 5), consequently, any overestimate of growth rate is likely to be small and would not qualitatively alter the results of the analysis, although it might have shifted the predicted position of $\mathbf{W}_{max}$ to a larger size.

This chapter will conclude with a brief discussion of the results of the simulations as they relate to habitat use and adult size.

Habitat Use

In the high encounter rate simulation, growth rate increased with temperature throughout the body size range. Conversely, in the low encounter rate simulation, growth rate decreased continuously with temperature. Between these extremes there must be a threshold food density above which growth increases with temperature and below which it decreases. The results of the simulations for the three food densities also indicate that this threshold is temperature-dependent as the temperature giving the highest growth decreased from 18 °C at the high food density to 12 °C at the intermediate density and to 5 °C at the lowest density. Assuming that there is an approximate correspondence between this threshold density and % ration, the temperature-dependence of this threshold can also be inferred from Fig. 6.9. This figure shows that % ration decreases continually with increasing temperature for any given food density or, equivalently, that if food density were decreased from a high value, any particular % ration would occur first at the highest temperature. Based on these results, it is expected that the temperature that maximizes growth will be a continuously decreasing function of food density over some intermediate food density range, a range that should include the feeding conditions normally encountered by salmonids. Consequently, movements to habitats of lower temperature would be expected as food density decreases, if such habitats are available. This prediction is consistent with the results of previous studies of habitat use reviewed in Chapter 2.

When food density and temperature are fixed, Fig. 6.9 also shows that % ration decreases continually as body mass increases. Thus, the effect on growth rate of increases in body mass at fixed food density and temperature should be similar to the effect of decreases in food density at fixed body mass and temperature. That is, at food densities within the range normally encountered by wild fish, the temperature that gives the maximum growth rate should decrease as body mass increases. In the absence of any changes in food density, this could produce a shift to habitats of lower temperature as body mass increases, if these are available. This is also consistent with the results of previous studies of habitat use reviewed in Chapter 2.

Adult size

As indicated in Chapter 1, the temperature-dependence of the size at which **ELRO** is maximized (**W_r**) will depend on the temperature-dependence of absolute growth rate. The above simulations indicate that there will be a threshold food density for qualitative changes in the effect of temperature on growth rate. Although the effect of temperature on **W_r** will thus depend on the value of food density relative to this threshold, neither the models of Chapter 1 nor the simulations give any indication as to the value of this threshold, beyond the probability that it will be below the threshold for growth to decrease with body mass. The effect of temperature on **W_r**, and any correlated sizes such as the size at maturity, is therefore problematic. Additional analyses of this question would require more complex models that quantified size-dependent and temperature-dependent mortality rates. Such models are beyond the scope of this thesis.

Chapter 7

REVIEW & SUMMARY

The objective of this thesis was to examine how temperature, body mass, and food availability may influence the behaviour, and growth of fish foraging under "natural conditions". The term "natural conditions" refers specifically to the constraint, in wild populations, that the rate at which a fish consumes food is directly linked to the time and energy that it expends searching for food. This was considered an interesting area of study, with relevance to both fish ecology and ecological theory, because this constraint is generally not present in experimental work on fish feeding and growth despite its fundamental importance in wild populations. Conversely, when it is present, as in field studies, it is difficult or impossible to quantify the relationships between foraging behaviour and (1) body size, (2) temperature, and (3) food availability. Consequently, previous work could not be used to address the question of how temperature changes influence the behaviour or growth of wild fish.

Although the constraint imposed by a natural foraging environment provided the rational for this study, it was difficult to address the effects of temperature and body mass on behaviour directly through field experiments because of the difficulty, noted above, of measuring and controlling critical variables. Alternatively, standard laboratory experiments on fish feeding and growth would not, by themselves, allow for the measurement of the behavioural variables important in the feeding of wild fishes.

In order to clarify the problems involved, identify critical parameters, and aid in experimental design, an initial analysis was carried out that involved the construction of a series of theoretical models (Chapter 1) that explored the relationships of the parameters involved using two different approaches; one based on optimal foraging assumptions, the other assuming the action of unknown constraints on optimal behaviour.

The critical variable identified by these models was distance swum during some fixed time period. Distance swum is important because it determines feeding rate which, in turn, determines growth rate. The effects of temperature, body size, and food availability on growth are thus largely mediated through their effects on distance swum.

Once the data requirements had been made explicit through analysis of the models, a literature review covering the effects of temperature, body size, and food availability on fish growth and behaviour was carried out. This review was intended to put the current work in perspective, and to highlight the relative lack of information on the effects of temperature, body size, and food availability on fish behaviour in wild populations, despite the enormous body of work on various aspects of temperature, body size, food availability, and behaviour in fishes.

Prior to carrying out behavioural experiments it was necessary to conduct an extensive series of preliminary laboratory studies on maximum feeding rates in brook trout and how these are influenced by body mass and temperature (Chapter 3). These studies were required to establish food delivery schedules for the experiments in Chapters 5 and 6 that would produce a range of feeding rates comparable to those expected in wild fish populations. In addition to providing these necessary baseline data, the feeding experiments yielded allometric exponents and thermal coefficients for maximum feeding rate. These parameter values, which for the allometric exponent were comparable to those for SMR, were used for subsequent comparisons with the allometric and thermal parameters obtained for swimming speed and distance swum.

The results presented in Chapter 3 were also relevant to an unresolved problem in fish ecology related to the measurement of maximum feeding rates.

The experiments described here used an equilibrium technique that had previously given feeding rates substantially lower than those obtained using non-equilibrium approaches. The results of the present study were consistent with these lower values, suggesting that many reported values may overestimate maximum feeding rates for live foods.

The behaviour experiments of Chapter 5, which formed the major contribution of the thesis, first required the development of a novel experimental technique and apparatus to carry out the detailed analyses of fish movements in real time. Although this was a complex and technically challenging problem, the system that was finally designed and constructed allowed for the measurement of aspects of fish behaviour that had not been investigated previously. This monitoring and control system (described in some detail in Chapter 4) was designed specifically for this study; however, the system could be used for a wide variety of time and energy budget studies requiring the detailed measurement of animal movements in real time.

The monitoring and control system was used to carry out the experiments described in Chapter 5. These experiments quantified the relationships between distance swum and temperature, body mass, and food availability; relationships identified (Chapter 1) as critical for investigating temperature, food density, and body size effects on behaviour and growth. Analyses of these experiments yielded the following results:

1. There was no significant relationship between food availability (delivery schedule) and distance swum or swimming speed.

This result is significant as it tests an optimal foraging model based on the maximization of net energy gain. The behaviour of experimental fish was clearly not what would be expected if behaviour was governed only by the requirement to maximize net energy gain. In this case, unidentified factors, in addition to pure energy maximization, must control foraging behaviour.

2. Distance swum increased with both body mass and temperature.

There were two components to the increase in distance swum with body mass and temperature: (1) an increase in the instantaneous swimming velocity with both body size and temperature, and (2) an increase in the amount of time spent actively swimming with both body size and temperature.

Although swimming speed increased with body size, the body mass exponent for swimming speed was well below that for SMR at all temperatures. When the energy costs of swimming were considered, the allometric exponent for instantaneous swimming costs was found to be similar to that for SMR. Therefore, swimming speed may be more closely related to the energy costs of the behaviour than the energy yield from foraging. This result was somewhat surprising because the actual energy costs of swimming appear to be small relative to the potential foraging gain from increased velocity and it would seem more energetically advantageous for swimming speed to scale in parallel with metabolic demands.

The allometric exponent for total distance swum exceeded that for instantaneous swimming speed because of the increase in active swimming time with body mass. Consequently, the body size scaling for daily swimming costs exceeded that for SMR. Although this reduced the difference between the body mass scalings for feeding rate and metabolic costs, the scaling of feeding rate was still substantially lower than that for SMR. Because of the relatively low cost of transport, it is again unclear why fish had such low activity levels.

The Van't Hoff thermal parameter for total distance swum was closer to that for **SMR** than was the thermal parameter for daily swimming costs (which exceeded that for **SMR**). The reasons for the similar scaling of total distance swum and SMR are unclear.

Regardless of the underlying reasons for the various behavioural responses to changes in body size and temperature, previous laboratory results would have suggested that changes in feeding rate with body mass should parallel changes in **SMR** (for example, as indicated by the similar scaling of maximum feeding rate and **SMR** seen in Chapter 3). The fact that this was not the case for these brook trout provides an empirical justification for the experimental approach taken here.

Although the experiments of Chapter 5 quantified the body mass and thermal dependence of swimming behaviour, it was not possible to immediately extend the analysis to the consequent effects on growth because the relationship between feeding rate and growth rate had not been precisely defined for these experimental conditions.

In order to do this, a series of experiments on the relationship between growth rate and (1) temperature, (2) body mass, and (3) feeding rate were carried out (Chapter 6). Once the results of these experiments were in hand, feeding rates, from Chapter 5, were converted to growth rates. Two approaches were then taken in the analysis of temperature and body size effects on growth rate, with comparable results.

The first approach used the actual feeding rates from the experiments of Chapter 5 and converted these into absolute growth rates (e.g. gm/fish/day) to produce a series of curves each relating growth rate to body mass at a particular temperature and food delivery schedule. This analysis showed that, under the experimental conditions, growth rate should decrease with body mass and temperature at low levels of food availability (close to and below maintenance feeding levels) and increase with body mass and temperature at high levels of food availability.

The second approach calculated predicted feeding rates indirectly from the distance swum results of Chapter 5. This second approach was used because it was felt that distance swum was a better predictor of feeding rate than the observed feeding rates, due to the variation with time in food density during individual trials(Chapter 5). Three "standard habitats" were defined at 12 °C that were characterized by food densities that produced high, intermediate, and low feeding rates in an 8 g fish. By using the distance swum relationships from Chapter 5 it was possible to calculate the growth rates of fish both smaller and larger than 8 g in the standard habitats, as well as in habitats differing in temperature and/or food density.

These results indicated that growth rate increased with temperature and body mass at high food densities and decreased with temperature and body mass at low food densities. At intermediate food densities, the qualitative effects of changes in temperature or body mass on growth rate were found to depend on temperature, body mass, and food density.

These simulations also indicated that the temperature at which growth rate is maximized should increase with increasing food density and decrease with increasing body mass. These results were consistent with the results of previous studies of the effect of temperature on habitat use reviewed in Chap. 2.

The effect of temperature and body mass on the size at which life time reproductive output is maximized ($\mathbf{W}_r$) could not be predicted from the experimental or theoretical results because it could not be determined if growth would increase or decrease with increasing temperature at $\mathbf{W}_r$.

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APPENDICES

A. Critical Subroutines in Automated Experimental System Software

1. Quickcapture Board (DT2855) Initializing Subroutine:

REM" This subroutine (Assembly language) will do :

1. initialize video control/status register;
2. clear busy and pass bits to stop board operation and turn off disply;
3. program input look-up tables which will binarize grey level during image acquisition;
4. program out look-up tables;
5. write to video control/status register and turn display on;
6. acquire a frame image."

```
     public initial
 code   segment
   assume   cs:code, es:code
 initial  proc  far
 ; initialize the board:
     push bp                          ;save registers
```

```
    push es

    push di

    push si

    mov  bp,sp

    mov  ax,3000h

    mov  es,ax

    mov  di,1f6h


;read video control/status register clear busy and pass bits:

busy_loop:

    mov  dx,240h              ;I/O base

    mov  ax,8000h

    out  dx,ax                ;set pass 0

    in   ax,dx                ;read video control/status register

    and  ax,8000h             ;check busy bit

    jnz  busy_loop            ;if busy not clear loop

    out  dx,ax                ;clear
```

```
;select input look-up table 0, send index value to ILUT 0:
    mov  bx,0                    ;index value
    mov  ch,0
    mov  cl,byte ptr es:[di]     ;times of loop (binarizing threshold)
ilut_loop1:
    mov  ax,bx
    mov  dx,240h+2               ;ilut index register
    out  dx,ax                   ;write index value
    inc  dx
    inc  dx                      ;ilut data register
    mov  ax,240
    out  dx,ax                   ;write data
    inc  bx                      ;increase index value
    loop ilut_loop1              ;decrease cx if cx=0 end loop
    mov  cx,10
    mov  si,0
 ilut_loop2:
    mov  ax,bx
    mov  dx,240h+2               ;ilut index register
```

```
  out  dx,ax                   ;write index value

  inc  dx

  inc  dx                      ;ilut data register

  mov  ax,si

  out  dx,ax                   ;write data

  inc  bx                      ;increase index value

  add  si,24

  loop ilut_loop2              ;decrease cx if cx=0 end loop

  mov  cx,246

  mov  ah,0

  mov  al,byte ptr es:[di]

  sub  cx,ax

ilut_loop3:

  mov  ax,bx

  mov  dx,240h+2               ;ilut index register

  out  dx,ax                   ;write index value

  inc  dx

  inc  dx                      ;ilut data register

  mov  ax,240
```

```
   out  dx,ax                    ;write data

   inc  bx                       ;increase index value

   loop ilut_loop3               ;decrease cx if cx=0 end loop


;write output look-up table:

   mov  al,0ffh

   mov  dx,240h+14h              ;olut pixel mask register

   out  dx,ax                    ;enable olut

   mov  dx,240h+10h              ;olut index register

   mov  al,0                     ;index and data value

   out  dx,ax                    ;write index value

   inc  dx

   inc  dx                       ;olut data register

   mov  cx,0ffh                  ;times of loop

 olut_loop:

   out  dx,ax                    ;write data to red entry

   out  dx,ax                    ;write datd to green entry

   out  dx,ax         ;write data to blue entry, index value increase automatically

   inc  al                       ;increase data
```

```
   loop olut_loop                 ;decrease cx, if cx=0 end loop
   mov  ax,8050h
   mov  dx,240h                   ;I/O base
   out  dx,ax                     ;write to video control/status, register
wait_loop:                        ;wait for video acquisition
   in   ax,dx
   and  ax,8000h
   jnz  wait_loop

;DT2855 now initialised and a frame input to buffer
   pop  si                        ;restore register
   pop  di
   pop  es
   pop  bp
   ret                            ;return to calling program
initial endp
code ends
   end
```

2. Read Pixel Data Subroutine:

REM" This subroutine (Assembly Language) will do:

1. access image memory onboard;

2. read pixel data through the pixel register;

3. determine dark pixels;

5. store coordinates of dark pixels."

```
      Public reading

code   segment  public 'code'

  assume   cs:code

reading  proc   far

    push bp                        ;save registers

    push es

    push di

    push si

    mov  bp,sp

    mov  ax,3000h                  ;data segment address

    mov  es,ax                     ;send to es

    mov  di,0                      ;offset to di
```

```
    mov  si,0               ;subscript of array X and Y
    mov  bx,9               ;line address
    mov  cx,9ah             ;times of line loop(154)

line_loop:
    push cx                 ;store cx value (times of line loop)
    mov  dx,240h+0ah        ;line address register
    mov  ax,bx
    out  dx,ax              ;write line address
    mov  ax,1ch             ;pixel address
    mov  cx,90h             ;times of pixel loop(144)

pixel_loop:
    mov  dx,240h+8          ;pixel address register
    out  dx,ax              ;write pixel address
    push ax                 ;store ax value (pixel address)
    mov  dx,240h+0ch        ;pixel data address register
    in   ax, dx             ;read pixel data
    cmp  ax,100             ;compare pixel data with a certain value
```

```
  jnb  next                      ;if the pixel is dark
  inc  di
  inc  di
  mov  dx,240h+8h                ;read pixel address
  in   ax,dx
  mov  word ptr es:[di],ax       ;save pixel address to memory
  inc  di
  inc  di
  inc  dx                        ;read line address
  inc  dx
  in   ax,dx
  mov  word ptr es:[di],ax       ;save line address to memory
  inc  si
  cmp  si,0fah
  jna  next
  mov  si,0fah
  mov  di,0
next:
  pop  ax                        ;return ax value (pixel address)
```

```
  inc  ax                       ;increase pixel address
  inc  ax
  inc  ax
  inc  ax
  loop pixel_loop               ;decrease cx, if cx=0 end loop
  pop  cx                       ;return cx value (times of line loop)
  inc  bx                       ;increase line address
  inc  bx
  inc  bx
  loop line_loop                ;decrease cx, if cx=0 end loop

  mov  ax,si                    ;send number of dark pixels to memory
  mov  di,0
  mov  word ptr es:[di],ax
  mov  ax,8050h
  mov  dx,240h                  ;I/O base
  out  dx,ax                    ;write to video control/status register
wait_loop:
  in   ax,dx                    ;check busy, wait for video acquisition
```

```
   and  ax,8000h

   jnz  wait_loop

   pop  si                          ;restore registers

   pop  di

   pop  es

   pop  bp

   ret                              ;return to calling program


reading endp

code ends

    end
```