Modelling the Growth and Resource Allocation Dynamics of Juvenile Salmonids

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“A Fo Ben Bid Bont”
–Y Mabinogion

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Abstract

Juvenile salmonids often begin their lives in seasonally harsh environments, and as such, have highly competing allocation demands for surplus energy. Individuals which allocate their resources to growing fast minimise the time that they are susceptible to a large array of size selective mortality effects. By contrast, individuals who allocate their resources to storage have an increased ability to withstand periods of intense food scarcity.

In this thesis, we investigate the success of three strategic physiological growth models to describe the resource allocation dynamics of juvenile salmonids. The net production allocation, reserve allocation and assimilation allocation models differ in their assumptions concerning the way salmonids utilise their resources for the physiological processes of maintenance, growth and storage. The main points of investigation include: the relationship between nutritional status and growth rate, what transpires when fish are starved or fed a maintenance ration, the effect of diet formulation and the sequence of recovery growth exhibited by weight compensating fish.

In all scenarios, the assimilation allocation model equals or betters the qualatative predictions of the net production and reserve allocation models. In addition to its qualitative success, we illustrate the assimilation allocation model's quantitative capability by successfully fitting it to a series of tank-based experiments, which encompass a wide range of different feeding regimes.

Using the assimilation allocation model we analyse the resource allocation strategies adopted by juvenile Atlantic salmon parr in a Scottish stream over a full annual cycle. The model highlights a seasonal pattern of resource allocation. At the onset of spring, juveniles primarily allocate to growth, but over the summer gradually change to a reserve accumulation strategy in anticipation of the ensuing winter period of food scarcity. The results are ecologically realistic and illustrate how salmonids use dynamic resource allocation in energy limiting environments.

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Part I

Introduction

Chapter 1

General Introduction

1.1 The Salmonid Family of Fish

The salmonidae are a family of fish which comprises the salmons, trouts, whitefishes, graylings, and chars (Nelson 1976). In general usage (and our usage), the term salmonid refers to salmon, trout and chars. Salmonids are a small family of fish characterised by high morphological homogeneity (Rankin and Jensen 1993). Salmonids are characterised by an elongate body covered with small cycloid (rounded, with smooth edges) scales and possessing an adipose (fleshy) fin between the dorsal fin and tail.

The amazing life histories of salmonids has captured the scientific and public imagination. Although quite variable in their life histories (within and among species), all salmonids begin their lives in freshwater (Boeuf 1993). Adult fish (migratory and non-migratory species) spawn in freshwater streams or lakes, usually in late summer or autumn (Groot and Margolis 1991). Their large yolky eggs are buried in the substrate, and the embryos develop overwinter. The juveniles emerge from the substrate the following spring as “fry” and are dependent on external food sources upon emerging.

Even at this early stage in life, the life history patterns of salmonids begin to diverge. Some sub-populations will remain in freshwater for all their lives but nearly all species of salmonids can adapt to life in salt water. These species are referred to as being anadromous, which is Greek for "running upwards" and alludes to the upstream spawning migrations many salmonids display. Some species must migrate or die, most of the others have races which deliberately migrate. A few species have not adapted to life in the sea, mainly because they inhabit isolated freshwaters (Sedgwick 1988).

Salmonids who will eventually migrate to sea can spend as little as a few months to many years in freshwater (Northcote 1984). The initiation of migration is preceded by the parr-smolt transformation (smoltification), in which the juveniles transform from a stage in their life history adapted to stream inhabitation to a stage adapted to downstream migration and eventually seawater inhabitation (Folmar and Dickhoff 1980). The Smoltification process is a series of morphological, physiological and behavioral changes (Boeuf 1993).

Anadromous salmonids carry out most of their growth at sea. Depending on the species and stock, the fish spend between one and seven years in the ocean (Groot and Margolis 1991). The migratory instinct of members of the salmonid family is remarkably specific, each generation returning to spawn in almost exactly the same breeding places as the generation before it. Even those species that do not migrate from fresh water to salt water spawn in the same freshwater streams as did their ancestors (although some straying is common (Quinn 1984)). The spawning ground of salmonids is usually a rapidly flowing, clear stream with gravel and rocks on the bottom. Many species of anadromous salmonids die shortly after spawning, but some small percentage of other species may return to sea and then return to spawn again. By contrast, non-anadromous salmonids can spawn repeatedly for many years (e.g. Hayes et al. (2000)).

The members of the salmonid family form the most commercially valuable group of the world's fish species (Sedgwick 1988). Most members of the salmonid family are valuable food fish and excellent game fish. Salmonids have always been an important source of food, and the last 30 years has seen the growth of large scale salmonid aquaculture which has coincided with a reduction in the commercial fishing of wild salmonids (Parrish et al. 1998). Wild salmonids are still considered a delicacy, but the continuous supply of salmonids to the world market in large quantities has eroded the previous prices paid for wild fish in former years (Youngson and Hay 1996). As a result, many previously marginal fisheries have been made unprofitable. Pressure on wild stocks for commercial fishing has been reduced (at least temporarily) on the ocean feeding grounds.

Fish farming is now a major global industry and the salmonids have become a world commodity. Arguably, however, the industry's most telling impact has been on a more local scale. For instance, in Scotland, the industry now directly employs over 2000 people and many of these live in remote areas where the local economy now depends on the income generated by aquaculture. The Scottish salmon industry alone produced over 86,000 tonnes of Atlantic salmon in 1998, and these sales were worth over £250 million to the Highland economy, a value that is greater than either lamb or beef (http://www.users.zetnet.co.uk/richd/Sintro.html). Wild stocks of salmonids are also an important natural resource for rural communities. Revenues from sport fishing provide a valuable source of income. In 1995, it was estimated that salmon angling on the River Dee in Scotland contributed between £5 million and £6 million to the local economy of the Grampian region (Anon. 1997).

In recent years, wild stocks of salmonids, all around the globe, have been in serious decline. For instance, wild Atlantic salmon populations throughout the North Atlantic are at their lowest levels in recorded history (Mills et al. 1999). There seems to be no single factor that can be blamed for falling numbers of wild stocks. It seems more likely, that falling numbers has resulted from the cumulative effects of man's different activities.

Although farming may have reduced fishing pressure in the open ocean, the industry has had some serious detrimental impacts on wild stocks. In most cases, fish farms are situated in areas frequented by wild salmonids. Within the intensive and confined conditions of sea rearing cages, high concentrations of sea lice are common. Migrating salmonids are very vulnerable to attack by these lice. In some rivers, wild stocks have virtually collapsed (Mills et al. 1999). Fish farms also spread diseases, such as Infectious Salmon Anaemia (ISA) and *Gyrodactylus salaris* to wild stocks (Mills et al. 1999). Uneaten food, fish faeces, or medications used to treat farmed fish, has been shown to heavily pollute the local water environment and have a detrimental effect on the local ecosystem (Mills et al. 1999).

Besides the obvious effects of fisheries, which directly catch salmonids or which remove the salmonids natural food in the sea, other detrimental factors to wild stocks include, pollution of rivers and silting up of spawning grounds, obstacles to migration (e.g. dams) and climatic change.

A number of organisations have been established to act as focal points for the identification and solution of the afore mentioned problems (e.g. The Atlantic Salmon Trust (http://www.atlanticsalmontrust.org/), Salmon and Trout Association (http://www.salmon-trout.org/), Salmon and Trout Conservation Network (SATCON) (http://www.satcon.org/)). These organisations encourage and give practical assistance to the conservation of salmonids in order that wild stocks of salmonids are preserved for the good of all.

1.2 The Juvenile Stage and the Competing Demands for Surplus Energy

For the purposes of this thesis we shall classify the juvenile stage to begin when the young fish has used up all their nutrients supplied in the egg sack and therefore are completely dependent upon external food for sustenance. There is a short phase (3-4 weeks) between hatching and reaching our classification of being a juvenile in which the individual is still dependent upon nutrients supplied in the egg sack. In this this stage, the individuals (called alevins) remain hidden from sight in the gravelly substrate of the spawning grounds and mortality rates are generally low (e.g. Mills et al. (1999)). We shall consider the individual to be classified as a juvenile until it has become fully sexually mature.

From a life-history perspective, the success of an individual organism is traditionally assessed by its lifetime reproductive output (Lika and Nisbet 2000). The exact factors that trigger full sexual maturity will almost certainly involve genetic and abiotic parameters, but in general are still poorly understood in fish. Nevertheless, sexual maturity is usually attributed to a satisfactory combination of size, nutritional condition and growth rate (Silverstein et al. (1997); Thorpe et al. (1998)). (The reason why it is hard to isolate one of these factors from another will become clear within this thesis.)

Before anadromous salmonids can reproduce they must first migrate out to sea (at least in the majority of cases, see later). It is generally agreed upon that anadromous salmonids must reach a critical minimum size (Elson 1957) by the time of the seasonally fixed migration period, to maximise their marine survival rate (e.g. Bilton et al. (1982); Lundqvist and Eriksson (1985); Lundqvist et al. (1994); Yamamoto et al. (1999)).

We can, from the above criteria, establish the main combined goals of juvenile salmonids. There are essentially two main goals juveniles must accomplish to reach the necessary (or reproductively advantageous) size to first reproduce or be able to migrate to sea. In order to be successful, juveniles must survive and grow (Wootton 1990).

For many species of animals the juvenile stage is a particularly precarious phase in its life, and for the salmonids, there is certainly no exception. Juveniles face the threat of mortality from a large variety of different causes. Consequently, mortality rates are at their highest levels in the juvenile phase, especially when the fish are very young (Mills et al. (1999); Egglishaw (1967); Gardiner and Geddes (1980)).

Small juvenile fish are the prey base on which piscivorous food webs depend (Mills (1962, 1964, 1965, 1989); Blackwell et al. (1997); Feltham and MacLean

(1996); Kennedy and Greer (1988)). As juveniles grow they become susceptible to a smaller range of predators (Post and Parkinson (2001); Sogard (1997)). A significant body of literature documents the common, inverse relationship between body size or growth rate and survival in young fish (Tonn et al. (1992); Persson et al. (1996); Post et al. (1999)).

Wild populations of juvenile salmonids often reside in seasonally harsh energy limited environments which means that starvation as well as predation is a common cause of mortality (Gardiner and Geddes 1980). On a specific size basis, smaller fish have higher metabolic costs than larger fish (Post and Parkinson 2001). There is substantial literature on metabolic allometry (as reviewed in Shuter and Post (1990)) which imply that larger bodied individuals, and those with the greater energy storage in a utilisable form (primarily lipids), have a greater likelihood of surviving intense periods of resource scarcity.

Small bodied juvenile salmonids are faced with strong competing demands for surplus energy (Post and Parkinson 2001). The above factors point out that for pre-reproductive organisms there are trade-offs between energy allocation to growth, predation avoidance, and storage products for periods of resource scarcity. Since energy availability is frequently limiting then there is a conflict between the benefits of maintaining somatic growth or allocating energy to storage. This conflict has important consequences for survival and therefore overall long-term fitness. Individuals or cohorts which grow fast minimise the time that they are susceptible to gape-limited and size dependent predators. Individuals or cohorts which maximise energy storage reduce their susceptibility to starvation.

The resource allocation dynamics of juvenile salmonids is of great practical importance to the aquaculture industry. The most influential and also controllable factor that affects growth and allocation is the formulation of the dietary feed. Prudent choice of diet formulation has been shown to increase growth efficiency and also yield the added benefit of a reduction in water pollution (see Steffens et al. (1998) and references therein). Poor choice of diet formulation can lead to retardations in growth, which will increase the time it takes to reach a harvestable size, thus increasing costs (Lovell 1989). Excessive levels of lipids in the diet lead to fat fish, which reduces flesh quality (Einen et al. 1998).

1.3 Thesis Aims and Objectives

Due to the recreational and commercial value of salmonids, and also their interesting life history strategies, there has been a huge amount of scientific research conducted on almost all aspects of their biology. Quite obviously, energy allocation strategies are very important, both to the survival of young wild fish and for the rearing practices of cultured fish. However, despite this, there have been extremely few mathematical modelling investigations into the energy allocation strategies adopted by juvenile salmonids.

The main aims and objectives of this thesis are to review the patterns of growth and energy allocation adopted by juvenile salmonids in a range of different environments and investigate which mathematical rules of energy acquisition, expenditure and (most importantly) allocation can best describe them.

There is an abundance of literature sources which report both morphological and biochemical observations of growth and allocation in a range of different environmental conditions. Therefore, a substantial part of this thesis will dedicated to reviewing, outlining and summarising the major consistent observed patterns of resource allocation in juveniles.

Having identified the major observed characteristics under a number of different environmental conditions, we shall, in turn, investigate the success of a range of different modelling assumptions to describe experimental observations. These models will differ in their assumptions concerning the way the organism utilises energy for the physiological processes related to maintenance, growth and allocation to storage.

Before we can begin fulfilling any of these objectives we must first identify a suitable modelling framework which can be utilised to investigate both growth and energy allocation. Therefore, in the next chapter we review the historical growth models which have been applied to salmonids. Having selected a suitable modelling framework we then move on to derive functional relationships which describe how the rate of energy expenditure (maintenance) and the rate of energy assimilation relate to the physical environmental and also the model state variables characterising the individual. The final section of the next chapter will be dedicated to introducing the (very few) tried and tested mathematical rules of energy allocation which can be applied to our model framework. In this section we also derive a completely new allocation scheme based on the nutritional principles of growth.

Chapter 2

Selecting a Suitable Modelling Framework

2.1 Introduction

In recent years there has been a large increase in the application of mathematical growth models in the field of fisheries science. Researchers investigating growth can now choose from a range of different model frameworks. The different modelling approaches have different goals and as a result vary greatly in the level of complexity. Therefore, the final choice of model is dependent upon the particular focus of research. For example, simple empirical models allow growth rates to be quantified, which is useful for making species and inter-population comparisons of growth rates.

Within this chapter we will investigate the variety of different modelling frameworks that have been applied to fish growth. We specifically want to identify a model framework that will allow us to investigate resource allocation.

2.2 Historical Fish Growth Models

2.2.1 Weight Based Empirical Growth Models

These models assume that the specific growth rate SGR of an organism is dependent on wet weight W, as in equation (2.1), and a selection of these types of models are shown in Table 2.1.

$$SGR = \frac{1}{W}\frac{dW}{dt} \tag{2.1}$$

Table 2.1: *Growth models based on achieved size, where specific growth rate is a function of wet weight, W.*

Model	$SGR^{\dagger}$
Logistic	$k_1(1 - W/W_{\infty})$
Gompertz	$k_1(log_e W_{\infty} - log_e W)$
Monomolecular	$k_1((W_{\infty}/W) - 1)$
Richards	$[1 - (W/W_{\infty})^{k_2}]k_1/k_2$

**Source:* Causton *et al.* (1978).

$^{\dagger}W_{\infty}$ asymptotic weight; k_1 and k_2 are constants.

These models can be fitted to data in order to determine their respective growth parameters, and can subsequently be used to predict the growth of fish raised in similar conditions (Baker et al. (1991); Schnute (1981)). Whilst these models point out there exists an important relationship between size and growth they give no insight into the causes of growth, or how growth varies with changes to the environment of the fish.

2.2.2 The Elliott and Hurley Functional Model for Maximum Growth

Theoretically, models of maximum growth are important as they provide an index of growth performance. They can be used to make useful inter-species comparisons and also be used to assess the quality of environmental conditions by comparing expected maximal growth to that of growth observed by wild fish populations (Elliott and Hurley 1997).

Elliott et al. (1995) have derived a statistical model which has been used to describe maximal growth rates of different sized fish at a range of different constant temperatures. The model was derived using results from tank based experiments in which the fish were supplied with excess ration and therefore assumed to be growing at their maximal rates.

The Elliott and Hurley (E&H) model has been successfully parameterised for immature stone-loach, (*barbatula barbatula* L.), brown trout, (*Salmo trutta* L.), Arctic charr, (*Salvelinus alpinus*) and juvenile Atlantic salmon (*Salmo salar* L.). Predictions from the model appear to reproduce tank based results in an excellent manner.

The model states that live weight specific growth rate (SGR) scales geometrically with live weight and increases linearly with temperature to a maximum and decreases linearly with temperature thereafter. The model is defined mathematically as follows:

$$SGR = cW^{-b}\left[\frac{T - T_0}{T_M - T_0}\right], \tag{2.2}$$

where,

$$T_0 = \begin{cases} T_L \text{ if } & T \leq T_M \\ T_U & \text{otherwise.} \end{cases} \tag{2.3}$$

All the parameters can be defined in biological terms. The temperature for optimum growth is T_M, and T_L and T_U are the lower and upper temperatures at which growth rate is zero. The weight exponent b is the power transformation of weight that produces linear growth with time, and c is the growth rate of a 1g fish at the optimum temperature. Table(2.2) displays the best fit parameter values for a number of salmonids.

Table 2.2: *Fitted Elliot and Hurley model parameter values for a number of juvenile salmonid species. Taken from Elliott et al. (1995), Larsson and Berglund (1998) and Elliott and Hurley (1995).*

Parameter	Units	Species		
		Brown trout	Atlantic salmon	Arctic Charr
b	–	0.31	0.31	0.24
c	g^b day^{-1}	0.028	0.035	0.064
T_M	^oC	13.11	15.94	15.09
T_L	^oC	3.56	6.0	3.25
T_U	^oC	19.48	22.51	28.5

The E&H model points out a number of important factors in the growth of juvenile salmonids. Firstly, that specific growth rate (SGR) exhibits a negative allometric relationship with fish size but absolute growth rate (g/day) exhibits a positive allometric relationship with fish size. In other words, as the size of the fish increases, growth rate increases but the specific growth rate decreases. Secondly, the model points out the fact that temperature is a very important abiotic factor governing the growth rate of salmonids. The optimum temperature for maximal growth is reported to range from 13-18^oC for salmonids. We can therefore conclude that in an environment with a plentiful supply of food juvenile salmonids exhibit geometric growth whose rate is heavily dependent upon water temperature.

2.2.3 Anabolic and Catabolic Models

Bertalanffy (1957) developed a physiologically dependent growth model that was used to predict weight and length. The model was the first to reflect that growth is an integrated process to which the principles of conservation can be applied. He popularised the balance equation which states that the rate of change of weight equals the rate of anabolism (build-up term) less the rate of catabolism (break-down term), such that

$$\frac{dW}{dt} = h_1 W^{n_1} - h_2 W^{n_2} \tag{2.4}$$

where h_1 and h_2 are the coefficients for anabolism and catabolism, and n_1 and n_2 are the allometric weight scalings for anabolism and catabolism. Bertalanffy (1957) noted that different combinations of values for the allometric scalings of anabolism and catabolism results in very different growth characteristics.

Exponential Growth

In the case where $n_1 = n_2 = 1$, that is, anabolism and catabolism both scale with weight, then equation(2.4) reduces down to

$$\frac{dW}{dt} = (h_1 - h_2)W \tag{2.5}$$

which can easily be solved to give

$$W(t) = W_0 \exp((h_1 - h_2)t) \tag{2.6}$$

which is exponential growth if $h_1 > h_2$ and exponential decay if $h_1 < h_2$.

Von Bertalanffy Growth

In the case, where, $n_1 = 2/3$ and $n_2 = 1$ then equation(2.4) is now given by

$$\frac{dW}{dt} = h_1 W^{2/3} - h_2 W. \tag{2.7}$$

To illustrate the growth dynamics of this particular case it is useful to exchange the currency of weight for length. The relationship between the weight and length of an organism can usually be represented by an allometric form

$$W = \chi L^q. \tag{2.8}$$

Therefore, if we assume that the organism grows with a constant shape and density (i.e. $q = 3$) then equation(2.7) can be rewritten as

$$\frac{dW}{dt} = h_1 \chi^{2/3} L^2 - h_2 \chi L^3 \tag{2.9}$$

Notice, that the organism will stop growing when its length reaches the value

$$L_{\text{max}} = \frac{h_1}{h_2 \chi^{1/3}}. \tag{2.10}$$

By recognising $W = \chi L^3$ we can write

$$\frac{dW}{dt} = 3\chi L^2 \frac{dL}{dt} \tag{2.11}$$

which from equation(2.9) implies

$$\frac{dL}{dt} = \frac{h_2}{3}(L_{\text{max}} - L). \tag{2.12}$$

From this equation we can solve for L, giving

$$L(t) = L_{\text{max}} - (L_{\text{max}} - L_0) \exp\left(-\frac{h_2}{3} t\right) \tag{2.13}$$

Hence, this particular choice of allometric scalings leads to asymptotic growth in length with the maximum achieved size being dependent upon the ratio of anabolic to catabolic coefficients. This type of growth is most commonly referred to as Von Bertalanffy growth.

Geometric Growth

In the case where $n_1 = n_2 < 1$ then equation(2.4) reduces down to

$$\frac{dW}{dt} = (h_1 - h_2)W^{n_1}. \tag{2.14}$$

Notice that the Elliott and Hurley maximal growth model is just a modification of this case, where, the difference in anabolic and catabolic coefficients has been replaced with a temperature response function.

If we assume h_1 and h_2 are constants, (or in terms of the E&H model a constant temperature) then weight will change according to

$$W(t) = \left(W_0^{1-n_1} + (1 - n_1)(h_1 - h_2)t\right)^{\frac{1}{1-n_1}} \tag{2.15}$$

which is geometric growth ($h_1 > h_2$) or decay ($h_1 < h_2$). It is interesting to note that unlike von Bertalanffy style of growth as long as $h_1 > h_2$ the organism will continue to grow indefinitely.

Further Adaptions

In its current format, equation(2.4) lacks any environmental input or dependence on rates of food consumption and is used more as a descriptive rather than a predictive model (e.g. Ismen (1995); Xiao (1994); Chen et al. (1992); Crisp and Beaumont (1995)). However, it is a simple case to make changes to the Bertalanffy format, such as making the anabolic and catabolic rates dependent upon temperature, as well as size (e.g. From and Rasmussen (1984); Kooijman (1993); Gurney and Nisbet (1998); Lika and Nisbet (2000)). Other adaptations have been used to predict density dependent (Lorenzen 1996) and seasonal (Fontoura and Agostinho 1996) effects on growth. The basic conservation principles of growth proposed by Bertalanffy have been extended to bioenergetic models that take into account very detailed aspects of fish growth.

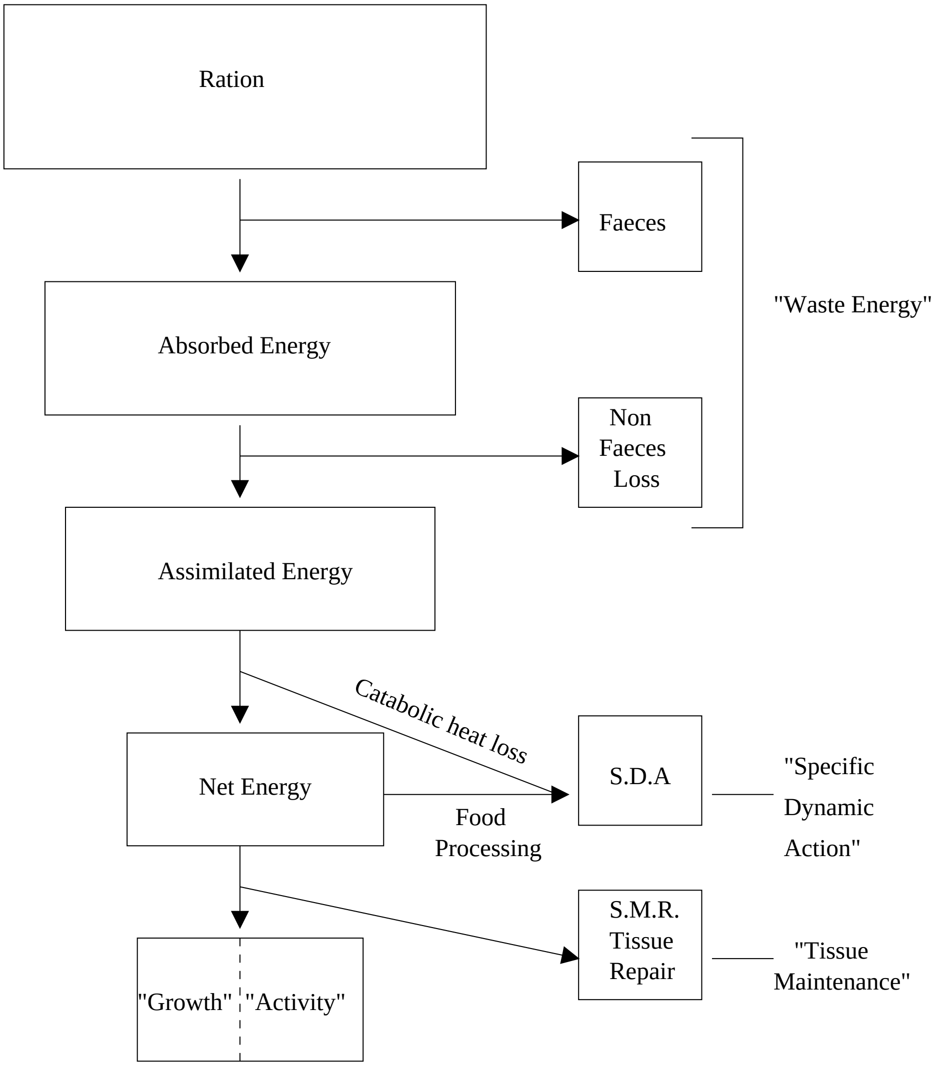

Figure 2.1: *Fish energy budget. Taken from Rogers (1982).*

2.2.4 Bioenergetic Models

Bioenergetic models are based on the following statement: “all the energy ingested (C_b) must turn up in one form or another as a result of metabolism (R_b), growth (G_b) and excretion (E_b)”. The balance of energy is therefore satisfied by the equality

$$C_b = R_b + G_b + E_b \tag{2.16}$$

which is commonly referred to as the balanced energy budget.

In order to use this model derivation successfully, it is necessary to have some understanding about the flow of energy through an organism. Numerous authors (e.g. see Elliott (1979), Tytler and Calow (1985), Brett and Groves (1979), Rogers (1982)) have proposed schematic diagrams of the passage of ingested food energy through a fish, figure(2.1) displays a typical scheme. This leads to the components of equation (2.16) being further subdivided.

Total metabolism (R_b) is subdivided as follows

$$R_b = R_s + R_a + R_d \tag{2.17}$$

where, R_S is the energy equivalent to that released in the course of metabolism in unfed and resting fish (standard metabolism), R_a is the energy required for swimming and other activity, R_d is the energy required for the process of digestion, movement and deposition of food materials (including specific dynamic action).

Total Excretion (E_b) is subdivided as follows

$$E_b = E_f + E_u \tag{2.18}$$

where E_f is the energy lost in faeces and E_u is the energy lost in excretory products (predominantly urea and ammonia).

Growth is subdivided into somatic growth (G_s) and gamete production G_g so that

$$G_b = G_s + G_g. \tag{2.19}$$

In the case where the fish is not allocating any energy to gamete production, $G_g = 0$.

If appropriate functional forms are assigned to these sub-components then bioenergetic models can be used to estimate the remaining unknown component. Kitchell et al. (1977), Stewart et al. (1983) and Hayes et al. (2000) used bioenergetic models to predict growth, Brodeur et al. (1992) and Stockwell and Johnson (1997) used bioenergetics to estimate food consumption rates, whilst Goyke and Brandt (1993) and Brandt and Kirsch (1993) used bioenergetics to predict foraging behaviour.

Due to the number of factors affecting growth that are included in bioenergetic models, they can be very complex. Functions together with parameter values are required for each subcomponent of equation (2.16). For this reason bioenergetic modelling can only be used to effect with extremely well researched fish species.

2.3 Modelling with Reserve and Structural Body Constituents

The above model frameworks have enjoyed numerous and widespread applications. However, where all these models have been applied (even the detailed bioenergetic models), invariably, the fish have been characterised as being homogeneous using either units of weight or energy. Such models are incapable of characterising the nutritional status of the fish, i.e. they cannot differentiate between two conspecifics of equal weight, one short and fat, one long and thin. Where they interest themselves in length a fixed weight-length relationship is assumed which is highly questionable when previously well fed fish have subsequently endured a period of nutritional restriction. Furthermore, maximum food uptake is expressed as a function of body weight which therefore assumes that conspecifics of equal weight posses the same capability to gather food irrespective of their lengths.

These models are inadequate because they characterise the instantaneous state of a fish with one state variable. It is therefore obvious we require a dynamic modelling framework that includes more than one state variable to incorporate the different biomass components of salmonids.

In response to this, Broekhuizen, Gurney, Jones, and Bryant (1994) laid the foundations of a two state variable fish growth model. They noted that a fish is composed of at least two fundamentally different types of tissue: those which can and those which cannot be remobilised once laid down. Following the practice used with considerable success in modelling the growth energetics of mussels

(Ross and Nisbet 1990) and *Daphnia* (Gurney et al. 1990) the total (carbon) tissue weight of an individual is partitioned into two components, reserve weight, denoted by R, and structural weight, denoted by S. The reserve weight is defined as that part of the body which can be remobilised and corresponds mostly to lipids and carbohydrates. Structural weight corresponds to tissues which, once formed, cannot be remobilised. These include skeletal, gut, circulatory and nervous tissues which mainly correspond to the majority of the total protein content of the fish.

By definition structural weight is non-decreasing and is therefore a useful surrogate for length which also does not significantly decrease with either short or prolonged periods of starvation. Following Broekhuizen et al. (1994) we shall relate the length (L) to structure (S) by the allometric relationship given as

$$L = \alpha S^{\beta}. \tag{2.20}$$

The total carbon weight (W_c) is by definition the sum of both reserve and structural components, $W_c = R + S$, which must therefore change according to

$$\frac{dW_c}{dt} = \frac{dR}{dt} + \frac{dS}{dt}. \tag{2.21}$$

We also recognise that the total change in carbon will be the difference (P) in current assimilation (anabolic term) and maintenance (catabolic term) rates, so we write

$$\frac{dW_c}{dt} = A - M = P \tag{2.22}$$

where, A and M are the current assimilation and maintenance rates, respectively. We shall discuss what factors mainly govern the rates of acquisition and losses of carbon from the body in greater detail within the next section.

In this model an individual dies when it can no longer meet its maintenance costs, which occurs when reserves have been fully depleted. As a meaningful and tractable measure of nutritional status, the ratio of reserve to structural weight will be used and is denoted by $X \equiv R/S$. Thus, the ratio X is a direct measure of the fish's ability to withstand periods of starvation.

This approach to modelling initiated by Broekhuizen et al. (1994) is conceptually akin to the Dynamic Energy Budget (DEB) model developed by Kooijman (1993). The models differ mainly in their choice of state variables with Kooijman (1993) choosing structural biovolume (V, a non decreasing quantity) and reserve density (R/V) rather than structure (S) and the reserve to structural ratio (X). We have chosen the Broekhuizen et al. (1994) model formulation because the state variables lend themselves to a more natural interpretation of the major fish body constituents (mainly in the form of lipids and proteins) of whose study of relative changes form an integral part of this thesis.

2.4 Modelling Anabolism and Catabolism

Before beginning to investigate different allocation schemes it is necessary to make some initial definitions that encapsulate the major terms of the fish's energy budget. In order to accomplish this objective it is necessary state functional forms that describe the rate at which carbon is assimilated into the body together with the rate at which carbon is lost from the body.

2.4.1 Assimilation

In an environment with excess food being supplied the maximum rate of food consumption of a fish is principally dependent upon water temperature and body size (Elliott 1976b). Studies on salmonids (e.g. From and Rasmussen (1984), Elliott and Hurley (1998b), Jobling et al. (1993)) have shown there to be an allometric relationship between body size and maximum uptake. The maximum uptake of a healthy (well fed) fish should be mainly correlated with the size of gut and mouth parts, which are clearly included within the definition of structural tissue. Considering temperature, it is known that maximum uptake increases rapidly with temperature to a maximum (15-18^oC) and thereafter decreases rapidly (e.g. From and Rasmussen (1984), Brett et al. (1969), Larsson and Berglund (1998)) with increasing temperature. Food consumption by its very nature is variable and there are substantial differences in both inter and intra species studies. Consequently, there are a number of different functional forms that are in use to model this relationship (e.g. Larsson and Berglund (1998); From and Rasmussen (1984); Elliott and Hurley (1998b)) and at this point we shall simply denote this uptake temperature (T) relationship as $f(T)$. From the combination of the above, the maximum uptake U_H of a healthy (well fed) fish can be represented as follows

$$U_H = U_{H0} S^d f(T) \tag{2.23}$$

where U_{H0} is the uptake scale and d is the allometric index.

When the daily food supply is supplied at a level below the maximum consumption it often convenient to express this ration as a fraction of its maximum uptake. Thus, we can state

$$U = U_H \phi \tag{2.24}$$

where U is the gross ration and $0 \leq \phi \leq 1$ is the fraction of its max potential consumption.

The actual realised Assimilation rate (A) is the product of the assimilation efficiency (ε) and the uptake rate (U) which we can write as

$$A = \varepsilon U_H \phi = \varepsilon U_H S^d f(T) \phi. \tag{2.25}$$

The assimilation efficiency (ε) denotes the proportional loss of ingestate from incomplete absorption (faecal losses) and also metabolic expenditure arising from apparent specific dynamic action (Beamish 1974). Losses incurred by specific dynamic action will include the costs of digestion, storage, deamination of amino acids and the synthesis of nitrogenous excretory products (Jobling 1994).

2.4.2 Maintenance

Maintenance costs stand for the collection of processes necessary to remain alive. The maintenance rate (M) incorporates the daily costs of tissue maintenance, locomotor activity and maintaining internal homeostatic balance (Jobling 1994). These processes are independent of growth rate and mainly dependent upon size and temperature.

On a unit weight basis, the expenditure related to maintenance reduces as fish size increases (Elliott (1976b); Jobling (1994); Hochachka and Mommsen (1995); Rankin and Jensen (1993)). Thus, as with maximum uptake maintenance has a negative allometric scaling with size (for a detailed discussion see Hochachka and Mommsen (1995)). Sedgwick (1988) reports that fat fish require more oxygen than lean fish–signifying that reserves also require maintenance. However, there is insufficient data to calibrate the differential maintenance costs for structural and reserve components. With no real evidence to the contrary we shall assume both reserves and structure demand equal costs such that maintenance costs scale with total carbon weight, $W_c = R + S$. An alternative assumption would have been to only accost structural tissues. This did not prove to be successful since this assumption produces linear weight loss in starving fish (under the assumption of no structural growth during starvation) which is in contrast to literature reports (Elliott 1975b).

Maintenance rates are heavily dependent upon water temperature and in most cases is found to be adequately described by an exponential temperature dependence (e.g. Elliott (1976b); Brett et al. (1969); Van Winkle et al. (1998) Lantry and Stewart (1993); Rand et al. (1993)).

By combining the above we derive the following term for maintenance (M):

$$M = M_{H0}(S+R)^{\nu}\exp(T/T_M), \tag{2.26}$$

where, T_M is the characteristic temperature for maintenance and M_{H0} is the maintenance scaling constant. Notice that maintenance is independent of the processes of growth and solely a function of total carbon weight and temperature.

2.5 Modelling Resource Allocation

Thus far we have presented a suitable modelling framework that uses the two intuitive state variables of reserves and structure. We have also described functional forms that dictate how the combination of these state variables together with water temperature will affect the processes of maximum food uptake and energy losses through metabolic processes.

Ultimately, all the required nutrients to support growth are derived from the food source. However, there are a number of different assumptions one can make in considering the flow of nutrients to and between reserve, structural and maintenance components. The one overriding constraint on the choice of allocation schemes is that (irrecoverable) maintenance costs, wherever possible, must be met in order that the organism remain alive. Our next step is therefore to present different classes of allocation schemes which are based on different assumptions.

2.5.1 Net Production Allocation

Following Broekhuizen et al. (1994) and Lika and Nisbet (2000) we introduce perhaps the most commonly used allocation scheme which we shall refer to as the net production allocation model. The net production allocation schemes principle assumption is that maintenance always has first call on assimilate. The excess is then partitioned between reserves and structure. In the case where

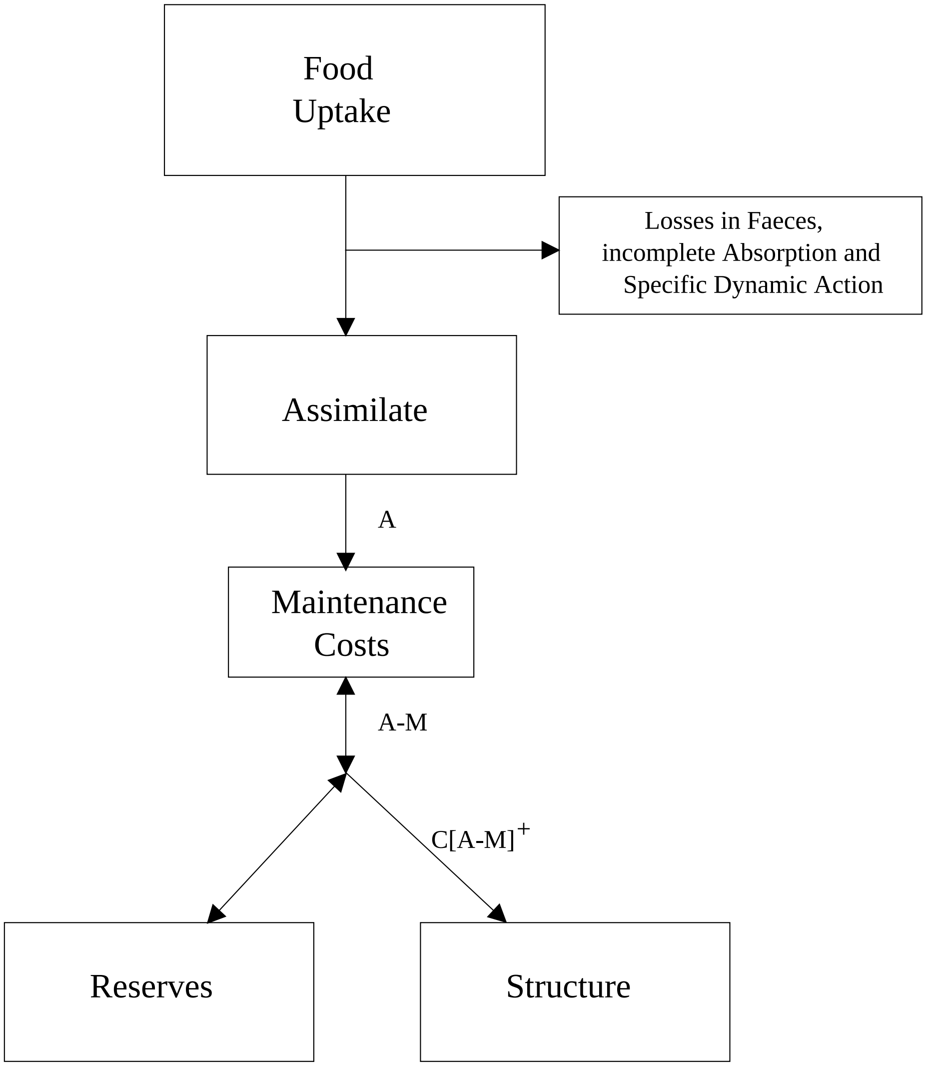

Figure 2.2: *Flowchart diagram illustrating the sequence of allocation assumed by a net production allocation scheme.*

assimilate cannot meet maintenance costs no allocation is made to structure and reserves make up the deficit. These assumptions yield the following balance equations for R and S, thus

$$\frac{dR}{dt} = A - M - \frac{dS}{dt} \tag{2.27}$$

$$\frac{dS}{dt} = C\,[A - M]^{+} \tag{2.28}$$

where $[x]^{+}$ denotes $\max\{x, 0\}$ and C represents the proportion of excess assim-

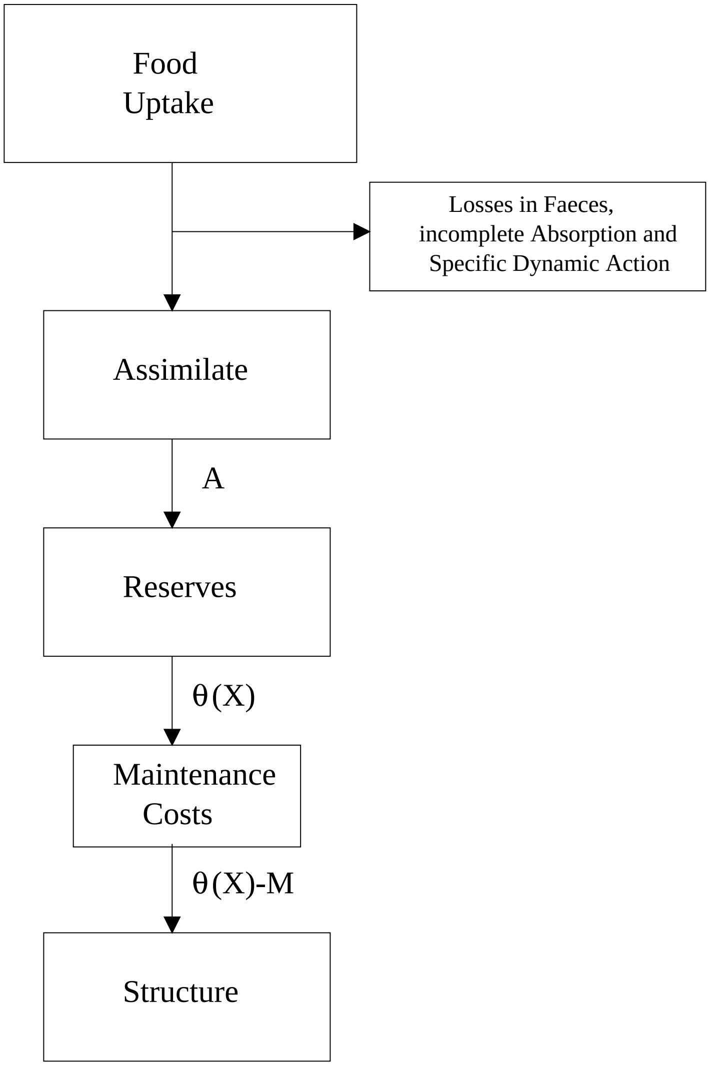

Figure 2.3: *Flowchart describing the sequence of allocation assumed by a reserve allocation scheme.*

ilate allocated to building structure. Figure(2.2) displays a flowchart diagram showing this sequence of allocation.

One of the major consequences of assuming a net production scheme is that structural growth can only be associated with an increase in the total carbon weight ($W_c = R + S$).

2.5.2 Reserve Allocation

The following class of model is based upon an energy allocation scheme developed by Kooijman (1993) which he incorporated into his DEB model framework. Although we are using different state variables the principles remain the same. All assimilate is first assumed to be directed into the reserve pool. All subsequent (irrecoverable) allocation to the combination of both maintenance and structure is made from this reserve pool. The main assumption of the reserve allocation model is that the rate of release of nutrients from reserves is dependent upon the individuals nutritional status assessed in our case in terms of reserve ratio, $X \equiv R/S$ (closely analogous to reserve density (R/V) used by Kooijman (1993)).

If we state that nutrients from reserves are released at a rate of $\theta(X)$ then for the individual to remain alive maintenance must have first call leaving the excess to be allocated to structure. This balance can be expressed mathematically as follows

$$\theta(X) = M + \frac{dS}{dt}. \tag{2.29}$$

If the reserves are being debited at a rate $\theta(X)$ but being accumulated at the assimilation rate (A) then reserves will change according to

$$\frac{dR}{dt} = A - \theta(R). \tag{2.30}$$

Figure(2.3) is a flowchart diagram summarising this sequence of allocation.

The major consequence of assuming this allocation scheme is that the rate of commitment to structure is not directly related to the immediate assimilate but mainly only dependent upon reserve status. Thus we shall call this allocation scheme the reserve allocation model.

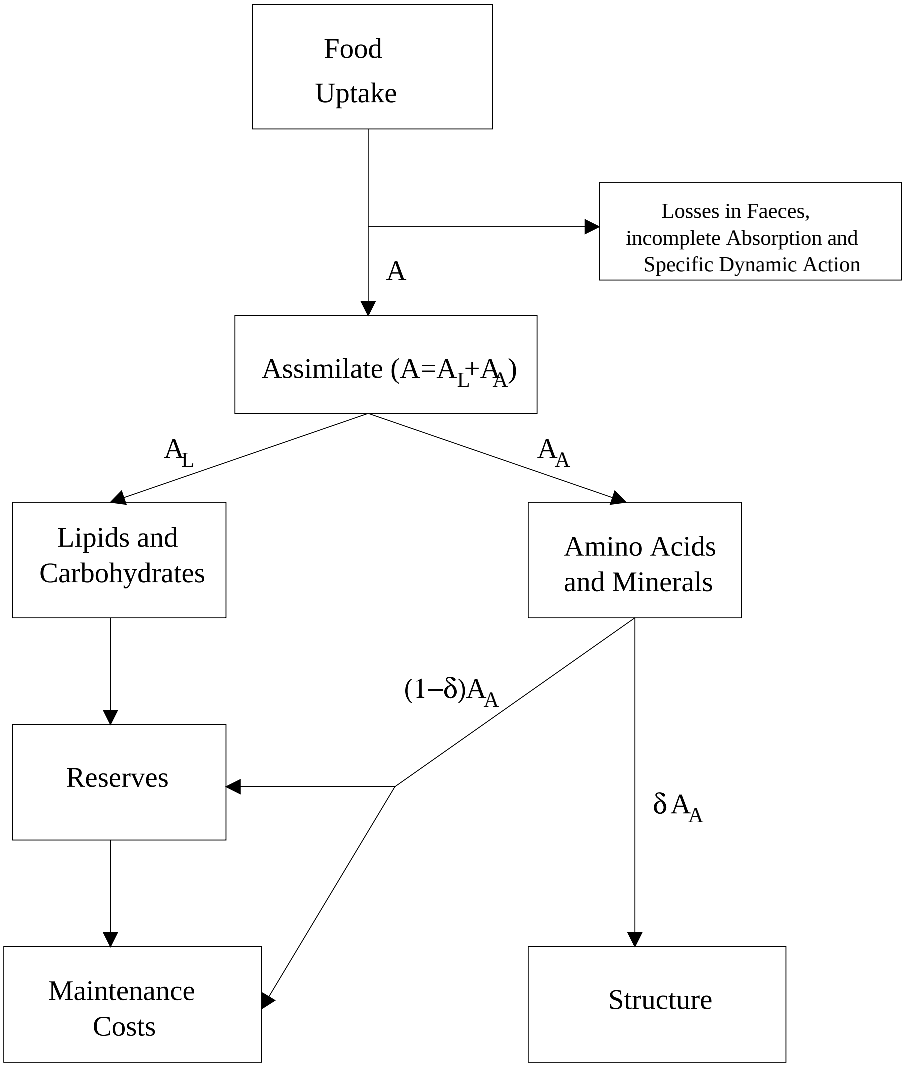

Figure 2.4: *Flowchart describing the possible routes of allocation for different nutritional components of the assimilate.*

2.5.3 Assimilation Allocation

The above net production and reserve allocation model frameworks have enjoyed numerous and widespread use. Their main assumptions, however, are based purely on energetic assumptions. They do not consider in any shape or form the physiological constraints imposed by the possible allocation of nutrients. Armed with a basic understanding of the nutrient flows within fish we shall derive a new model with the express aim of encapsulating these important nutritional principles.

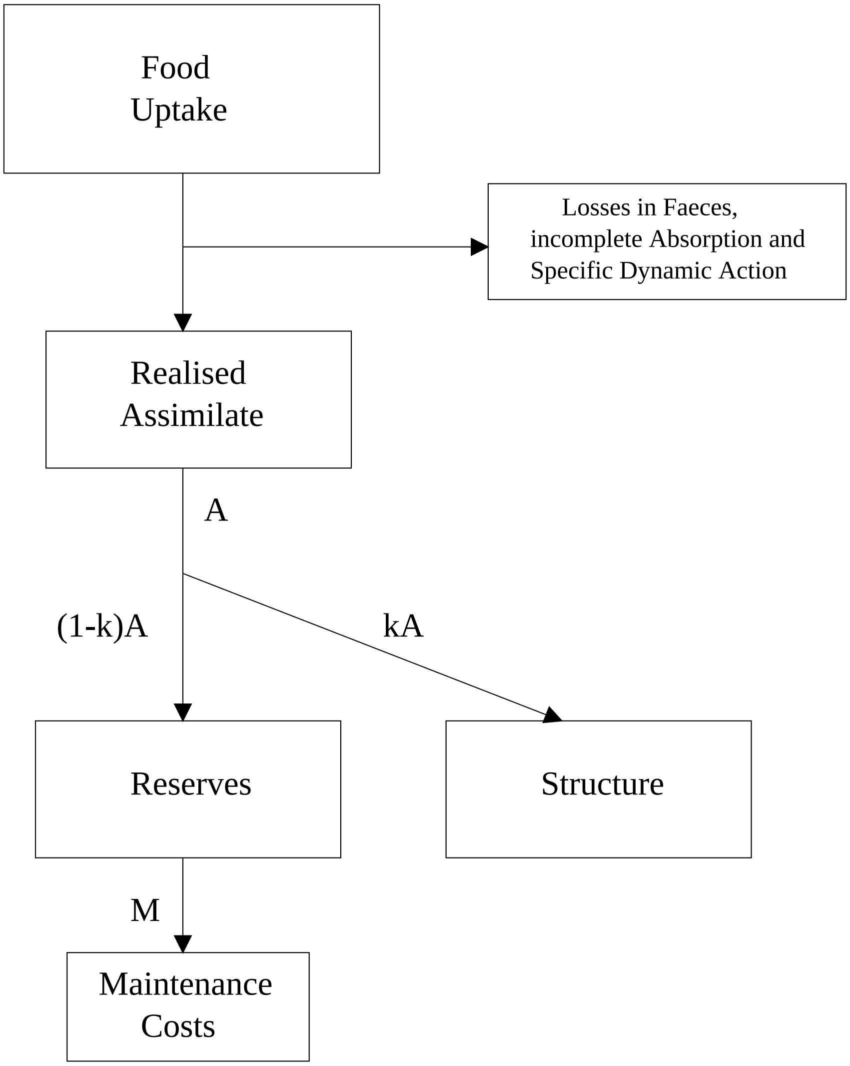

Figure 2.5: *Flowchart describing the flow of carbon in a fish where, allocation to structure is made from the immediate assimilate. Function definitions are given in the text.*

We shall first partition the realised assimilate A into two components such that

$$A = A_{\mathrm{L}} + A_{\mathrm{A}} \tag{2.31}$$

where A_{L} is the component that cannot possibly be converted into structure and A_{A} is the component of the assimilate that can possibly be converted into structure. A_{L} is mostly composed of lipids but also a relatively small amount of carbohydrate, whereas, A_{A} is mostly composed of amino acids but also a small component of inorganic elements (e.g. calcium and phosphorus) necessary to build the skelature.

The component A_{L} of the assimilate can only be used to meet maintenance expenditure and also be stored in reserves. On the other hand, the component A_{A} can be used to build structure but also be used to meet maintenance costs and also be stored as reserves in the form of lipid.

We can express these two terms as a function of the total assimilate A as follows

$$A_{\mathrm{A}} = \gamma A \tag{2.32}$$

$$A_{\mathrm{L}} = (1-\gamma)A \tag{2.33}$$

where $0 \leq \gamma \leq 1$ signifies the proportion of total assimilate A which can possibly be used to build structural tissues.

If we now state that a proportion δ of A_{A} is committed to structure then we can write

$$\frac{dS}{dt} = \delta A_{\mathrm{A}} = \delta\gamma A \tag{2.34}$$

The remaining $(1-\delta)$ is then used to meet maintenance costs and also be stored as reserves. This together with A_{L} can then be used to meet maintenance costs and if there is an excess can be stored as reserves. The flowchart diagram (2.4) graphically displays this structure of resource allocation. This means that reserves will change according to

$$\frac{dR}{dt} = A_L + (1-\delta)A_A - M = (1-\delta\gamma)A - M. \tag{2.35}$$

If we know introduce a new variable $k \equiv \delta\gamma$ then the full system dynamics reduce down to

$$\frac{dS}{dt} = kA \tag{2.36}$$

$$\frac{dR}{dt} = (1-k)A - M. \tag{2.37}$$

We shall call this model the assimilation allocation model for obvious reasons. Figure(2.5) is a flowchart summarising the assimilation allocation sequence of allocation.

2.6 Thesis Structure

The remainder of this thesis is split up into four parts. In the next three parts (parts II-IV) of this thesis we will investigate and model the growth and allocation patterns adopted by juvenile salmonids in three broad categories of environments. The first of the three parts is dedicated to investigating and modelling growth and allocation in a near constant environment which we define as environmental conditions where the food supply of a constant dietary formulation is supplied at a fixed ration level at a range of different constant temperatures. We first consult a large body of literature sources reporting the results of tank based experiments in order to identify the major consistent observed patterns of resource allocation and growth. We then move on to investigate the relative success of each of the above allocation schemes to model these growth and allocation characteristics.

In part III we investigate the growth and allocation dynamics of individuals reared in variable environments. This part is dedicated to investigating the phenomenon of compensatory growth: the ability of individuals to compensate for lost periods of growth by exhibiting higher rates of growth than continuously well fed conspecifics. As in part II we first consult a large body of literature to identify the major observational patterns of growth and allocation. We then move on to investigate an historical compensatory growth model which is a special case of the net production class of model. We identify several cases in which this model will not predict any growth compensation in contrast to the literature reports and so move on to the process of deriving a new model. Each class of the above growth models is assessed in its ability to reproduce the qualitative properties of compensatory growth as reported by the literature. In the final chapter within this part we fit the most successful model to published data sets in order to asses its quantitative capability to model compensatory growth.

In part IV we investigate the production dynamics and allocation patterns of juvenile salmonids in their natural habitat. This is afforded by access to high resolution individually tagged juvenile Atlantic salmon parr data from the Girnock Burn, a tributary of the River Dee in Scotland. In the first chapter of this part we carry out an exploratory data analysis in order to identify the major temporal patterns of growth and its relation to the parr's physical environment. In the second chapter of this part we investigate the patterns of energy allocation adopted by the parr by fitting a simple model to the individual growth data which is based on the modelling results of the parts II and III.

In the final part of this thesis we take the opportunity to discuss the ecological implications of resource allocation and attempt to explain why salmonids partake in energy partitioning strategies that at first appear to be counter-intuitive. Following this, we discuss the success of our three different allocation schemes to emulate these energy allocation strategies. To complete the thesis we make suggestions for future research.

Part II

Growth and Allocation in a Constant Environment

Chapter 3

A Review of Growth and Allocation in a Constant Environment

3.1 Introduction

The aim of this chapter is to investigate the growth and resource allocation patterns of juvenile salmonids subjected to a near constant environment. The main points of investigation will be the effects of temperature, ration level, growth rate, age and diet formulation. The term "constant environment" refers to individuals reared at a constant temperature on a single diet formulation supplied at a constant ration level. Thus all the literature is drawn from artificial tank-based experiments which were necessarily devised to try and exclude seasonal effects.

3.2 Body Composition Analysis

Before reviewing the literature in further detail it is useful to point out what researchers use to assess salmonid nutritional status. There are essentially two types of analysis, namely, non-destructive and destructive measures.

Non-destructive correlates of fish condition are morphological measures which mainly use the relationship between the wet weight and length of the fish. It is often assumed that the relationship between a healthy well-fed organism's live weight and length is well described by the allometric relationship

$$W = \chi L^q \tag{3.1}$$

with $q = 3$, which implies isometric growth at a constant density.

Since length is a non-decreasing quantity then any reduction in weight for a given length will cause a corresponding deviation away from this relationship. Therefore, as a useful non-destructive measure of a fish's nutritional condition the following measure has been suggested

$$K = \frac{100W}{L^3} \tag{3.2}$$

which is commonly referred to as the condition factor. It has enjoyed much use for workers who require a non-destructive indicator of nutritional condition and has been especially useful in indicating lipid content (for discussion see Weatherley and Gill (1987)). For salmonids the condition factor can range by as much as 0.8 to 2. The greatest virtue of the condition factor as a measure of nutritional condition is that it does not require the fish to be killed but is not as accurate as a fully destructive analysis.

Growth is the sum of a series of biochemical, physiological and behavioural processes which involve the assimilation of consumed food into the deposition of body material (Brett 1979). The major material constituents of fish are similar to those of other animals: water (which greatly predominates), lipid, protein and to a lesser extent carbohydrate, plus minerals (the latter frequently termed ash, which includes skeletal bone) as signifying what remains after the body has been burned in oxygen during calorimetry. The live weight of fish usually consists roughly of water, 65-85%; protein, 10-20%; lipid, 1-12%; ash, 1-3%; and carbohydrate, 0.5-2%. There may be substantial variation of these values.

A full biochemical analysis allows the amounts of these different body constituents to be estimated. The relative proportions of each biochemical constituent can then be found. The obvious disadvantage of biochemical tests is that the fish require to be destroyed.

3.3 Growth and Allocation in Relation to Temperature and Ration Level

Nicieza and Metcalfe (1997) subjected juvenile Atlantic salmon (*Salmo salar* L.) to two different types of growth restriction. The first group was subjected to restricted ration (app. 1% of body mass) at ambient temperature (mean ± 1 SD: 13.7 ± 0.9^{o}C) whilst the second group were held at a depressed temperature (5.6 ± 1.7^{o}C) with plentiful food. For comparisons to be made between growth treatments a control group were fed in excess at ambient temperature. The manipulation period lasted for 37 days. The initial and final, weights and lengths for each treatment group is given in table(3.1).

Nicieza and Metcalfe (1997) reported that while all growth manipulated fish (i.e. depressed temperature or restricted ration) grew during the growth manipulation period both groups maintained skeletal growth at the expense of labile tissue, resulting in a low body mass for a given length as compared to control fish. Controls exhibited the most rapid growth and maintained the highest ratios of mass-to-length growth rates, whereas the low temperature treatment exhibiting the lowest growth rates also had the lowest ratio of mass-to-length growth rates. The restricted feed group had both intermediate growth rates in terms of mass and mass-to-length ratio growth rates. These differing mass-to-length growth

Table 3.1: *Data from Nicieza and Metcalfe (1997).*

	Control	Restricted Feed	Low Temperature
Initial Sample			
Wet weight (g)	4.0	4.1	4.2
Length (mm)	71.50	72.1	72.85
Condition Factor (K)	1.0975	1.092	1.086
Final Sample			
Wet weight (g)	8.2	6.0	4.8
Length (mm)	89.29	82.14	77.5
Condition Factor (K)	1.152	1.082	1.031
SGR-Weight/SGR-Length	1.85	1.525	1.180

rates resulted in the faster growing fish (controls) having the greatest mass for a given length and the slowest growing fish (depressed temperature) having the lowest mass for a given length. The intermediate growth rate of the restricted ration fish resulted in an intermediate mass for a given length.

These results imply differing allocation patterns with varying opportunity for growth, and in general, the greater the growth rate the greater the mass for a given length. Similar patterns of allocation have been noted by Weatherley and Gill (1981), Weatherley and Gill (1983), McDonald et al. (1998), Johansson et al. (2000), Einen et al. (1998), Rondscholt (1998) and Weatherley and Gill (1983) who all observed that restricted ration or low temperatures result in slow growth with a significantly lower mass-to-length relationship compared to fully fed controls.

The relationship between weight and length for salmonids is regarded as a good indicator of fat reserve content (Elliott (1976a); Weatherley and Gill (1987);

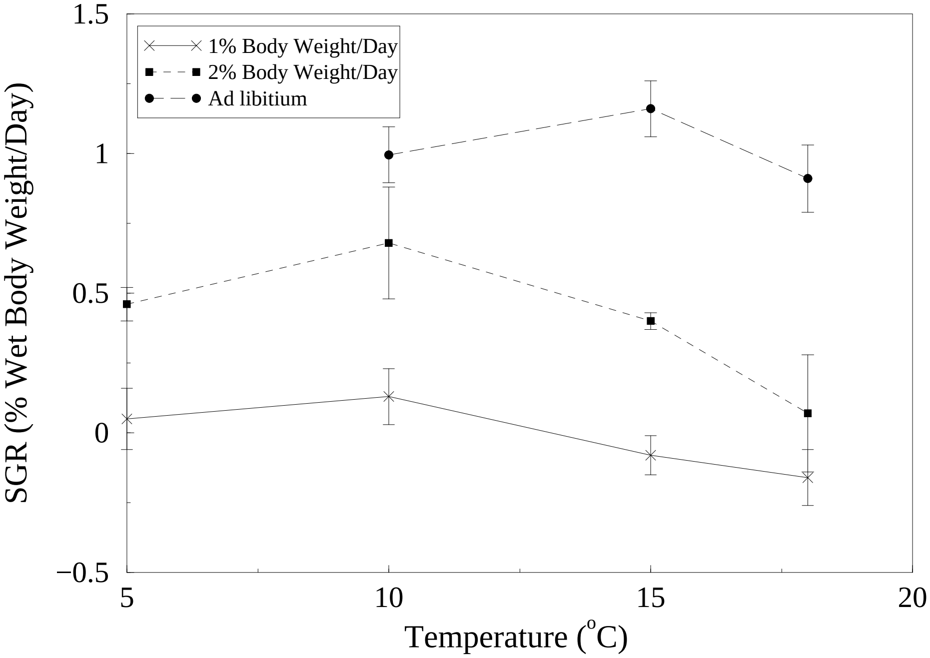

Figure 3.1: *The specific growth rate (SGR) of juvenile coho salmon at different ration levels and temperatures. The bars denote 95% confidence limits. Taken from Edsall et al. (1999).*

Simpson et al. (1992); Thorpe et al. (1998)). With this in mind, the above experiments imply that under reduced opportunity for growth there is a preferential allocation to structural body masses resulting in a leaner individual. This observation is further corroborated by biochemical body composition analysis carried out on fish held on differing restricted growth regimes.

Edsall et al. (1999) investigated the combined effects of temperature and ration size on the growth and body composition of juvenile Coho salmon (*Oncorhynchus kitsuch*). At four different constant temperatures (5, 10, 15 and 18^oC) yearling juveniles (initial weight approx 170g) were fed freshly thawed juvenile alewives (*Alosa pseudoharen*) at three different ration levels (1% and 2% wet body weight per day and *ad libitum*) for a period of 53 days.

The specific growth rate (SGR) for each feeding regime is shown in figure(3.1). At all temperatures the effect of increasing ration size was to (perhaps, not surprisingly) increase growth rate. The highest growth rate occurred at all temperatures when fish were given an *ad libitum* supply of food (fig(3.1)). With *ad libitum* food supply the optimal temperature for growth was $15^{o}C$. However, on the reduced ration levels the optimum temperature for growth reduced to $10^{o}C$. In addition to calculating growth rate Edsall et al. (1999) carried out a biochemical analysis. The results of the chemical analysis are given in table(3.2).

Water content was found to be more variable (68.6-76.4%) than other body constituents; lipid also varied widely (3.5-10.4%), whereas ash (1.8-3.1%), carbohy-

Table 3.2: *Final body constituents and energy content of yearling Coho salmon following different feeding regimes. Values are means based on a sample of five fish. No measure of variability was published. Taken from Edsall et al. (1999).*

Temp	Ration	Body Constituents				Energy content	
(^{o}C)	% WW/day	Water	Lipid	Ash	Prot.	KJ/g DW*	KJ/g WW†
5	1%	76.4	3.5	2.2	17.8	26.53	5.68
	2%	74.2	5.0	2.2	17.3	26.93	6.11
10	1%	74.5	4.8	2.3	18.4	27.24	6.32
	2%	71.9	6.8	2.4	18.5	28.05	7.21
	ad-lib	71.0	8.2	2.3	18.1	28.39	8.15
15	1%	73.8	5.9	3.1	18.1	27.86	6.69
	2%	72.7	7.4	2.1	18.0	28.59	7.86
	ad-lib	70.1	10.2	2.0	18.1	29.70	8.41
18	1%	73.2	4.8	2.3	18.7	26.78	6.56
	2%	71.1	7.7	2.2	18.0	28.27	7.89
	ad-lib	68.6	10.4	1.8	18.0	29.26	8.66

* Kj/g ash free dry weight.

† Kj/g wet weight.

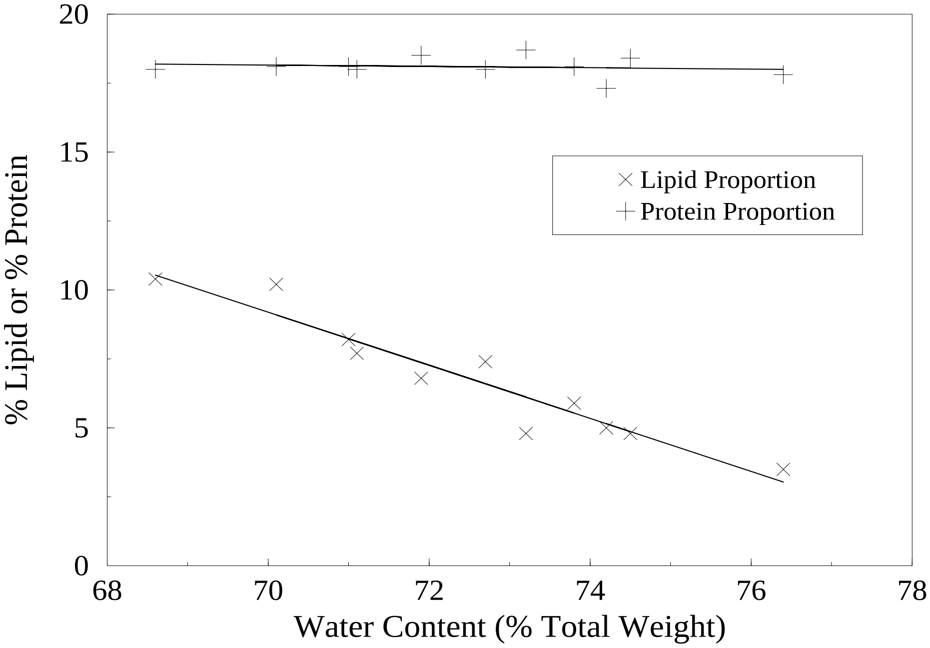

Figure 3.2: *The relationship between lipid and protein proportions (% wet weight) to water content (% wet weight) for juvenile Coho salmon. Calculated from Edsall et al. (1999).*

drate (0.1-1.9%), and protein (17.3-18.7%) did not vary greatly. Water content (% body weight) was negatively correlated with lipid, energy content, SGR, ration and water temperature. Energy content (Kj/g ash free dry weight) was positively correlated with ration and SGR but negatively correlated with water content. From table(3.2) it can be seen that the major changes in energy status were due to the relative changes in lipid and water content. Figure(3.2) displays the relationship between body water content (% body weight) and the proportion of lipid and protein constituents present. It can be seen there is a strong negative linear relationship between water content and lipid ($P < 0.01$) but no such relationship exists between water content and protein content ($P > 0.05$). This relationship has resulted in the energy content on a wet weight basis (Kj/g wet weight) being more variable than energy content on a dry weight basis (see table(3.2)).

A similar set of experiments has been conducted by Brett et al. (1969) but using

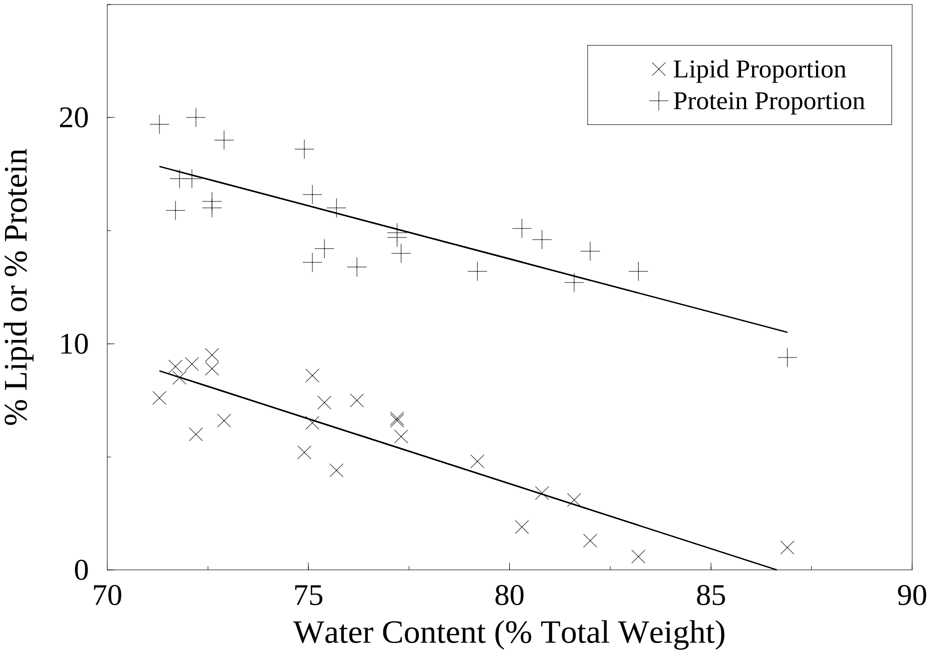

Figure 3.3: *The relationship between lipid and protein proportions (% wet weight) to water content for juvenile sockeye salmon (Oncorhynchus nerka). Taken from Brett et al. (1969).*

smaller fish (initial weight app. 6g) and also a longer experimental time period. Brett et al. (1969) investigated the growth rate and changes in body composition of young sockeye salmon (*Oncorhynchus nerka*) in relation to temperatures ranging from 1 to 24^oC and rations that ranged from 0 to 6% of dry body weight per day and also excess rations. The experiments lasted between 83-99 days.

Brett et al. (1969) reported that maintenance requirements exponentially increased with temperature being 7 times greater at 20^oC than at 1^oC. The strong temperature dependence of maintenance requirements resulted in the temperature for optimum growth reducing as the ration supply was reduced, moving from 15^oC on excess ration to approximately 5^oC for a ration of 1.5%/day. In contrast to the experimental findings of Edsall et al. (1999) ration level and temperature had a considerable effect on all body constituents. They ranged from 86.9% water, 9.4% protein, and 1.0% fat at 20^oC for fish starved for 83 days, to 71.3% water, 19.7% protein, and 7.6% fat for fish fed on an excess ration

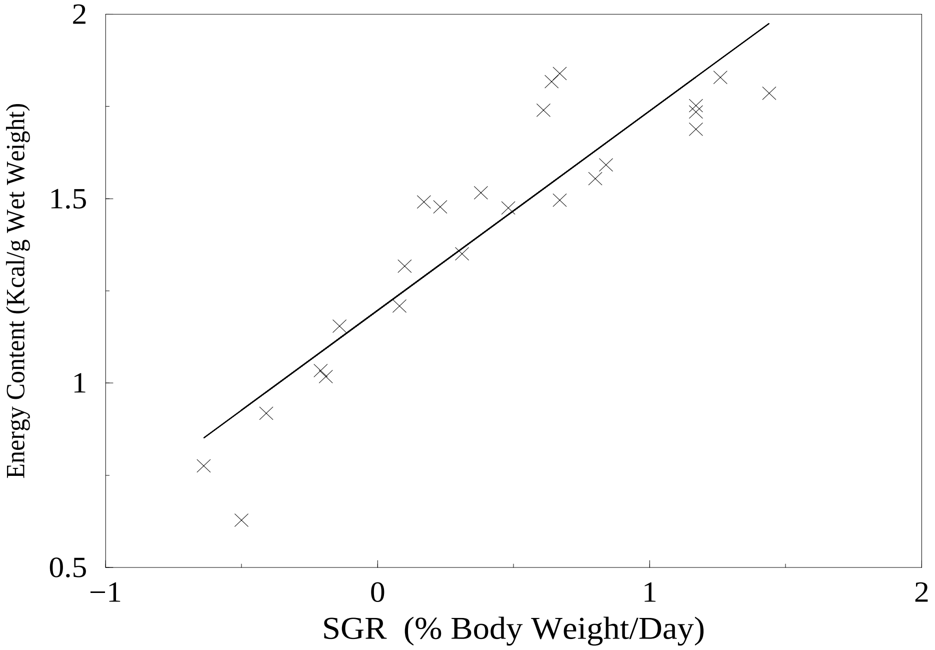

Figure 3.4: *The relationship between body energy content (Kcal/g wet weight) and specific growth rate for juvenile sockeye salmon (Oncorhynchus nerka). Calculated from Brett et al. (1969).*

for 99 days at 15^oC - the optimum temperature for growth.

There was found to be a strong negative relationship between lipid and water content. However, in contrast to the findings of Edsall et al. (1999) there was also found to be a strong negative linear relationship between protein content and water content. Figure(3.3) displays the relationship between water content and lipid and protein proportions. Although protein content varied over a relatively large range (9.4-19.7%) it was in the starved individuals where the greatest reduction in protein content was found, being particularly noticeable at 20^oC.

In contrast to the greatest majority of other studies (see section(3.5)), Brett et al. (1969) found a strong linear relationship between water and protein content. This signifies that a significant portion of body protein in the starved fish had been burnt to meet maintenance costs. The primary reason for this is the length (83-99 days) and severity (i.e. high temperatures) of the imposed food restriction. Furthermore, this study used fish of very small size, which, on a unit weight basis have higher maintenance rates. Therefore we can conclude that this strong protein-water relationship has been provoked by the length and severity of the imposed nutritional restriction, resulting from body protein being used as an energy source after the more labile reserves have been almost exhausted.

Figure(3.4) displays the relationship between the final specific energy content and specific growth rate for all treatment groups of fish. It can be seen that there exists a strong positive correlation between growth rate and energy content. This correlation not only exists for individuals losing weight but also for individuals who have managed to maintain growth. This signifies that under a reduced opportunity for growth, precedence is given to maintaining leaner structural body masses with a corresponding reduction in the rate of reserve accumulation.

Elliott (1976a) studied the changes in body composition of brown trout *Salmo trutta* growing for 14-42 days at nine temperature levels between 3.8 and 21.7^{o}C, five ration sizes between zero and maximum for fish of initial weights of 11, 50, 80 and 250g. Maintenance requirements were found to increase exponentially with water temperature (Elliott 1975b). The optimal temperature for growth decreased progressively from about 13^oC (Elliott 1975a) at maximum ration to about 4^oC at a ration size just above the maintenance ration (Elliott 1975b).

Elliott found that whole body water (%) decreased linearly and whole body protein (%) and lipid (%) increased linearly with ration size. Body constitution was markedly effected by temperature. At intermediate temperatures ranging from 7-15^{o}C, definite changes in the body constituents occurred between differing ration levels. When the trout were fed at maximum ration and body constituents expressed in terms of wet weight the water content decreased and both protein and lipid content increased. This relationship was reversed when the trout were kept on zero rations. At the lowest temperatures of 3.8 and 5.6^{o}C, the body constituents remained fairly constant over the whole range of ration level. However, Elliott states, that if the experiment had been carried out for more than 42-days it is possible that significant changes in body constituents would have occurred. In any case, the low temperature experiments serve to show that rates of change in body constituents are slower than at intermediate temperatures. At the higher temperatures of 17.8 and 19.5^{o}C rates of change in body constituents were high for trout kept on zero rations whilst the trout fed on maximum ration showed little change in body constituent proportions. At the highest temperature of 21.7^{o}C rates of change were typical of those on zero ration irrespective of ration level, i.e. water content increased whilst protein and lipid proportions decreased.

Lipid content (2-7% wet body weight) and water content (72-80% wet body weight) was found to vary more than protein content (14-17% wet body weight). This in agreement with Edsall et al. (1999) and Brett et al. (1969) caused the wet weight energy content (1100-1700 cal g^{-1} wet weight) to vary more than dry weight energy content (5400-6400 cal g^{-1} dry weight). Elliott also noted there was a tendency for larger trout to posses higher proportions of lipid and protein with a corresponding reduction in water content.

The relationship between body constituents and percent water content was found to be well described by the simple regression equation:

$$Y = a - bX \tag{3.3}$$

where a and b are constants, X is the percent water content, Y is the percent

Table 3.3: *Values of the constants a and b in equation(3.3) and the variance due to regression (P %) for the relationship between the body constituents (% lipid, % protein, energy values) and the % water content for brown trout.*

	% Lipid	% Protein	Energy value (cal g^{-1})	
			Dry weight	Wet weight
a	51.63	42.92	12100	7303
b	0.613	0.353	83.5	77.9
P(%)	96.1	85.2	85.2	98.8

lipid, percent protein or energy value (cal g^{-1} dry weight or wet weight). The value of the parameters for equation(3.3) are given in table(3.3). It can be seen that this simple expression explained a large amount of the variability in body constituents. Thus, Elliott concluded that if the water content is known then the remaining proportions of body constituents can be estimated relatively accurately.

In some situations it may not be possible to estimate water content. For example, it may be necessary to keep the fish alive. Elliott recognised the need for a non-destructive estimate of body composition and noted that an estimate of the body constituents could be made from the combination of weight and condition factor (K).

The following statistical representation was found to work well

$$Y = aK^{b_1}W^{b_2} \tag{3.4}$$

where, Y is either % water % fat, % protein of whole body weight and also energy value per gramme wet and dry weight. The value of the parameters for equation(3.4) are given in table(3.4). Elliott (1976a) found this representation very satisfactory in predicting body composition results and also in estimating

Table 3.4: *Values of the constants a, b_1 and b_2 in equation(3.4) and the variance due to regression (P %) for the relationship between the body constituents (% lipid, % protein, energy values) and the wet weight and condition factor for brown trout.*

	% Water	% Lipid	% Protein	Energy value (cal g^{-1})	
				Dry weight	Wet weight
a	81.11	2.732	14.56	5374	1053
b_1	-0.0705	0.771	0.138	0.0907	0.317
b_2	-0.0174	0.157	0.0259	0.0178	0.0711
P(%)	74.7	74.0	52.0	63.0	72.0

Table 3.5: *Changes in body composition of juvenile Arctic charr held on a restricted ration (0.2% wet body weight day^{-1}) for 8 weeks at a constant temperature of 8°C. Taken from Miglavs and Jobling (1989a,b).*

Week	WW (g)	Total Energy Kj	Lipid energy:Protein energy
0	8.65	38.0	1.16
8	9.6	37.1	0.80

body constituents of different sized trout fed a variety of different diets.

Miglavs and Jobling (1989b) investigated the pattern of energy deposition with juvenile Arctic charr (*Salvelinus alpinus*) fed a restricted ration for eight weeks at a temperature of 8^0C. Restricted feeding for 8 weeks resulted in slow growth with (wet) weight gain appearing to result from an increase in eviscerated carcass tissue. By contrast, lipid content of both viscera and liver fell during the experiment, with the decrease in visceral lipid being particularly noticeable. Growth in carcass tissue was maintained during the period of restricted ration, even though metabolic demands resulted in some depletion of both visceral and liver reserves. The changes in biochemical composition which occurred during restricted feeding led to a marked decrease in the proportion of body energy present as lipid, with the lipid energy: protein energy ratio decreasing from 1.16 in the initial sample to a value of 0.80 after the period of restricted feed (table(3.5)). Although wet weight had increased slightly over the experimental period the total energy content of the fish had remained the same (if not decreased slightly). Thus, even though there was no net gain in energy the juvenile charr were still able to maintain protein growth resulting in a leaner individual.

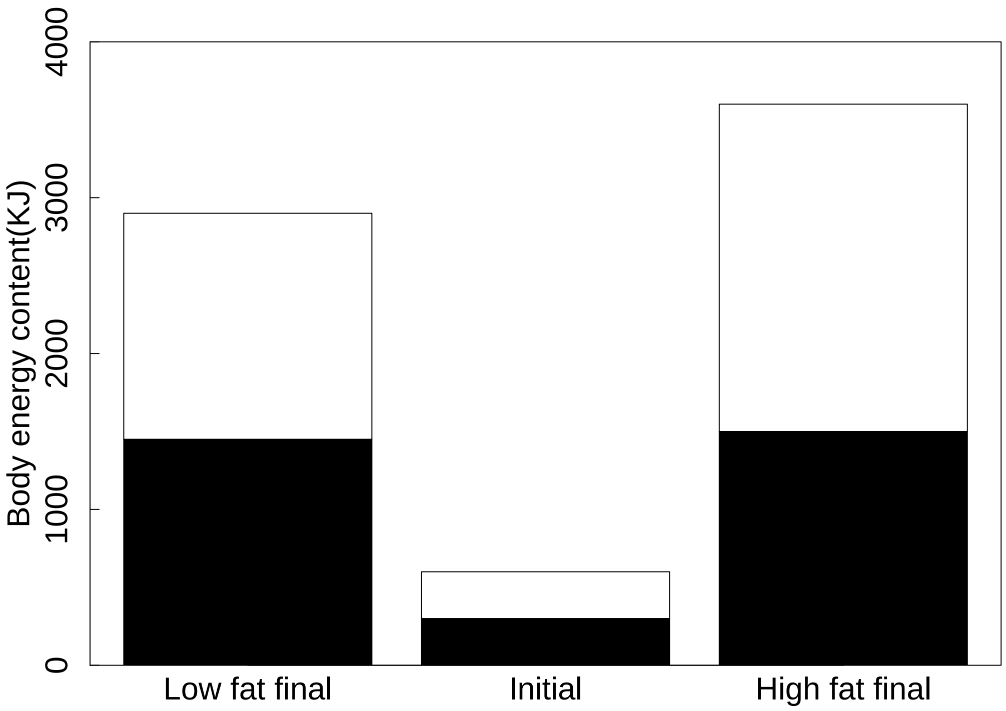

Figure 3.5: *Body energy contents and contribution of lipid energy (open sections of the bars (KJ)) to the energy content in rainbow trout fed diets with differing fat contents. Taken from Jobling et al. (1998).*

3.4 The Effect of Feed Formulation

Jobling et al. (1998) investigated the influence of dietary fat level on the growth and body composition of rainbow trout, *Oncorhynchus mykiss* (Walbaum). Two groups of fish (initial weight app. 90g) were fed diets differing in fat content for 11 weeks at a constant temperature of 14.5^oC. Each feed formulation was supplied to both experimental groups in excess for a period of 4 hours (0800 to 1200h) each day. The high fat diet consisted of: protein, 50.3%; fat, 27.5%; energy 24.4KJ g^{-1} and the low fat diet consisted of: protein, 59.1%; fat, 12.6%; energy 21.2KJ g^{-1}. At the end of the experiment there was no significant difference in wet weight of each diet treatment (treatment means±SD, 360.7± 7.7 versus 348.7± 18.7 g for the fish on the high and low fat diets, respectively). Although the two groups of fish grew at similar rates, dietary treatment had a marked influence on the chemical composition of the body tissues (table(3.6)).

Table 3.6: *The initial and final % fat and % moisture and energy content of two group of fish fed a high fat diet or low fat diet. Data are presented as means±SD. Taken from Jobling et al. (1998).*

	Initial	High Fat	Low Fat
Fat(%)	8.9 ± 1.5	15.4 ± 1.6	10.5 ± 0.7
Moisture (%)	75.3 ± 4.4	64.5 ± 2.0	69.4 ± 1.2
Gross energy(Kj g^{-1})	6.6 ± 1.2	10.1 ± 0.6	8.3 ± 0.4

The high fat diet treatment group had a significantly greater proportion of fat present than the low fat diet treatment group. Figure(3.5) displays the initial and final total body energy contents and contribution of fat energy for both dietary treatments. The increase in non lipid energy (predominantly protein) content is practically equal for both dietary treatments. However, the high fat diet fed fish have a greater final energy content by virtue of an increased accumulation of fat reserves.

Similar results have been found by Boujard et al. (2000) who reports on the effects of diet composition and ration level on body composition in juvenile rainbow trout (*Oncorhunchus mykiss*). Two experimental diets (high energy (HE) and low energy (LE)), were formulated to contain a constant protein level and different proportions of lipid and indigestible starch (table(3.7)). Groups

Table 3.7: *Chemical composition of HE (High Energy) and LE (Low Energy) experimental diet formulations used by Boujard et al. (2000).*

	HE	LE
Dry matter(DM)(%)	95.0	93.8
Protein(% DM)	40.6	40.5
Lipid(% DM)	22.9	6.6
Gross energy(Kj g DM^{-1})	22.6	18.9

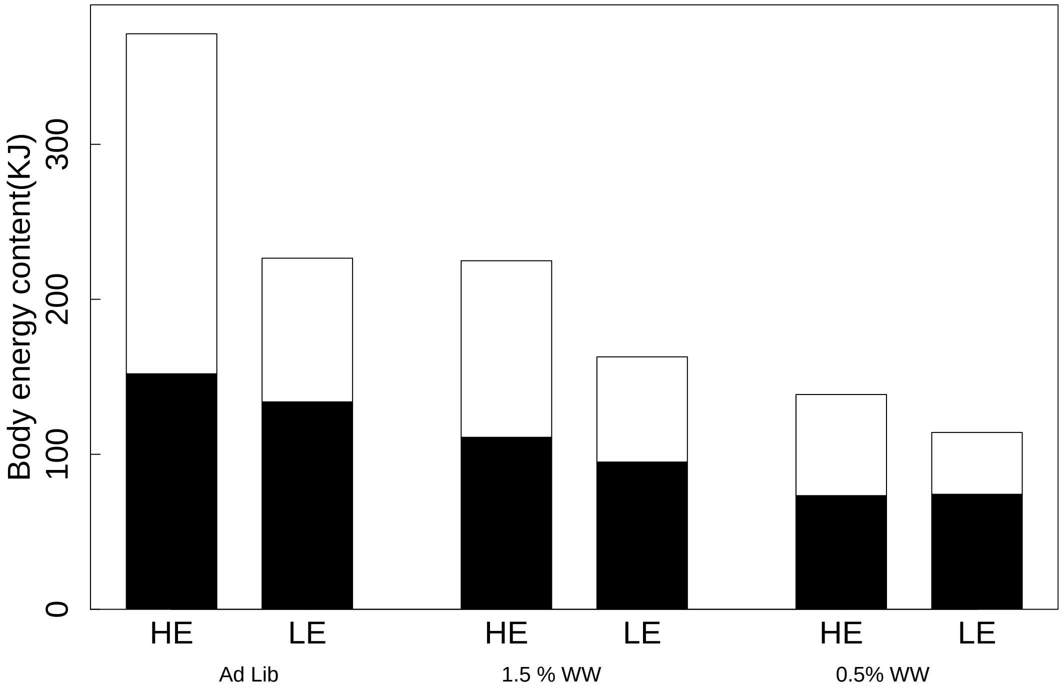

Figure 3.6: *Total body energy content and contribution from lipid energy (open sections of the bars (KJ)) and protein energy (closed sections of the bars (KJ)) in rainbow trout fed diets with differing fat contents (high energy (HE) and low energy (LE)) at three different ration levels. Recalculated from Boujard et al. (2000).*

of fish (initial weight approx. 20g) were fed both feed formulations at three different ration levels (0.5% or 1.5% initial body weight, to satiation) for 34 days at a constant temperature of 16^0C.

Growth rate (wet weight) increased with ration size for both diets. The high energy diet fed fish exhibited moderately greater growth rates than low energy diet fed fish at all ration levels. The proportion of protein present was found to be relatively stable (14.2-15.5%) in comparison to changes in lipid (5.0-12.3%). Increased ration level (and therefore increased growth rate) resulted in an increase in the proportion of lipid present for both diet formulations. However, the high energy diet fed fish had a greater percentage of lipid present than low energy diet fed fish, signifying that the majority of the extra energy gain was sustained from an increase in lipid deposition.

Figure(3.6) displays the contribution of lipid and protein energy to the total final total energy content of each group of fish. It can be seen that increasing the lipid fed to the fish has had little effect on the rate at which protein is accreted. The increased levels of lipids has only really served to increase the body adiposity.

There have been numerous experimental investigations into the effects of increasing dietary lipid content. The greatest majority of investigations report that increasing lipid levels in the diet always serves to increase adiposity (e.g. Silverstein et al. (1999); Shearer et al. (1997); Shearer (1994); Reinitz (1983); Weatherup et al. (1997)).

We now move our attention to discussing the effects of changing the proportion of protein in the diet. We have already shown that increasing the lipid proportion in the diet serves to always increase the rate of lipid accumulation. However, the same cannot be said about the deposition of body proteins. When the dietary feed has a fixed proportion of protein then it is ration level that has the greatest effect on the rate of protein growth (e.g. see fig.(3.6)). Obviously as the ration supply is increased the dietary supply of protein increases, however, one needs to ask what relationship there exists between these two variables.

Using a constant diet formulation a number of investigators have found a linear relationship between protein consumption and protein growth rate (e.g. Rankin and Jensen (1993); Hochachka and Mommsen (1995); Tytler and Calow (1985)). For example, Mcarthy at al. (see chapter 2, Rankin and Jensen (1993)) investigated the relationship between protein consumption (% day^{-1}) and protein growth rate (% day^{-1}) in rainbow trout (*Oncorhuchus mykiss*) of initial weight 40g at a constant temperature of 8^oC supplied a range of different ration levels. A significant linear relationship between protein consumption and protein growth rate was exhibited with the linear regression equation being

$$y = 0.276 * x - 0.0110 \qquad (n = 37, r^2 = 0.691, P < 0.001). \tag{3.5}$$

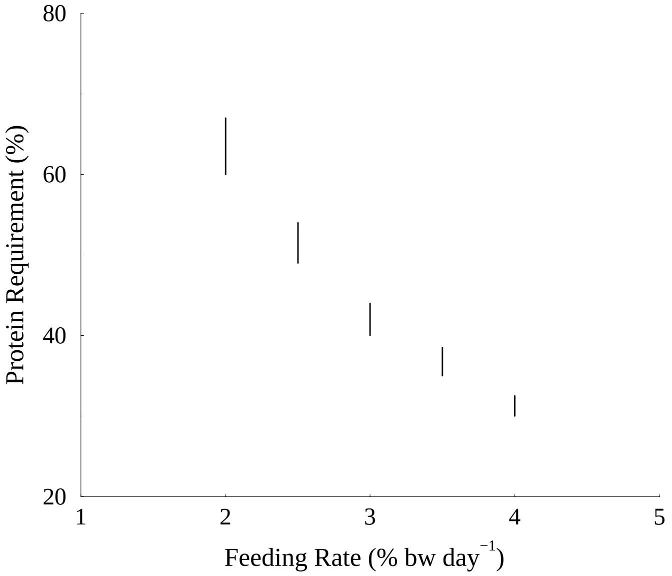

Figure 3.7: *Relationship between feeding rate and the dietary protein level needed to satisfy the protein requirements of common carp and rainbow trout (12-13 g protein per kilogram body wet weight per day). Each vertical line represents the combined limits of protein requirement for both species at each feeding level. Taken from Ogino (1980).*

where y is protein growth (% day^{-1}) and x is protein consumption (% day^{-1}). The intercept does not significantly differ from zero and even fish given a very low ration of protein managed to exhibit positive protein growth.

An interesting alternative question is what may transpire when the proportion of protein in the diet is altered whilst feed is supplied in excess. Perhaps, not surprisingly, protein growth rate has been reported to initially increases as the proportion of protein in the diet is increased (as you would expect from the above relationship). However, this pattern does not continue indefinitely and above a certain protein proportion in the diet no further increase in protein growth is found (Anderson et al. (1981); Jauncey (1982); Ogino (1980); Austreng and Refstie (1979); Cai et al. (1996)).

Ogino (1980) investigated the dietary optimum requirement of protein for rainbow trout and common carp at a range of different ration levels whilst also varying the proportion of protein in the diet. Figure(3.7) displays the relationship between the optimal percentage protein requirement (the point at which no further protein growth is found with increasing protein content) with ration level. It can be seen that as the ration supply is reduced the percentage requirement of protein in the diet to maximise protein growth reduces so that the gross optimal protein requirement remains the same (app. 12-13 g protein per kilogram body wet weight per day).

This study, in agreement with many other studies (for review, see chapter 6, Tytler and Calow (1985)), shows that fish have a well defined maximum rate at which they can accrete body proteins. This study also shows that in healthy fish, whether this maximum rate is achieved or not is governed solely by the gross intake of protein and not any other constituent of the diet.

3.5 General Conclusions

Changes in the Relative Proportions of Body Constituents

Studies that have investigated salmonid body composition in relation to temperature, ration and body size are in general agreement about a number of observations (Elliott (1976a); Parker and Vanstone (1966) Brett, Shelbourn, and Shoop (1969); Gardiner and Geddes (1980); Weatherley and Gill (1983); Weatherley and Gill (1981); Berg and Bremset (1998)). The major changes in body composition and energy status brought about by nutritional imbalance are chiefly due to variations in the relative proportions of fat and water content. When lipids levels are being depleted there is a concomitant increase in water uptake and when lipids levels are being repleted there is a concomitant decrease in water content.

Protein content, which is so vital a constituent of the living cell tends to vary relatively little in healthy fish, unless drawn upon during particular demands of reproduction or during prolonged periods of extreme nutritional restriction (Weatherley and Gill 1987). Lipid stores are far more labile than proteins and

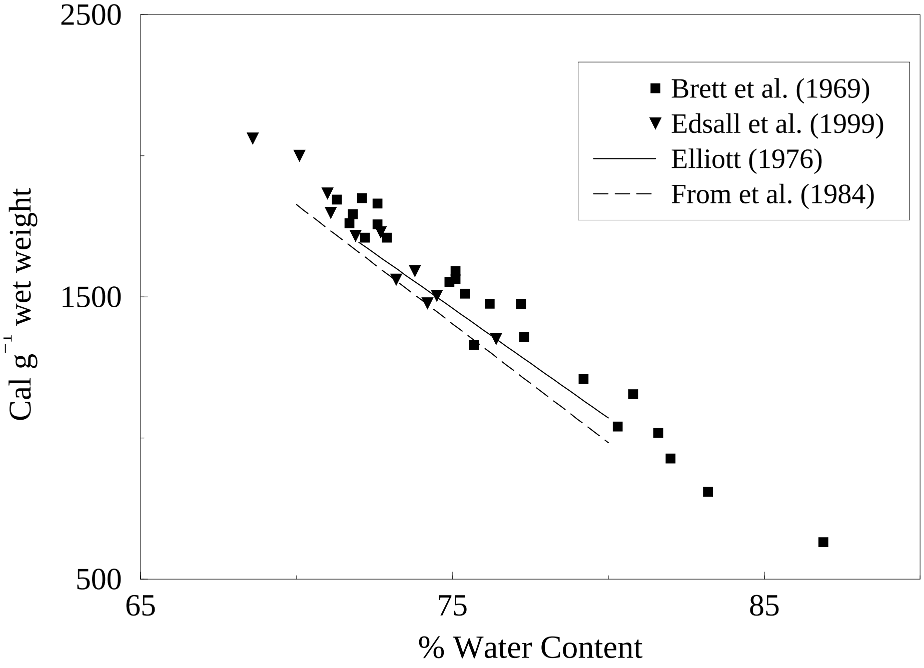

Figure 3.8: *The relationship between energy content and % water content for a number of salmonid species. The straight lines are least squares linear regression fits displayed in each case for the range of values reported in the respective studies.*

also have a greater specific energy content. This means that the changes in the fish's specific energy content is more closely related to the changes in lipid content rather than the protein content (Elliott 1976a). As a consequence of this, wet weight on its own is a very poor indicator of energy content.

Figure(3.8) displays the relationship between specific energy content and percentage water content for a number of salmonid species. It can be seen that there exists a strong negative linear relationship between the water content and the energy content of the fish, inclusive of the Edsall et al. (1999) study in which no relationship between protein content and water content was found. Furthermore, this relationship is very similar for each of the species of salmonid studied.

Growth Restriction

If the above biometric and biochemical observations are combined, then it can be seen that reduced opportunity for growth leads to a disproportionate increase in length together with a continuation of protein deposition and a reduction in the rate of lipid accumulation. Since length constitutes a measure of structure then it is clear that salmonids under reduced opportunity for growth are seeking to maintain somatic growth at the cost of reducing levels of somatic energy reserves. This leads to a longer, leaner organism with a significant decrease in the more labile lipid reserves.

Growth is restricted when water temperature is reduced and also when the ration supply is reduced. Studies of energy allocation most commonly point out the relationship between ration level and nutritional condition, i.e. when the ration level is reduced growth continues but with a corresponding reduction in lipid accumulation. Our review has also pointed out the fact that this relationship also occurs when growth is restricted through lower temperatures.

The observation by Miglavs and Jobling (1989a,b) that current lipid reserves can actually be depleted to make way for somatic growth is important because it means that the proportion of lipid present need not only decrease because body weight is still increasing whilst lipid deposition has ceased. It is therefore clear that salmonids give a high degree of priority to maintaining somatic growth, even at the cost of reducing lipid levels, which, will almost certainly decrease the time the individual can survive for when faced with a starvation challenge. We shall discuss possible ecological reasons for this in chapter 11.

Starvation

When fish are starved, there is an immediate decrease in lipid content whilst the water content increases (e.g. Swift (1955); Idler and Clemems (1959); Philips et al. (1966); Hochachka and Mommsen (1995)). Salmonids amongst other fish are very reluctant to use body proteins proteins for energy purposes and it is the last body constituent to begin being mobilised (Hochachka and Mommsen 1995). At the beginning of the fast protein reserves are spared. As the starvation period is prolonged and when lipid reserves have been significantly depleted only then do protein reserves begin to be utilised. The time period in which proteins are spared will likely depend upon the maintenance requirements of the fish (size and temperature) and also its initial lipid content (Hochachka and Mommsen 1995). In a similar manner to lipids, when proteins are mobilised water moves in to partially take its place. The fact that mobilised body constituents are partially replaced by water means that body wet weight loss is partially offset by the uptake of water. Thus, under starvation conditions, weight loss on its own is a poor representation of the actual energy losses incurred.

The results of the Brett et al. (1969) study with the small coho salmon (*Oncorhynchus nerka*) are a good illustrative example of the above sequential mode of remobilisation. The greatest depletion of protein was found for the fish enduring the starvation at the highest temperatures which also had by far the greatest depletion of lipid reserves (see figure(3.3)).

Body Composition and Age

A number of studies report that there is a tendency for well fed fast growing fish to exhibit a slight increase in lipid content and also sometimes protein content with increasing weight (e.g. Weatherley and Gill (1987); Elliott (1976a); Pfeffer (1982)). Amongst initially equally sized groups of fish the effect of fish size may be partially confounded by other factors, because as we know from this review, faster growing fish maintain a higher nutritional status. Also, if fish were not adequately fed before the growth experiments then a return to better growing conditions would also elicit an increase in lipid levels.

Groves (1970) studied the changes in the body composition during growth of young sockeye salmon ranging from 0.5 to 2500g. Groves reported that protein, water, and ash–the major components of the lipid-free mass–were closely related to each other and to fork length. Groves derived the following expressions to account for the relationship between protein, water and ash content

$$W_a = 0.00571L^{3.118} \tag{3.6}$$

$$P = 0.204W_a^{1.038} \tag{3.7}$$

$$FFDM = 1.113P \tag{3.8}$$

where W_a is total water, L is fork length, P is protein, $FFDM$ is lipid-free dry material (protein and ash).

Groves stated that

$$F = W - (W_a + FFDM) \tag{3.9}$$

where body lipid (F) is the difference in body wet weight (W) and the lean mass ($W_a + FFDM$). Groves reported that body composition could be estimated by use of the above equations and that (for non-starving fish) the protein value derived from fork length was as accurate as that derived from body water, typically $R^2 > 80\%$. As for lipid, Groves (1970) noted that body lipid tended to increase with body size but was not closely related to the body's other components because lipid is more a function of nutritional history of the fish. A corollary of this is that since lipid is the main determinant of condition ($K = (100W)/L^3$), "at any given fish length a non-starving salmon of a given species contains a precisely specified amount of protein, water and ash, and therefore has a closely predictable fat-free mass."

As in the studies we have reviewed, Groves notes that lipid content is more a function of nutritional history than any other factor. Similar conclusions have been drawn by Reinitz and Hitzel (1980) and Reinitz (1983). As we have already highlighted, even in non-starving individuals lipid content is the most variable body constituent (e.g. Edsall et al. (1999)). Lipids reserves being remarkably labile are more sensitive than any other body constituent to growing conditions.

We therefore conclude, that there is a tendency for lipid content to increase with fish size but that lipid content is much more greatly influenced by the previous growing conditions such as temperature, ration level and diet composition.

Diet Effects

The greatest majority of experiments conducted to investigate the effects of diet composition have been carried out by aquaculturists. Proteins are the single most expensive ingredient in fish diets. Therefore, one of the main aims of aquaculturists is to reduce the amount of protein the fish utilise for energy purposes and increase the protein retention efficiency.

Our review has shown that proteins act as both a nutrient source and an energy source. Indeed, salmonids being carnivorous are highly adapted to using protein as an energy source. On the other hand, lipids seem mainly only able to serve as an energy source to fuel metabolic processes and for all intents and purposes cannot be directly converted into protein. Therefore, one would not immediately expect an increase in the dietary lipid content to have any beneficial effect on structural body protein growth. Nevertheless, increasing the ratio of dietary energy to protein energy supplied in the feed has in some cases been shown to increase protein efficiency (Steffens et al. (1998); Steffens (1996); Beamish and Medland (1986); Desilva et al. (1991)). We shall investigate why this protein "sparing" effect may occur in a further chapter.

The effects of different diet formulations on growth and allocation patterns gives us a particularly good insight into the physiology of salmonids. It highlights the constraints imposed by nutritional pathways rather than purely energetic conservation arguments. Obviously, nutritional factors in growth are important but yet they remain practically un-modelled because the majority of growth models are based purely on energetic assumptions.

Chapter 4

Resource Allocation Model Properties

4.1 Introduction

In section(2.5) we introduced three different classes of allocation scheme which can be applied to our modelling framework. Each of these models are based on differing assumptions concerning the way an organism utilises energy for the processes related to maintenance, growth (structure) and storage (reserves). In this chapter we shall analyse the behaviour of each of these three allocation schemes with respect to growth and allocation in a "constant environment". We aim to investigate which class of model will best reproduce or emulate the growth and allocation patterns of juvenile salmonids reared in a near constant environment as described by the literature.

Until now only the general form of the system dynamics for each class of model have been described. The next step will be derive particular allocation rules for each class of allocation model. The step from the general case to a particular case is useful as it allows one to generate growth simulations, from which valuable inferences and comparisons can be made in considering each class of model. However, there is probably a great number of different particular growth allocation rules that we could choose for each class of model. With this in mind, we will aim to derive simple allocation rules that we deem indicative of each class of model.

Once the particular cases have been derived we shall move on to investigate the growth and allocation behaviour in different constant growth environments. Of particular interest is how the models behave in cases where positive growth is sustainable (but to varying degrees), when supplied a maintenance ration and also what may transpire under starvation conditions.

4.2 Simulations

In the ensuing analysis of each growth allocation scheme we shall run a number of numerical growth simulations. For brevity, clarity and standardisation we dedicate this short section to outlining the simulation procedure, associated functional forms for assimilation and maintenance and also their respective trial parameter values.

Reductions in maximum uptake usually only occur at quite high temperatures which we can mostly attribute to the effects of thermal stress. In general, maximum uptake is adequately described as being an exponential function of temperature (e.g. Higgins and Talbot (1985); Brett and Groves (1979); Broekhuizen et al. (1994)).

From section(2.4.1) we can therefore express the assimilation rate as follows

$$A = \varepsilon U_H \phi = \varepsilon U_{H0} \exp\left(\frac{T}{T_H}\right) S^d \phi. \tag{4.1}$$

The allometric scaling for uptake (d) is usually found to lie in the range of 0.66-0.83 for salmonids. Elliott (1976b) found the allometric uptake scaling to lie in the range 0.731-0.770. Similar results have been found by From and Rasmussen (1984). Therefore, we choose a value of 0.75. Based on the work of Elliott

Table 4.1: *Parameter values to be used in growth simulations unless explicitly stated otherwise.*

Param.	Interpretation	Units	Value	Source
M_{H0}	Maintenance cost rate scale	mgC$^{(1-v)}$ day^{-1}	0.02	-
T_M	Maintenance characteristic temperature	^{o}C	12.0	Elliott (1976b) Brett (1979) From et. al. (1984)
v	Maintenance cost allometric index	—	0.75	From et. al. (1984) Elliott (1976b)
d	Maximum uptake allometric index	—	0.75	Elliott (1976b) From et. al. (1984)
ε	Assimilation efficiency	—	0.4	Broekhuizen et al. (1994)
U_{H0}	Uptake scale	mgC$^{(1-d)}$ day^{-1}	0.24	Broekhuizen et al. (1994)
T_H	Uptake rate characteristic temperature	^{o}C	6.0	Elliott (1976b) Brett (1979)

(1976b) we choose a temperature scaling (T_H) of 6.0. A similar value has been reported by Brett and Groves (1979).

For trial values of assimilation efficiency (ε) and uptake scaling (U_{H0}) we choose a pair of values from the work of Broekhuizen et al. (1994), which we display in table(4.1).

As introduced in section(2.4.2), for daily maintenance we use the following functional form

$$M = M_{H0} \exp(T/T_M)(R + S)^v. \tag{4.2}$$

The allometric scaling for maintenance (v) is similar to that of uptake and is usually found to lie in the range of 0.66-0.85. Elliott (1976b), From and Rasmussen (1984) and Jobling (1985) find the appropriate value index of 0.75 for trout, and we shall set our maintenance cost rate allometric index to this value. For the exponential temperature scaling (T_M) we use the value of 12.0 from Elliott (1976b) but Jones (1976), From and Rasmussen (1984) and Brett (1979) all give similar values. The chosen value of 0.02 for the maintenance cost rate scaling (M_{H0}) is based on a fitting analysis which we report on in detail within a further chapter.

The values of the default trial parameters are all displayed in table(4.1). These values will all be used in the ensuing growth simulations, unless explicitly stated otherwise. For each class of model, growth simulations were predicted by numerically integrating the two paired differential equations, respectively. We used a fourth order Runge-Kutta algorithm with a fixed time step of 0.1 of a day.

4.3 Growth Efficiency

A number of studies have pointed out that as the ration supply is reduced the optimum temperature for growth also reduces (Brett et al. (1969); Elliott (1976b); Edsall et al. (1999)). We shall now show that this is a general growth property that will be exhibited by all the different classes of allocation model.

The total change in carbon weight is described by equation(2.22) together with the functional forms for assimilation and maintenance described in the previous section. At a constant temperature the maximum growth rate will obviously be achieved when the fish are fed a plentiful supply of food allowing them to consume their maximum uptake. However, when an individual is fed a restrictive ration supply below its maximum uptake an interesting relationship developes between growth rate, ration size and temperature.

From equation(2.22) we can write the change in total carbon weight as

$$\frac{dW_c}{dt} = P = \varepsilon U - M. \tag{4.3}$$

which states that net production (P) is the difference in assimilation and maintenance. The maximum uptake rate (U_H) and maintenance rate (M) have both been described by monotonic increasing functions of temperature such that $\frac{\partial U_H}{\partial T} > \frac{\partial M}{\partial T}$, that is, maximum growth rate increases with temperature (see equation(4.1) and equation(4.2) with table(4.1)). Now suppose an individual is offered a constant ration of, say R, then we can write the individual's uptake U as follows

$$U = \begin{cases} U_H(T) & \text{if} \quad R > U_H(T) \\ R & \text{if} \quad R \leq U_H(T) \end{cases} \tag{4.4}$$

that is, any food supplied beyond its maximum uptake capacity $U_H(T)$ is rejected. This means there exists a temperature T_{opt} where $R = U_H(T_{\text{opt}})$ such that

$$R > T \quad \forall \quad T \leq T_{\text{opt}} \tag{4.5}$$

$$R \leq T \quad \forall \quad T \leq T_{\text{opt}} \tag{4.6}$$

that is, T_{opt} is the temperature at which this fixed ration level R is equal to the maximum uptake. If we assume that ε is constant and since $\frac{\partial U_H}{\partial T} > \frac{\partial M}{\partial T}$ then at any fixed ration R,

$$T < T_{\text{opt}} \Leftrightarrow R > U_H(T) \Rightarrow \frac{\partial P}{\partial T} > 0 \tag{4.7}$$

$$T > T_{\text{opt}} \Leftrightarrow R < U_H(T) \Rightarrow \frac{\partial P}{\partial T} < 0. \tag{4.8}$$

The first of the above expressions means that if the fixed ration R is greater than maximum uptake then an increase in temperature will serve to increase maximum uptake and in turn increase net production (see equation(4.3)), at least until $T = T_{\text{opt}}$. The second expression means that if the fixed ration R is below maximum uptake then a reduction in temperature would serve to increase net production because uptake would remain constant but maintenance would reduce, at least until $T = T_{\text{opt}}$. We can conclude from this that at any constant ration supply R, T_{opt} is the optimum temperature for weight gain at any fixed total carbon weight W_c. Consequently, as the ration level R is reduced the optimum temperature for growth also reduces.

This analysis is based on the instantaneous change in total carbon weight and illustrates how very simple assumptions concerning the differing ways temperature affects the processes of uptake and maintenance can help elucidate some very strong observed growth dynamics. Basically, this relationship between ration supply, temperature and growth reported by Brett et al. (1969), Elliott (1976b) and Edsall et al. (1999) develops because the fish have a maximum uptake rate dependent upon temperature and that maintenance costs must always be met, are independent of the processes of growth and are heavily temperature dependent. However, it is also worth noting that maximum uptake is also a function of structural carbon weight, which means that over time differing patterns of allocation will modify this relationship. Nevertheless, in short term experiments it is the above relationships that are dominating the patterns of growth.

4.4 Net Production Allocation

4.4.1 Derivation

The principle assumption of the net production allocation scheme we introduced in section(2.5.1) is that maintenance always has first call on assimilate. Since maintenance costs must always be met then the system dynamics are described as follows

$$\frac{dR}{dt} = A - M - \frac{dS}{dt}, \qquad \frac{dS}{dt} = C[A - M]^{+} \tag{4.9}$$

where, C denotes the proportion of excess assimilate allocated to structure. A useful alternative statement is to recast the model in terms of reserve ratio and structural carbon weight as follows

$$\frac{dS}{dt} = CP^{+} \tag{4.10}$$

$$\frac{dX}{dt} = \frac{1}{S}\Big(P - P^{+}(C + X)\Big) \tag{4.11}$$

where net production $P \equiv A - M$.

Following Lika and Nisbet (2000) we shall state that a healthy individual in an environment where growth is sustainable (i.e. $A > M$) directs a fixed proportion C_1 of net production to building structure.

4.4.2 Analysis

To investigate the changes in reserve ratio with varying growth opportunity we shall solve for the steady state reserve ratio X^* by setting $\frac{dX}{dt} = 0$ in equation(4.11). Following some trivial algebra we find

$$X^* = \frac{1}{C_1} - 1. \tag{4.12}$$

The most important point to note here, is that the steady state reserve ratio value is independent of both assimilation and maintenance. Therefore, in an environment where growth is sustainable (i.e. $A > M$) individuals will always head to a constant steady state reserve ratio value which is independent of ration level and temperature and thus growth rate. This means that individuals who are faced with a reduced growth opportunity will reduce their structural growth rate but will not reduce reserve status.

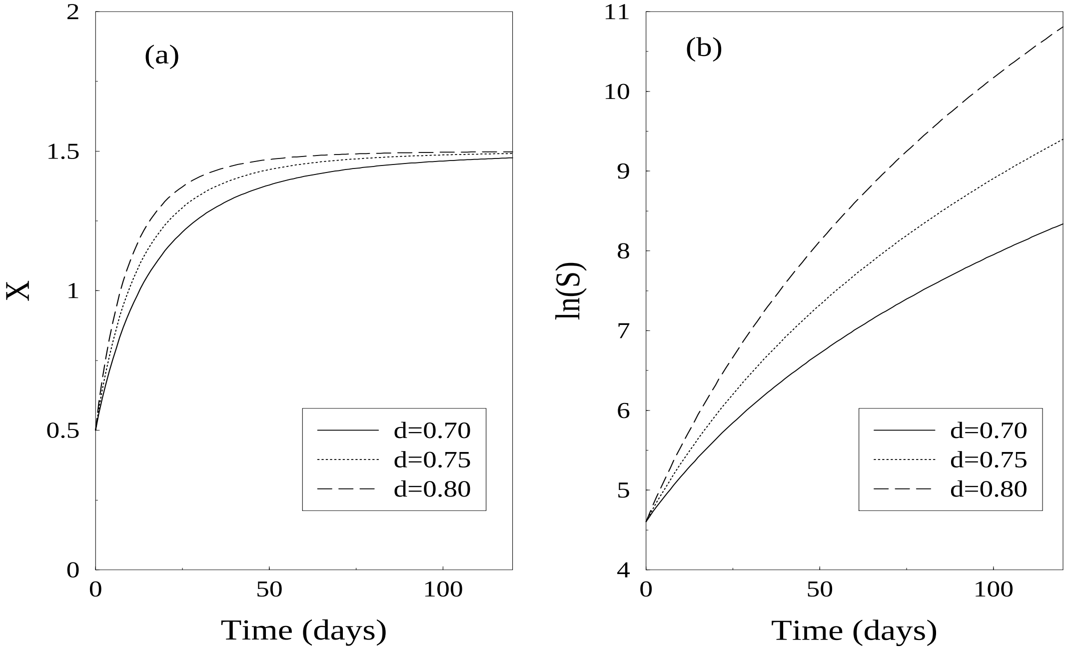

Figure 4.1: *Net production allocation: the effect of varying the maximum uptake allometric scaling d in equation(4.1) on individuals fed an excess ration and allocating a fixed proportion C_1 of net production to structural growth. Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $C_1 = 0.4$, $T = 12.0^oC$, $\phi = 1.0$, $X_0 = 0.5$, $v = 0.75$, $S_0 = 100$ *mg C.*

4.4.3 Simulation

Figure(4.1) displays the changes in structural weight and reserve ratio for a set of maximal growth simulations (i.e. $\phi = 1.0$) using a constant value of C_1 and different values for the uptake allometric constant d in equation(4.1) with a constant value of $v = 0.75$ for the maintenance allometric scaling in equation(4.2). It can be seen that even superficially small changes in the scaling values for uptake can cause quite large changes in the structural growth rate. However, even though structural growth rate varies greatly each reserve ratio trajectory asymptotically heads to the same steady state value of 1.5 predicted by equation(4.12).

Figure(4.2) displays the change in structural weight and reserve ratio for individ-

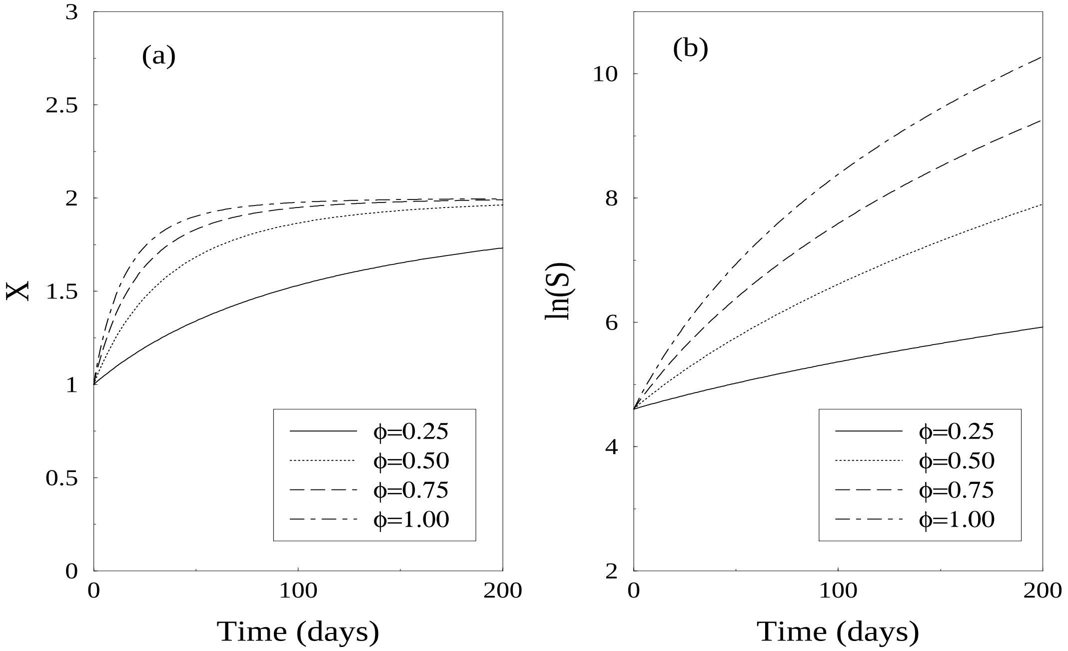

Figure 4.2: *Net production allocation: the effect of varying ration level on individuals allocating a fixed proportion C_1 of net production to structural growth. Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are $C_1 = 0.333$, $T = 12.0^oC$, $X_0 = 1.0$, $v = d = 0.75$, $S_0 = 100$ mg C.*

uals supplied a range of different ration levels (using identical allometric scalings of $v = d = 0.75$). Again, each reserve ratio trajectory heads asymptotically to the same steady state value which is independent of ration level. In this simulation all individual reserve ratio trajectories head to X^*=2.0, solely in response to the change in value of C_1=1/3. Individuals supplied a plentiful amount of food, grow faster but merely approach X^* quicker, as opposed to maintaining a different nutritional status than more poorly fed conspecifics.

4.4.4 Maintenance Dynamics

We could possibly derive a new and different allocation rule whose reserve ratio dynamics are in better accordance with literature reports. However, there is one system dynamic which no particular case of the net production allocation scheme can reproduce.

Under a net production allocation scheme, when an individual is fed a maintenance ration (i.e. $A = M$) then by definition net production $P = A - M$ is zero. Since both the change in reserve ratio and structure is proportional to P then equation(4.11) and equation(4.10) are both set to zero, irrespective of what particular functional form we may choose for C. Thus, we are able to conclude that the whole class of net production models cannot predict a change in body constituents when an individual is fed a maintenance ration (i.e. remaining in a stationary energy balance), which is in contrast to that reported by Miglavs and Jobling (1989b) (see table(3.5)).

4.5 Reserve Allocation

4.5.1 Derivation

The principle assumption of the reserve allocation scheme we introduced in section(2.5.2) is that all the immediate assimilate A is first directed into the reserve pool, from which all subsequent (irrecoverable) allocation to maintenance and structure is made. The two general differential equations that describe the changes in reserves and structure according to this scheme are given as follows

$$\theta(R) = M + \frac{dS}{dt}, \qquad \frac{dR}{dt} = A - \theta(R) \tag{4.13}$$

where $\theta(R)$ denotes the rate of release of carbon from the reserve pool. For analytical purposes we shall recast the system dynamics in terms of reserve ratio and structure, which leads to

$$\frac{dX}{dt} = \frac{1}{S}\left(A - \theta(R) - X\frac{dS}{dt}\right), \tag{4.14}$$

where

$$\frac{dS}{dt} = \theta(R) - M. \tag{4.15}$$

Maintenance (M) stands for the collection of processes necessary to stay alive. Therefore, whenever possible (i.e. $R > 0$) maintenance costs must be met. Hence maintenance costs must have first call on $\theta(R)$ and only the excess can be allocated to build structure. We shall subdivide $\theta(R)$ to further express this order of resource allocation such that

$$\theta(R) = M + \Gamma(R) \tag{4.16}$$

where $\Gamma(R)$ is the excess allocate remaining from $\theta(R)$ once maintenance costs have been debited. This leads to equations (4.14) and (4.15) reducing to

$$\frac{dX}{dt} = \frac{1}{S}\left(P - (1+X)\Gamma(R)\right), \tag{4.17}$$

and

$$\frac{dS}{dt} = \Gamma(R) \tag{4.18}$$

where net production $P \equiv A - M$. This new model statement allows us to directly identify the resource allocated to structure, namely, $\Gamma(R)$.

A sensible and reasonable assumption would be that an individual in a good nutritional condition would allocate more to structural growth than a conspecific in a poorer nutritional state. Hence, we shall suggest that the rate and proportion of reserves that are converted to structure per unit time is very likely to be a function of the organisms reserve level. It might be suggested that below a defended value, say R_μ, no further conversion will be maintained so as to reduce the immediate risk of starvation. Since the model will take into account many different size ranges of fish it is convenient to express this critical energy level as a threshold reserve ratio μ defined by

$$\mu \equiv \frac{R_\mu}{S}. \tag{4.19}$$

If it further assumed that the rate of allocation to structure from reserves is proportional to the difference in the current reserve level and the defended energy level then the depletion of reserves resulting from conversion to structure can be written as

$$\Gamma(R) = b[R - R_\mu]^+ = bS[X - \mu]^+ \tag{4.20}$$

where, $R_\mu \equiv S\mu$ and b is a non-negative constant of proportionality.

Numerical simulations showed that this particular reserve allocation model had some encouraging properties. However, there was a persistent trend for the reserve ratio value to decline with size, which is certainly not supported by the literature. The reason why will become clear in the ensuing analysis section. By making a minor adjustment we obtained a much more satisfactory model. For brevity we shall introduce this minor adjustment here.

We found the model dynamics to a much more satisfactory model by modifying b such that

$$b = b_1 S^{g-1} \tag{4.21}$$

where b_1 is a constant of proportionality and g is a structural allometric scaling constant. This means that $\Gamma(R)$ is now newly defined as

$$\Gamma(R) = b_1 S^g [X - \mu]^+. \tag{4.22}$$

Notice that the previous function for $\Gamma(R)$ given by equation(4.20) is just a special case of this new functional form with $g = 1$.

4.5.2 Analysis

In a similar manner to that of the previous section we shall investigate the reserve ratio dynamics by setting $\frac{dX}{dt} = 0$ in equation(4.17) and solving for the steady state reserve ratio value X^*, assuming sustainable growth (i.e. $A > M$). Following some algebra we find

$$X^* = \frac{1}{2}\left[(\mu - 1) + \sqrt{(1+\mu)^2 + 4\left(\frac{P^+}{b_1 S^g}\right)}\,\right]. \tag{4.23}$$

The steady state reserve ratio X^* in this case is dependent upon the defended reserve ratio for structural growth μ and the quotient of net production over the product of current structural weight (S) and b_1 the constant of proportionality in equation(4.22). In contrast to the net production model, this particular scheme predicts that reserve status will change with varying opportunity for growth.

It is now also clear why the original formulation for $\Gamma(R)$ equivalent to $g = 1$ in equation(4.22) predicted a decrease in reserve ratio with size. Net production is the difference in assimilation and maintenance, both of which exhibit strong negative allometric relationships (equations(4.1) and (4.2)). Therefore, as the organism was growing the quotient P^+/S^1 in equation(4.23) was reducing. By introducing a more appropriate scaling constant we yield a model whose reserve ratio dynamics remain steadier with increasing size. To further investigate the change in reserve status with varying opportunity for growth and differing sizes we shall run a number of numerical simulations.

4.5.3 Simulation

Figure(4.3) displays the changes in structural weight and reserve ratio for a set of maximal growth simulations (i.e. $\phi = 1.0$) using a constant value of $g = 0.75$ and different values for the uptake allometric constant d with a constant value of $v = 0.75$ for the maintenance allometric scaling. It can be seen that the differences in uptake allometric scaling change the rate of structural growth rate quite significantly. However, faster growing individuals maintain a higher reserve status than slower growing conspecifics. The long term reserve ratio values are also dependent upon the choice of allometric scalings. In the case

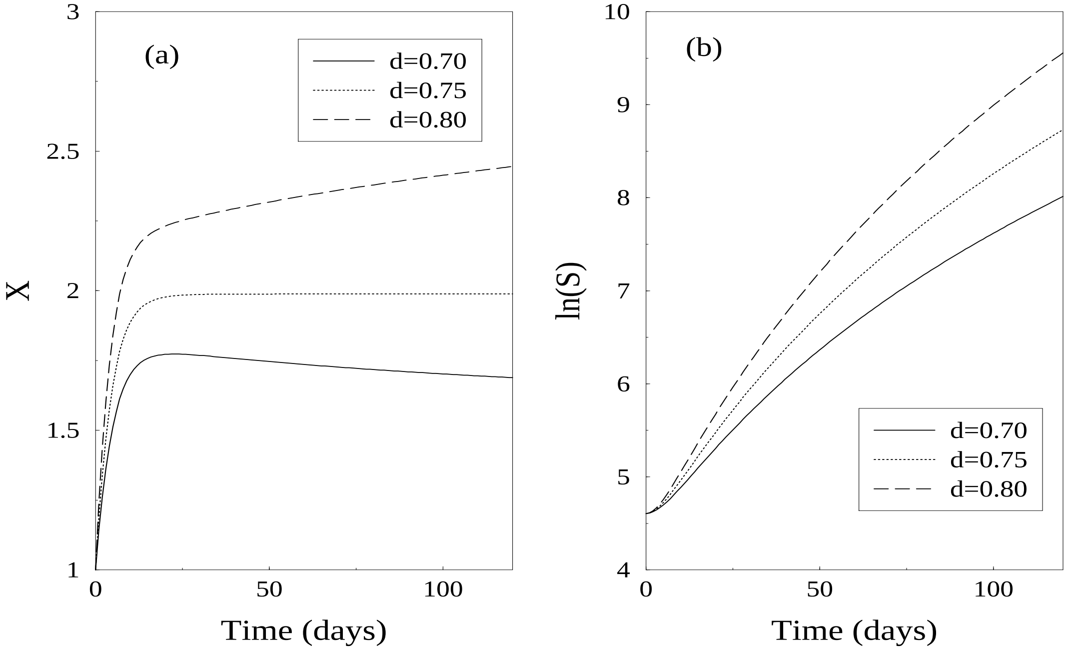

Figure 4.3: *Reserve allocation: the effect of varying the maximum uptake allometric scaling d in equation(4.1) on individuals fed an excess ration and committing to structure according to equation(4.22). Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values in conjunction with table(4.1) used to simulate these trajectories are* $b_1 = 0.2$, $T = 12.0^oC$, $\mu = 1.0$, $X_0 = 1.0$, $S_0 =$*100mgC*, $\phi = 1.0$, $g = 0.75$, $v = 0.75$.

where, $d > v = g$ the reserve ratio increases with size, if $d < v = g$ then reserve ratio decreases with size. If all three allometric scalings are equal then the reserve ratio heads to a steady state.

The particular values of the allometric scaling constants dictate the long term behaviour of reserve ratio, whilst other factors control the "fast" dynamics of the system. To investigate these additional factors we shall choose the case in which $v = g = d$. In this scenario a steady state reserve ratio is achieved for a constant ration level ϕ and temperature as illustrated in figure(4.4). We can see that the effect of increasing the ration supply level is to increase growth rate but also for the individual to maintain a higher reserve ratio value than less well fed conspecifics. Thus, the effects of increasing the ration level are in accordance with the literature.

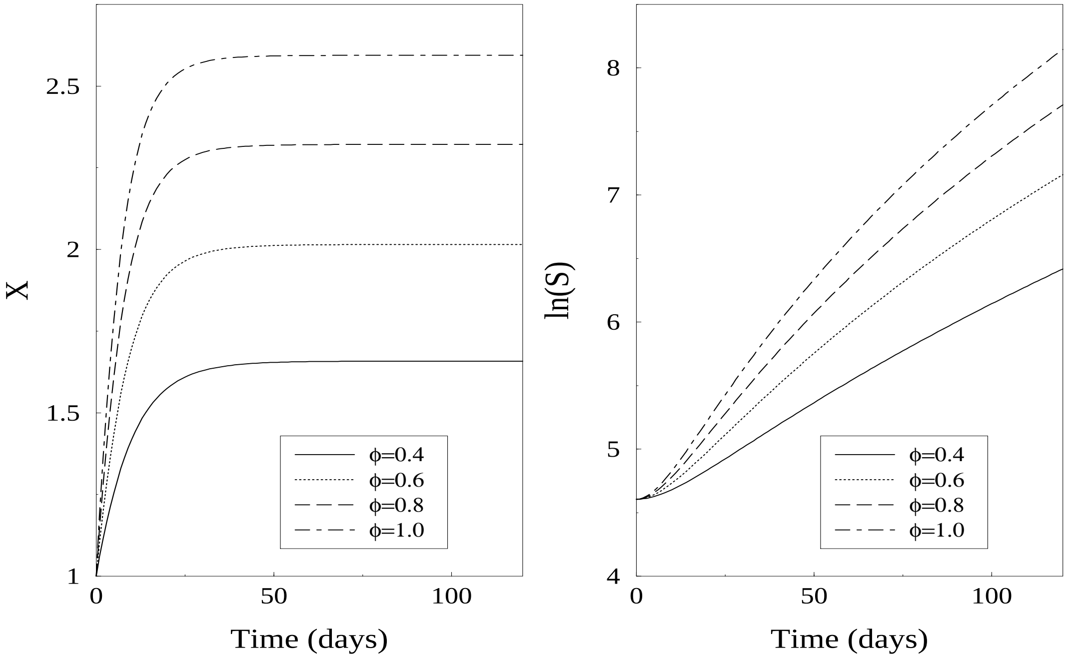

Figure 4.4: *Reserve allocation: the effect of varying ration level on individuals allocating to structure according to equation(4.22). Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values in conjunction with table(4.1) used to simulate these trajectories are* $b_1 = 0.1$, $T = 12.0^oC$, $\mu = 1.0$, $X_0 = 1.0$, $S_0 =$ *100mgC*, $g = d = v = 0.75$.

We can make predictions about how different environmental factors will affect the steady state reserve ratio value and growth rate from equation(4.23). The effect of decreasing the ration level is to decrease the assimilation rate (A) and in turn reduce net production (P), thus as predicted equation(4.23) the reserve ratio falls. However, another factor that constrains net production is temperature. We have used an exponential temperature dependence for both maintenance and maximum assimilation which predicts increasing net production with increasing temperature. Thus, according to equation(4.23) a change in temperature should also effect the reserve ratio and growth. Figure(4.5) displays simulations of individuals reared at different constant temperatures with a plentiful food supply (i.e. $\phi = 1.0$). The effect of increasing temperature from 6-14^oC is to both increase growth rate and also increase the steady state reserve ratio.

The two remaining factors that will alter the growth dynamics are b_1, the con-

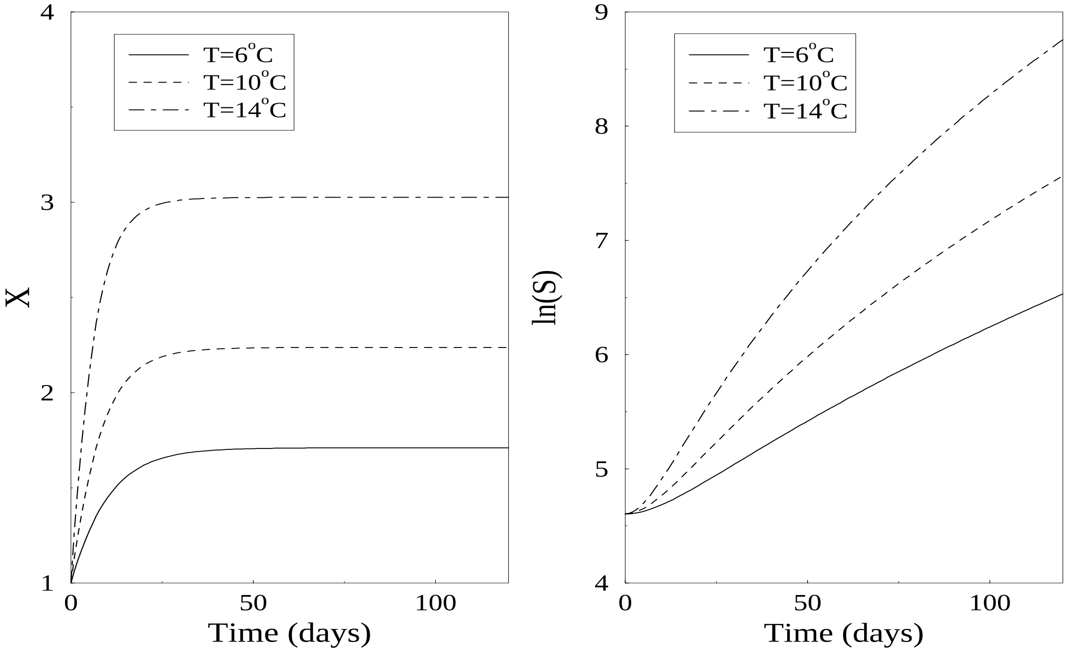

Figure 4.5: *Reserve allocation: the effect of varying temperature on individuals fed excess food and allocating to structure according to equation(4.22). Trajectories of a) reserve ratio and b) structural carbon. Additional parameter values in conjunction with table(4.1) used to simulate these trajectories are* $b_1 = 0.1$, $\phi = 1$, $\mu = 1.0$, $X_0 = 1.0$, $S_0 =$*100mgC*, $g = d = v = 0.75$.

stant of proportionality in equation(4.22) and μ, the defended reserve ratio value for which no further structural growth is maintained. Figure(4.6) displays growth simulations for different values of b_1. We can see that the effect of decreasing b_1 is to reduce the rate of structural growth whilst maintaining a higher reserve ratio value. The effect of increasing b_1 is to increase the rate of structural growth whilst maintaining a lower reserve ratio value. These differences arise because b_1 contributes to the rate of commitment to structure, i.e. for individuals who posses identical reserve ratios a conspecific with a higher value of b_1 would commit more to structure per unit time. Hence, increasing b_1 increases the structural growth rate. The increased rate of commitment to structure leads to a shift in the steady state reserve ratio as is predicted by equation(4.23).

Changes in the defended reserve ratio value (μ) act on the rate of structural

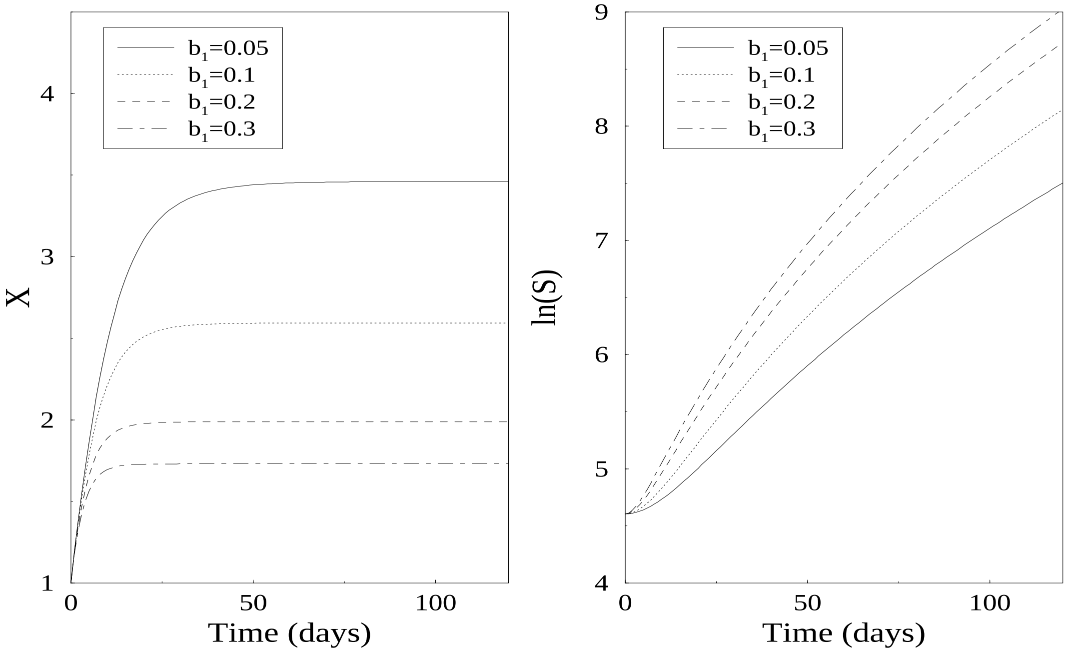

Figure 4.6: *Reserve allocation: the effect of varying b_1 in equation(4.22) on individuals fed excess food. Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are $\phi = 1.0$, $T = 12^oC$, $\mu = 1.0$, $X_0 = 1.0$, $S_0 =$100mgC, $g = d = v = 0.75$.*

growth and changes in reserve ratio values in a similar manner to that of changing b_1. For two conspecifics possessing identical reserve ratio values the one with the lower value of μ would have the greatest difference between current and defended reserve ratio value. Thus, by definition the rate of commitment to structure would be greater for the individual possessing the lowest value of μ. Figure(4.7) shows growth simulations using different values of μ. It can be seen that a decrease in μ serves to increase structural growth rate whilst maintaining a lower reserve ratio threshold. The changes in the steady state reserve ratio values with changes in μ can be ascertained from equation(4.23).

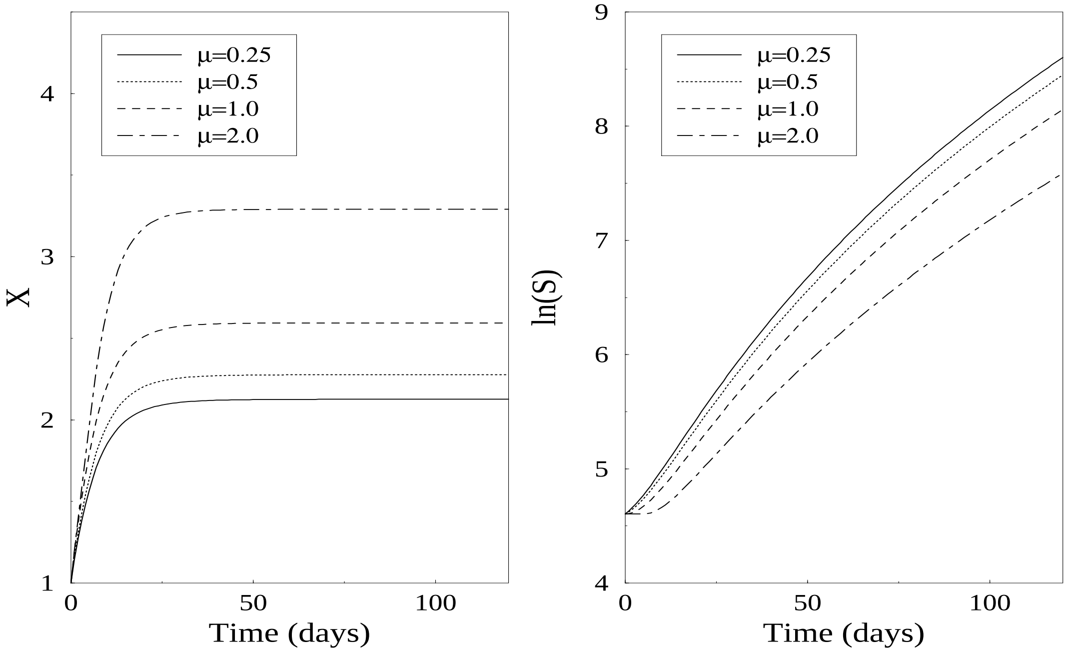

Figure 4.7: *Reserve allocation: the effect of varying μ in equation(4.22) on individuals fed excess food. Trajectories of a) reserve ratio and b) structural carbon. Additional parameter values in conjunction with table(4.1) used to simulate these trajectories are $b_1 = 0.1$, $\phi = 1.0$, $T = 12^oC$, $X_0 = 1.0$, S_0 =100mgC,* $g = d = v = 0.75$.

4.5.4 Maintenance Dynamics

Of special interest is how the reserve allocation model framework will behave when a maintenance ration is supplied (i.e. $A \equiv M$). In the reserve allocation model framework commitment to structure is predominantly governed by reserve status and is not directly related to food supply. Therefore, when a maintenance ration is supplied to initially reserve rich fish commitment to structure continues. When a maintenance ration is supplied then the system dynamics in terms of changes in structure and reserve ratio reduces to

$$\frac{dX}{dt} = -b_1 S^{g-1}(1+X)[X-\mu]^+ \tag{4.24}$$

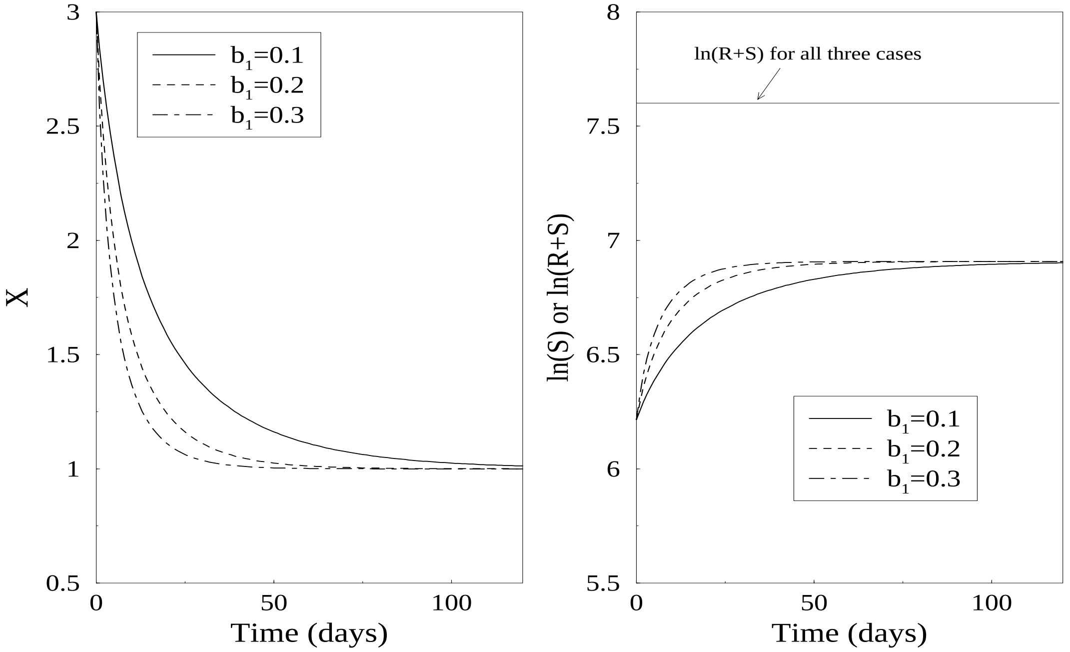

Figure 4.8: *Reserve allocation: the effect of changing* b_1 *in equation(4.22) on individuals fed a maintenance ration (i.e.* $A = M$*). Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $\mu = 1.0$, $T = 12^oC$, $X_0 = 3.0$, $S_0 = 500mgC$, $g = d = v = 0.75$.

$$\frac{dS}{dt} = b_1 S^g [X - \mu]^+. \tag{4.25}$$

Figure(4.8) shows the changes in reserve ratio and structure for initially reserve rich fish with differing values of b_1 in equation(4.22). At the onset of the food restriction period structural growth rate is initially high. Since the net production ($P \equiv A - M$) of the system is zero then this commitment depletes the amount of reserves present. The combination of increasing structural weight with decreasing reserve weight reduces the reserve ratio. As the reserve ratio decreases the rate of commitment to structure decreases because X is heading towards the defended threshold value μ. This is why we observe the reserve ratio to head asymptotically to its defended level whilst structural growth rate gradually reduces until its reaches zero at $X = \mu$. The speed at which X approaches

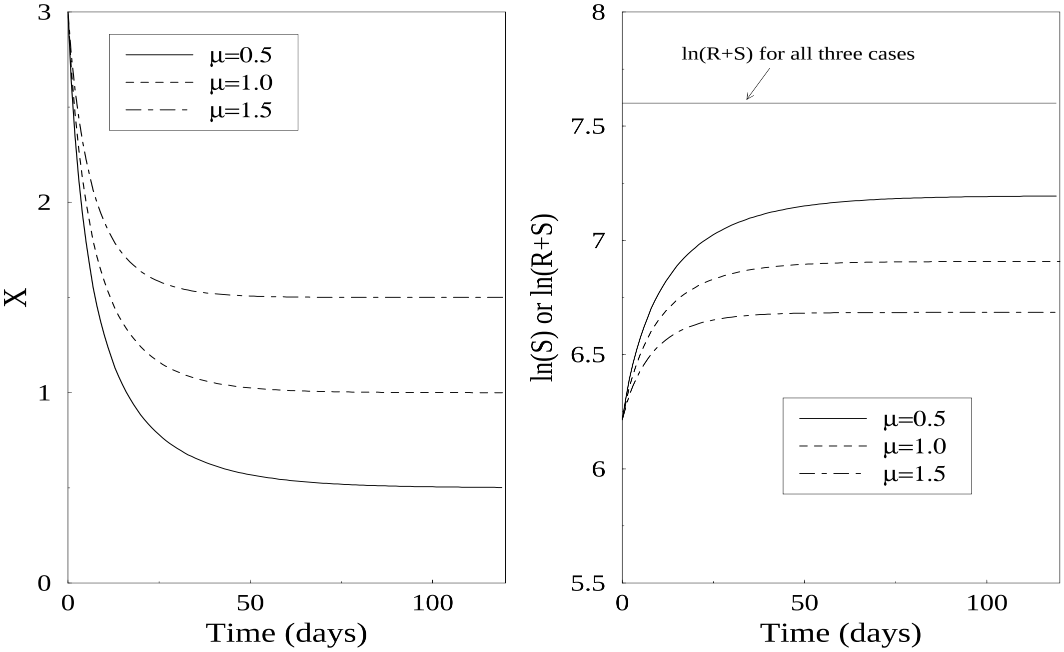

Figure 4.9: *Reserve allocation: the effect of varying* μ *in equation(4.22) on individuals fed a maintenance ration (i.e.* $A = M$*). Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $b_1 = 1.0$, $T = 12^oC$, $X_0 = 3.0$, $S_0 =$*500mgC*, $g = d = v = 0.75$.

μ is affected by the particular value of b_1 chosen. As we have pointed out earlier, increasing b_1 increases the rate of commitment to structure amongst individuals possessing similar reserve ratio values. Hence, increasing b_1 effectively increases the rate at which the reserve ratio heads to μ.

We may also investigate the effect of changing μ the defended reserve threshold for structural growth. Figure(4.9) shows the changes in reserve ratio, structure and also the sum of reserves and structure for initially reserve rich individuals possessing different values of threshold reserve ratio who are subsequently fed a maintenance ration. Since net production is zero for each case the change in the total carbon weight is zero. Once more, for each case the decline in X and hence the rate of structural growth is initially fast. However, the individual with the lowest value of μ obtains the fastest reduction in reserve ratio because the difference in the initial and defended reserve ratio is greatest. Furthermore, this individual with a low value of μ also commits more to structural growth than its cousins with higher values of μ (see figure(4.9)). We shall summarise the major properties of the reserve allocation model and compare these with all other models in section(4.8).

Individuals with high structural growth threshold values (i.e. μ) begin to defend their reserve status much earlier and also commit far less to structure than their cousins with lower reserve ratio threshold values for maintaining growth. By a comparison of figures(4.13) and (4.14) it is clear that changes in μ have a much greater effect on commitment to structure than changes in a_1.

4.6 Assimilation Allocation

4.6.1 Derivation

The assimilation allocation scheme first presented in section(2.5.3) was derived on the principle of strong nutritional constraints on the possible routes of allocation. We stated that the assimilate was composed of two fundamentally different types of nutrients: those which can (structural nutrients) and those that cannot (reserve nutrients) be converted into structure. However, structural nutrients can be converted into reserve tissues or be used directly to meet maintenance. Following a simplifying procedure the model dynamics reduce down to

$$\frac{dS}{dt} = kA, \qquad \frac{dR}{dt} = (1-k)A - M \tag{4.26}$$

where, $k \equiv \delta\gamma$ and γ is the proportion of structural nutrients in the total assimilate A and δ is the proportion of structural nutrients allocated to structure.

Once again, as in the previous model derivations, we shall recast the assimilation class of model in terms of structure and reserve ratio dynamics

$$\frac{dS}{dt} = kA \tag{4.27}$$

$$\frac{dX}{dt} = \frac{1}{S}\left(P - (1+X)kA\right). \tag{4.28}$$

On the basis of there being an observed linear relation between protein consumption and protein growth with an intercept very close to zero (see section(3.4)), we might propose that a constant proportion δ of the structural nutrients $A_{\mathrm{A}} = \gamma A$ in the realised assimilate A is allocated to building structure. For a constant diet formulation this means that $k = \delta\gamma$ is a constant.

4.6.2 Analysis

To investigate the reserve ratio dynamics of the assimilation allocation model with varying opportunity for growth we shall solve for the steady state reserve ratio value X^* by setting $\frac{dX}{dt} = 0$ in equation(4.28) and assume that growth is sustainable (i.e. $A > M$). Following some simple algebra we arrive at

$$X^* = \frac{1}{k}\left(1 - \frac{M}{A}\right) - 1 = \frac{P^+}{kA} - 1. \tag{4.29}$$

The steady state reserve ratio X^* is inversely proportional to k and negatively dependent upon the ratio of maintenance to assimilation rates. From this expression we can predict the effect of ration level will have on reserve status. An increase in ration supply will increase assimilation A and because maintenance is independent of growth rate the net result will be a decrease in the ratio M/A which will in turn increase the steady state reserve ratio value in accordance with equation(4.29).

We can also predict the effect of temperature on reserve ratio with individuals supplied an excess of food. An increase in temperature will serve to increase both maintenance and maximum assimilation. However, maximum assimilation

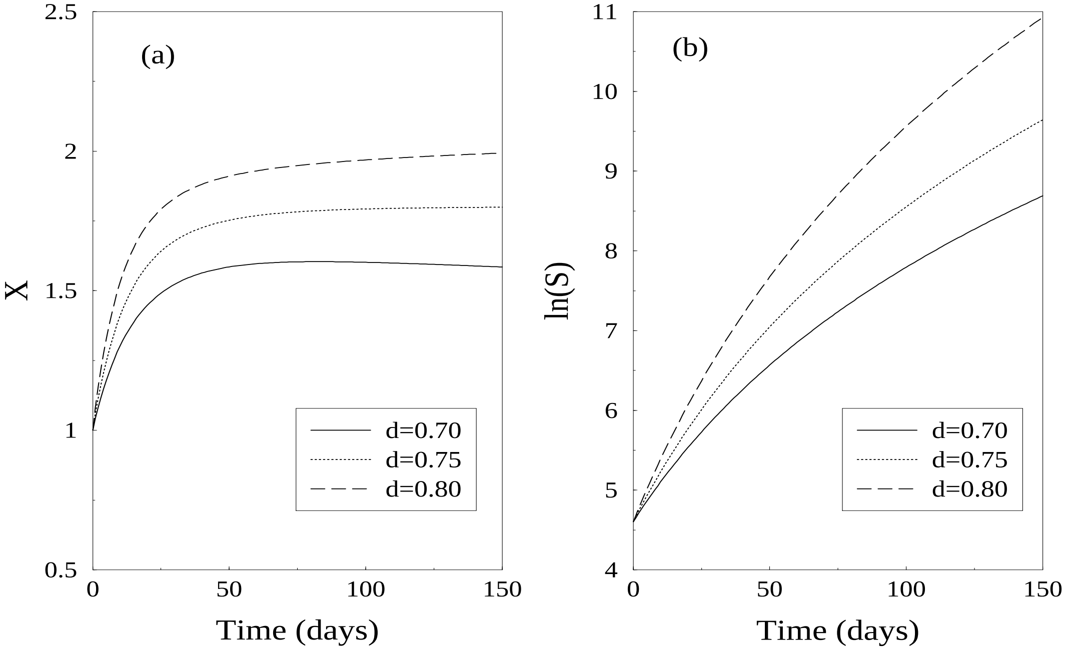

Figure 4.10: *Assimilation allocation: the effect of varying the maximum uptake allometric scaling d in equation(4.1) on individuals supplied with excess food and allocating a fixed proportion k of assimilate to structure. Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $k = 0.3$, $T = 12.0^oC$, $\phi = 1.0$, $X_0 = 1.0$, $S_0 = 100\ mgC$.

will increase faster than maintenance (this must be so, in order that growth rate increases with temperature), which will result in a reduction in M/A and in turn increase X^*.

The reserve ratio dynamics of the assimilation allocation model looks promising because the reserve ratio is related to oppurtunity for growth. To further investigate this model we shall run a number of numerical simulations.

4.6.3 Simulation

Figure(4.10) displays the changes in reserve ratio and structural growth for a set of maximal growth simulations using a constant value of k and different values for the uptake allometric scaling constant d with a constant value of $v = 0.75$ for the maintenance allometric scaling. As in the previous classes of model the small changes in the allometric scaling for uptake can cause large differences in the rate of structural growth.

For each case there is an initial increase in the initially low values of reserve ratio until they eventually pretty much settle down. The faster growing individuals maintain higher reserve ratio values than slower growing conspecifics. Notice also that there is a slight tendency for the long term behaviour of the reserve ratio to change with different choices of allometric scalings. Numerical simulations show that for a constant ration level at a constant temperature then a steady state reserve ratio is achieved if the allometric scalings are equal. In the case where $d > v$ then there is a slight increase in reserve ratio as the organism grows, whereas, if $d < v$ there is a slight decrease as the organism grows (see fig(4.10)).

Figure(4.11) displays the structural growth rate and changes in reserve ratio when fish allocating a fixed proportion of assimilate are fed at a variety of different ration levels. It can be seen that the effect of increasing the ration level is to both increase structural growth rate and for the fish to maintain a higher reserve status. Individuals fed a poorer ration supply have a lower structural growth rate but also maintain a lower reserve status. As predicted by equation(4.29) the steady state reserve ratio value is correlated with ration level and thus growth rate.

Figure(4.12) displays a number of maximal growth simulations for fish allocating a constant proportion k of assimilate to structure held at a range of different temperatures. As the temperature is increased, growth rate increases and the fish maintain a higher reserve status. Individuals held at a low temperature exhibit slower growth but also head to lower reserve value. Again, as predicted by equation(4.29) individuals who are fed an excess ration posses steady state reserve ratio values which are correlated with temperature and thus growth rate.

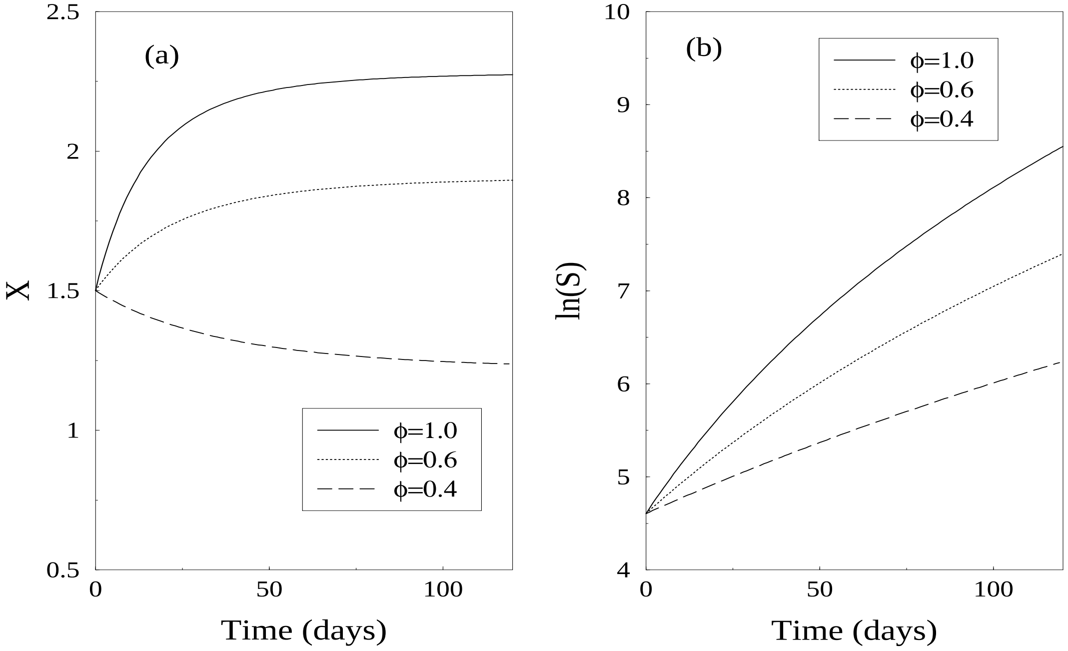

Figure 4.11: *Assimilation allocation: the effect of varying ration level on individuals allocating a fixed proportion k of assimilate to structural growth. Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are $k = 0.25$, $d = 0.75$, $T = 12.0^oC$, $X_0 = 1.5$, $S_0 = 100$ mgC.*

4.6.4 Maintenance Dynamics

When a maintenance ration (i.e. $A = M$) is supplied the assimilation allocation model dynamics reduce down to

$$\frac{dS}{dt} = kA \tag{4.30}$$

$$\frac{dX}{dt} = \frac{-(1+X)kA}{S}. \tag{4.31}$$

Since commitment to structure is made directly from assimilate then structural growth continues. Indeed, under the current rules of allocation the fish would continue allocation to structure indefinitely, which would eventually result in death.

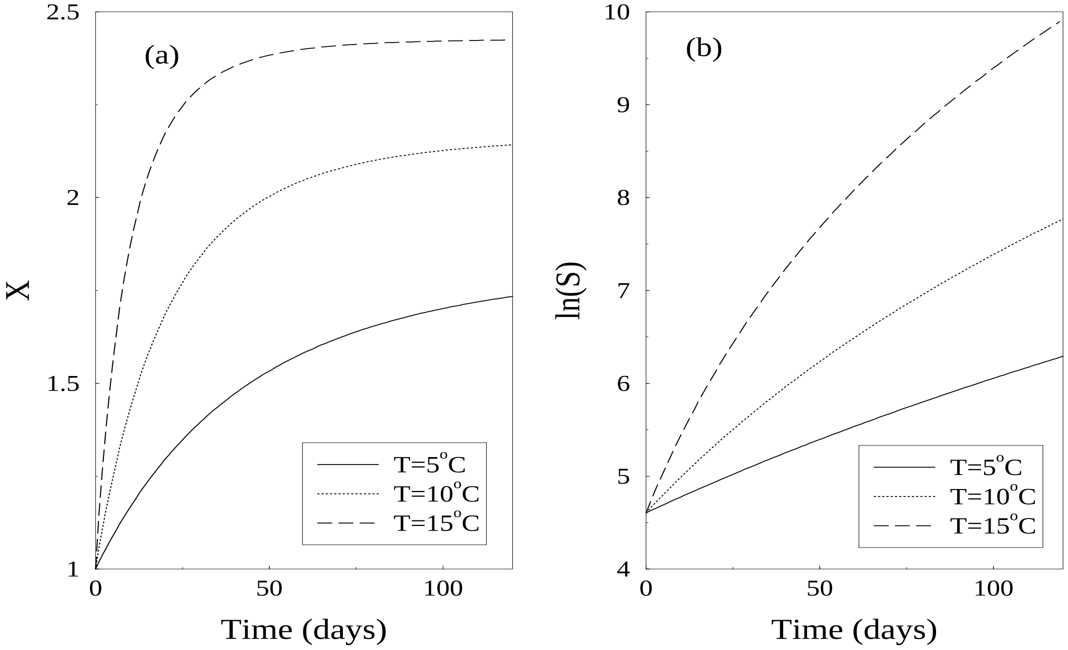

Figure 4.12: *Assimilation allocation: the effect of varying temperature on individuals fed excess food and allocating a fixed proportion* k *of assimilate to structural growth. Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $k = 0.25$, $\phi = 1.0$, $d = 0.75$, $X_0 = 1.0$, $S_0 = 100$ *mgC.*

It is therefore clear that the assimilation allocation model requires a control mechanism to decrease and eventually cease any further allocation to avoid this unreasonable scenario. A reasonable assumption is that this control mechanism should be a function of reserve ratio X.

We shall implement the following mechanism to control allocation

$$\delta(X) = \min\left\{\delta_1, \frac{[X-\mu]^+}{a}\right\} \tag{4.32}$$

where $\delta(X)$ is the proportion of structural assimilate the fish allocates to structure. This function is zero below μ and increases linearly to the nominal constant value of δ_1 with increasing reserve ratio. The reserve ratio value at which $\delta(X)$ begins to decrease is therefore $X = \mu + a\delta_1$.

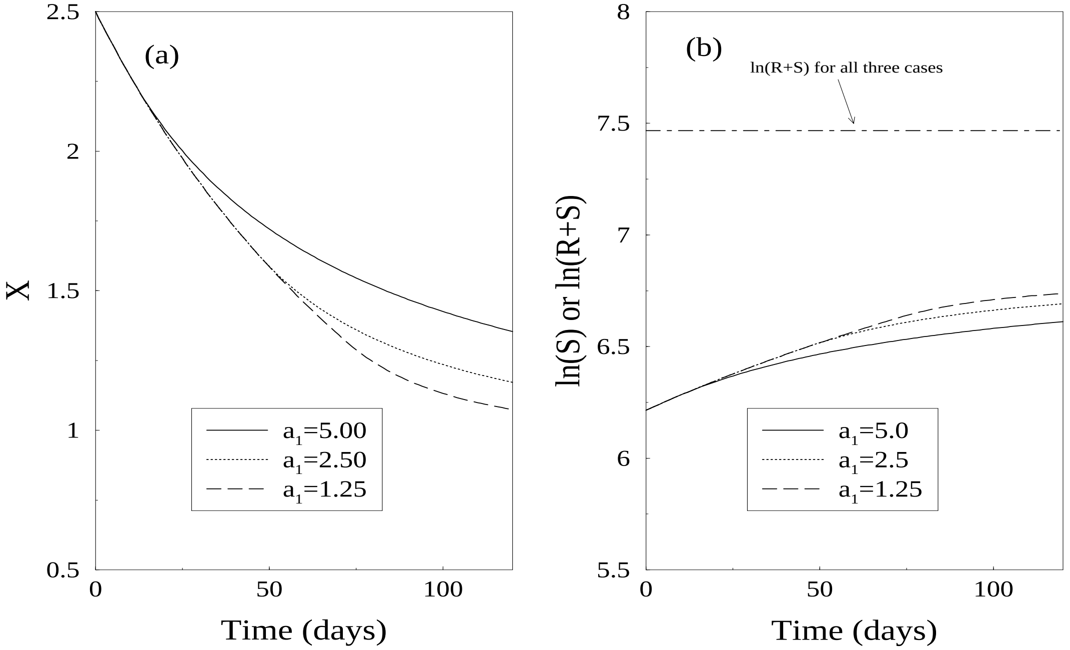

Figure 4.13: *Assimilation allocation: the effect of varying a_1 in equation(4.33) on individuals fed a maintenance ration with the proportion of assimilate allocated to structure now given by equation(4.33). Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are $A = M$, $k_1 = 0.25$, T=12ºC, $v = 0.75$, $X_0 = 3.0$, $\mu = 1.0$, $S_0 = 500$ mgC.*

This means that $k = \gamma\delta(X)$ will change according to

$$k(X) = \min\left\{k_1, \frac{\gamma[X-\mu]^+}{a}\right\} = \min\left\{k_1, \frac{[X-\mu]^+}{a_1}\right\} \tag{4.33}$$

where

$$a_1 = \frac{a}{\gamma} \tag{4.34}$$

which means the organism begins to defend its reserve ratio (i.e. reducing commitment to structure below the nominal proportion of k_1) when $X = \mu + a_1 k_1$.

It is worthwhile noting that this condition need not only be activated when the fish are fed a maintenance ration. If the organism is given a ration such that non-negative growth was possible (i.e. $A \geq M$) yet not enough to maintain a

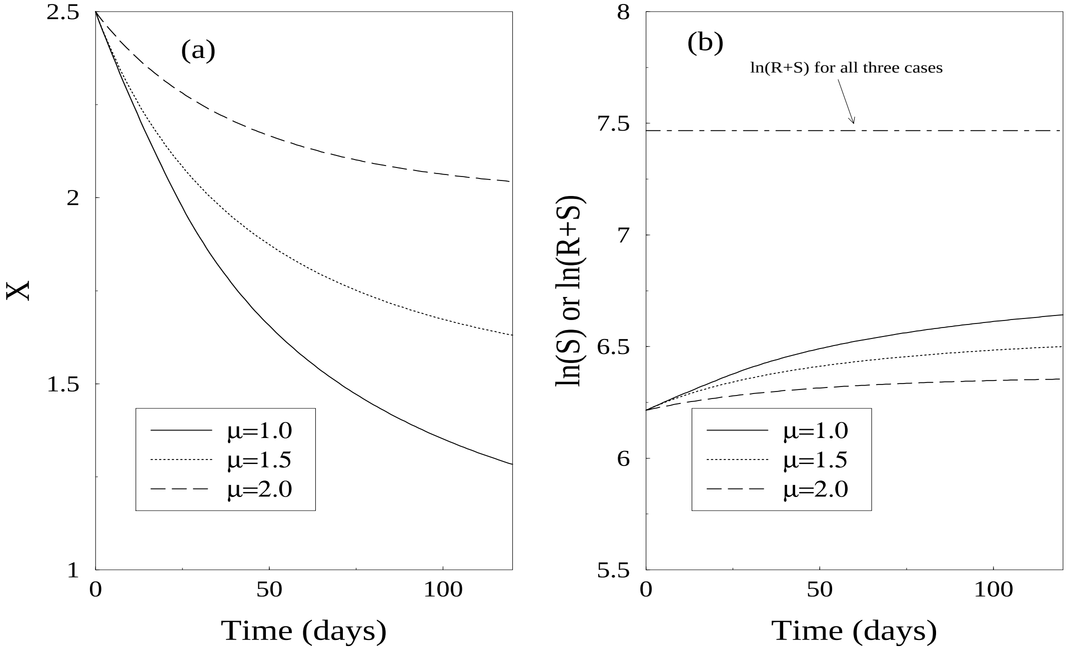

Figure 4.14: *Assimilation allocation: the effect of varying μ in equation(4.33) on individuals fed a maintenance ration with the proportion of assimilate allocated to structure now given by equation(4.33). Trajectories of a) reserve ratio and b) structural carbon weight. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are $A = M$, $k_1 = 0.25$, T=12°C, $v = 0.75$, $X_0 = 3.0$, $a_1 = 2.5$, $S_0 = 500$ mgC.*

value of X greater than $X = \mu + a\delta_1$ then the steady state reserve ratio value is given by

$$X^* = \frac{1}{2}\left[(\mu - 1) + \sqrt{(1+\mu)^2 + \left(\frac{4a_1P^+}{A}\right)}\,\right]. \tag{4.35}$$

Notice the similarity between this expression and the corresponding expression for the reserve allocation model (equation(4.23)). In this transient phase the assimilation allocation model behaves in much the same way as the reserve allocation model, principally because commitment to structure is being controlled by reserve status. However, the difference is that the assimilation allocation model can only control commitment to structure from the immediate assimilate A.

Figure(4.13) displays the changes in reserve ratio and structure for individuals supplied a maintenance ration which possess different values of a_1. Initially, all individuals commit to structure at the same rate resulting in a decrease in reserve ratio from the need to burn reserves to meet maintenance costs. Individuals with higher values of a_1 begin to defend their nutritional condition earlier than individuals with lower values resulting in a reduced rate of commitment to structure.

Figure(4.14) displays the changes in reserve ratio and structure for individuals supplied a maintenance ration whom possess different values of μ. Individuals with high structural growth threshold values (i.e. μ) begin to defend their reserve status much earlier and also commit far less to structure than their cousins with lower reserve ratio threshold values for maintaining growth. By a comparison of figures(4.13) and (4.14) it is clear that changes in μ have a much greater effect on commitment to structure than changes in a_1.

4.7 Starvation Conditions

4.7.1 Net Production and Assimilation Allocation

When a fish is starved of food then by definition the assimilation rate (A) is set to zero. In both the net production and assimilation classes of model, the ultimate commitment to structure is made from the immediate assimilate (A) either before or after maintenance costs have been met. Therefore, for both models, the absence of any external food source ceases any further structural growth immediately and hence the models reduce to the same case.

To remain alive, under starvation conditions, maintenance costs must still be met and thus in the absence of any externally derived nutrients reserves have to be remobilised. For both the net production and assimilation allocation schemes the depletion of reserves from the resultant need to meet maintenance costs means the reserve ratio will change according to

$$\frac{dX}{dt} = -\frac{M}{S} = -\frac{M_{H0}}{S} \exp(T/T_M)(R+S)^v. \qquad (4.36)$$

Since there is no further change in S we can for a constant temperature regime find an analytical solution for the reserve ratio X as a function of time. More interestingly, however, we can solve for the time to death from starvation t_S which occurs when reserve ratio X falls to zero. Following some simple calculus the time to death from starvation is satisfied by

$$t_S = \frac{S_0^{1-v}}{M_{H0}} \left(\frac{(1+X_0)^{1-v} - 1}{1-v} \right) \exp(-T/T_M), \qquad v \neq 1, \qquad (4.37)$$

where S_0 and X_0 denote the structural weight and reserve ratio at the onset of the starvation period ($t = 0$), respectively.

The time to starvation t_s is inversely proportional to the product of both the maintenance cost scaling M_{H0} and exponential temperature scaling – which essentially states that the less the organism has to pay in maintenance the longer it can survive. t_s is also related to the initial reserve ratio indicating the unsurprising result that similarly sized individuals who possess a higher reserve ratio can survive for longer. Perhaps, more interestingly, t_s is also related to a geometric function of the initial structural weight which predicts that larger individuals can survive for longer than smaller individuals.

The latter observation does not imply in anyway that growth restricted individuals who allocate more to structure reduce their risk of starvation. In fact, they are most definitely increasing the risk of starvation, because, maintenance rates are still dependent upon the total carbon weight. As an illustration of this, consider the following scenario. Consider two individuals who initially possess the same size and condition which are both subjected to an equal degree of nutritional restriction and then subsequently starved of food. At the end of the growth-restriction period we can reasonably assume their total carbon weights to be equal (since maintenance rates are dependent upon total carbon weight). However, the nutritional condition of the fish will depend on the degree

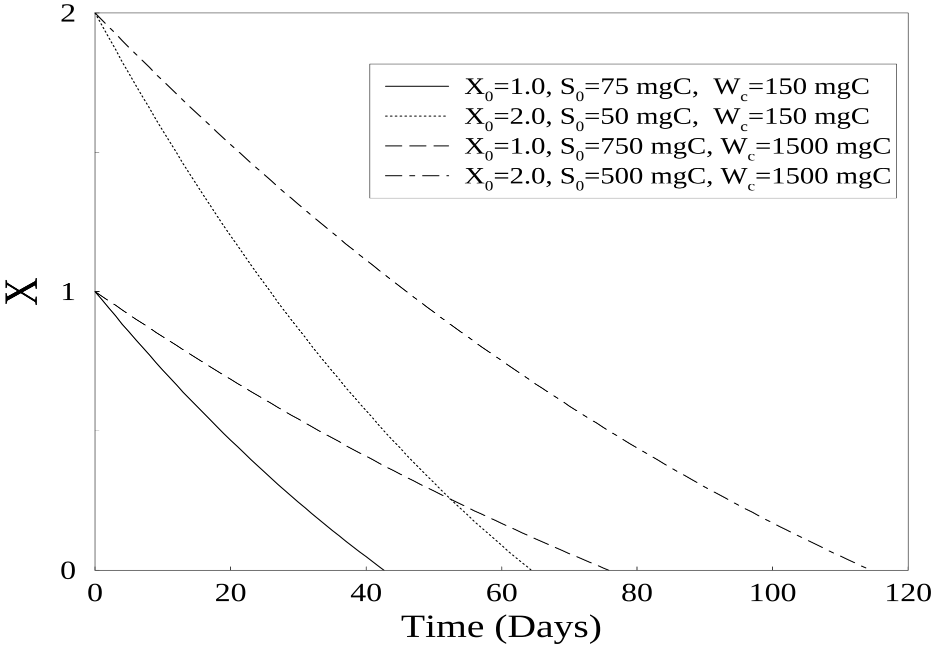

Figure 4.15: *Reserve ratio trajectories for starved individuals of initially different size and condition. All individuals are not allocating any resource to structure. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $A = 0$, *T=12.0* ^oC, $v = 0.75$

of commitment to structure.

Figure(4.15) displays the rates of change in reserve ratio in groups of starved fish whom initially possess equal total carbon weights but different initial values of reserve ratio. Within groups of initially identical values of total carbon weight, individuals with the highest initial value of reserve ratio survive for much longer than individuals who have committed more to structure (and thus reduced levels of reserves). However, it is still clear from this figure that larger individuals can survive for longer than smaller individuals initially possessing identical reserve ratio values.

4.7.2 Reserve Allocation

Within the reserve allocation model, commitment is not made from assimilate but from reserves. This means that the absence of any food does not immediately stop structural growth. When a starvation period is imposed the model dynamics reduce down to

$$\frac{dX}{dt} = -\frac{1}{S}\left(M + X\frac{dS}{dt}\right) \tag{4.38}$$

$$\frac{dS}{dt} = b_1 S^g [X - \mu]^+. \tag{4.39}$$

Therefore, structural growth will continue until $X \leq \mu$. Indeed, at the onset of the starvation period the instantaneous structural growth is at its pre-deprivation rate. When structural growth is cessated (i.e. $X \leq \mu$) then the system dynamics reduce down to the same case as the net production and assimilation allocation model. Therefore, we shall concentrate on the effects of differing initial reserve ratio values on subsequent model behaviour.

Figure(4.16) displays a number of simulations illustrating the behaviour of the reserve allocation model under starvation conditions. Because reserves are being depleted both through conversion to accrete structure and also from the need to meet maintenance costs then the initial decrease in reserve ratio is quick. Individuals with initially high values of reserve ratio do not survive for much longer than less well fed conspecifics, because, this extra energy reserve is allocated to structure.

4.8 General Conclusions

Using simple sensible particular rules of allocation we have investigated the growth and allocation characteristics of each class of allocation scheme in a range of different constant environments. In this section we shall compare and

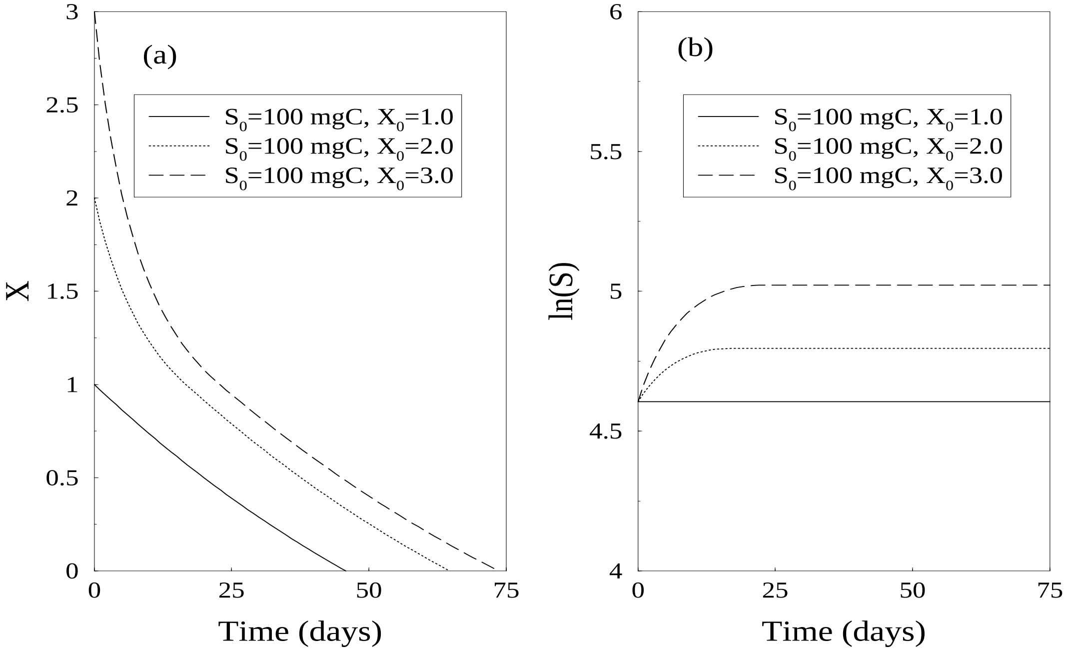

Figure 4.16: *Reserve allocation: trajectories of a) reserve ratio and b) structural carbon weight for starved individuals possessing different initial reserve ratio values and allocating to structure according to equation(4.39). Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $A = 0$, $g = 0.75$, $T = 12.0\ ^oC$, $v = 0.75$, $b_1 = 0.1$, $\mu = 1.0$.

contrast the modelling results with the general qualitative properties of salmonid growth and allocation as reviewed in the previous chapter.

4.8.1 Growth in Relation to Temperature and Ration Level

Assuming a constant proportion of net production is allocated to structure results in the organism heading to a steady state value of reserve ratio which is independent of growth rate, ration and temperature, which is clearly not in agreement with literature reports. By contrast, both the reserve and assimilation allocation models have reserve ratio dynamics which are much more sensitive to growing conditions, although, for completely different reasons.

In the reserve allocation model an increased opportunity for growth first results in an increase in reserves, which, subsequently increases commitment to structure. When opportunity for growth is reduced, commitment to structure initially continues at the same rate, reducing reserve status, and subsequently reducing commitment to structure. This pattern of allocation leads to the long term reserve ratio dynamics being dependent upon net production, which, means that the nutritional condition of the fish is a function of ration level and temperature. Thus, the steady state reserve dynamics are in accordance with the literature.

By assuming that a constant proportion of assimilate is allocated to structure we again arrive at a system in which reserve status is dependent upon growing conditions. At a constant temperature an increase in consumption immediately serves to increase structural growth rate. However, this increased consumption increases the rate of reserve accumulation in greater proportion to structure leading to an increase in reserve ratio until eventually a balance is struck. When the ration supply is reduced, commitment to structure continues in proportion to consumption rate which means that commitment to reserves is reduced leading to a decrease in the reserve status. These allocation dynamics means that the steady state reserve ratio value is dependent upon the ratio of net production to assimilation. Since a reduction in temperature serves to decrease assimilation faster than net production then this still results in a decreased value of reserve ratio. Thus, in accordance with the literature, the nutritional condition of the fish is related to the ration supply and temperature.

4.8.2 Restricted Growth

The ability of animals to maintain structural (protein) growth when fed a low ration has been noted for other animals as well as for fish. In some cases it is even possible for the animals to be in a negative energy balance when fed a low ration yet still be accreting protein, that is, burning lipid stores to meet metabolic costs and using the amino acids in the food supply to maintain structural protein growth (e.g. Jones and Farrell (1992b); Jones and Farrell (1992a); Hornick et al. (2000); Yu et al. (1990)).

By its very definition the net production model cannot predict a change in body constituents when a fish is fed a maintenance ration or less. On the other hand, both the other models predict the fish to always maintain structural growth until the no growth boundary is reached (i.e. $X = \mu$) when fed a maintenance ration. Individuals do not always maintain structural growth when fed a very low ration. Perhaps, because the achieved growth does not warrant the costs in maintaining the biochemical machinery necessary to sustain growth. It is hard to legislate for such inconsistencies. Nevertheless, the net production model cannot possibly predict a change in body constituents when fed a maintenance ration, whereas, a slight modification to the other models would make them behave differently when a low ration level is supplied.

It is worthwhile noting that with the assimilation allocation scheme changes in body constituents on a low ration take place quite slowly because allocation can only be made from assimilate. Changes in the reserve allocation model take place more quickly because allocation is made from reserves and is not directly limited by the current food supply.

4.8.3 Starvation

Under starvation conditions the net production and the assimilation allocation models reduced down to the same case because structural growth is ceased immediately and independently of reserve status. This meant that we could find an analytical solution for starvation energy losses in a constant temperature regime. The final solution gives some strong predictions about the rate of energy losses and therefore the time to starvation. The most intriguing being, that larger individuals can survive for longer than smaller individuals. These modelling predictions are in good accordance with literature reports.

For example, Sogard and Olla (2000) found that large body size, high initial condition and cold temperatures all increased survival rates in starving fish. Similar conclusions have been made by Miranda and Hubbard (1994) and Post and Parkinson (2001), whilst Cargnelli and Gross (1997) noted that larger individuals emerged from winter in a better nutritional condition.

This strong relationship between starvation risk and size exists because of the negative allometric relationship between metabolism and body size (Post et al. 1998). This means that young small fish are at a particular high risk of starvation ((Gardiner and Geddes 1980); Post et al. (1998)). Yet, despite this, slower growing smaller individuals still maintain lower levels of reserves than faster growing larger conspecifics. The relationship between body size and the ability to withstand periods of starvation is an important contributing factor to size-selective mortality effects (Sogard 1997).

The reserve allocation model predicts a continued deposition of structural masses when fish are starved. This essentially negates any nutritional advantage possessed at the onset of the starvation period. Studies mostly show that length increases in starving fish are miniscule if present at all (e.g. see figure(6.5) and table(9.3)), even amongst individuals whom initially posses a high nutritional condition (Einen et al. 1998). This is probably one of the principal motivations behind the net production model (e.g. Broekhuizen et al. (1994)).

Chapter 5

Modelling the Effects of Diet Formulation

5.1 Introduction

It is clear from the literature that the composition of the diet has a substantial effect on the relative tissue deposition patterns of fish. In particular, diet formulations with high levels of lipid lead to an increase in lipid deposition but do not lead to any great, if any, increases in protein deposition. The route cause of changes in deposition patterns attributable to different diet formulations occur as a physiological consequence of nutrient and not energy allocation in fish. Basically, these changes arise because lipid cannot be directly converted into protein. Hence, the reason why the inclusion of high levels of lipid in the diet only has a weak interaction with the processes involved in protein accretion.

In the reserve allocation scheme all assimilate is first directed into a common reserve pool. At this point any nutritional information regarding the food supply is lost. Therefore, it is clear that the reserve allocation scheme will not be suitable for modelling the effects of diet formulation. By contrast, the assimilation allocation class of model was specifically derived on the basis of nutrient allocation in fish making it the obvious candidate for modelling the effects of diet formulation.

5.2 The Composition of the Diet

Under normal healthy conditions, when food supply is in abundance, fish are able to compensate for high levels of water in their diets but are less able to immediately compensate for low energy high dry weight feeds (Larsson and Berglund (1998); Elliott and Hurley (1998b); Bromley and Adkins (1984); Hilton et al. (1972)). Therefore, we should mainly expect the uptake U to correspond to the dry (carbon) weight of the ingested feed.

The fish's uptake U will consist of several different components whose relative quantities will depend upon the formulation of the diet or the composition of the prey. However, we can initially partition the uptake into two different components such that

$$U = U_{\mathrm{D}} + U_{\mathrm{N}} \tag{5.1}$$

where U_{D} is the digestible component of the dietary uptake and U_{N} is the non-digestible component of the dietary uptake. These two quantities can be expressed as a proportion of the total uptake as follows

$$U_{\mathrm{D}} = \gamma_{\mathrm{D}} U \tag{5.2}$$

$$U_{\mathrm{N}} = (1 - \gamma_{\mathrm{D}}) U \tag{5.3}$$

where γ_{D} is the digestible fraction of the total uptake U and is thus a measure of the quality of the diet.

We can partition the digestible proportion of the diet into essentially two components such that

$$U_{\mathrm{D}} = U_{\mathrm{A}} + U_{\mathrm{L}} \tag{5.4}$$

where U_{A} is the component of the diet that can possibly be converted into structural assimilate and U_{L} is the component of the diet that cannot be converted into structural assimilate. U_{A} will be mostly composed of protein and a small amount of inorganic minerals necessary to build the skelature. U_{A} will be mostly composed of lipids but also a small amount of carbohydrates.

We can now recast the proportion of structural and non-structural nutrients in the total uptake as follows

$$U_{\mathrm{A}} = \gamma_{\mathrm{D}}\gamma_{\mathrm{A}}U \tag{5.5}$$

$$U_{\mathrm{L}} = \gamma_{\mathrm{D}}(1-\gamma_{\mathrm{A}})U \tag{5.6}$$

where γ_{A} is the proportion of structural nutrients in the digestible part of the diet.

5.3 Equal Processing Costs for Reserve and Structural Nutrients

5.3.1 Derivation

Our next step will be to investigate the relationship between diet composition and the growth and allocation patterns predicted by the assimilation allocation model. As a first approximation we shall assume that the costs in making one unit of non-structural assimilate (A_{L}) from the non-structural nutrients supplied in the diet are the same as making one unit of structural assimilate (A_{A}) from the structural nutrients supplied in the diet. This assumption allows one to write the total assimilate (A) as

$$A = \epsilon(U_{\mathrm{A}} + U_{\mathrm{L}}) = \epsilon\gamma_{\mathrm{D}}U \tag{5.7}$$

where ϵ is the efficiency of converting structural and/or non-structural nutrients in the diet into one unit of structural and/or non-structural assimilate.

This assumption means that we can now write the different nutrient components of the total assimilate as follows

$$A_{\mathrm{A}} = \epsilon U_{\mathrm{A}} = \epsilon \gamma_{\mathrm{A}} \gamma_{\mathrm{D}} U \tag{5.8}$$

$$A_{\mathrm{L}} = \epsilon U_{\mathrm{L}} = \epsilon (1 - \gamma_{\mathrm{A}}) \gamma_{\mathrm{D}} U. \tag{5.9}$$

Having identified the different nutritional components of the assimilate as a function of the quality and relative proportions of nutrients in the diet we shall apply the assimilation allocation model.

The assimilation allocation model states that a healthy fish allocates a constant proportion δ of the structural assimilate (A_{A}) to building structure which together with equation(5.8) can be related directly to the food supply by

$$\frac{dS}{dt} = \delta A_{\mathrm{A}} = \delta \epsilon \gamma_{\mathrm{A}} \gamma_{\mathrm{D}} U. \tag{5.10}$$

The remaining $(1 - \delta) A_{\mathrm{A}}$ plus the non-structural nutrients in the assimilate are added to reserves from which maintenance expenditure is debited. We can relate the change in reserves directly to the food supply by using equations(5.8) and (5.9) as follows

$$\begin{aligned} \frac{dR}{dt} &= A_{\mathrm{L}} - (1 - \delta) A_{\mathrm{A}} - M \\ &= \epsilon \gamma_{\mathrm{D}} (1 - \gamma_{\mathrm{A}} \delta) U - M. \end{aligned} \tag{5.11}$$

If we now use equation(5.7) to relate the dietary uptake (U) to the assimilate (A) we can redefine the assimilation efficiency ε as follows

$$\varepsilon = \epsilon \gamma_{\mathrm{D}}. \tag{5.12}$$

Furthermore, if we now redefine k such that

$$k \equiv \delta \gamma_{\mathrm{A}} \tag{5.13}$$

then the full system dynamics reduce down to the familiar assimilation allocation form as follows

$$\frac{dS}{dt} = kA \tag{5.14}$$

$$\frac{dR}{dt} = (1 - k)A - M. \tag{5.15}$$

5.3.2 Increasing the Proportion of Lipid in the Diet

Changes in the diet quality will change γ_{D}. An increase in the proportional digestible components of the diet will increase γ_{D} and a decrease in the proportion of dietary digestible components will decrease γ_{D}. Changes in the relative proportions of nutrients in the diet formulation will change γ_{A}. An increase in the proportion of lipid with a corresponding reduction of protein will reduce γ_{A}. Likewise, an increase in the protein proportion with a corresponding reduction in lipid will increase γ_{A}.

Because the assimilation rate is independent of γ_{A} (see equation(5.7)) then as long as the quality of each diet remains the same the only effect of changing the relative proportions of structural and non-structural nutrients in the diet will be to change γ_{A}. Therefore, an increase in the relative proportion of lipid in the diet will reduce γ_{A} and in turn reduce $k \equiv \delta\gamma_{\mathrm{A}}$.

Figure(5.1) displays a number of maximal growth simulations using several different values of k. The effect of decreasing k (increasing lipid proportion) is to reduce the rate of structural growth and increase the rate of reserve accumulation. Individuals fed a low fat diet (increasing k) accumulate more structure

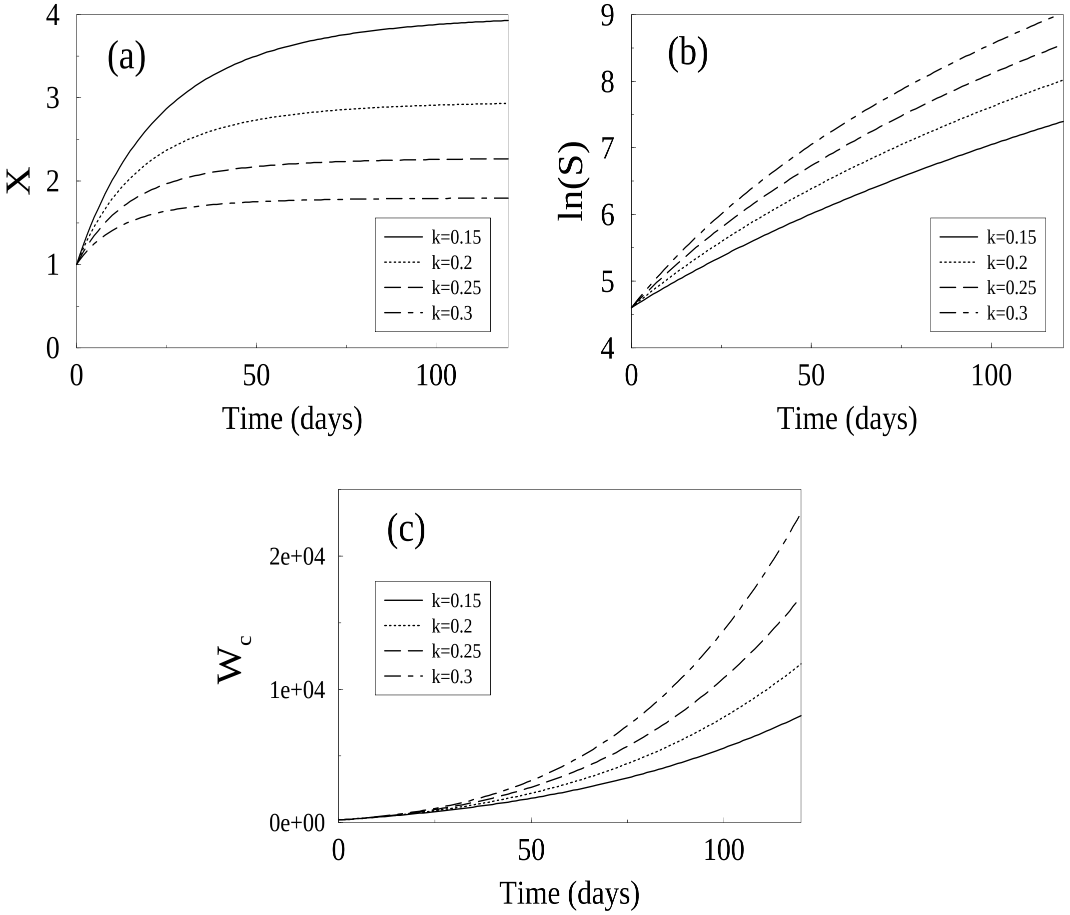

Figure 5.1: *Trajectories of a) reserve ratio, b) structural carbon weight and c) total carbon weight for the assimilation allocation model using several different constant values of* k*. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $\phi = 1.0$, $T = 12^oC$, $X_0 = 1.0$, S_0 *=100mgC,* $d = v = 0.75$.

and maintain a lower reserve ratio. However, low fat fed individuals have a significantly greater final carbon weight because the increased rate of commitment to structure has allowed them to make better use of the excess food supply.

The usual experimental protocol when investigating the effects of high lipid levels in the diet is to feed groups of fish the same amount of protein but differing amounts of lipid (e.g. Boujard et al. (2000)). To accomplish this the usual procedure is to add a non-digestible diet filler (such as cellulose) to the low fat feed so that both diet formulations have the same percentage protein on a dry weight basis. The experimenter then feeds both groups of fish an equal or excess ration supply. We shall investigate what effect this has on the composition of the assimilate and apply it to the assimilation allocation model.

Consider a unit of dietary uptake (U) which has a constant proportion ($0 \leq c_1 \leq 1$) of structural nutrients ($U_{\rm A} = c_1 U$) but a variable proportion of non-structural nutrients and a corresponding variable non-digestible proportion. We can write the three components of the diet as follows

$$U_{\rm A} = c_1 U, \qquad U_{\rm L} = \eta U, \qquad U_{\rm N} = (1 - c_1 - \eta) U \tag{5.16}$$

where $0 \leq \eta \leq 1 - c_1$.

Now consider the effect of changing η on $\gamma_{\rm D}$ and $\gamma_{\rm A}$. From equation(5.2)

$$\gamma_{\rm D} = \frac{U_{\rm A} + U_{\rm L}}{U} = \frac{c_1 U + \eta U}{U} = c_1 + \eta \tag{5.17}$$

and we can write

$$\gamma_{\rm A} = \frac{U_{\rm A}}{U_{\rm A} + U_{\rm L}} = \frac{c_1 U}{c_1 U + \eta U} = \frac{c_1}{c_1 + \eta}. \tag{5.18}$$

If we apply these functions to the assimilation allocation model then we (using equation(5.10)) that the structural weight will change according to

$$\frac{dS}{dt} = \delta\epsilon \frac{c_1}{c_1 + \eta}(c_1 + \eta) U = \delta\epsilon c_1 U \tag{5.19}$$

and from equation(5.11) reserves will change according to

$$\frac{dR}{dt} = \epsilon(c_1(1 - \delta) + \eta) U - M. \tag{5.20}$$

Notice that structural growth rate is independent upon η with all the benefit of increasing the lipid content being placed on reserves. As long as the amount of structural nutrients in the diet is constant the product $\gamma_{\rm D}\gamma_{\rm A}$ remains constant.

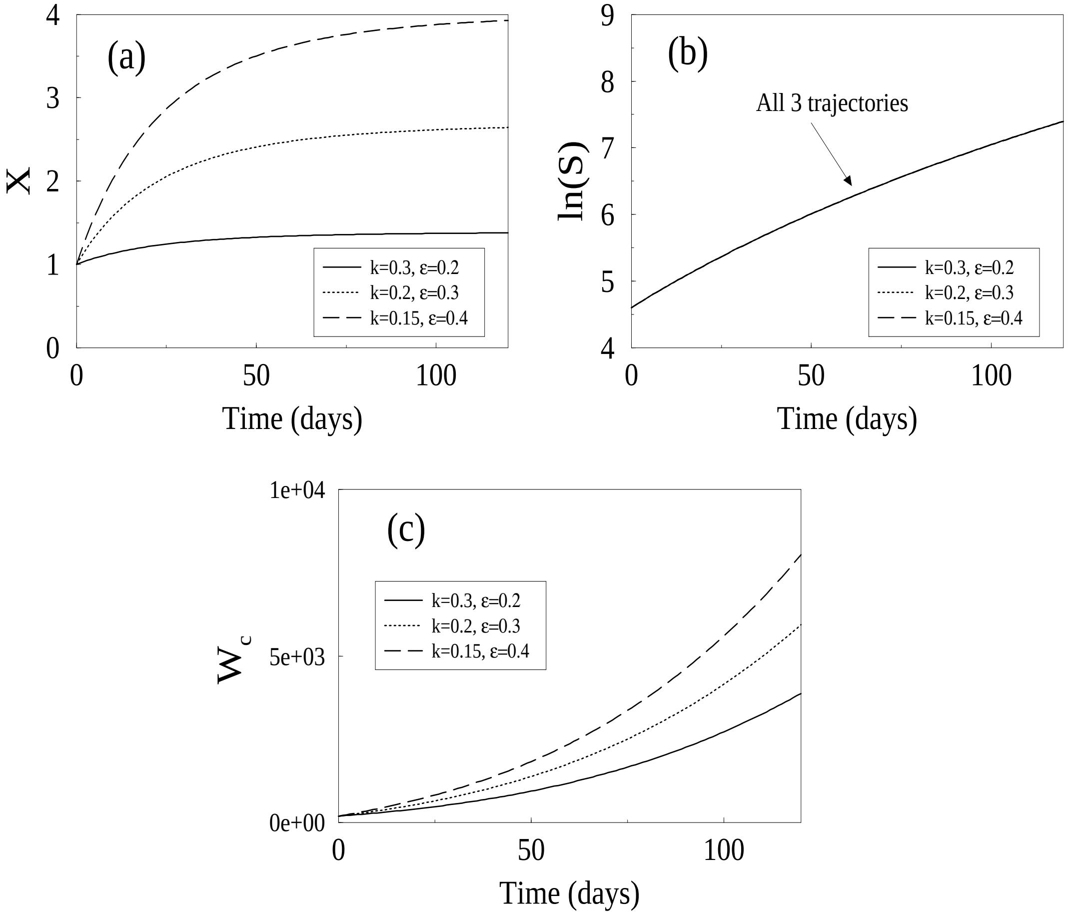

Figure 5.2: *Trajectories of a) reserve ratio, b) structural carbon weight and c) total carbon weight for the assimilation allocation model using composite values of* k *and* ε *such that their product* $k\varepsilon$ *remains constant at 0.06. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $\phi = 1.0$, $T = 12^oC$, $X_0 = 1.0$, $S_0 =$ *100mgC,* $d = v = 0.75$.

As the lipid in the diet is increased γ_{D} increases and γ_{A} reduces. This will cause $k = \delta\gamma_U$ to reduce and assimilation $A = \epsilon\gamma_{\mathrm{D}}U$ to increase such that kA remains constant. Because γ_{D} has been absorbed into the assimilation efficiency term (i.e. $\varepsilon = \epsilon\gamma_{\mathrm{D}}$) then we can express the effect of increasing the lipid in the diet whilst holding the protein content constant by choosing different values of k and ε such that their product remain constant.

Figure(5.2) displays a number of maximal growth simulations using different values of ε and k such that their product remains the same. The effect of increasing the proportion of non-structural nutrients whilst holding the proportion of structural nutrients constant (increasing ε, decreasing k) is simply to increase the reserve growth rate. For all three growth trajectories the structural growth rate has remained the same and the difference in the final total carbon weights is only as a consequence of an increase in reserve carbon weight.

5.3.3 Increasing the Proportion of Protein in the Diet

Unlike the mechanisms involved in the deposition of lipids there seems to be a clear cut maximum rate at which protein can be accreted into the body. Without this phenomena being incorporated into the model a continual increase in the structural nutrients within the diet (i.e. increasing γ_{A}) will always serve to increase growth rate (see fig(5.1)) which certainly does not comply with the literature. Therefore, the assimilation allocation scheme needs to be modified to incorporate this upper limit on structural growth.

We can incorporate an upper limit on structural growth rate by stating

$$\frac{dS}{dt} = \min\left\{\delta A_{\mathrm{A}}, \Omega\right\} \tag{5.21}$$

where Ω is the maximum possible rate of structural growth for a given size and temperature. When the attempted commitment to structure (δA_{A}) is greater than the maximum possible we shall assume that the excess is redirected to the reserves pathway. To satisfy this conservation of nutrients and because A_{A} is only a function of the diet and ration size it is clear that δ must reduce to satisfy $\delta A_{\mathrm{A}} = \Omega$ when the attempted commitment to structure is greater than maximal growth will allow. This means that δ must now be modified such that it is some function of the maximal structural growth rate Ω.

We can recast the rate of structural growth as follows

$$\frac{dS}{dt} = \Omega \phi_S \tag{5.22}$$

where $0 \leq \phi_S \leq 1$ is the fraction of maximum structural growth at which the individual is growing.

Under normal conditions the rate of structural growth within the assimilation allocation scheme is proportional to the assimilation rate which using a constant diet formulation is proportional to the uptake rate. Therefore a reasonable assumption would be that the maximum structural growth rate scales with maximum uptake such that

$$\Omega = \omega U_H = A_{H0} S^d f(T) \tag{5.23}$$

where $A_{\mathrm{H0}} = \omega U_{H0}$ is the maximum structural growth rate scaling and $f(T)$ is the temperature scaling function for maximum food uptake.

Using equations(5.21) and (5.22) we can ascertain under what combination of conditions structural growth will approach maximum i.e. $\phi_A = 1.0$. By using equations(5.8) and (2.23) we can express the fraction of maximum structural growth as follows

$$\phi_S = \frac{\delta \epsilon \gamma_{\mathrm{D}} \gamma_{\mathrm{A}} U_{H0} \phi}{A_{H0}} \tag{5.24}$$

which is a function of many different parameters. However, there are essentially only three parameters which are under exogenous control, namely, the quality of the diet γ_{D}, the relative amount of structural nutrients in the diet γ_{A}, and the ration level ϕ. It is the product of these three parameters that will determine whether the maximum structural growth rate is achieved. Consequently, there are a number of different situations under which ϕ_S can reach one. For instance, if a certain diet type possessed a proportional amount of structural nutrients to accomplish maximal structural growth rate on a maximum uptake ($\phi = 1$) then a reduction in ration with a corresponding increase in the relative proportion of structural nutrients would still keep $\phi_S = 1$, as has been reported by Ogino (1980)(see figure(3.7)).

When the attempted commitment to structure is greater than maximal will allow

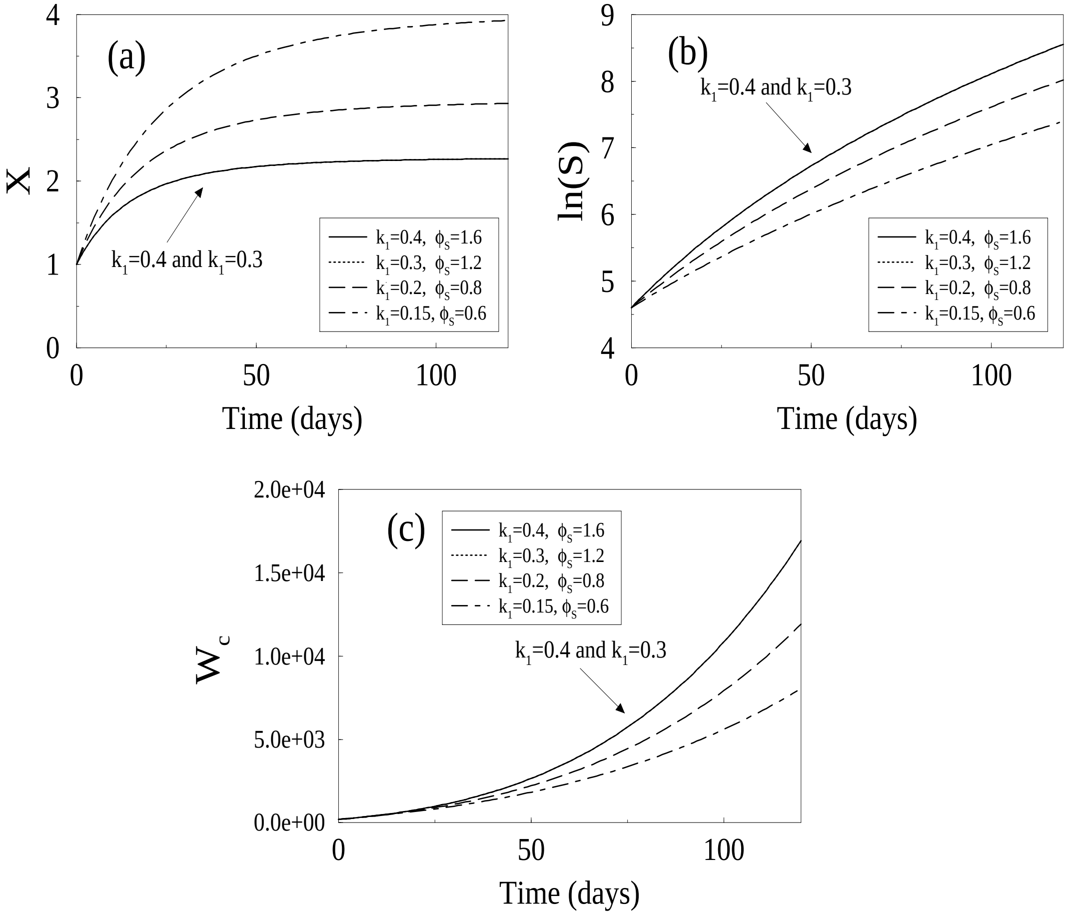

Figure 5.3: *Trajectories of a) reserve ratio, b) structural carbon weight and c) total carbon weight for the assimilation allocation model using different values of k_1 where there is an imposed upper limit on the rate of structural growth. The quantity ϕ_S is the attempted proportion of maximum at which structural growth is trying to be achieved. The actual proportion of the total assimilate allocated to structure k is defined by equation(5.26). Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are $A_{H0} = 0.024$, $\phi = 1.0$, $T = 12^oC$, $X_0 = 1.0$, $S_0 =$100mgC, $d = v = 0.75$.*

we shall use the following function to limit commitment to structural growth

$$\delta(\phi_S) = \min\left\{\delta_1, \frac{\delta_1}{\phi_S}\right\} \tag{5.25}$$

where δ_1 is the nominal constant proportion of structural assimilate a healthy fish commits to structure. This will have a similar effect on the proportion of the total assimilate allocated to structure k which we can write as

$$k(\gamma_{\mathrm{A}}, \phi_S) = \min\left\{k_1, \frac{k_1}{\phi_S}\right\} \tag{5.26}$$

where k_1 is the nominal constant commitment of total assimilate to structure a healthy fish feeding on a constant diet commits to structure.

Figure(5.3) displays a number of maximal growth simulations using different values of k_1. As k_1 is increased (i.e. an increase in the proportion of structural nutrients within the diet) there is an increase in the rate of structural growth. However, growth rate only increases until the maximum structural growth rate has been reached. Once the proportion of structural nutrients in the diet are enough to achieve the maximum structural growth rate any further increase in k_1 has no effect on the rate of accumulation of reserves or structure. Individuals on a low protein diet (low values of k_1) have a lower structural growth rate but maintain a higher reserve ratio. However, once again the final carbon weight is greater for the individuals on the high protein diet because the increased rate of commitment to structure has allowed them to make better use of the plentiful food supply.

5.4 Differential Processing Costs for Reserve and Structural Nutrients

5.4.1 Derivation

Until now we have assumed equal processing costs for the reserve and structural nutrients supplied in the food. This has allowed us to simplify the dynamics and investigate what major consequences different diet formulations will have on the behaviour of assimilation allocation model. However, it is likely that the costs associated with processing structural nutrients will be more than the costs associated with processing reserve nutrients.

One of the major reasons for this is that the mechanisms involved in the synthesis of proteins into the body are more complex than the processes involved with the deposition of lipids into the body (Tytler and Calow (1985); Hochachka and Mommsen (1995)). Also, the amino acids supplied in the diet which are not synthesised into protein must first be deaminated (the process of removing the nitrogen from the nitrogen rich amino acids) before being used as an energy source or being converted into lipid (Hochachka and Mommsen 1995). This means that the conversion efficiency in using protein as an energy source will be less than for using lipids as an energy source.

We shall incorporate these differential costs by using different assimilate conversion efficiencies for the different nutrients supplied in the diet. Thus, we write

$$A_{\mathrm{A}} = \epsilon_{\mathrm{A}} U_{\mathrm{A}} \tag{5.27}$$

$$A_{\mathrm{L}} = \epsilon_{\mathrm{L}} U_{\mathrm{L}} \tag{5.28}$$

where, ϵ_{A} is the conversion efficiency in processing structural nutrients to structural assimilate and ϵ_{L} is the conversion efficiency in processing non-structural nutrients to non-structural assimilate. The total assimilate can now be written as

$$A = \gamma_{\mathrm{D}}(\epsilon_{\mathrm{A}} U_{\mathrm{A}} + \epsilon_{\mathrm{L}} U_{\mathrm{L}}). \tag{5.29}$$

If the digestible proportion of the diet consists of γ_{A} structural nutrients then the total assimilate can be written as

$$A = \gamma_{\mathrm{D}} U(\epsilon_{\mathrm{A}} \gamma_{\mathrm{A}} + \epsilon_{\mathrm{L}}(1 - \gamma_{\mathrm{A}})). \tag{5.30}$$

If we now say that $\epsilon_{\mathrm{L}} = \zeta \epsilon_{\mathrm{A}}$, where, $\zeta > 1$ then the total assimilate can be recast as follows

$$A = \gamma_{\mathrm{D}}\epsilon_{\mathrm{A}}U(\gamma_{\mathrm{A}} + \zeta(1-\gamma_{\mathrm{A}})). \tag{5.31}$$

Notice that for a unit of a constant quality uptake the total amount of assimilate changes with the relative proportion of different nutrients.

We shall now apply this to the assimilation allocation model. Structural carbon weight will change according to

$$\frac{dS}{dt} = \delta A_{\mathrm{A}} = \delta\epsilon_{\mathrm{A}}\gamma_{\mathrm{D}}\gamma_{\mathrm{A}}U \tag{5.32}$$

and the change in reserve carbon weight (following some simplification) can be described as

$$\frac{dR}{dt} = \epsilon_{\mathrm{A}}\gamma_{\mathrm{D}}U\left(\zeta(1-\gamma_{\mathrm{A}}) + \gamma_{\mathrm{A}}(1-\delta)\right) - M. \tag{5.33}$$

It can be seen that the previous derivation assuming equal processing costs is just a special case of the above system dynamics with $\zeta = 1$, that is, $\epsilon_{\mathrm{L}} = \epsilon_{\mathrm{A}}$. Under the new more realistic assumption the structural growth rate is still proportional (under healthy non-limiting conditions) to the proportion of structural nutrients in the diet and is independent of the amount (not proportion) of non-structural nutrients in the diet supply. As ζ is increased all the gain in the assimilate (see equation(5.31)) is only benefitted by reserves. This means that for any fixed proportion of relative nutrients in the diet (i.e. γ_{A}) the assumption of equal processing costs can only predict a leaner individual than would be predicted by assuming differential processing costs with $\epsilon_{\mathrm{L}} > \epsilon_{\mathrm{A}}$.

We can illustrate this further by solving for the steady state reserve ratio (X^*) which gives

$$X^* = \frac{1}{\delta\gamma_{\mathrm{A}}}\left(\zeta(1-\gamma_{\mathrm{A}}) + \gamma_{\mathrm{A}}(1-\delta) - \frac{M}{\epsilon_{\mathrm{A}}\gamma_{\mathrm{D}}U}\right). \tag{5.34}$$

As long as the allometric scalings for uptake and maintenance are identical the above steady state will be achieved (see section(4.6)). From this expression we can gather that for any fixed cost of producing structural assimilate (i.e. $\epsilon_{\rm A}$) the effect of an increase in ζ can only be to increase the reserve ratio (with the obvious proviso that $\gamma_{\rm A} < 1$).

In this new modified assimilation allocation model we cannot group together δ and $\gamma_{\rm A}$ to form the composite parameter k, that is, the proportion of total assimilate allocated to structure. The actual proportion of the total assimilate, say $k_{\rm A}$, which is committed to structure is now given by

$$k_{\rm A} = \frac{\delta\gamma_{\rm A}}{\gamma_{\rm A} + \zeta(1-\gamma_{\rm A})} \tag{5.35}$$

which reduces down to the earlier definition of k when $\zeta = 1$.

The assimilation efficiency defined by $\varepsilon = A/U$ using equation(5.31) can be expressed as

$$\varepsilon = \gamma_{\rm D}\epsilon_{\rm A}(\gamma_{\rm A} + \zeta(1-\gamma_{\rm A})) \tag{5.36}$$

which once again reduces down to the earlier definition when $\zeta = 1$.

The dynamics of the new assimilation allocation model which accounts for different processing costs can still be written in the following form

$$\frac{dS}{dt} = k_{\rm A}\varepsilon U = k_{\rm A}A \tag{5.37}$$

$$\frac{dR}{dt} = (1-k_{\rm A})\varepsilon U - M = (1-k_{\rm A})A - M \tag{5.38}$$

but with $k_{\rm A}$ and ε newly defined by the above expressions. Notice, that for healthy fish, $k_{\rm A}$ and ε are still constants when a constant diet formulation is

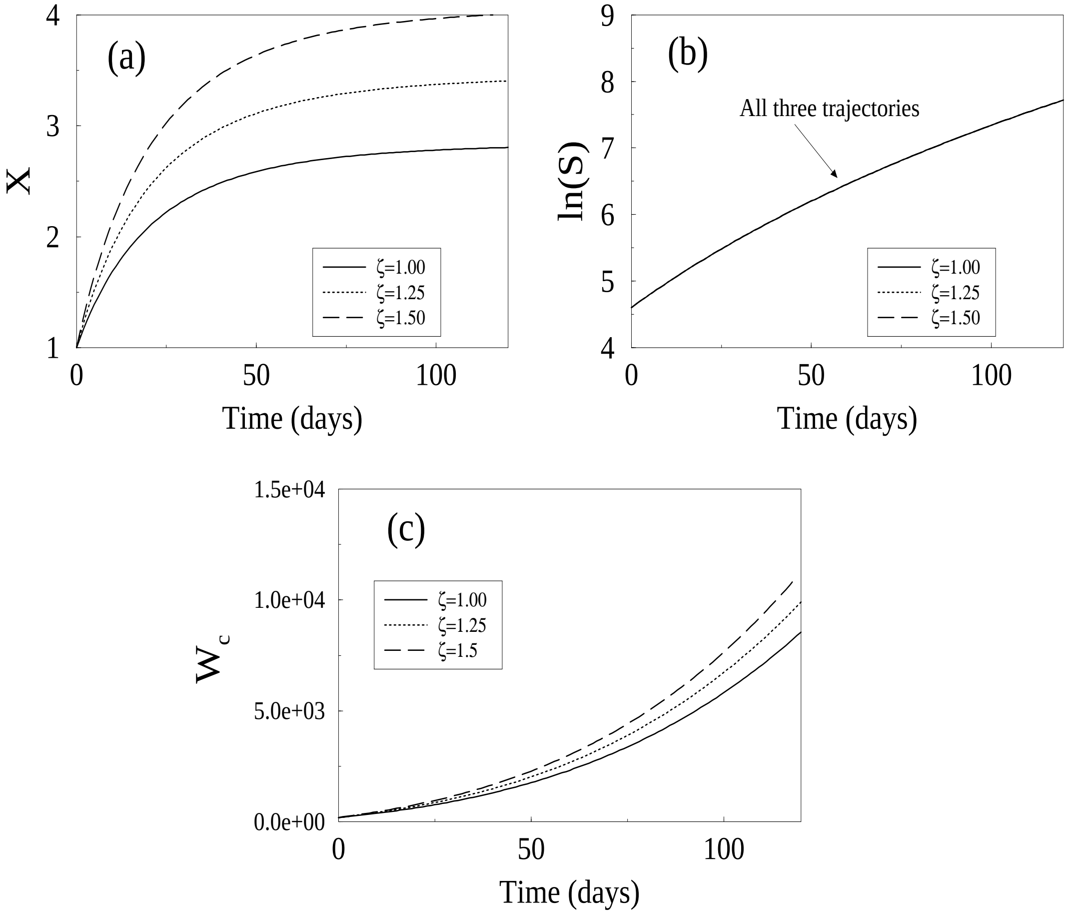

Figure 5.4: *Trajectories of a) reserve ratio, b) structural carbon weight and c) total carbon weight for the assimilation allocation model using equations(5.32) and (5.33). With* $\zeta = 1$ *the model reduces down to the previous assumption of equal processing costs. With increasing* ζ *the costs for non-structural nutrient processing become less. Structural growth is not being limited by the fish's maximum structural growth rate with* $\phi_S = 0.7$ *for all three trajectories. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $A_{H0} = 0.024$, $\gamma_A = 0.4$, $\gamma_D \epsilon_A = 0.35$, $\delta = 0.5$, $\phi = 1.0$, $T = 12^oC$, $X_0 = 1.0$, $S_0 =$*100mgC*, $d = v = 0.75$.

supplied leaving the earlier analysis of how ration level and temperature change reserve ratio and growth completely viable.

Because there is no longer a one to one relationship between k and the relative proportions of structural and non-structural nutrients in the digestible proportion of the uptake we shall run simulations using equations(5.32) and (5.33). We shall first point out the difference concerning the different assumptions about processing costs. This can be achieved quite simply by changing the value of ζ, where, $\zeta = 1$ for equal processing costs and $\zeta > 1$ for lower reserve nutrient processing costs.

Figure(5.4) displays a number of maximal growth simulations with different values of ζ. With increasing ζ, the extra assimilate gain from the lowered non-structural nutrient processing is only added to the reserves. No gain is given to structure and the difference in the final total carbon weights are only attributable to an increased accumulation of reserves.

In essence, the inclusion of differential processing costs has the same dynamic effect as increasing the non-structural proportion of nutrients whilst holding the amount of structural nutrients in the diet constant with the assumption of equal processing costs. As the difference in processing costs is increased, k_{A} reduces according to equation(5.37) and increases ε according to equation(5.36). The fact that differential processing costs only serve to change the reserve dynamics means that the main dynamic effects of changing diet formulation described in the previous section with the assumption of equal processing costs still hold true. With, however, the proviso that equal processing costs would under predict the growth rate of reserve carbon weight.

5.4.2 Structural Nutrient Sparing Effects

Thus far we have shown why high levels of lipid in the diet should not benefit structural growth. Indeed, the assimilation allocation model was specifically derived on this basis. However, protein "sparing" effects (an increased proportion of the protein supplied in the diet being accreted into the body) have been reported with an increase in the dietary lipid:protein ratio, most commonly, when the ration is reduced below maximum (pers. comm. Kim Jauncey [1]).

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[1] Kim Jauncey, Institute of Aquaculture, University of Stirling, Stirling, FK9 4LA

When the fish is growing near its maximum structural growth rate then it should perhaps not be surprising that lipids have no "sparing" effects. However, under reduced ration levels the assimilation allocation model is capable of showing some structural nutrient "sparing" effects with an increase in the relative proportion of non-structural nutrients within the diet.

We first need to point out the relationship between reserve ratio, ration level and diet formulation. For a fish allocating a fixed proportion (δ) of structural assimilate to structural growth we can with some rearrangement recast the steady state reserve ratio as follows

$$X^* = \frac{1}{\delta}\left(1 - \zeta - \delta + \frac{1}{\gamma_{\mathrm{A}}}\left(\zeta - \frac{M}{\epsilon_{\mathrm{A}}\gamma_{\mathrm{D}}U}\right)\right). \tag{5.39}$$

It can be seen that the steady state reserve ratio is inversely related to the proportion of structural nutrients within the digestible portion of the diet (γ_{A}). This means that although individuals may be fed the same ration of equal quality food the individual supplied with the high protein diet would maintain a lower value of reserve ratio. There are two reasons for this relationship. Firstly, the individual fed the high protein diet would (under the current rule) be allocating more to structure in accordance with equation(5.32). Secondly, the increased proportion of structural nutrients in the ration supply would incur higher processing costs reducing the total assimilate in accordance with equation(5.31).

In terms of diet effects, we have thus far only considered healthy growing individuals which we assume allocate a constant proportion of structural assimilate to building structure. In such circumstances there cannot possibly be any structural nutrient "sparing" effects. However, should the reserve ratio fall below the threshold value where the fish begins to defend its nutritional status then it is perfectly possible for an adjustment in the diet to have some structural nutrient "sparing" effects.

The assimilation allocation model needs a control mechanism to decrease and eventually cease any further allocation to structure in order to avoid death from

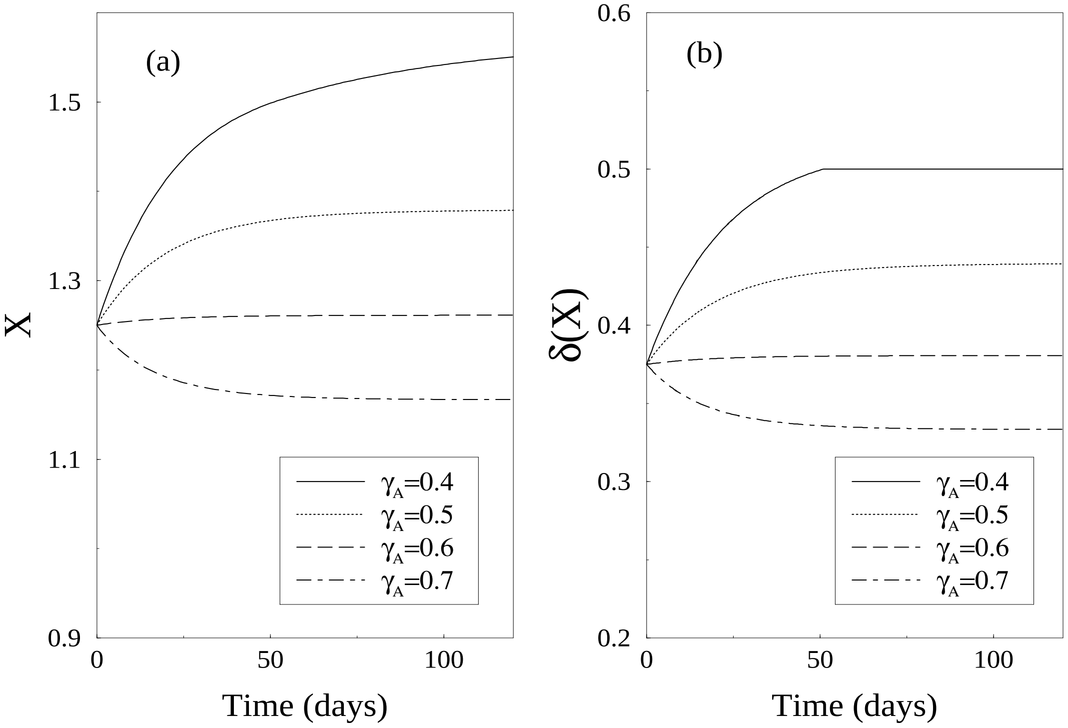

Figure 5.5: *Trajectories of a) reserve ratio and b) proportion of structural assimilate allocated to building structure for the assimilation allocation model using equations(5.32) and (5.33) with different values of relative proportions of structural nutrients in the diet. Structural growth is not being limited by the fish's maximum structural growth rate. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $A_{H0} = 0.024$, $\gamma_D \epsilon_A = 0.30$, $\mu = 0.5$, $a = 2.0$, $\zeta = 1.3$, $\delta_1 = 0.5$, $\phi = 0.3$, $T = 12^oC$, $X_0 = 1.25$, $S_0 =$ *100mgC*, $d = v = 0.75$.

starvation even though there may be an adequate supply of food for maintenance purposes. We have implemented the following mechanism to control allocation

$$\delta(X) = \min\left\{\delta_1, \frac{[X-\mu]^+}{a}\right\}. \tag{5.40}$$

This function is zero below μ and increases linearly to δ_1 with increasing reserve ratio. The reserve ratio value at which $\delta(X)$ begins to decrease is therefore $X = \mu + a_1\delta_1$. If a feeding regime of a particular diet formulation elicited such a reduction below this threshold then an increase in the non-structural nutrients would increase the reserve ratio above this threshold, thus, maintaining a higher structural growth efficiency.

Figure(5.5) displays a number of growth simulations for groups of fish each fed a constant ration level but with diets differing in the proportions of structural nutrients. Individuals who are feeding on the high structural nutrient diet initially undergo a reduction in the reserve ratio which the function $\delta(X)$ responds to by decreasing allocation to structure. With an increasing relative proportion of non-structural nutrients in the diet the individuals are able to maintain a higher reserve ratio which increases the proportion of structural nutrients allocated to until eventually the nominal constant proportion δ_1 is reached.

5.4.3 The Optimal Ration and Diet Formulation

Aquaculture Goals

The greatest majority of studies investigating the effects of diet formulation have been carried out by aquaculturists who are seeking to maximise the following goals

1. Increase production
2. Reduce costs
3. Increase flesh quality
4. Reduce pollution levels

Armed with the simple nutritional principles of the assimilation allocation model we shall seek a ration level and diet formulation which will aim to simultaneously maximise these clear objectives.

Optimal Ration Level

An increase in growth rate would increase production and an increase in growth efficiency would reduce costs. These objectives are simultaneously accomplished when the fish are fed at their maximum ration level. It is obvious why this should be so for growth rate, but to understand why this should also be the case for efficiency consider the quotient of net production per unit uptake as follows

$$\frac{P}{U} = \frac{A - M}{U} = \frac{\varepsilon U_H \phi - M}{U_H \phi} = \varepsilon - \frac{M}{U_H \phi} \tag{5.41}$$

It can be seen that for any given diet formulation (i.e. constant ε) the net production per unit uptake is maximised when the ration is supplied at its maximum level. Basically, this relationship occurs because maintenance costs always have to be met and are independent of growth rate. Therefore, any increase of intake above that needed to meet maintenance costs will increase growth efficiency. This simple theoretical reasoning is backed up by numerous experimental studies which report energy conversion efficiency to be increased when the ration level is increased (e.g. Brett et al. (1969); Elliott and Hurley (2000); Huisman (1976); Saether and Jobling (1999); Staples and Nomura (1976)).

The Optimal Relative Proportion of Nutrients

Since in an increase in diet quality (increasing γ_{D}) will obviously increase growth rate the only other possible variable we need study is the relative combination of structural and non-structural nutrients supplied in the diet.

Figure(5.6) displays a number of maximal growth simulations for individuals who are supplied different diet formulations. The effect of increasing γ_{A} is to initially increase the rate of structural growth until the maximum structural growth rate has been achieved, whereupon, no further increase in structural growth is achieved with increased proportions of structural nutrients.

Protein as a food source is more expensive to supply than either lipid or car-

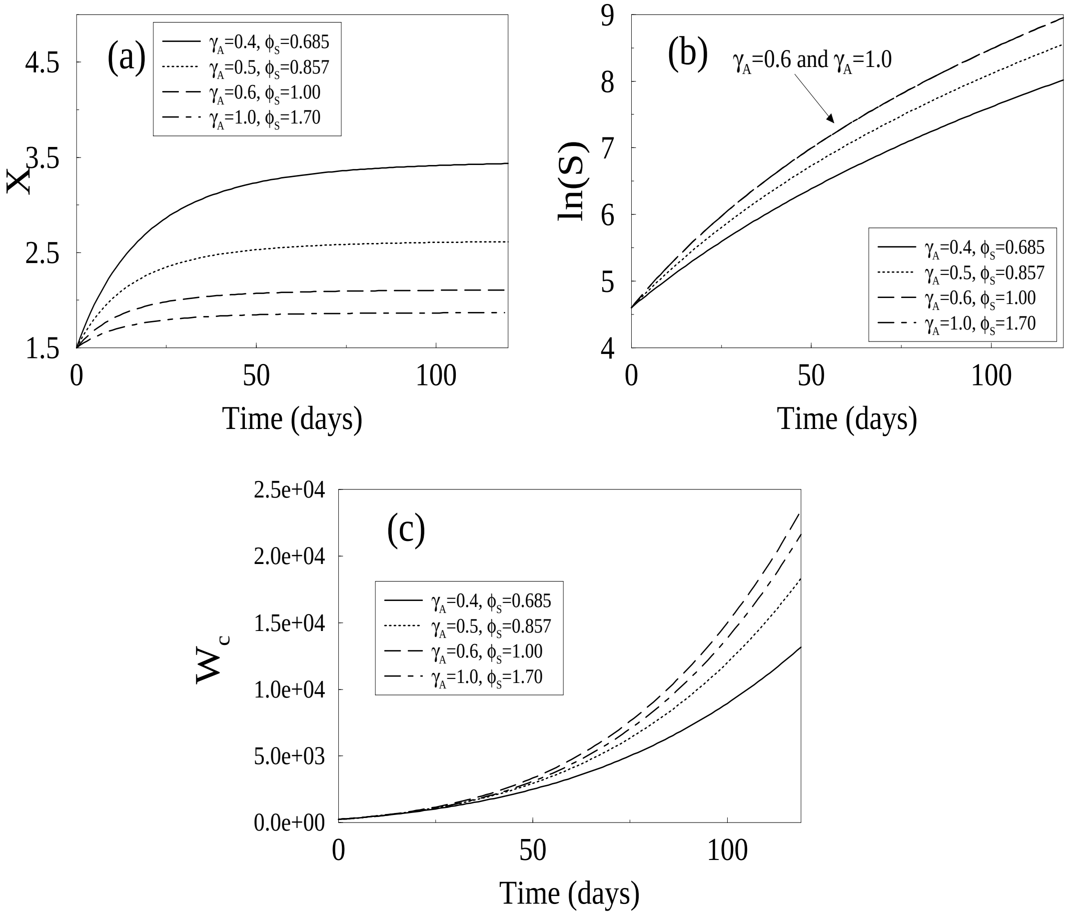

Figure 5.6: *Trajectories of a) reserve ratio, b) structural carbon weight and c) total carbon weight for the assimilation allocation model using different relative proportions of structural nutrients within the diet. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $A_{H0} = 0.028$, $\gamma_D \epsilon_A = 0.4$, $\mu = 0.5$, $a = 2.0$, $\delta_1 = 0.5$, $\zeta = 1.2$, $\phi = 1.0$, $T = 12^o C$, $X_0 = 1.5$, $S_0 =$ *100mgC*, $d = v = 0.75$.

bohydrate (Amanat and Nasser 2001). Thus, we can immediately point out to save costs there is no point in feeding an excess of protein. Furthermore, an excess supply of proteins more than necessary to achieve maximum structural growth will add to pollution effects through an increased output of ammonia produced through the deamination of amino acids (Kelly et al. 1996). Notice also, that the reserve ratio for the excess protein fed fish is less than that of the optimally protein level fed fish leading to a lower final total carbon weight.

This is due to the increased costs associated with structural nutrient processing which may possibly lead to a reduction in structural growth through the fish defending its reserve ratio. It is also important to note that if the amount of reserve nutrients supplied in the diet were reduced, then this again would cause the fish to begin defending its reserve status and start burning more structural nutrients for energy purposes which would in turn reduce structural growth rate.

There are two consequences of reducing the proportion of structural nutrients below the optimal value for maximal structural growth. Firstly, the rate of structural growth decreases. This means that the fish are not able to make the best use of the plentiful food supply since they are being supplied with less of the nutrients necessary to build the biochemical machinery to process food. This results in the final total carbon weights being less for individuals fed with a sub-optimal proportion of structural nutrients in the diet (see fig(5.6)). Furthermore, the greatest majority of the total carbon weight is composed of reserves, mainly in the form of lipids. High levels of lipids within the body of the fish are not a desirable property and reduce the quality of the flesh (Einen et al. 1998). As the proportion of non-structural nutrients within the diet are increased further, these effects compound leading to smaller fatter fish. The net result is that the fish take longer to reach a harvestable size and are of a poorer quality.

From our investigations a clear optimal diet formulation has emerged in satisfying the main goals of aquaculture. It is the optimal ratio of reserve to structural nutrients that supplies enough structural nutrients to keep structural growth rate near maximum whilst simultaneously supplying enough energy in the form of the more digestible non-structural nutrients to help meet maintenance costs and maintain a healthy reserve ratio.

5.4.4 Conclusions

We have investigated what effects different diet formulations will have on patterns of growth and allocation using the assimilation allocation model. The model is based on the very simple principle that some nutrients can be used only for energy purposes (mostly lipids), whereas, others (mostly protein) are of a genuine nutrient value for growth purposes but can also be used for energy purposes. We manipulated the composition of the diet by simultaneously changing the values of a small number of exogenous parameters. The conclusions we can draw from the assimilation allocation model are in good agreement with published experimental studies as outlined in section(3.4).

From our modelling investigations we initially found that increasing the lipid levels in the diet only serves to increases adiposity and has no direct benefit on structural growth. Whereas, the attained rate of structural growth is governed by the amount of structural nutrients supplied in the uptake and not reserve nutrients.

Further investigations revealed that reserve nutrients in the diet act indirectly to support structural growth. Lipids are more easily utilised for energy purposes than protein. This makes them a valuable commodity to meet the costs of metabolic processes and also maintain a good nutritional status. If the energy supplied in the diet is low then the reduction in nutritional condition will force an increase in the proportion of structural nutrients being used for energy purposes. However, if there are not enough structural nutrients supplied in the diet then this retards growth below its potential maximum. These strong growth and allocation dynamics resulted in a clear optimal ration and diet formulation to satisfy the main aquacultural goals.

As our model predicts, excessive levels of lipid in the diet have been shown to reduce fish growth and produce fatty fish (Lovell (1989); Chou and Shiau (1996); Garling and Wilson (1977) Takeuchi et al. (1983)). Low energy diets have also been shown to reduce protein retention efficiency (Amanat and Nasser 2001). Optimum growth for salmonids is reported to be achieved when 40-55% of the dietary energy is in the form of protein (Jobling 1994). Whilst this value may change slightly with different fish species, the principles remain exactly the same.

The optimum diet formulation (at least for aquaculture) is one which supplies enough nutrients for the process of protein growth with enough energy, primarily in the form of the more easily digestible lipids, to maintain a healthy nutritional condition and avoid any extraneous catabolism of proteins for energy purposes.

Part III

Growth and Allocation in a Variable Environment

Chapter 6

A Review of Compensatory Growth

6.1 Introduction

Studies have illustrated that following periods of growth restriction a broad variety of different animal species are able compensate by displaying a growth spurt on subsequent re-alimentation (see, e.g. Wilson and Osbourne (1960); Bilton and Robins (1973); Perrin et al. (1990); Bradley et al. (1991)). This catch-up growth commonly referred to as compensatory, catch-up or recovery growth has a magnitude greater than that of fully fed controls.

This increased growth has been shown to be achieved by increasing food intake rate beyond that of normal maximum (a hyperphagic response) and also in some cases increasing food conversion efficiency. Recovery from restricted ration or starvation is usually complete (on re-alimentation animals achieve the same body size as con-specifics), or partial (figure(6.1)). However, in some rare cases recovery growth can result in a greater weight gain than fully fed controls (e.g. Hayward et al. (1997); Dobson and Holmes (1984)).

The obvious potential utility of compensatory growth to fish aquaculture has led

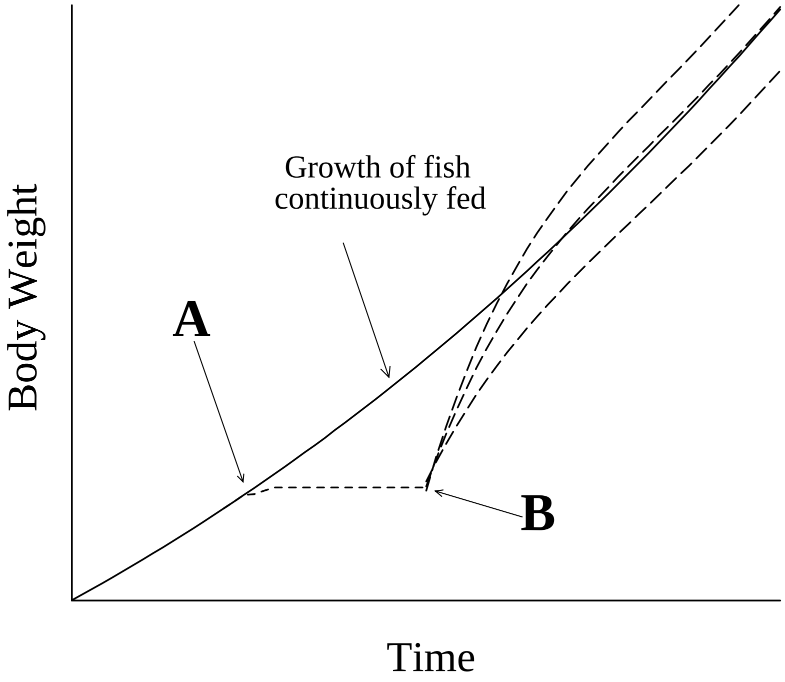

Figure 6.1: *Growth of control fish(solid line) together with deviations from the control growth trajectory during periods of restricted ration and catch-up, recovery or compensatory, growth. A feeding restriction is imposed at time point A, and the fish are returned to full feeding at point B. After the return to full feeding, growth rate is initially rapid, but then slows. The recovery of body weight may be either partial, complete and in some rare cases over compensation is exhibited.*

to a substantial research effort. However, many physiological and behavioural aspects of compensatory growth are still poorly understood. The aim of this chapter is to review the broad research literature so that the most evident factors influencing compensatory growth can be pointed out and noted for future growth modelling objectives.

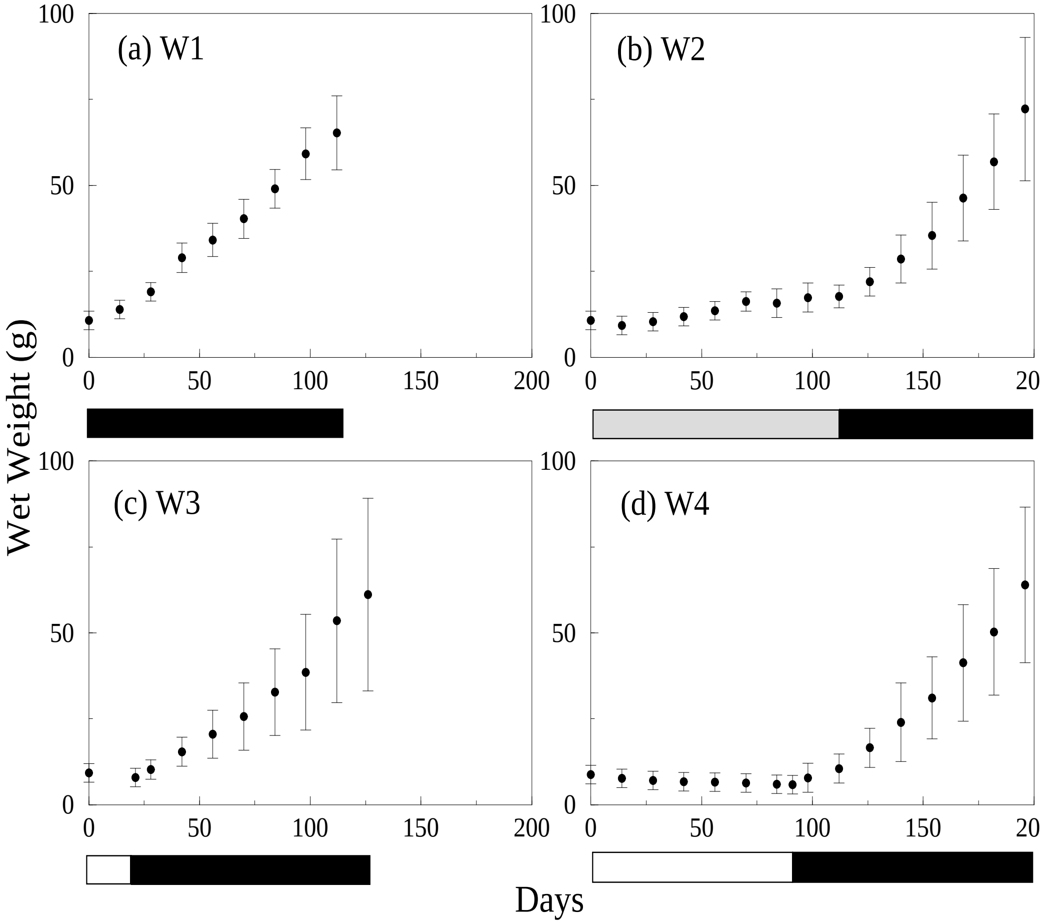

Figure 6.2: *Observed weight for the fish of Weatherley and Gill (1981). Vertical bars denote 95% confidence intervals. The bar below each figure denotes the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

6.2 Studies of Compensatory Patterns of Growth

The aim of this section is to investigate and review a number of the more detailed studies of compensatory growth. Studies have mostly been conducted to try and ascertain what factors, in particular feeding regime, influence the extent to which growth losses are recovered.

Weatherley and Gill (1981)

Weatherley and Gill (1981) subjected juvenile rainbow trout (*Salmo gairdneri* Richardson) to different feeding regimes at a constant water temperature of 12^oC (see figure(6.2)). The trout were distributed into four groups: W1: fed to excess for a period of 13 weeks; W2: restricted ration for 13 weeks followed by a 13 week excess ration; W3: 3 weeks of starvation followed by 13 weeks excess ration; W4: 13 weeks of starvation followed by 13 weeks of excess ration. The wet weight growth trajectories for each group are displayed in figure(6.2).

Weatherley and Gill (1981) concluded that following feed restriction, the young rainbow trout were rapidly able to retain pre-starvation sizes, and were then able to grow at a similar rate to that of controls, which were never less than well fed. The weights of each group were not significantly different from one another following equal time periods of excess supply of food with previous different lengths and severity of food restriction. Therefore, the compensatory response must be viewed as being only a partial recovery of body size, because the feed cycling experiments had been conducted for longer and yet did not out perform the weight gain of the controls.

Miglavs and Jobling (1989a,b)

Miglavs and Jobling (1989a,b) studied the pattern of compensatory growth of juvenile Arctic charr (*Salvelinus alpinus*) over an equal time period at a constant temperature of 8^oC. The charr were fed according to three different feeding regimes: M1: excess food for 16 weeks; M2: restricted ration for 8 weeks followed by 8 weeks of excess ration; M3: starved for 16 weeks. The weight trajectories for each group are displayed in figure(6.3).

Following re-alimentation, the restricted-refed group (M2) exhibited significantly greater rates of growth than controls for 6 of the 8 week refeeding period. In the final two weeks of the experiment restricted-refed fish had growth rates equal to

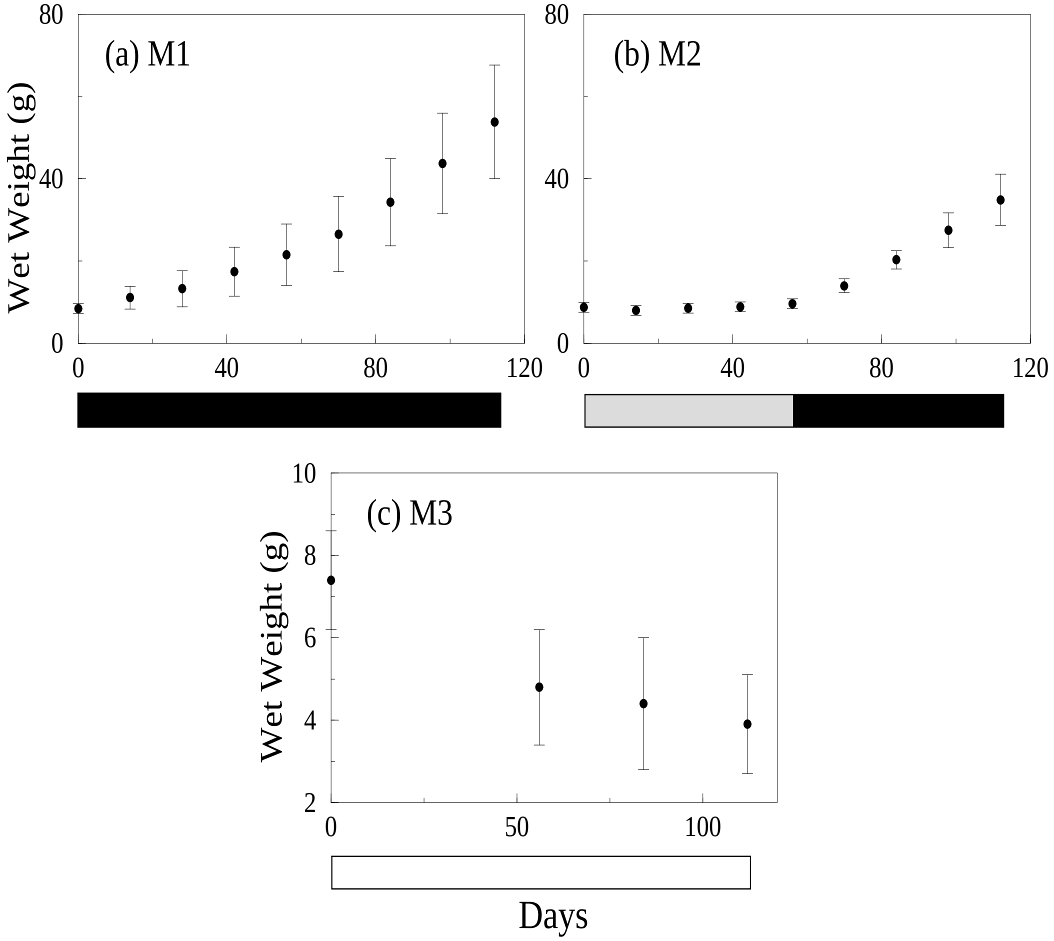

Figure 6.3: *Observed weights for Arctic charr of Miglavs and Jobling (1989,a,b). Vertical bars denote 95% confidence intervals. The bar below each figure denotes the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

that of controls. Despite this prolonged increased rate of growth, the final mean weight was still significantly lower than controls, who were supplied with excess ration throughout the experiment.

Quinton and Blake (1990)

Some investigations have been conducted with an express interest in what feeding regimes may maximise the compensatory growth response. Quinton and Blake (1990) studied the effects of feed cycling rainbow trout (*Oncorhynchus*

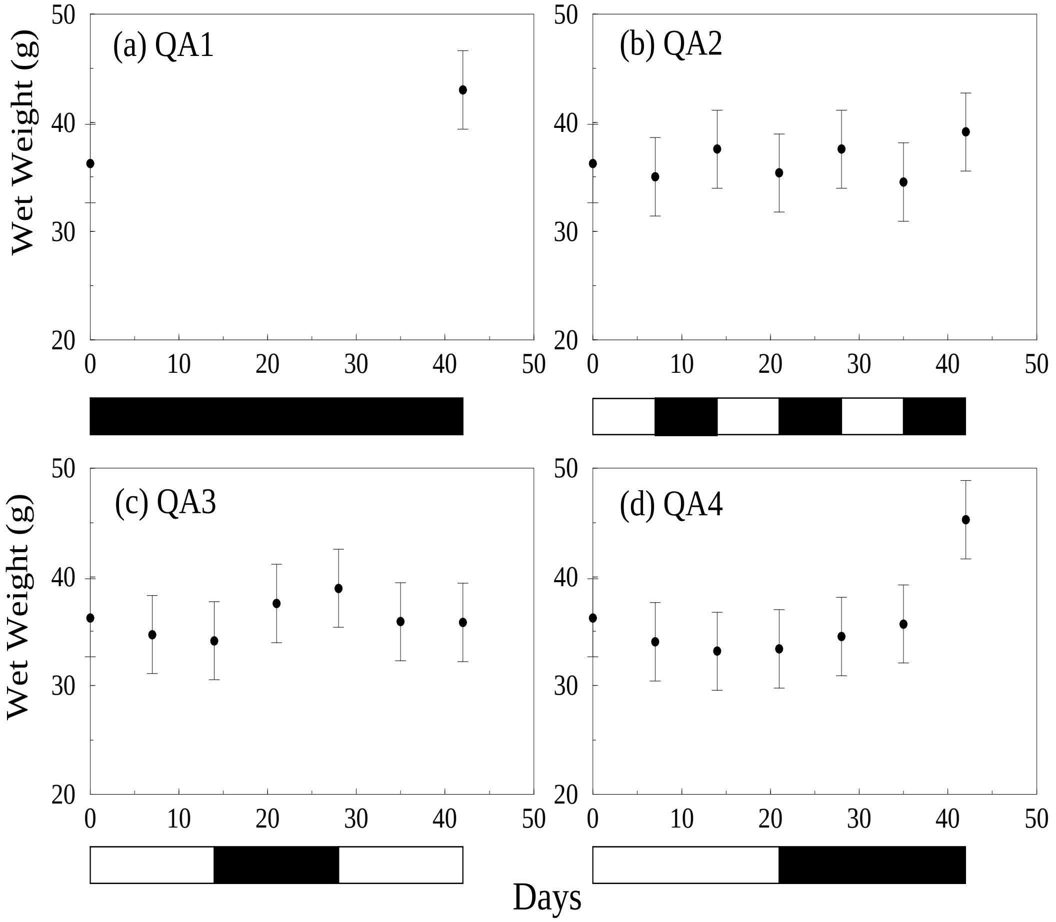

Figure 6.4: *Observed weights for the fish of Quinton and Blake (1990), Exp. A. Vertical bars represent 95% confidence intervals (based upon the statement that the final weights of the control and starved fish were not significantly different). The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

mykiss) at a water temperature of 13^oC. The first of their experiments (initial mean fish weight 36.24g) investigated the effects of a 1:1 week, 2:2 week and 3:3 week alternating periods of food deprivation and excess food provision. The experiment continued for six weeks. Figure(6.4) displays the wet weight trajectories for control (QA1) and the different feed cycled groups of fish.

The 3:3 cycling pattern emerged as the most successful at inducing compensatory growth with the final weight being slightly greater than controls. The 1:1 and 2:2 week cyclically fed fish both had similar final mean weights, which were both

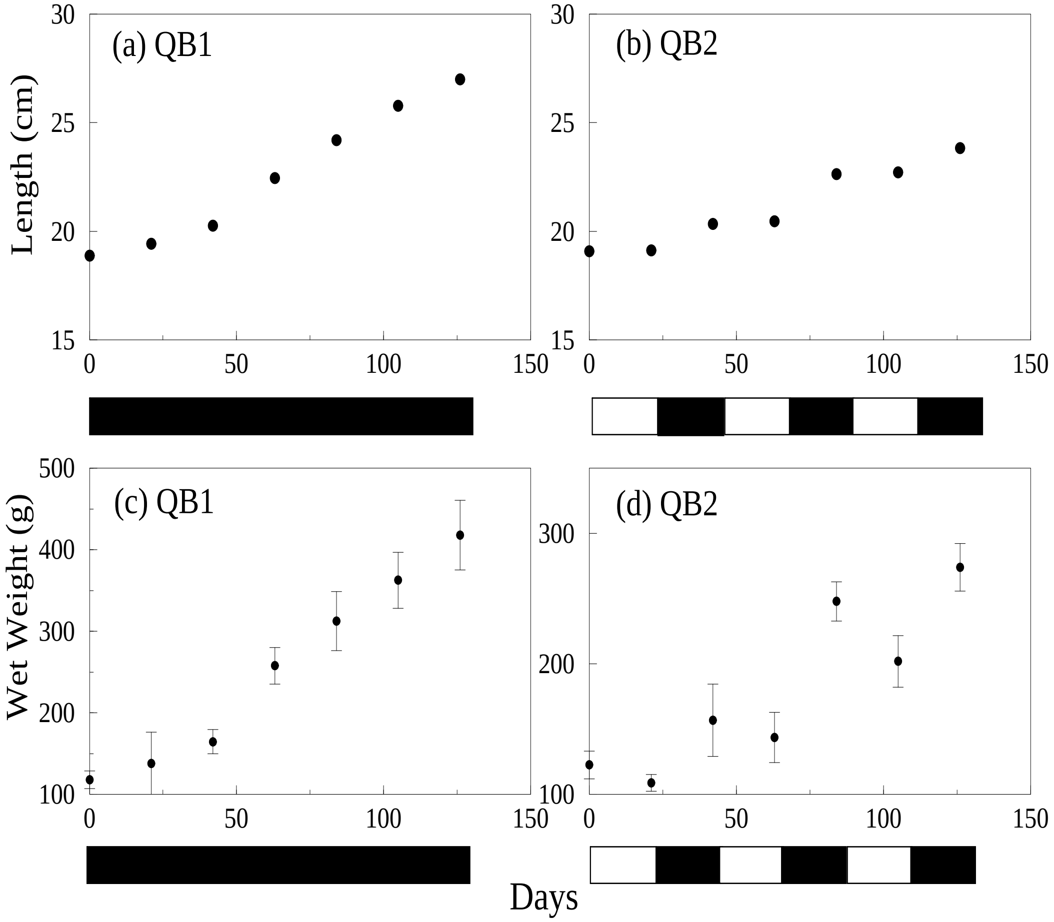

Figure 6.5: *Observed lengths and weights for the fish of Quinton and Blake (1990), Exp. B. Vertical bars denote 95% confidence intervals. Quinton and Blake give no measure of the variance associated with the quoted mean lengths. The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

lower than continuously fed controls. No significant weight change was found in the first week or two weeks after refeeding in all feeding regimes. Quinton and Blake (1990) remarked that the majority of the gain in weight and length of the 3:3 cycle was achieved on the third week of refeeding.

In a further experiment (Exp. B; initial mean fish weight 120.22g) they continually repeated the 3:3 week cycles of food deprivation and food in excess for a period of 18 weeks. Figure (6.5) displays both weight and length trajectories for control (QB1) and 3:3 week feed cycled (QB2) fish. Following the first cycle (three weeks of starvation and 3 weeks of refeeding), the mean weight was not significantly different from controls who had been continuously fed in excess. After the second cycle, again, the mean weight did not significantly differ from controls (week 12). Unfortunately, during the 17th week there was a mechanical failure of the thiosulphate pump and a large chlorine treatment of the water supply. The water quality problem was so severe that all fish in both groups had died 3 days after the final measurements, so the data for the last 3 weeks should not be included when examining the effects of repetitive cyclic feeding. Ignoring the final 3 weeks this is an example of complete compensation motivated by a 3 week feed deprivation and 3 week excess food supply. In a similar experiment Dobson and Holmes (1984) using the rainbow trout, *Salmo gairdneri* Richardson, also found 3 weeks of starvation and 3 weeks of refeeding to equal and sometimes better the weight gain of controls fed in excess throughout out a number of 6 week experiments.

Kindschi (1988)

Kindschi (1988) also conducted an experiment to investigate possible feeding regimes that induce compensatory growth. Rainbow trout (initial weight 15.9g), *Salmo gairdneri* Richardson, were divided up into 4 groups and given different feeding schedules: (K1) Fed every day to excess; (K2) Fed a restricted ration every day; (K3) every day for 3 days in excess and then deprived of food for 4 days each week; (K4) alternate 4 week cycles of plentiful food and no food. The experiment continued for 16 weeks at a constant temperature of 12.2^oC. The wet weight growth trajectories for each group are displayed in figure(6.6).

At the termination of the experiment the mean weights of each group were all found to be significantly different from one another. Continuously fed controls (K1) had outperformed all other groups. Alternate 4 week cycles of food and no food (K4) had the second greatest final mean weight followed by the fish continuously fed a continuous restricted ration (K2) and the lowest final mean

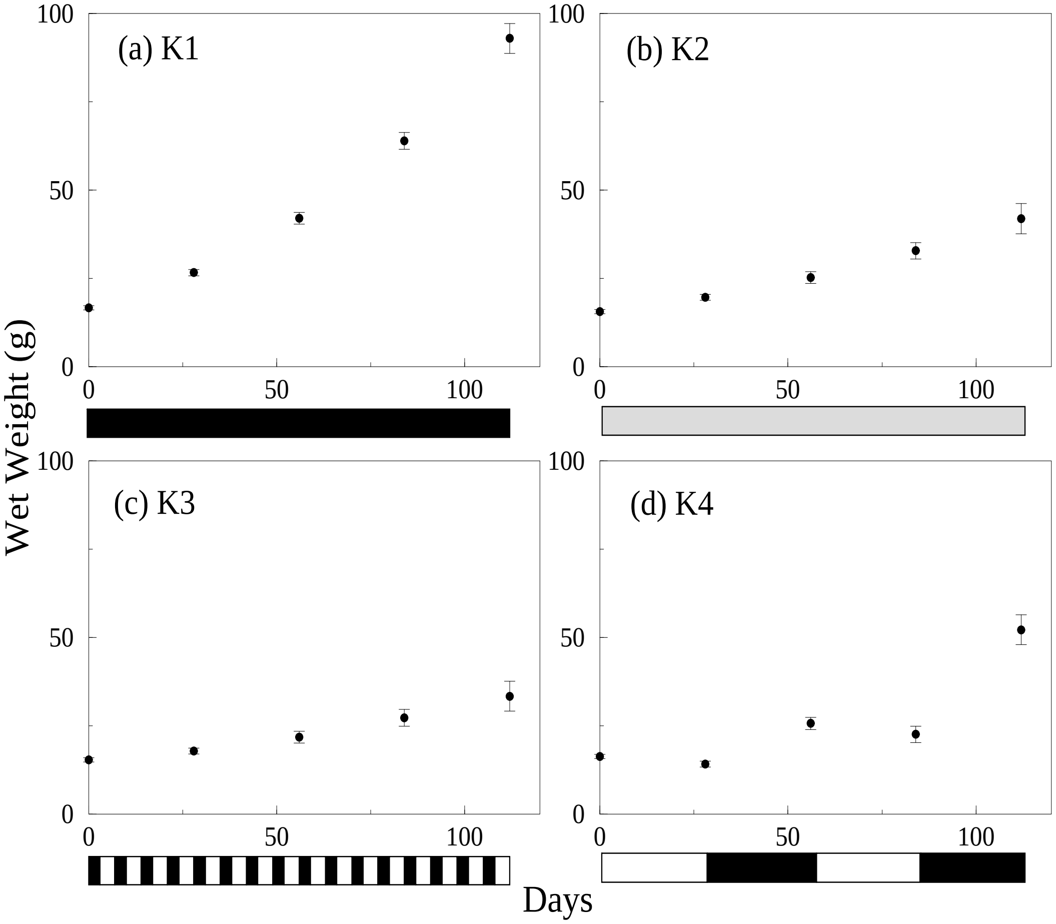

Figure 6.6: *Observed wet weights for the fish of Kindschi (1988). Vertical bars are approximate 95% confidence bounds (based upon halving the difference between means quoted as not being significantly different). The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

weight was elicited by the 3:4 day cycles of excess and no food. From this study it is clear that the compensatory growth response elicited by the different feed cycles did not match the growth of control fish. However, it can be seen that that the longer alternate 4 week cycles of supplying plentiful food and no food evoked the greatest compensatory growth response in comparison to the short feed of 3 days of feeding and 4 days of starving.

Jobling et. al. (1993)

Jobling et al. (1993) conducted a similar experiment to investigate the effects of feed cycling in Arctic charr *Salvelinus alpinus* using a constant temperature of 9.5^oC. Groups of fish were subjected to fixed length alternating periods of food deprivation and unlimited food provision with a period of 1, 1.5 and 3 weeks. The wet weight growth trajectories are displayed in figure(6.7). All cyclic feeding regimes depressed growth to below that of controls continuously fed. Fish that were deprived of food and then fed on alternate weeks (1:1) were slightly larger than those that were exposed to periods of 1.5 or 3 week deprivation feeding (1.5:1.5 or 3:3).

On receiving excess food supplies following 24 weeks on the restricted feeding regimes the previously restricted fish grew more rapidly than controls. The greatest compensatory growth was displayed after the 3:3 regime, followed by the 1.5:1.5 and then the 1:1 feeding regime. At the termination of the experiment there was no significant differences in body weight between fish fed according to each of the cyclic feeding regimes during the period that food restriction was imposed.

Discussion

In reviewing the literature, it becomes clear that there are inconsistencies in the extent to which growth losses are recovered by the compensatory growth response. Recovery is most often only partial (Weatherley and Gill (1981); Miglavs and Jobling (1989a); Kindschi (1988)), sometimes complete (Quinton and Blake (1990), Exp. B.), and in some rare cases over-compensation is exhibited (Dobson and Holmes (1984)).

Studies have shown that both the length and severity of the food restriction play a part in the ensuing growth response. In general, the greater the length and severity of the growth retardation the greater is the resultant compensatory

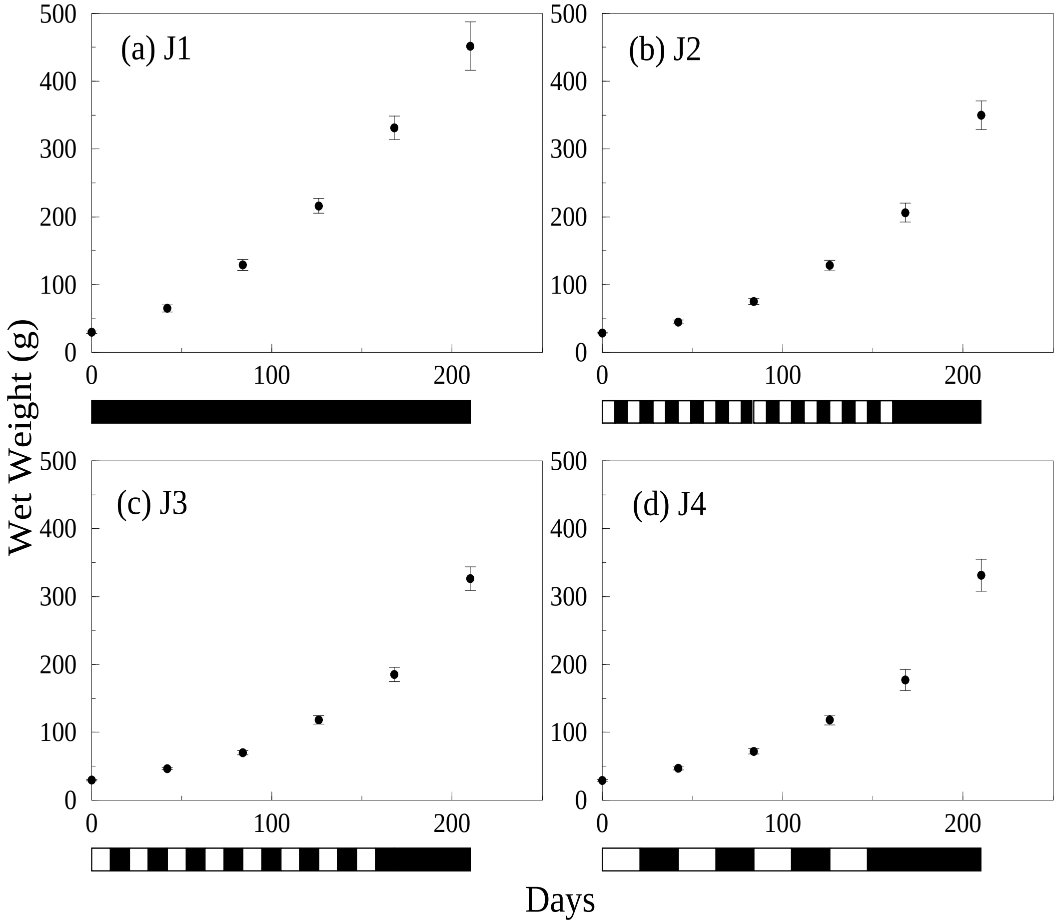

Figure 6.7: *Observed weights for the fish of Jobling et. al. (1993). Vertical bars denote 95% confidence intervals. The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food.*

response (e.g. Jobling and Koskela (1996)). However, if the applied growth restriction is too severe then the extent of recovery begins to decrease. For example, Bilton and Robins (1973) found that sockeye salmon fry, *Oncorhynchus nerka*, were capable of showing full recovery following 3 weeks, but not following longer periods of starvation.

It is important to note that compensatory growth need not only be elicited by a severe growth restriction. Several studies have pointed out that even individuals who have managed to remain in a stationary or positive energy balance within the growth restriction period exhibit increased rates of growth (above that of controls) on subsequent realimentation (e.g. Jobling and Koskela (1996);

Nicieza and Metcalfe (1997); Jobling and Johansen (1999); Miglavs and Jobling (1989a,b)). It is also important to note that growth restrictions applied by a reduction in temperature also elicits a compensatory growth when the fish are reintroduced to warmer more favourable temperatures for growth (Mortense and Damsgard (1993); Nicieza and Metcalfe (1997))

We have relayed the results of a number of experiments investigating compensatory growth in more detail than others (the studies in which we have graphically depicted the data). Particular attention has been paid to these studies as they are amongst the most detailed published data sets that incorporate a large number of different feeding regimes, thus, making them particularly good candidates for future model fitting. However, the conclusions we draw from these studies are inconsistent with one another. In particular, the conflicting results of Exp. A, Quinton and Blake (1990) and the Jobling et al. (1993) study.

The results of Exp. A, Quinton and Blake (1990) suggest that there exists a delayed reaction to refeeding on realimentation with the most rapid gain in weight occurring in the third week of recovery. This resulted in the 3:3 week cycled fish being the more successful. In contrast, with the Jobling et al. (1993) experiment there cannot have been much of a delayed response to refeeding since the 1:1 week cycled fish grew just as well (if not better) as the 1.5:1.5 and 3:3 week cycled fish.

Quinton and Blake (1990) report there were large differences in the growth rate of control fish between Exp. A and Exp. B. Controls of Exp. A. only managed to change in weight from 36g to 42g and in length from 13.3 cm to 13.8 cm in a 6 week growing period with a plentiful supply of food at a temperature near optimal for growth. Comparison of these growth rates with that published by Austreng et al. (1987) for rainbow trout of similar weight and temperature conditions reveal the fish of Exp A. Quinton and Blake (1990) to be growing some 8 times slower. Therefore, the delayed reaction to refeeding could in some way have been related to these extremely slow rates of growth.

6.3 Hyperphagia and Growth Efficiency

Irrefutably, the cause of compensatory growth is either an increase in food uptake and/or a reduction in costs. On realimentation following nutritional restriction fish species have been shown to exhibit a hyperphagic response (e.g. Miglavs and Jobling (1989a); Russel and Wooton (1992); Hayward et al. (1997); Nicieza and Metcalfe (1997)) and also in some cases increased growth efficiency is reported (e.g. Qian et al. (2000); Boujard et al. (2000)). In order to gather any information on these mechanisms it is necessary to collect fine scaled food consumption data. As a consequence of this fewer data sources exist.

Following a restrictive ration for a period of 8 weeks Miglavs and Jobling (1989a) report that juvenile Arctic charr displayed a sharp increase in rates of food intake when presented with excess food supply. With the exception of the last two weeks of the 8 week realimentation period, food consumption was significantly greater than that of fish fed to satiation throughout. In a similar experiment Russel and Wooton (1992) subjected the European minnow (*Phoxinus phoxinus*) to a 16 day period of either restricted ration or starvation. Both treatments groups exhibited significantly greater rates of food intake than controls in 4 out of 5 days immediately following refeeding. In addition to elevated food consumption an increase in gross food conversion efficiency (g.f.c.e = weight change/food fed) was reported to have occurred in the initial period of refeeding. Restricted refed minnows values of g.f.c.e had declined to that of controls by the second week, whilst the starved refed minnows were not significantly different from the controls until the third week of refeeding. Concordantly, Miglavs and Jobling (1989a) also reported increased values of g.f.c.e in the first two weeks of the realimentation period in Arctic charr.

Animals can adapt to periods of food deprivation by reducing energy expenditure. It has been hypothesised that following refeeding metabolic rates may not immediately return to the same level as that of a continuously fed animal. The consequence of this would be as follows. Low rates of metabolic expenditure occurring concurrently with high rates of food intake would result in large amounts of food intake being available for growth. Thus, rates of weight gain should be rapid during the initial phase of recovery. Maintenance of low rates of metabolic expenditure would expect to lead to a large weight gain per unit food intake, i.e. efficient food conversion.

Although the afore mentioned argument is an attractive proposition, experimental results do not always agree (Jobling 1994). If the hypothesis of depressed maintenance were to be true to such an extent as outlined above, then restricted-refed fish would show a significantly higher values of growth efficiency as compared to that of continuously well fed controls. Whilst this may be observed in the recovery phase it should also be present (admittedly, to a lesser extent) at the end of the recovery period.

Further investigation of the food conversion efficiency of restricted-refed Arctic charr (Miglavs and Jobling (1989b)) as compared to continuously well fed controls revealed that there was no significant difference between each treatment group over the complete experimental period, both, in terms of a live weight and an energetic basis. Similar results were found by Russel and Wooton (1992) with the European minnow (*Phoxinus phoxinus*). The mean total food consumption over the whole experimental period did not differ significantly between each treatment group (including controls). At the end of the experiment (in which treatment group fish had returned to normal controls levels of feeding) the restricted-refed fish had fully compensated their weights to that of controls. Thus, there cannot have been any significant increase in growth efficiency. Further, whilst Hayward et al. (1997) were able to double hybrid sunfish growth rates by using cyclic feeding patterns they did not detect any increase in growth food conversion efficiency over the full experimental period.

In many studies on compensatory growth, efficiency is estimated by means of a biometric measure such as g.f.c.e. Therefore it is possible that the improvements in conversion observed in restricted-refed animals (section 6.2) could be related to differences in the composition of the tissues deposited during recovery

Table 6.1: *Arctic charr biochemical body composition from Miglavs and Jobling (1989a,b). Fat levels are expressed as % live body weight.*

Week	Group	Wet Weight (g)	Fat(%)	FAT:LBM
0	initial	8.65	6.0	0.063
8	M2	9.6	4.5	0.047
12	M2	19.7	5.9	0.062
16	M2	34.9	7.2	0.078
	M1	53.8	7.4	0.079

and normal growth (Jobling 1994). Furthermore, many studies merely imply increased growth efficiency even though food intake was not monitored (Quinton and Blake (1990); Dobson and Holmes (1984)).

Based on the above evidence, the bulk of the accelerated rates of growth exhibited by weight compensating fish was attributable to increased food uptake above that of normal or control levels and was not as a result of increased food conversion efficiency. In general, the high rates of achieved growth are most consistently achieved through an increase in food uptake (Nicieza and Metcalfe 1997). Therefore, all future model derivations will assume that the increased rates of growth are achieved from an increase in uptake rather than food conversion efficiency.

6.4 Recovery Growth and Changes in Nutritional Status

On subsequent re-alimentation, following growth restriction, rates of growth are increased to levels above that of continuously well-fed controls. Studies have invariably shown there to be a concomitant increase in nutritional condition with the ensuing recovery growth. Since compensatory responses have been shown to be inconsistent with one another, the nutritional condition of the fish when the accelerated rates of growth have returned to normal levels is of particular interest.

Miglavs and Jobling (1989a,b) also conducted a biochemical analysis of body constituents. Their experiment was terminated once growth rates of restricted-refed fish had returned to levels of controls. Fully fed controls (M1) were sampled at the end of the experiment, and samples of feed restricted fish (M2) were taken after 8, 12 and 16 weeks. Table(6.1) displays the changes in wet weight, lipid levels and the ratio of lipid to lean body mass (LBM: inclusive of water, protein and ash). Restricted ration for 8 weeks resulted in a reduced levels of lipid (% body weight) with an increase in protein content (we have already discussed this result in section(3.3)). Change from the restricted feeding regime to excess food ration resulted in an accelerated growth rate facilitated by hyperphagia. By week 12 restricted-refed fish had increased in wet weight and also accomplished an increase in lipid content. At the end of the experiment (when the growth compensation period has ceased) the restricted-refed fish had not completely compensated for lost growth, however, fat levels (% body weight) were not significantly different from the larger continuously fed controls.

Table(6.2) displays the result of a feed cycling experiment conducted with post smolt Atlantic salmon (initial weight 75g) reported in Jobling and Johansen (1999). Fully fed fish were fed in excess throughout the 16-week trial (JJ1). For the first 8 weeks, the restricted fish (JJ2) were fed half the ration predicted to support maximum growth and, during the second half of the trial, these fish

Table 6.2: *Post-smolt Atlantic salmon body composition from Jobling and Johansen (1999). Fat levels are expressed as % live body weight.*

Week	Group	Wet Weight (g)	Fat(%)	FAT:LBM
0	initial	75	NA	NA
8	JJ1	170	7.5	0.080
	JJ2	135	6.0	0.066
16	JJ1	276	8.5	0.094
	JJ2	281	8.0	0.087

were given an unlimited feed supply. During the restriction phase the increase in body weight was only 65% of that of fully fed controls. There were differences between the groups in both LBM and proximate chemical composition. By the end of the trial restricted-refed fish had fully compensated for body wet weight losses and also possessed lipid levels similar to that of fully fed controls.

Thus far, we have illustrated that the compensatory growth phase includes the recovery of nutritional status. However, it is important to note that compensatory growth also includes a genuine degree of recovery in structural growth. Numerous studies have pointed out that, during the recovery phase of growth, growth rate in length is increased to levels greater than that of continuously fed controls (e.g. Sogard and Olla (2000); Dobson and Holmes (1984); Pedersen and Jobling (1989); Quinton and Blake (1990)).

In conclusion, the period of rapid growth following growth restriction facilitates a recovery of nutritional status and a degree of recovery in lost structural growth.

6.5 Conclusions

In this chapter, we have reviewed the results of a large number of compensatory growth studies conducted with juvenile salmonids. The results of these experiments are not always in universal agreement with one another. Indeed, some experiments are completely inconsistent with one another (i.e. Quinton and Blake (1990), Exp A. and Jobling et al. (1993)).

Our eventual goal is to derive a model for compensatory growth. However, before we can do this we need to point out what dynamic properties this model should posses. Given the complexity of factors that may be involved in compensatory growth, together with the fact that no model could possibly hope to explain every single experimental result, we feel that producing a concise summary of the most consistent properties of compensatory growth is the best strategy to aid future model derivations.

After much deliberation and thought we feel that the most important conclusions of this review which have the greatest repercussions for future modelling objectives are as follows:

1. Compensatory growth is exhibited by individuals who have endured a period of growth restriction either through low temperatures or a reduced ration supply.
2. Compensatory growth can still be exhibited by individuals who have remained in a positive energy balance through the growth restriction as well as individuals who have sustained energy losses during the growth restriction period.
3. The increased growth rate above that of controls is more consistently shown to be achieved through an increased uptake of food and not through an increase in growth efficiency.
4. The strength of the resultant compensatory growth response is related to length and severity of the growth restriction. In general, the greater the

growth restriction the stronger the compensatory response. However, if the growth restriction is too harsh then growth losses are not fully recovered.

5. There are clear inconsistencies in the extent to which growth losses are recovered. The majority of studies report partial or complete recovery of body weight.
6. There is evidence to suggest that the compensatory growth response is ablated when nutritional status has been recovered.
7. Recovery growth is structural compensation as well as a recovery of reserve status.

Thus, our modelling objectives are clear.

Chapter 7

Modelling Compensatory Growth

7.1 Introduction

The aim of this chapter is to derive a model that encapsulates the strong growth characteristics of compensatory growth. To accomplish this we first need a mechanism for how compensatory growth is regulated. Therefore, our first step will be to investigate the (few) hypothesised mechanisms that can explain experimental observations.

Having identified the most logical and immediately successful mechanism we will then move on to a more detailed modelling investigation. We then, in turn, asses the ability of each class of allocation model to exhibit the major characteristics of compensatory growth.

Our final model should be able to display the major qualitative observations as listed in the previous section and also, perhaps explain why we observe some of these strong growth characteristics.

7.2 Hypothesised Mechanisms of Compensatory Growth

7.2.1 Pre-determinate Growth Characteristics

One of the most popular hypothesised mechanisms for compensatory growth is that growth follows a predetermined course (e.g. Wilson and Osbourne (1960); Wilbur and Collins (1973); Hubbell (1971)). Deviations away from this predetermined growth trajectory would elicit a compensatory growth response until individuals have returned back to the given size at age.

Such a mechanism requires individuals to have a knowledge of future size at age which must be adhered to by a knowledge of what growth losses have been sustained, thus, a memory of past growing conditions must be involved. Such a mechanism would predict a full compensation of body weight and could not explain why compensation is often only partial. In a similar manner, such a mechanism could not explain why body weight over-compensation sometimes occurs. We give this mechanism as a full qualitative explanation of compensatory growth pretty short shrift.

7.2.2 The Lipostat Model

In his lipostatic model Kennedy (1953) proposed that a change in energy balance sufficient to alter adiposity elicited a compensatory change in food intake as a result of changes in negative feedback signals originating from the brain that inhibits feed intake. Thus, after a period of food restriction, the negative feedback that inhibit feeding are reduced because of a change in fat content. The result is elevated food intake that is maintained until fat levels are restored.

It is now accepted that adipose tissue mass influences food intake in mammals (Weigle (1994); Matson et al. (1996); Blum (1997); Schwartz and Seeley (1997); Friedman (1998); Hossner (1998)) and in the light of recent work there is evidence that the size of body fat stores plays a role in the feeding of salmonid fishes (Jobling and Johansen (1999); Metcalfe and Thorpe (1992); Simpson et al. (1996); Jobling and Miglavs (1993); Silverstein et al. (1999); Shearer et al. (1997)).

Jobling and Johansen (1999) have recently reviewed the role that the lipostatic principles proposed by Kennedy (1953) may play in the compensatory growth responses of fish. Jobling and Johansen (1999) state that the lipostatic model could contribute to an explanation of the disparate results in the extent to which body weight is recovered in fish. They support this claim with results from the experiments which have been re-displayed in table(6.1) and (6.2). As a measure of body nutritional status they use the fat:LBM ratio which they closely analogies with the reserve to structure to ratio in our modelling framework initiated by Broekhuizen et al. (1994).

Jobling and Johansen (1999) note that in fish that repleted their body lipid reserves rapidly during catch-up growth, there would be a rapid ablation of hyperphagia resulting in a quick restoration of fat:LBM ratio. The net result would be an incomplete recovery of body weight, relative to fully fed controls (e.g. table(6.1)). On the other hand, if lipid accumulation took place more slowly during catch-up growth, the hyperphagic response would be of longer duration, and changes in the fat:LBM ratio would occur gradually, enabling a complete restoration of body weight (e.g. table(6.2)). In cases of a very slow repletion of body reserves, body weight over-compensation might be predicted because the imbalance in the fat:LBM ratio would remain for a prolonged period.

The principles of the lipostatic model can instantly explain why the strength of the compensatory growth response is related to the length and severity of the growth restriction period. From our review in chapter 3 we know that growth and nutritional status are intimately related with one another, where, the greater the growth restriction (depressed temperatures or reduced ration levels) the greater the reduction in reserve status. Thus, when returned to better growing conditions, individuals in a poorer nutritional state will take longer to recover nutritional status than conspecifics in a better nutritional state. The net result would be that individuals who have sustained the greatest growth losses would show the strongest compensatory growth response. This would act as a regulatory mechanism for controlling growth. Furthermore, individuals need not have sustained energy losses during the growth restriction period, because, the increased appetite is elicited by a shift in nutritional status.

In conclusion, a model based on appetite being regulated by changes in reserve status can immediately explain almost all the major qualitative dynamics of compensatory growth. Therefore, in the absence of any other satisfactory mechanisms all future model derivations will be based upon this mechanism. A model based on the same principles has already been derived, and so our next step will be to investigate this model in more detail.

7.3 The Broekhuizen Compensatory Growth Model

7.3.1 Explanation of Model

The Broekhuizen et al. (1994) compensatory growth model is based on a particular case of the net production sequence of allocation. The baseline model is defined as follows

$$\frac{dR}{dt} = A - M - \frac{dS}{dt} \tag{7.1}$$

$$\frac{dS}{dt} = C(X)\,[A - M]^{+} \tag{7.2}$$

where $C(X)$ is the proportion of excess assimilate that is allocated to structure and is assumed to be a function of the current reserve ratio X.

Table 7.1: *The Broekhuizen et al. (1994) starvation response functions.*

State	Reserve range	Uptake response	Maintenance response
Healthy	$X/X_0 > \tau_1$	$\lambda(X) = 1.0$	$\gamma(X) = 1.0$
Hungry	$\tau_1 \geq X/X_0 > \tau_2$	$\lambda(X) = \xi_{\lambda H} > 1.0$	$\gamma(X) = 1.0$
Torpid	$\tau_2 \geq X/X_0$	$\lambda(X) = \xi_{\lambda L} < 1.0$	$\gamma(X) = \xi_{\gamma L} < 1.0$

One of the major assumptions of the model is that the fish wish to maintain an "ideal" reserve to structural ratio (X_0) so long as there exists an opportunity for positive growth. To do this an individual whose current reserve ratio is at the ideal (X_0) must allocate a fixed proportion:

$$C_0 \equiv \frac{1}{1 + X_0} \tag{7.3}$$

of excess assimilate ($[A - M]^+$) to structural tissue.

The most important aspect of the model is how a fish changes its rate of assimilation and maintenance in response to deviations below the ideal reserve ratio. Small deviations from X_0 result in the fish entering a "hungry" state. If there is a plentiful supply of food the fish increase the rate of uptake (a hyperphagic response) whilst maintenance rate remains unchanged as to that of a healthy (well fed) fish. A further reduction in X below a critical limit results in the fish entering a "torpid" state whereby the rate of assimilation and maintenance are both reduced. The magnitudes of both assimilation and maintenance rates in the nutritionally depleted states of "hungry" or "torpid" are assumed to be scalar products of assimilation and maintenance rates of healthy (well fed) fish such that:

$$M = \gamma(X) M_H \tag{7.4}$$

and

$$A = \varepsilon \min\{\Phi, U_{\max}\} = \varepsilon \min\{\Phi, \lambda(X) U_H\} \tag{7.5}$$

The response functions are summarised in table(7.1).

In terms of allocation, Broekhuizen et al. (1994) chose the following function to control the proportion of excess assimilate to structure

$$C(X) \equiv \min\left\{1, C_0\left[1+\theta(X-X_0)\right]^+\right\}. \tag{7.6}$$

We shall discuss this in further detail below.

7.3.2 Analysis

Broekhuizen et al. (1994) arrived at this model formulation through a process of elimination. They, reportedly, formulated a range of different models (inclusive of models that incorporate a memory of past feeding conditions) and tested each model in both its qualitative and quantitative power to model compensatory growth. Each model was tested in its quantitative success by fitting the model to published growth studies which included a total of 16 different feeding regimes. Not only was the final presented model reportedly less complicated than other models but was, more importantly, the most successful in predicting both the qualitative and quantitative observed patterns of compensatory growth. The final result was a model based on the same lipostatic principles proposed by Kennedy (1953). Seeing as they did not make any explicit reference to any published reports of lipostatic involvement then we can pretty much conclude that this model was independently derived. For an objective analysis we shall compare this models properties with that of the major observed characteristics of compensatory growth we have listed in section(6.5).

The major draw back of this model is that it cannot predict a compensatory growth on realimentation following an initially well fed fish being growth restricted but who had yet managed to remain in a non-negative energy balance. This problem does not arise because of the general model, but from the particular choice of allocation scheme.

Under the current rules of allocation (see equations(7.1), (7.2) and (7.6)), fish initially possessing a reserve ratio at their "ideal" level whom are subsequently faced with a period growth restriction would reduce structural growth rate but not reserve status. Therefore, the reserve ratio would remain at its "ideal" value. Consequently, the lack of any reduction in nutritional status would not elicit a compensatory growth response.

We could, perhaps, modify this particular allocation scheme so that individuals reduced nutritional condition when growth restricted. However, for reasons we have explained in section(4.4.4), the whole class of net production models cannot predict a change in the body constituents of fish whom are fed a maintenance ration. This means that the changes in body constituents reported by Miglavs and Jobling (1989a,b) (see table(3.5)) in fish held in a stationary energy balance could not be predicted. Therefore, on subsequent realimentation no compensatory growth response would be elicited.

The assumption that fish can turn down their maintenance costs was principally noted from Exp. A. of the Quinton and Blake (1990) study, who noted that weight loss was quickest in the first week of starvation of the three week starvation period. Quinton and Blake (1990) mostly attributed this to an emptying of the gut. Nevertheless, this lead Broekhuizen et al. (1994) to postulate that this sequence of weight loss occurred because maintenance rates were being down regulated. Based on the observations of Priede (1985) that the maintenance rates of brown trout (*Salmo trutta*) was approximately four time greater in summer than in winter they derived a value of $\gamma(X) = 0.3$ when the fish is in a torpid state (see table(7.1)). Almost certainly, these large differences are mostly due to the large differences in summer and winter temperatures of 15.0^oC and 5.5^oC, respectively. However, fish are capable of down regulating maintenance rates, but not to such an extent as proposed by Broekhuizen et al. (1994). A recent experiment found that one month starved juvenile Atlantic salmon had managed to reduce maintenance rates by around 20% in comparison to continuously fed conspecifics (O'Connor et al. 2000). This would be equivalent to

$\gamma(X) = 0.8$ when the fish is in a torpid state.

The assumption that maximum uptake was down regulated when the fish were in a torpid state was again principally based on the observations of Exp A. Quinton and Blake (1990), who noted that following three weeks of starvation the majority of the growth occurred in the third week of re-feeding, with only very low growth rates in the first two weeks of feeding. The 1:1 and 2:2 week cycled starvation and re-fed experiments did not produce an equivalent growth response. To accommodate for this Broekhuizen et al. (1994) proposed that once the fish were in a torpid state the cost of a turn-down in maintenance was a turn down in maximum uptake. Within this model framework, this down regulation in feeding, therefore, serves to delay the growth response.

There is no refuting that in this experiment, a delayed reaction to re-feeding was exhibited. However, such delayed responses are actually quite rare, and in the majority of cases compensatory growth occurs very quickly after re-feeding (Jobling and Johansen 1999). The delayed reaction to re-feeding is not unheard of, but even within experimental treatments it can be inconsistent (e.g. Zhu et al. (2001)). We might therefore interpret this phenomenon as belonging more to the behavioural repertoire of compensatory growth rather than a major and consistent observation of feed cycling experiments. One clue to this is that the control fish of Exp. A, Quinton and Blake (1990) only exhibited very slow growth (only growing 0.5cm in length over a period of six weeks).

One of the major constraints Broekhuizen et al. (1994) placed on this model was that individuals exhibited a hyperphagic response to mainly recover lost reserves. This lead them to choose the allocation scheme given by equation(7.6). This scheme changes the proportion of net production committed to structure when X falls below its “ideal” value. As the reserve ratio falls the individual would consider allocating less to structure. Such an allocation scheme makes for a quick recovery in nutritional condition and only a low degree of structural compensation.

7.4 A New Compensatory Growth Model

7.4.1 Derivation

We have reviewed the Broekhuizen et al. (1994) compensatory growth model, which is based on principle that fish are responding to changes in nutritional status. The major drawback of this model is that a compensatory growth response can only be predicted if fish have sustained a negative energy balance during the period of growth restriction, where the literature states quite clearly otherwise. This inadequacy results from the particular rules of allocation and not the general model. However, no matter what particular rules of allocation we choose based upon the net production scheme we cannot predict a change in the body constituents of fish fed a maintenance ration. As a consequence of this no compensatory growth response would be predicted on subsequent realimentation. Therefore, we shall aim to derive a new compensatory growth model based upon fish responding to changes in nutritional status but using either the reserve or assimilation allocation scheme.

Rather than the fish being in one of three nutritional states we shall consider there to be only two, namely, hungry or healthy. We shall not include a torpid state. Whilst we do not deny that fish reduce metabolic expenditure, we consider the effect of this small reduction to be small in comparison to the major observed patterns of growth. Furthermore, the inclusion of a turn down in maintenance will always serve to increase food conversion efficiency which is not generally supported by experimental results. We shall consider the hyperphagic response (when elicited) to be immediately effective when the fish are re-fed.

The Broekhuizen et al. (1994) model assumed that fish become hyperphagic in response to a depression below a fixed threshold reserve ratio value. We in accordance with Kennedy (1953) shall consider that individuals become hyperphagic in response to a reduction in reserve status. Both the reserve and assimilation allocation models posses steady state reserve ratio values which are dependent upon the fish's growing conditions, both in relation to temperature and ration level such that $X^* = X^*(T, \phi)$ (see section(4.5) and (4.6)). This means that well fed fish will approach a steady state reserve ratio value given by $X^* = X^*(T, \phi = 1.0)$. A reduction in nutritional condition will ensue if either the temperature is depressed or the ration level is reduced, thus, initiating an increase in appetite. If we assume that appetite returns to a normal level when the reserve ratio is near $X^* = X^*(T, \phi = 1.0)$ then we can simply incorporate a hyperphagic response by restating the fish's maximum uptake as

$$U_{\text{max}} = \lambda(X) U_H \tag{7.7}$$

where U_H is the normal healthy maximum uptake and $\lambda(X)$ is the hyperphagic response function given by

$$\lambda(X) = \begin{cases} 1.0 & \text{if} \quad X > X^*(T, \phi = 1.0) - \Delta \\ \xi_{\lambda H} & \quad \text{otherwise.} \end{cases} \tag{7.8}$$

where, $\xi_{\lambda H} > 1$.

7.4.2 Reserve Allocation

Figure(7.1) displays a number of compensatory growth simulations using the reserve allocation model with different values for the hyperphagic constant $\xi_{\lambda H}$. Initially, the starvation period leads to a quick decrease in reserve status since commitment to structure continues and also maintenance costs must be met. On subsequent realimentation, the hyperphagic response function becomes active. (By choosing a value of $\xi_{\lambda H} = 1.0$ we display the growth response with no hyperphagic response.) For all simulations, recovery of nutritional condition is very quick with no structural growth compensation exhibited in the recovery growth phase, which, is contrary to the literature reports.

For analytical purposes we shall re-display the reserve allocation model dynamics

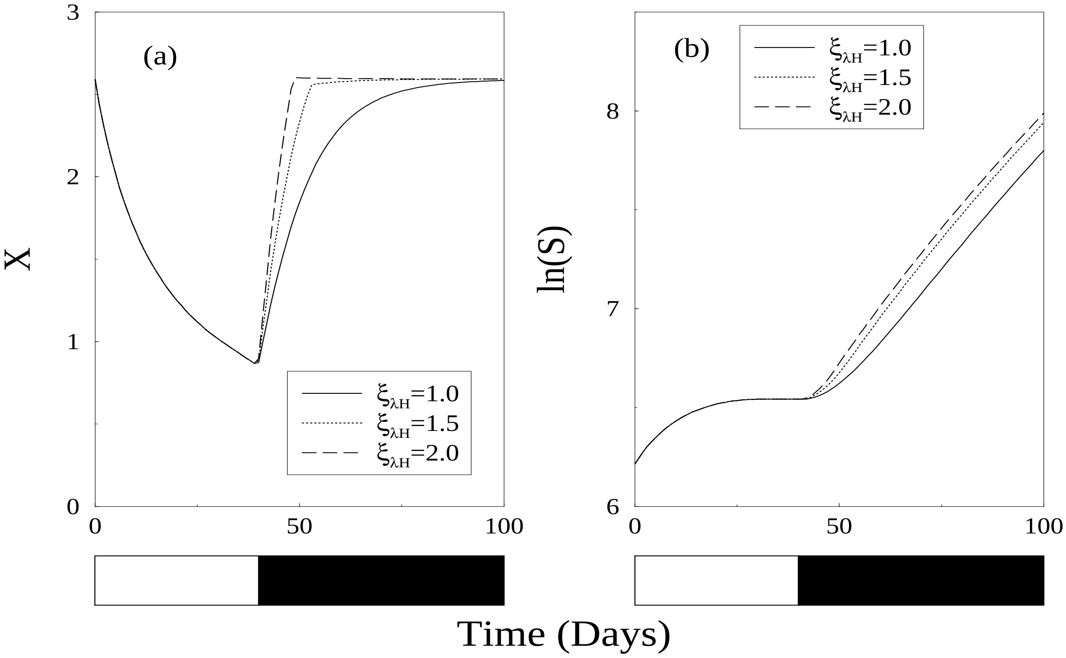

Figure 7.1: *Trajectories of a) reserve ratio and b) structural carbon weight for starved - refed individuals committing to structure according to the reserve allocation scheme with the hyperphagic response function given by equation(7.8). The bars denote the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $b_1 = 0.1$, $g = 0.75$, $\mu = 1.0$, $T = 12.0^oC$, $X_0 = X^* = 2.59$, $\Delta = 0.05$, $S_0 = 500\ mgC$.

which are given by

$$\frac{dR}{dt} = A - M - \frac{dS}{dt} \tag{7.9}$$

and

$$\frac{dS}{dt} = b_1 S^g [X - \mu]^+ . \tag{7.10}$$

From equation(7.10), we can see that this very quick recovery in reserve status and no structural compensation occurs because the rate and degree of commitment to structure is governed by reserve status. This means that hyperphagic recovering individuals, initially in poor condition, show only very poor growth in structure. The reduced commitment to structure leads to a very quick recovery in nutritional condition, which, quickly ablates the hyperphagic response. This results in individuals who became hyperphagic only being slightly larger at the end of the simulation and only by virtue of a quicker recovery of condition, allowing them to begin committing to structure at the normal control levels, earlier.

In conclusion, without any additional changes in parameter values, the characteristics of recovery growth predicted by the reserve allocation scheme are not in accordance with the literature reports. Thus, we shall move on to investigate the assimilation allocation model.

7.4.3 Assimilation Allocation

For a constant diet formulation (and assuming the structural nutrients supplied in the fish's normal uptake are not excessive, i.e. k does not change directly with ration level) the assimilation allocation model dynamics can be written as follows

$$\frac{dR}{dt} = (1-k)A - M, \tag{7.11}$$

and

$$\frac{dS}{dt} = kA \tag{7.12}$$

with

$$k(X) = \min\left\{k_1, \frac{[X-\mu]^+}{a_1}\right\} \tag{7.13}$$

The reserve allocation scheme was not successful because it could not predict any genuine structural compensation. However, with this model an increase in uptake will increase assimilation rate and therefore structural growth rate. Since we have assumed that the fish's maximum structural growth rate is pro-

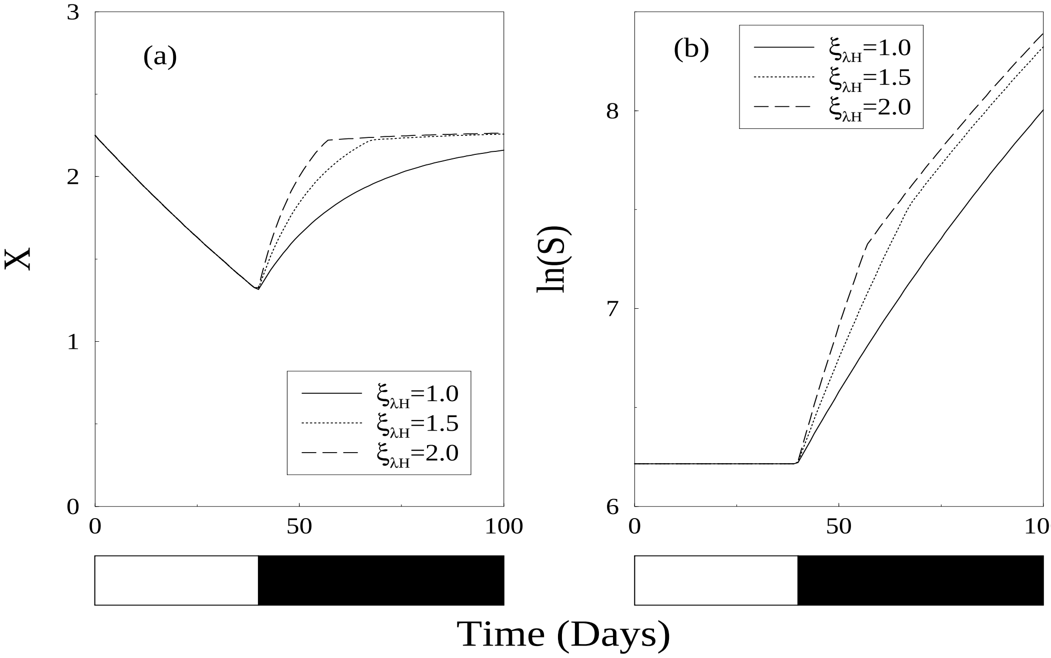

Figure 7.2: *Trajectories of a) reserve ratio and b) structural carbon weight for starved - refed individuals committing to structure according to the assimilation allocation scheme with the hyperphagic response function given by equation(7.8). The bars denote the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $b_1 = 0.1$, $g = 0.75$, $\mu = 1.0$, $a_1 = 0.5$, $T = 12.0^oC$, $X_0 = X^* = 2.28$, $S_0 = 500\ mgC$.

portional to maximum uptake (see equation(5.21)) then maximum structural growth rate will also increase in hyperphagic fish. This means ϕ_S will remain unchanged in equation(5.24) and so k_1 will remain constant when the individual is hyperphagic.

Figure(7.2) displays compensatory growth simulations using the assimilation allocation model with different values of the hyperphagic uptake constant $\xi_{\lambda H}$. It can be seen that individuals who become hyperphagic on realimentation undergo a quicker recovery than non-hyperphagic fish but also undergo structural compensation. However, because the fish are immediately committing the same proportion of assimilate to structure when hyperphagic, the compensation period is more prolonged than in the reserve allocation scheme. This results in

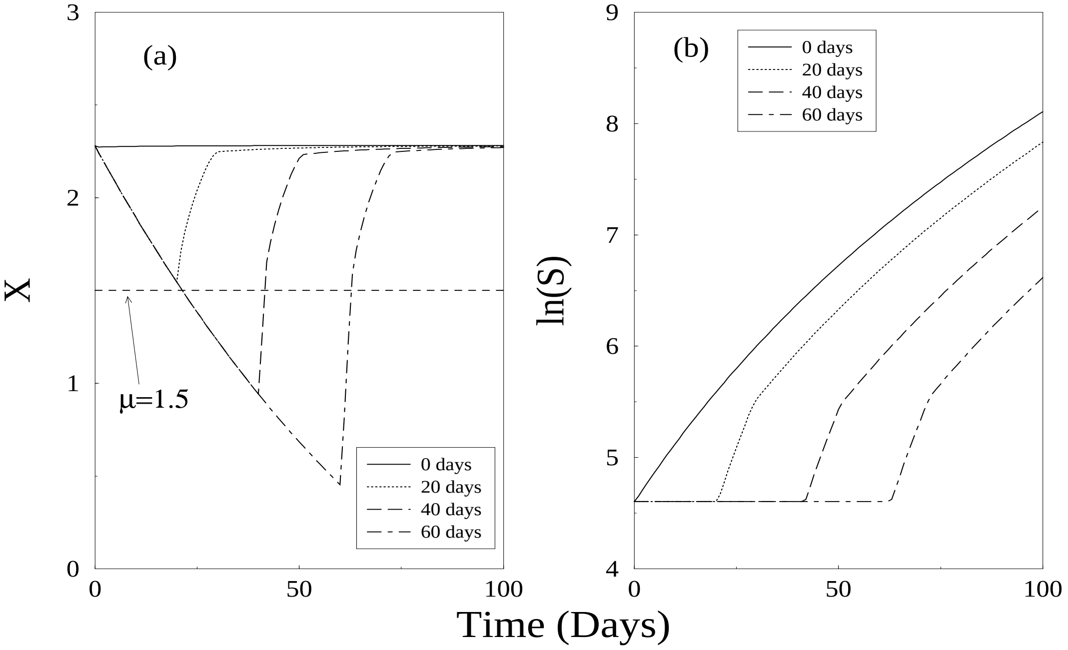

Figure 7.3: *Trajectories of a) reserve ratio and b) structural carbon weight for starved - refed individuals committing to structure according to the assimilation allocation scheme with the hyperphagic response function given by equation(7.8). The bars denote the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration. Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $T = 12.0^oC$, $a_1 = 0.5$, $\mu = 1.5$, $\xi_{\lambda H} = 2.0$, $X_0 = X^* = 2.28$, $S_0 = 100$ *mgC.*

hyperphagic fish being larger at the end of the simulation whilst still having fully recovered reserve status. The effect of increasing the hyperphagic constant $\xi_{\lambda H}$ from 1.5 to 2.0 is to mainly make for a quicker recovery of reserve status and only a slightly higher degree of structural compensation.

Figure(7.3) displays a number of compensatory growth simulations with different periods of starvation using a constant value of $\mu = 1.5$. It can be seen that, in this case, if the starvation period is moderate then structural growth losses are not too severe as compared to fully fed controls. However, if the reserve ratio falls below the threshold for maintaining growth μ then growth losses become great. For example, consider the individuals in figure(7.3) who were starved for

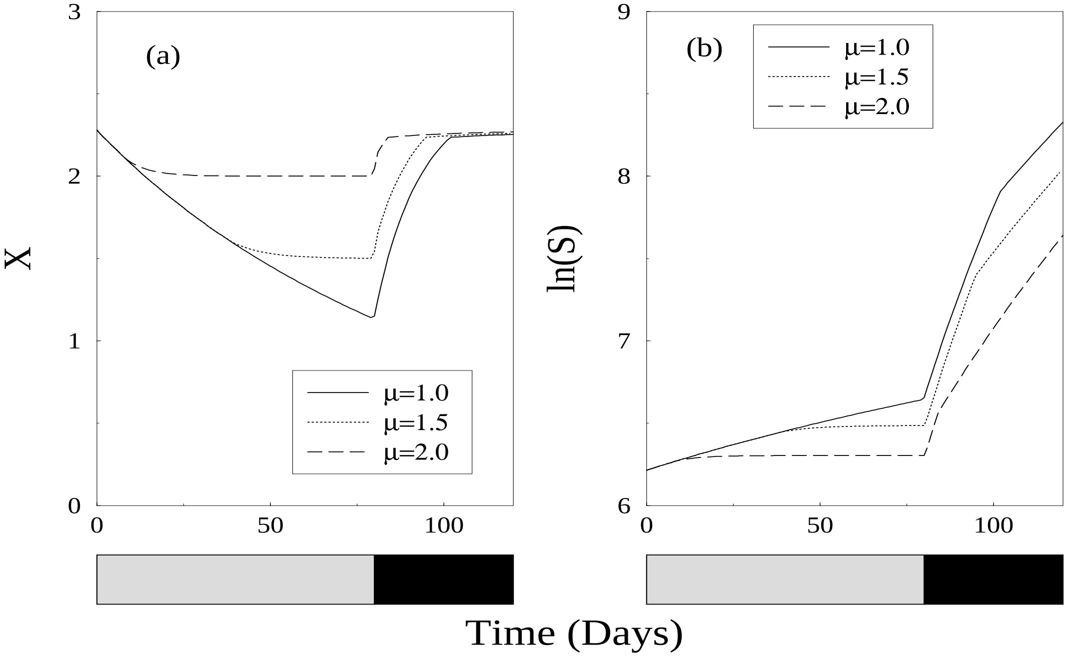

Figure 7.4: *Trajectories of a) reserve ratio and b) structural carbon weight for starved - refed individuals committing to structure according to the assimilation allocation scheme with the hyperphagic response function given by equation(7.8). Additional parameter values used in conjunction with table(4.1) to simulate these trajectories are* $T = 12.0^oC$, $a_1 = 0.5$, $X_0 = X^* = 2.28$, $\xi_{\lambda H} = 2.0$, $S_0 = 500\ mgC$.

40 and 60 days. Although the 60 days starved individual exhibited the greatest depletion of reserve status the degree of structural compensation is identical (see figure(7.3,b)).

Growth losses begin to be great as compared to fully fed controls once the reserve ratio falls below μ because all assimilate on subsequent realimentation is first allocated to reserves in order to reduce the immediate threat of starvation. It is only when the reserve ratio rises above μ when structural growth compensation is initiated. This means that any depletion of the reserve ratio below μ does not benefit the ensuing structural compensation one jot. That is, no matter how far below μ the reserve ratio falls, the degree of structural compensation will always be the same. Thus, in accordance with the literature, if the growth restriction is too harsh then growth losses begin to be severe in comparison to fully fed controls.

Jobling and Johansen (1999) hypothesise that inconsistencies in the amount growth losses are recovered may arise from differences in the composition of the weight gain during compensation. An alternative and equally interesting hypothesis is that such inconsistencies could arise from the extent individuals will maintain structural growth during the growth restriction period. Figure(7.4) displays a number of compensatory growth simulations for individuals whom posses different values of μ and fed a maintenance ration ($A = M$) during the growth restriction period. It can be seen that individuals with the lowest defended reserve ratio allocate the most to structure and hence receive the greatest reduction in nutritional condition. On realimentation, these individuals undergo the longest hyperphagic response. The end result is large size differences at the end of the simulation.

7.5 Discussion

We have analysed the net production, reserve and assimilation allocation models in their respective abilities to model the dynamic behaviour of compensatory growth. The net production model failed because it could not predict a change in nutritional status in individuals fed a maintenance ration. The reserve allocation model failed because it could not predict any genuine structural compensation with an increase in uptake. Our final model, based upon the assimilation allocation scheme, is capable of displaying all the major characteristics of compensatory growth as listed in section(6.5). In this model, growth losses begin to be substantial as soon as the reserve ratio breaches the no growth boundary μ. Perhaps, surprisingly, there is experimental evidence of this growth dynamic in action.

Results from broiler chickens have suggested that the success of a restricted feeding programme in allowing full recovery of body weight may be dependent upon the birds experiencing a negative energy balance during the restriction, whilst, at the same time, being in positive protein balance. In other words, the bird mobilises stored body fat during the restriction period, but the amino acids in the supplied in the low ration allow continued protein deposition. Upon a return to *ad libitum* feeding conditions there is a rapid compensatory growth of lean tissues. However, if the protein deposition is prevented during the restriction phase, either because the restriction is too severe or is of long duration, complete compensatory growth of the lean tissues does not occur (Jones and Farrell (1992a,b)).

The point at which protein deposition ceases would be in accordance with our threshold reserve ratio value for maintaining growth. This threshold would be breached if the restricted food supply was not enough to support the cost of living, that is, the restriction is too harsh. Also, if the restricted ration supply was enough to support maintenance costs, but applied for too long then growth would eventually cease when condition reached the no growth boundary and the organism would remain in a stationary state thereafter. No matter how long the individual was kept on the no-growth boundary the degree of compensation would remain the same. Therefore, growth losses would begin to be lost in comparison to continuously fed conspecifics.

Chapter 8

Testing the Compensatory Growth Model

8.1 Introduction

In the previous chapter we derived a candidate compensatory growth model that explains how the phenomenon of compensatory growth may be regulated. Our model, based upon the assimilation allocation scheme, displays all the most widely reported qualitative features of compensatory growth as listed in section(6.5). Our next step is to test whether this model is feasible. This will involve investigating two quantitative aspects of the model. First, how well can the assimilation allocation scheme predict the growth of fish reared under normal conditions? Second, how well can the model predict the compensatory response on realimentation following a period of growth restriction.

To accomplish this we shall attempt to fit the model to observed growth trajectories of salmonids reared in tank-based environments and given a fluctuating supply of food. These experiments will include a range of temperatures, different feed cycling regimes and a variety of fish sizes. The model will be tested in its quantitative capability to predict both changes in wet weight and length.

8.2 The Test Data Set

We have found five studies which are suitable to test our model. Two of these concern the growth of Arctic charr, *salvelinus alpinus* L. (Miglavs and Jobling (1989a,b); Jobling et al. (1993)). The three remaining studies are observations on rainbow trout, *Oncorhynchus mykiss* (Weatherley and Gill (1981); Quinton and Blake (1990); Kindschi (1988)). We have already discussed the experimental protocols and results of these studies in chapter 6 and have also displayed the wet weight growth trajectories. We shall not include the results of exp.A from the Quinton and Blake (1990) study since the controls only exhibited very slow growth and we deem the delayed reaction to re-feeding as uncharacteristic.

Length measurements for all survey points are available for the Jobling et al. (1993) and Quinton and Blake (1990) studies. Kindschi (1988) supplies lengths for the initial and final survey points. Weatherley and Gill (1981) give length measurements for initial, final and at transition point in feeding regimes. No length measurements are given for the Miglavs and Jobling (1989a,b) study. No direct measure of variance for length data is reported in any of the studies.

The key features of all these experiments are summarised in table(8.1).

Table 8.1: *Characteristics of the test data set.*

Study	Exp.	Species	Temperature ^oC	Low ration % wet wt day^{-1}	High ration % wet wt day^{-1}	Feed cycle low:high(weeks)
Miglavs and Jobling (1989a,b)	M1	*Salvelinus alpinus*	8	Satiation	Satiation	Control
	M2		8	0.2	Satiation	8:8
	M3		8	Nil	Nil	–
Weatherley and Gill (1981)	W1	*Oncorhynchus mykiss*	12	*ad libitum*	*ad libitum*	Control
	W2		12	3.0 (of dry weight)	*ad libitum*	16:12
	W3		12	Nil	*ad libitum*	3:15
	W4		12	Nil	*ad libitum*	13:15
Quinton and Blake (1990), Exp. B	QB1	*Oncorhynchus mykiss*	13	5.0	5.0	Control
	QB2		13	Nil	5.0	3:3
Kindschi (1988)	K1	*Oncorhynchus mykiss*	12.2	58.06 length^{-1}(cm)	58.06 length^{-1}(cm)	Control 1
	K2		12.2	29.03 length^{-1}(cm)	29.03 length^{-1}(cm)	Control 2
	K3		12.2	Nil	58.06 length^{-1}(cm)	3 days:4 days
	K4		12.2	Nil	116.1 length^{-1}(cm)	1:1:1:1[*]
Jobling et al.[†] (1993)	J1	*Salvelinus alpinus*	9.5	Satiation	Satiation	Control
	J2		9.5	Nil	Satiation	1:1
	J3		9.5	Nil	Satiation	1.5:1.5
	J4		9.5	Nil	Satiation	3:3

[*] The cycle in this experiment was nil:58.06 length^{-1}:nil:116.1 length^{-1}.

[†] Following 24 weeks of cyclic feeding all groups (J1-J4) were fed to satiation for a further 6 weeks.

8.3 Energetic Considerations

The test data set provides wet weights and in most cases length measurements for a number of salmonids held on a large variety of feeding regimes. Therefore, from a combination of both total carbon weight and reserve ratio the new model derivations need to able to predict wet weight and length. The variable conditions for growth will induce a multitude of different nutritional states which will be related to both the length and severity of the restricted growth regime. Because the specific energy content of fish change significantly with different growth environments then it is not feasible to simply derive a constant carbon to weight conversion ratio. That is, we cannot assume that wet weight is a constant scalar value of total carbon weight. The aim of this section is to introduce a method for more accurately assessing the energetic content of the fish.

Since it is often argued that the nutrient value of a food item is proportional to its carbon weight (Gurney and Nisbet 1998) it would be desirable to derive a carbon weight energy conversion ratio. Based on the dry weight and carbon weight analysis of juvenile Atlantic salmon (*Salmo Salar* L.) fed 4 different ration sizes ranging from zero to maximum for a period of 60 days and the strong negative linear relationship between water content and energy which is similar for a number of different salmonids (figure(3.8)) we derive a conversion ratio of 12.0 cal/mg$C$ (Carter et al. 1992).

In the absence of any other statistical models that estimate the energy content of salmonids based on a combination of weight and length we shall use Elliott (1976a) statistical representation parameterised for brown trout. Although a different species we should expect the estimates to be reasonable since the salmonid family group of fish is often characterised by their highly morphological homogeneity (Rankin and Jensen 1993). Furthermore, we have shown the relationship between energy content and specific water content to be similar for a number of different species figure(3.8).

By substituting energy for carbon weight in equation(3.4) we can with some rearrangement arrive at

$$W = \left(\frac{12.0 L^{3b_1} W_c}{a 100^{b_1}} \right)^{\frac{1}{(1+b_1+b_2)}} \tag{8.1}$$

where, W_c is the total carbon weight (mg), L is fish length (cm) and W is the wet weight (g). Since length will be predicted from the structural carbon weight (equation(2.20)) then equation (8.1) can subsequently be used to predict wet weight. Therefore, given a total carbon weight and reserve ratio both the length and the wet weight of the fish can be predicted and hence the models can be fitted to the test data set.

8.4 Parameterisation

The aim of this chapter is to test whether the model is feasible. Although we aim to find a good fit we must also recognise that to obtain the very best optimum fit would almost certainly require that most parameter values would change across studies. To simplify the fitting process (and gain more confidence in our model) we will aim to reduce the number of free fitting parameters. To do this we shall assume that some parameters can be held constant across all species and studies, whilst other parameters are more likely to be study specific.

The model will first be fitted to the control portions of the data and then will be extrapolated (using the same parameters) to asses the difference between normal growth and the exhibited compensatory growth. This means that the greatest majority of the parameter values have to be estimated from the controls (i.e. food supply is constant). This means that there is relatively little starvation data in which to parameterise maintenance rates of each study. Therefore, we shall assume that maintenance is constant across all studies. In view of the relatively small temperature range (8-13^oC) we derive an exponential temperature scaling value from the literature of 12^oC based on observations by Elliott (1976b) and Jones (1976). For the maintenance allometric scaling we shall use a value of 0.75

Table 8.2: *Independently determined parameters.*

Parameter	Interpretation	Units	Value	Source
T_M	Maintenance characteristic temperature	^{o}C	12.0	Jones (1976)
v	Maintenance cost allometric index	—	0.75	From and Rasmussen (1984)
d	Maximum uptake allometric index	—	0.75	Elliott (1976b)
T_H	Uptake rate characteristic temperature	^{o}C	6.0	Elliott (1976b)
Δ	see equation(7.8)	—	0.05	—

based on the observations of From and Rasmussen (1984) on rainbow trout. The maintenance cost rate scaling (M_{H0}) will be treated as a global fitting parameter which will be held constant over all studies.

The Broekhuizen et al. (1994) approach was to assume that the fish all had the same ideal reserve ratio and therefore to treat the parameters values of α and β in the relationship between structure and length as study specific fitting parameters. In view of the high morphological homogeneity of different species of salmonids we shall take a different approach and assume that the values of α and β are a more generic property of the fish. Hence, we shall treat them as global fitting parameters held constant across studies.

One of the most likely factors that will differ between studies is the diet formulation. The effects of different diet formulations will be to change assimilation efficiency ε and allocation k. k is a function of both reserve ratio and fraction at which structural growth is being achieved. If the attempted commitment to structure is above that of the maximum rate then k must reduce. Whether, maximum structural growth is achieved or not will depend on the ration level and diet composition (i.e. quality of diet and proportion of structural nutrients). Unfortunately, there was neither the resolution of length or weight data or diet composition data to investigate this effect. However, since in all studies, feeds were obtained from commercial sources then we should not expect the protein to be supplied in the diet to be too wasteful. Therefore, even if structural growth was at maximum we should not expect a great reduction in the value of k. Hence, we shall assume the value of k to be independent of ration level and treat it as a study specific fitting parameter as a reflection of the differences in the relative proportions of structural and non-structural nutrients supplied in the diet. In a similar manner, the quality and composition of the diet will also affect the assimilation efficiency ε and so its value will also be treated as a study specific fitting parameter.

Considering uptake, we shall assume an exponential temperature dependence and use a global value of 6.0 derived from Elliott (1976b) for the temperature scaling. In view of the reported similarities in both uptake scaling and maintenance scaling and also given the fact that the greatest majority of changes in nutritional condition will be as a result of changes in growth conditions we use the same allometric scaling value of 0.75 for uptake Elliott (1976b). Unfortunately, it was not possible to assign a global value of uptake scaling for all studies and when we attempted to do so, controls did not give a good fit. Therefore, we treated U_{H0} as a study specific fitting parameter. In such circumstances where food supply was alternated between excess and starvation rations (i.e. Quinton and Blake (1990);[1] Jobling et al. (1993)) the product of assimilation efficiency and uptake scaling were mutually confounded by one another. In this case we

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[1] Strictly speaking, the daily ration provision in the Quinton and Blake (1990) exp.B study was not supplied in excess (see table(8.1)). However, under no circumstances (including hyperphagic fish) did the model predict the rate of food consumption to rise above the 5% wet body weight per day. Therefore, the product of assimilation efficiency and uptake were still mutually confounded by one another.

merged the product of these two parameters into a single fitting parameter which we treated as a study specific fitting parameter.

We have identified the value of μ, the threshold for maintaining growth, to possibly be a factor in explaining why there may be disparate results in the extent to which growth losses are recovered. However, with our resolution of data, the direct effects of μ on growth are very hard to fit to, making μ somewhat of a poorly defined fitting parameter. More precisely, with the relatively low resolution of length data in the control portion of data, its effects (such as the reserve ratio at which structural growth (length) ceases) cannot be directly measured and thus fitted to. Therefore, we shall attempt to fit a global value of μ and a_1.

All the above free fitting parameters were estimated by fitting to the control portions of the complete data set. The one remaining parameter value to be estimated was the hyperphagic uptake constant. In such circumstances where compensatory growth was conclusively shown to have occurred (see later) we (using the same parameter values) extrapolated the recovery growth phases using our hyperphagic response function. We treated the hyperphagic constant $\xi_{\lambda H}$ as being a global fitting parameter for all studies in which compensatory growth was definitely found to occur.

In conclusion, based upon our assumptions we were left with a total of 19 free fitting parameters. With the exception of the global hyperphagic constant $\xi_{\lambda H}$, all parameters were derived from the control portion of the data. Of these parameters, 13 were study specific and the remaining 5 were global, i.e. assumed to be equal for all experimental groups of fish.

8.5 Error Measure

The models are to be fitted to mean weight and length measurements for each study. It is invariably found that the variability of weight and length within growing cohorts increases with fish size (see all figures). Since this violates the assumption of homoscedasticity (the assumption that variance remains constant), minimising the square error is not an option. A prudent error measure would need to weight the point error with the variance of the mean observation. Therefore, the following point error measure would be desirable

$$E_{i,j} = \frac{(O_{i,j} - P_{i,j})^2}{\sigma_{i,j}^2} \tag{8.2}$$

where, $P_{i,j}$ is the predicted weight or length, $O_{i,j}$ is the mean observed weight or length and $\sigma_{i,j}^2$ is the sample variance of the data point j from study i.

Unfortunately, the exact values of variability associated with each mean weight and length are not given for all the published studies. In the absence of detailed variability data it will be assumed that the coefficient of variation remains constant in each study both for mean weights and lengths. The great advantage of this assumption is that c.v. can be removed from the error measure since its only function is multiply the error by a scalar quantity. Further, if equation(8.2) is modified by taking the positive square root it will yield a more intuitive measure defined as

$$E_{i,j} = \frac{|O_{i,j} - P_{i,j}|}{O_{i,j}} \tag{8.3}$$

which is the proportional error in predicting the observed mean value. This measure will be used for calculating point errors for every mean weight and length observation in each study.

The models are to be fitted to a number of different data sets which each contain a varying number of data points. To be fair and consistent, equal precedence must be given to each data set. Therefore, for each data set the mean proportional error will be minimised and summed to establish a total. If this total is further divided by the number of studies it yields a more intuitive measure, namely, the average mean proportional error between studies, which is an as-

Table 8.3: *Composition of diets fed to fish of Kindschi and Weatherley.*

	Experiment	
%	W	K
Water	35.4	11.2
Protein	41.6	59.6
Lipid	13.0	5.3
Ash	7.5	10.2
Other	2.5	13.7

sessment of the quality of fit to a typical data point. This error is summarised mathematically as

$$E_G = \frac{1}{N_S}\sum_{i=1}^{N_S}\frac{1}{N_i}\sum_{j=1}^{N_i}\frac{|O_{i,j} - P_{i,j}|}{O_{i,j}} \tag{8.4}$$

where, N_i is the number of data points in study i and N_S is the total number of studies.

8.6 Initial Conditions

All fish were, reportedly, well fed before the beginning of each experiment. Therefore, we assumed that all groups of fish started each experiment with a value of reserve ratio equal to that of its steady state value. For each experimental group, this was calculated from the combination of an estimate of initial total carbon weight and the values of the trial parameters. This practice allowed us to calculate the initial values of reserve and structural carbon weight. However, since the state variable initial conditions were not calculated directly this meant that the predicted initial length and thus weight (see equation(8.1)) were not equal to the reported initial conditions. This meant we had to include the initial weight and length measurements as fitting points in order to force the parameter values to comply with the initial conditions. This actually proved to be an advantage since we could add the initial length measurements to the already sparse number of length fitting points. This practice was necessary because the initial length measurements were not given for the Miglavs and Jobling (1989a,b) study, but from the body composition analysis we could predict the initial total carbon weight. Broekhuizen et al. (1994) adopted a similar approach but set the initial reserve ratio value to its "ideal" value in each study.

Only two of the five studies report the composition of the feed (Weatherley and Gill (1981); Kindschi (1988); see table(8.3)). To convert these into units of carbon we used our energy conversion factor of 12 cal/mgC. Where the composition of the diet is not given, we assume, following Broekhuizen et al. (1994) that the feed is 40% carbon by weight.

8.7 Simulations

Growth trajectories were predicted for each experimental protocol by integrating the model equations (7.11) and (7.12). We used a fourth order Runge-Kutta algorithm (Press et al. 1989) using a fixed time step of 0.1 of a day. For minimising the above error function we used the downhill simplex method of optimisation (Nelder and Mead 1965) backed up with bootstrap restarting (Wood 2001) to avoid spurious local minima. Details of both these schemes are given in the appendices.

Model parameters were estimated by fitting to the control section of each study. Since the models shared a common set of parameters we minimised all parameters simultaneously. We then extrapolated the growth simulations to the refeeding portions of the data. To ascertain whether any significant compensatory growth responses were found we compared predicted with observed weight and length trajectories assuming that the fish did not become hyperphagic.

Following this analysis we fitted the complete compensatory growth model in-

Table 8.4: *Best fit study specific parameter values.*

		Experiment				
Parameter	Units	W	M	QB	K	J
k_1	-	0.18	0.19	0.15	0.25	0.33
ε	-	0.65	0.60	–	0.28	–
U_{H0}	mgC^{1-d} day^{-1}	0.12	0.19	–	0.20	–
εU_{H0}	mgC^{1-d} day^{-1}	0.078	0.114	0.085	0.056	0.098

clusive of the hyperphagic response function and treated the hyperphagic uptake constant $\xi_{\lambda H}$ as a global fitting parameter.

8.8 Results

The best fit study specific and global fitting parameters are given in tables (8.4) and (8.5), respectively. The fitted growth trajectories for each study are displayed in figures(8.1) to (8.8). In each case, the long dashed lines represent the extrapolated growth trajectories assuming no hyperphagic response on realimentation. It can be seen that the control portions of the studies were fitted in an

Table 8.5: *Best fit parameter values held constant across all experiments.*

Parameter	Interpretation	Value	Units
M_{H0}	Maintenance cost rate scale	0.02	mgC^{1-v} day^{-1}
$\xi_{\lambda H}$	Hungry uptake/healthy uptake	1.40	—
μ_S	Structural growth reserve ratio threshold	0.87	—
b_1	Structural growth sensitivity parameter	0.89	—
α		1.99	cm mg $C^{-\beta}$
β		0.28	—

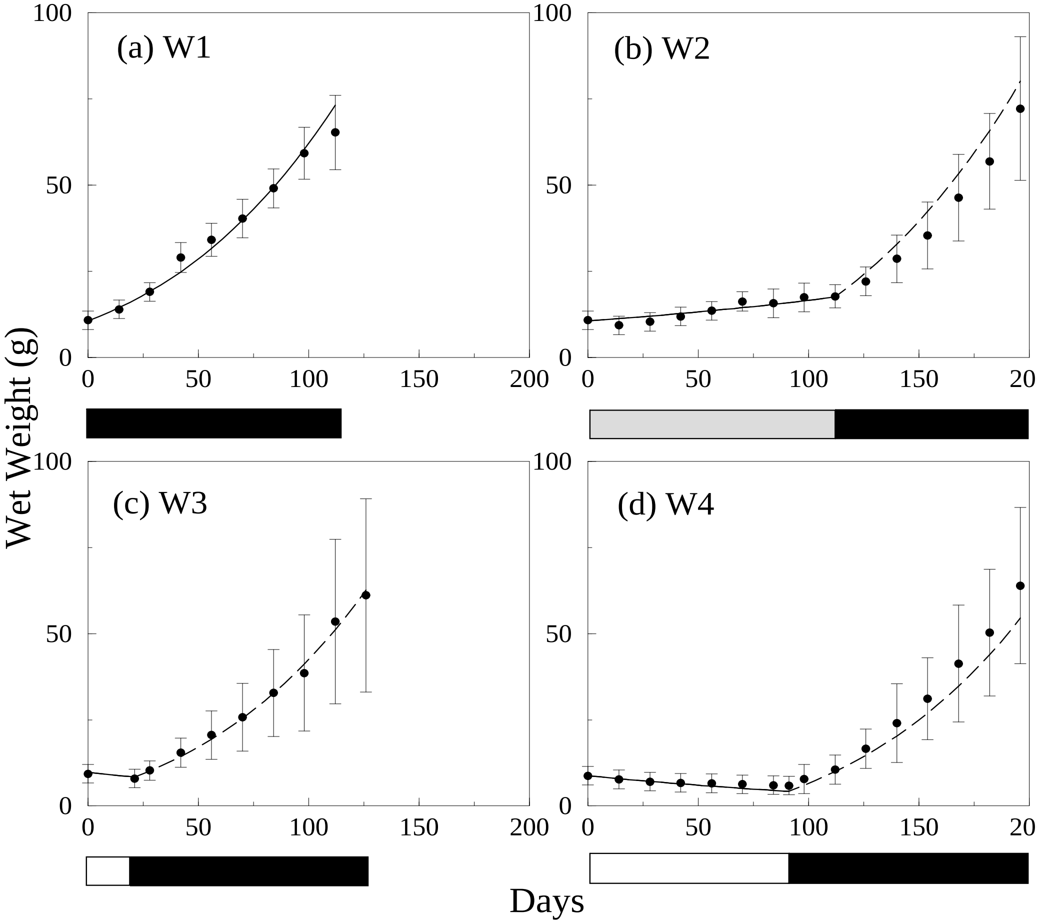

Figure 8.1: *Observed and predicted weights for the fish of Weatherley and Gill (1981). The model has been fitted to the control section (solid line) and using the same parameter values has been extrapolated forward (long dashed line) assuming there is no hyperphagic response. It can be seen that there is no evidence of a hyperphagic response. The bar below each figure denotes the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

excellent manner. The one exception is the prediction for the final data point of the control portion to the Jobling et al. (1993) study. However, a brief analysis found the SGR to decrease in a linear manner rather than geometrically with increasing size. This could possibly be related to the fish reaching a sexually mature age, although, we only included the reportedly non-maturing fish in our data set.

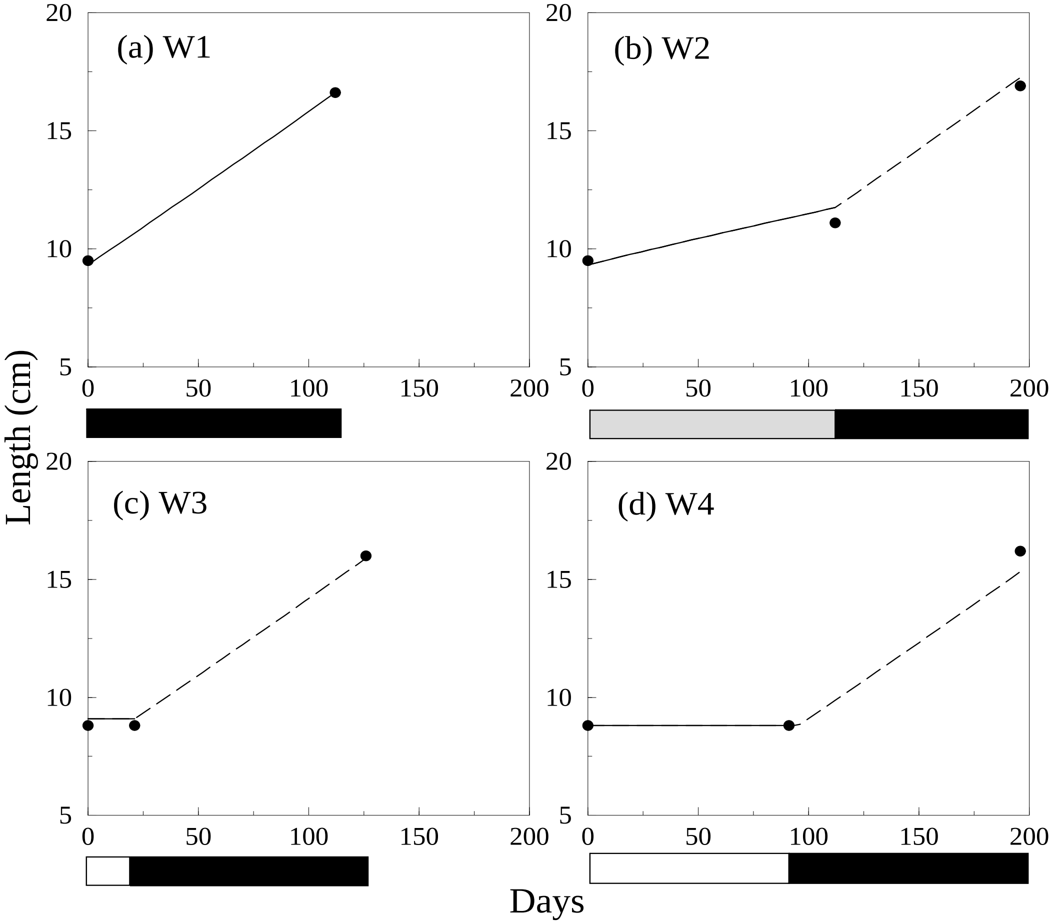

Figure 8.2: *Observed and predicted lengths for the fish of Weatherley and Gill (1981). The model has been fitted to the control section (solid line) and using the same parameter values has been extrapolated forward (long dashed line) assuming there is no hyperphagic response. It can be seen that there is no evidence of a hyperphagic response. Vertical bars denote 95% confidence intervals. The bar below each figure denotes the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

We could find no evidence of any significant compensatory growth response within the Weatherley and Gill (1981) study. The extrapolated growth trajectories (assuming no hyperphagia) all did not significantly differ from the re-fed growth phases (see figure(8.1)). Length predictions were also in good agreement (see figure(8.2)). A further analysis showed this still to be the case even when μ_S and b_1 (two parameters which we can possibly explain disparities in which growth losses are recovered; see section(7.4.3)) were assumed to be study specific fitting parameters. Since food intake was not monitored then it impossible to conclude whether there was a hyperphagic response or not. With no real evidence to the contrary we assumed that no significant compensatory growth response was exhibited (in view of their conclusions we should perhaps not be surprised) and thus omitted this study from the secondary fitting procedure.

Weatherley and Gill (1981) fed experimental groups of fish a daily *ad libitum* supply of food (see table(8.1)) and give no mention of any special provisions for weight compensating fish. It is therefore possible that during the recovery growth phase the food supply was not sufficient to meet the maximum uptake of hyperphagic fish. This may be one reason why a genuine compensatory growth response was not exhibited.

In all other studies, significant compensatory patterns of growth were found to have occurred. It can be seen from the figures that the forward extrapolated predictions consistently and significantly under predicted both weight and length observations. By applying our simple hyperphagic uptake function, that is, increased uptake until the previous nutritional condition has been recovered we obtained a much better fit to both the remaining length and weight observations in all studies (dot dashed lines).

The greatest majority of the predictions lie within the 95% confidence intervals but there are a few exceptions. The final weight observation within the Quinton and Blake (1990) study has been over predicted. However, given that there was a problem in water quality (as explained in section(6.2)) we should not be surprised. The one remaining minor discrepancy is the final observation from the Kindschi (1988) study (exp. K4).

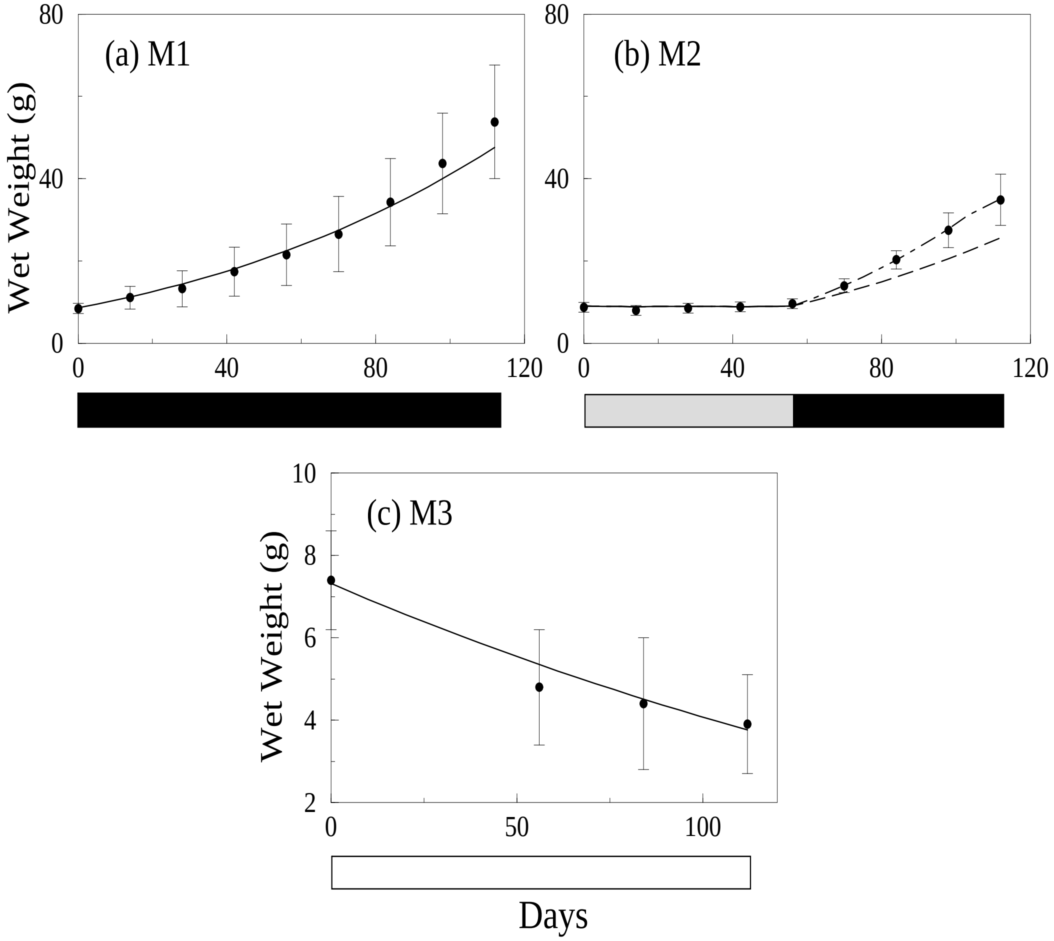

Figure 8.3: *Observed and predicted weights for Arctic charr of Miglavs and Jobling (1989,a,b). Vertical bars denote 95% confidence intervals. The model has been fitted to the control section (solid line) and using the same parameter values has been extrapolated forward (long dashed line) assuming there is no hyperphagic response. The dot dashed line is the fitted model predictions including a hyperphagic response to refeeding. The bar below each figure denotes the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

8.9 Summary

In the first chapter of this part we reviewed the literature in order to identify the major characteristics of compensatory growth. This resulted in a well defined target set of modelling objectives.

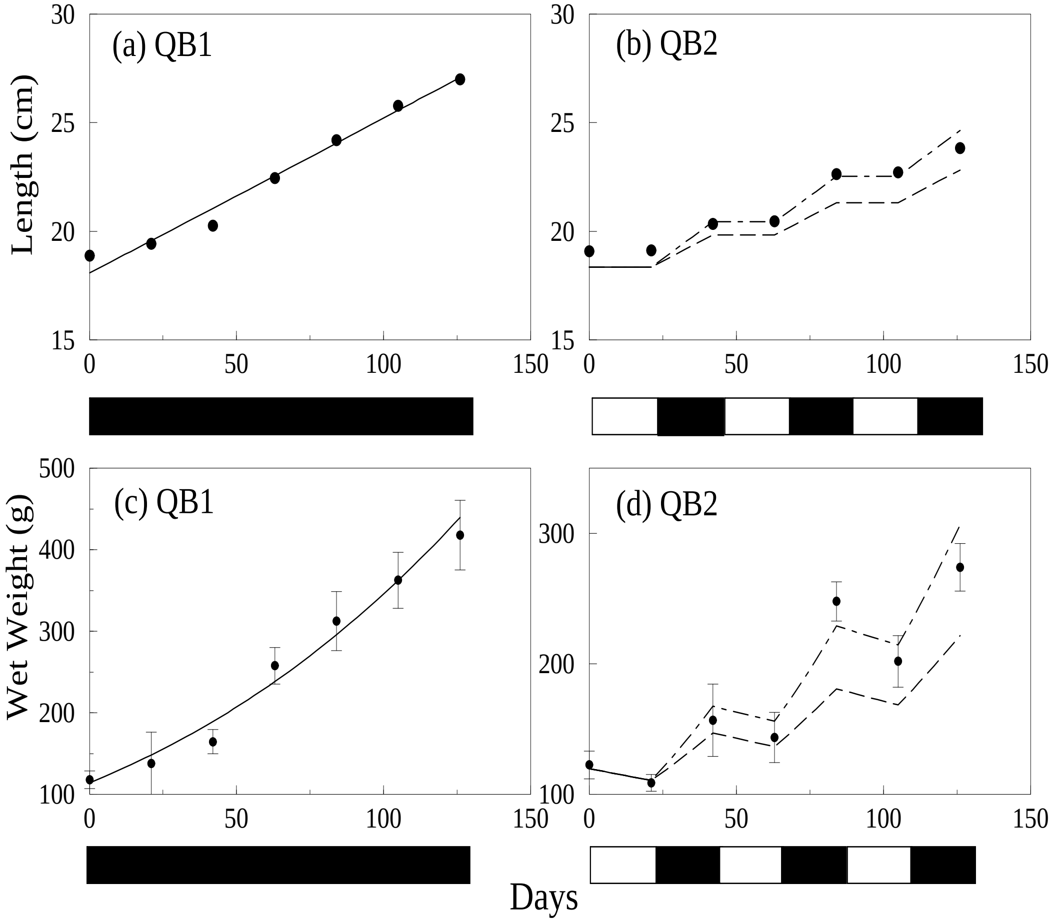

Figure 8.4: *Observed and predicted lengths and weights for the fish of Quinton and Blake (1990), Exp. B. The model has been fitted to the control section (solid line) and using the same parameter values has been extrapolated forward (long dashed line) assuming there is no hyperphagic response. The dot dashed line is the fitted model predictions including a hyperphagic response to refeeding. Vertical bars denote 95% confidence intervals. Quinton and Blake give no measure of the variance associated with the quoted mean lengths. The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food; (grey bar) restricted ration.*

In the second chapter we moved on to the process of deriving a model which could exhibit the major qualitative properties of compensatory growth. Our first step, was to identify a general mechanism for explaining how compensatory growth is regulated. We decided on a framework where the fish were reacting to

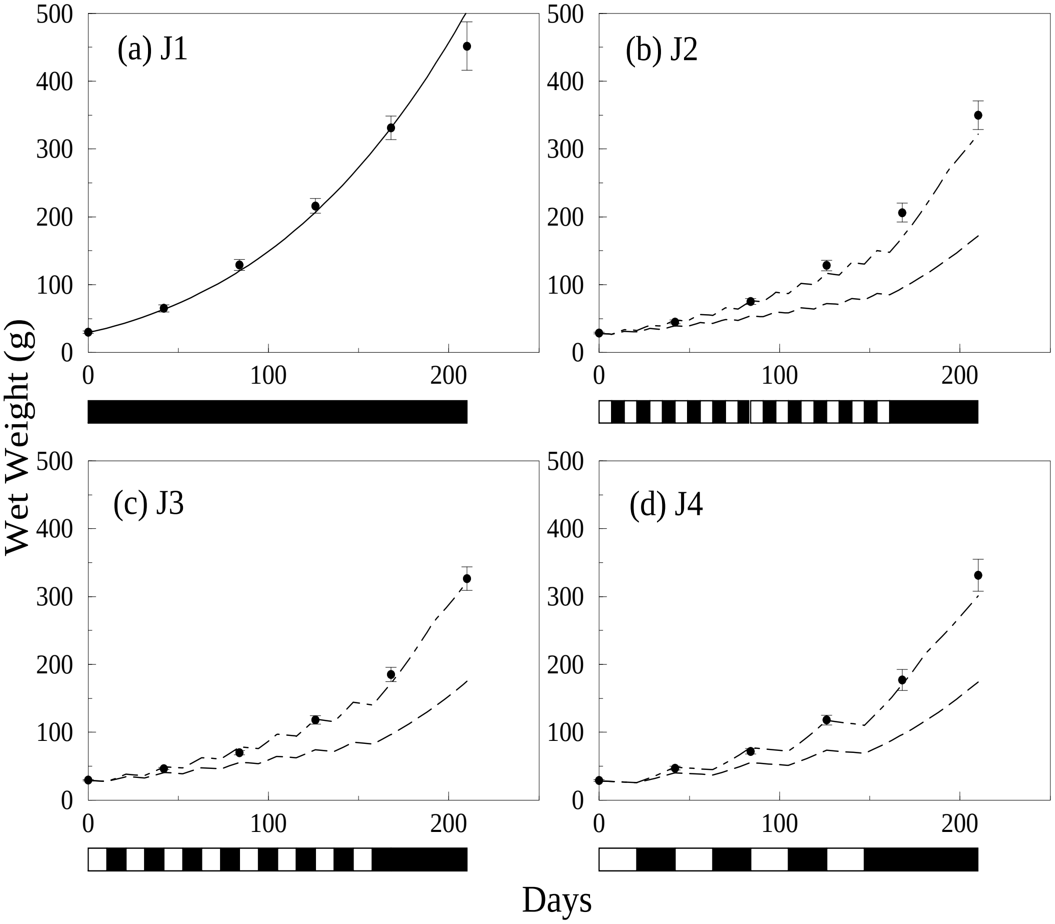

Figure 8.5: *Observed and predicted weights for the fish of Jobling et. al. (1993). The model has been fitted to the control section (solid line) and using the same parameter values extrapolated forward (long dashed line) assuming there is no hyperphagic response. The dot dashed line is the fitted model predictions including a hyperphagic response to refeeding. Vertical bars denote 95% confidence intervals. The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food.*

changes in nutritional status, principally, because it could possibly explain the disparate results in the extent to which growth losses are recovered. We then moved on to investigate an historical model already based on these principles which uses the net production sequence of allocation. Several situations were identified where this model could not predict compensatory growth in contrast to literature reports. Furthermore, we also identified a situation where the net

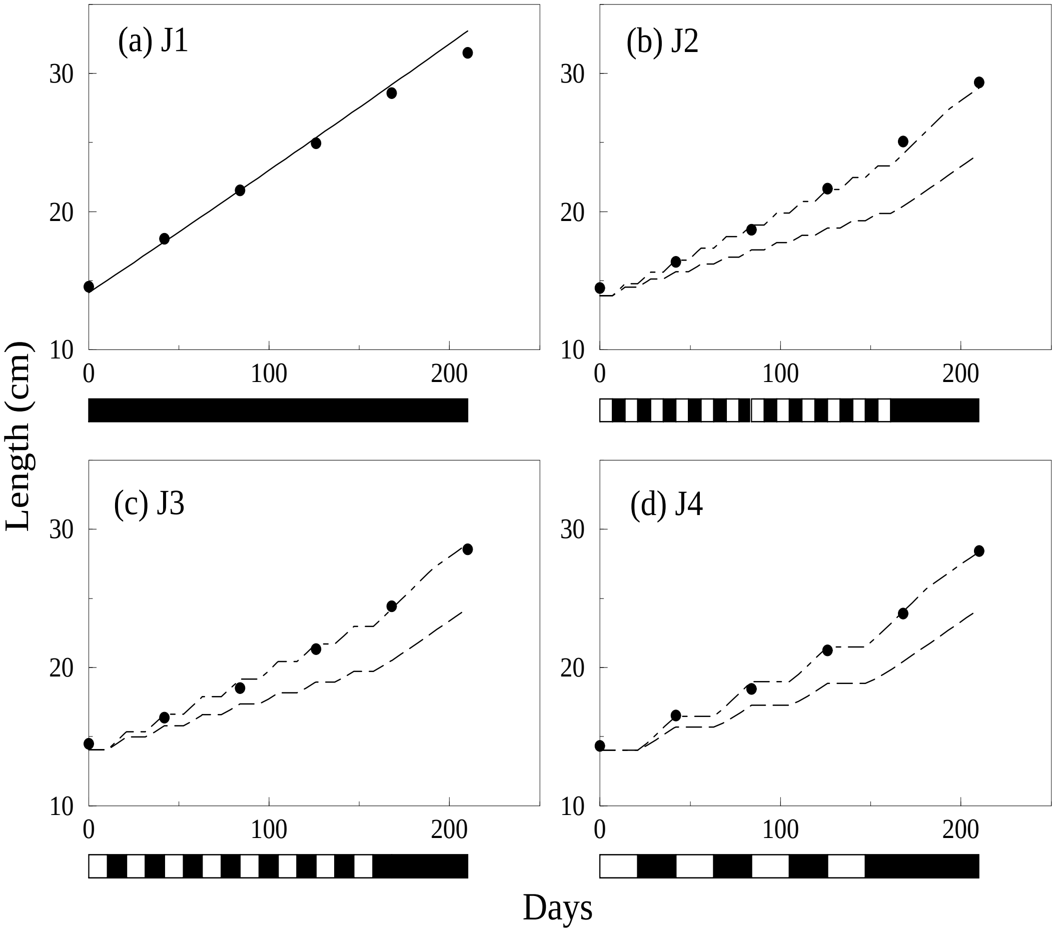

Figure 8.6: *Observed and predicted lengths for the fish of Jobling et. al. (1993). The model has been fitted to the control section (solid line) and using the same parameter values has been extrapolated forward (long dashed line) assuming there is no hyperphagic response. The dot dashed line is the fitted model predictions including a hyperphagic response to refeeding. Vertical bars denote 95% confidence intervals. The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food.*

production model would fail to predict compensatory growth.

Following this we went on to derive a new criteria for triggering an increase in appetite which could accommodate fish maintaining low rates of growth but still remaining in a non-negative energy balance becoming hyperphagic on realimentation. We applied this simple function to both the reserve and assimilation allocation models and in turn assessed their qualitative characteristics to model

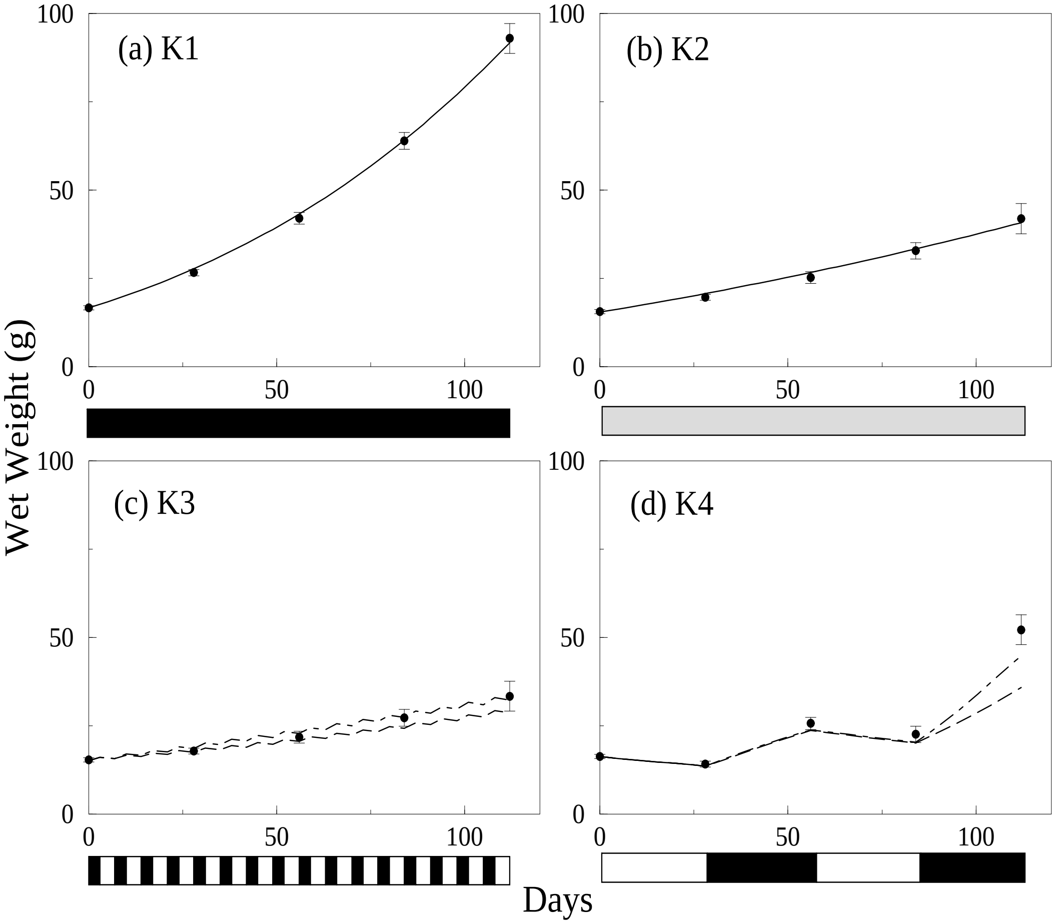

Figure 8.7: *Observed and predicted weights for the fish of Kindschi (1988). The model has been fitted to the control section (solid line) and using the same parameter values has been extrapolated forward (long dashed line) assuming there is no hyperphagic response. The dot dashed line is the fitted model predictions including a hyperphagic response to refeeding. Vertical bars denote 95% confidence intervals. The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food.*

compensatory growth.

The reserve allocation model was not successful as it could not predict any genuine structural compensation during recovery growth phase, principally, because allocation to structure is governed by reserve status. With the assimilation allocation model commitment to structure is made from the immediate assimilate, which meant that structural compensation could be predicted with

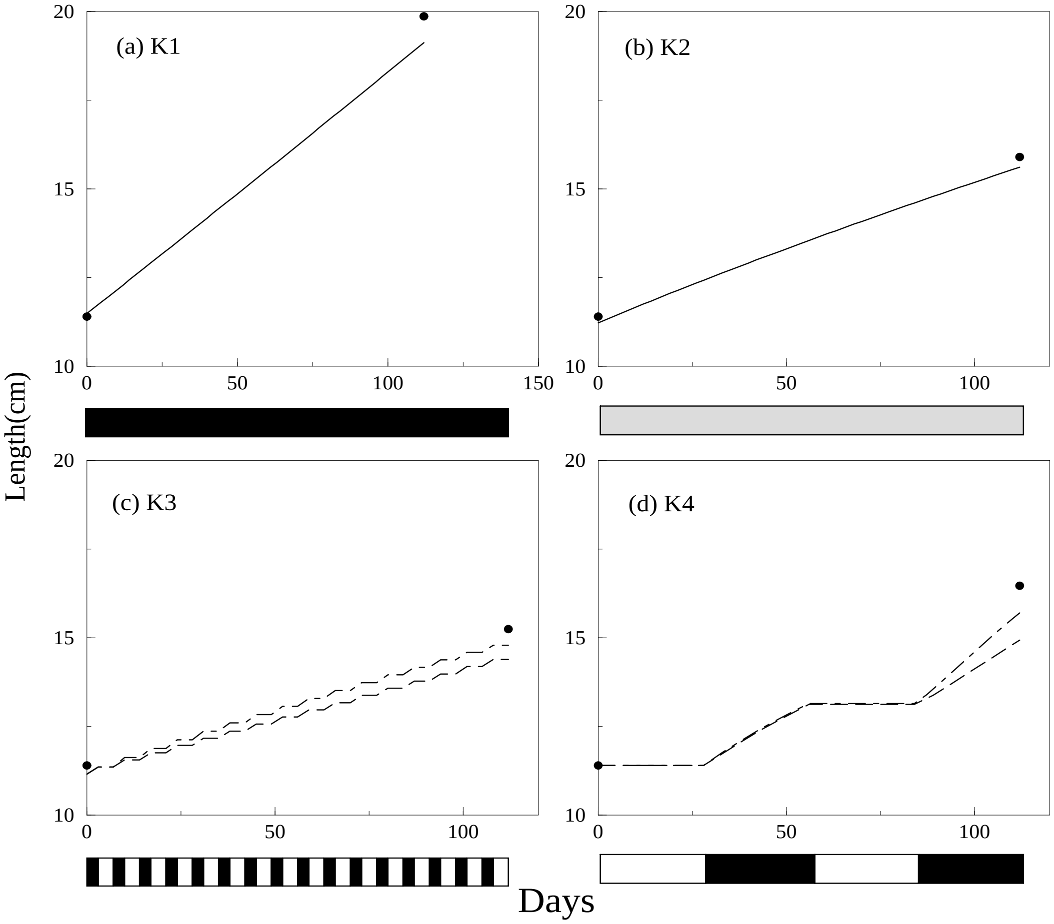

Figure 8.8: *Observed and predicted lengths for the fish of Kindschi (1988). The model has been fitted to the control section (solid line) and using the same parameter values has been extrapolated forward (long dashed line) assuming there is no hyperphagic response. The dot dashed line is the fitted model predictions including a hyperphagic response to refeeding. The bar below each figure indicates the feeding regime: (black bar) excess food; (white bar) no food.*

an increase in uptake. Further investigation of the model revealed that all the major qualitative characteristics of recovery growth could be predicted.

In this final chapter our main aim was to test whether this model is feasible. We first fitted our model to the control portions of the data and obtained a good fit. Using the same parameter values we extrapolated these growth trajectories to the refeeding portions of the data to asses for any compensatory responses. With the exception of one study, experimental groups of fish exhibited a significant compensatory response, both in terms of weight and length. By simply stating that the fish had an increased appetite until their previous nutritional condition had been recovered, we gained a much better fit to the remaining data points, both in weight and length. Our best fit value of the hyperphagic uptake constant $\xi_{\lambda H}$ of 1.4 is similar to that reported by Jobling and Miglavs (1993) who note that food intake of juvenile charr with some 4.5% body fat was some 1.5 times greater than charr with 6.5% body fat. Similar results have been found by Silverstein et al. (1999) for juvenile Atlantic salmon.

Part IV

Growth and Allocation in the Field

Chapter 9

The Growth of Juvenile Atlantic Salmon in the Girnock Burn

9.1 Introduction

Wild populations of salmonids are most commonly found in temperate and sub-arctic climates. In such environments, water temperature, photoperiod, predation pressure and food availability change with the changing seasons. Periods of high food abundance are inter-dispersed with sometimes longer periods of low or negligible food supply. During winter the food supply becomes particularly scarce. The lack of nutrient supply poses a nutritional challenge to the individual that must be endured until the natural food supply once again becomes more abundant. If food uptake is not enough to meet metabolic expenditure then somatic reserves have to be remobilised to make up the deficit. If accumulated reserves are not of a sufficient level to last through the winter period then starvation will ensue, and indeed, overwintering starvation is thought to be one of the major causes of mortality amongst juveniles (e.g. Gardiner and Geddes (1980)), especially in very young small fish.

On the other hand, individuals can only grow when the environmental conditions are favorable. Both temperature and food supply, which are major determinants of maximal growth, fluctuate throughout the year. The temporal changes in natural prey abundance combined with temperature will therefore be a major factor in determining when and to what magnitude growth can be accomplished. This window of opportunity when both abiotic and biotic conditions are favorable for allowing significant growth to be accomplished is commonly referred to as the growing season.

To survive, grow and flourish in such a precarious and fluctuating environment necessitates a quite specialised life history strategy that is not only adapted to the geographical location but also to the local ecosystem (Youngson and Hay (1996); Rickardsen and Elliott (2000); Post and Parkinson (2001)). Consequently, growth and survival strategies are diverse and a source of continuing interest for the scientific community.

In the previous two parts of this thesis we first reviewed the literature and then went on to investigate the success of different classes of models to synthesise the noted observed patterns of growth and allocation. In this part we shall apply what we have learnt to patterns of growth and allocation observed in the field. This will be afforded by access to detailed, high resolution, temporal data of the growth rates of juvenile Atlantic salmon (*Salmo Salar* L.) in a Scottish stream. We shall investigate this data in detail and then, towards the end of this part, we shall relate our results to findings published in the literature for salmonids living in similar seasonally driven environments. Hence, our approach will be the reverse to that of the previous two parts: we shall specialise a study to a particular species in a particular geographical location and then relate our findings to the literature.

Before we can begin our analysis it is a necessary requirement to give an (albeit brief) introduction to the life history of the Atlantic salmon. Following this, we shall explain the geography of the Girnock Burn - a stream in North-East Scotland and our study site. We shall then move on to outline the data gathering procedure and conclude this chapter with a general description of the data and a growth analysis.

9.2 Life History of the Atlantic Salmon

The Atlantic salmon (*Salmo salar* L.) is a species that leads its life in the rivers and oceans of the northern hemisphere (Youngson and Hay 1996). They were originally found in all countries whose rivers flowed into the North Atlantic Ocean and the Baltic Sea (Mills 1989). Over the past century, however, wild populations have been seriously depleted: an effect which is mostly attributable - directly or indirectly - to man's activities. For example, populations of Atlantic salmon have disappeared from some of Europe's major rivers, such as those along the northern coast of continental Europe from Poland to France, and in southern England, all of whom which once supported substantial numbers (Parrish et al. 1998). Wild populations are still to be found in Europe as far north as Russia, Norway, Iceland, Finland and as far south as northern Spain and Portugal, and in North America from Greenland and Northern Canada to New England in the U.S.A (Folt et al. 1998).

Most populations of Atlantic salmon are anadromous. They usually spend one or two years (rarely three or four) feeding in the nutrient rich waters of the North Atlantic Ocean. It is within the ocean phase where the greatest increase in size occurs and is due to a plentiful food supply, being capitalized upon.

It has been known for many years that the Atlantic salmon posses a well developed homing ability, enabling successful individuals to return to their natal rivers to spawn (Mills 1989). It is in the freshwater phase of their return journey at which they are at most visible, for example, leaping up water falls to reach their final destination upstream, which is an impressive spectacle for all who observe. The returning adults have already begun to become sexually mature out at sea (Youngson and Hay 1996) and spawning in freshwater usually commences in the autumn. The adult females construct (cut) a nest, called a redd, in which she will lay her eggs. Males compete with each other for position alongside the female for the best mating privileges. Once fertilisation has taken place, the female covers the redd with gravel and may move on to construct several more redds (Fleming et al. 1997) and repeat the spawning process. Most adults die shortly after spawning, (on average 89% of the total, and 78% of the females and 96% of the males Fleming (1998)), but the survivors, known as kelts, return to sea, and may spawn again.

The fertilised embryos develop slowly throughout the winter and hatch in the spring well before the yolk supply is exhausted. The rate of egg development and thus the incubation period is mainly dependent upon temperature (e.g. Egglishaw and Shackley (1977); Brannas (1986); Elliott and Hurley (1998a)). The young fish, called alevins, remain in the gravel of the redd for several more weeks. During this time they rely on their remaining yolk supply for nutrition and development. As the reserves of the yolk become diminished they move up out of the gravel to begin life in the stream itself. During this time competition is at its severest and mortality rates at their highest.

Juvenile Atlantic salmon are solitary creatures that each require enough space on the river bed to give adequate shelter and food. Failure to seize a suitable territory deprives the juvenile of the resources needed to survive and mortality ensues from predation and starvation (Youngson and Hay 1996). When the fry reach about 6.5-7.0 cm in length they start to develope dark blotches along their sides, and are now defined as parr.

It is from within these defended territories that they capture and consume their food (Kalleberg (1958); Keenleyside and Yamamoto (1962)). The majority of their diet consists of invertebrates captured from the water column (Allen (1941); Egglishaw (1967)). They are also able to capture invertebrates of terrestrial origin which fall onto the water surface, as well as being able to forage amongst the substrate (Stradmeyer and Thorpe (1987); Wankowski and Thorpe (1979)) and the larger parr have been known to take fry and ova (Egglishaw 1967).

It is possible for both male and female anadromous salmon to become sexually mature whilst they are still parr. This is rare for females, (Gibson (1983); Youngson and Hay (1996)) and may be due to the benefits (e.g. pre-reproductive survival) not being great enough to outweigh the costs (e.g. reduced fecundity and competitive ability) (Fleming 1998). However, early maturation of males is common, and in some populations, up to 100% of males have been estimated to have matured early as parr during their life history (Fleming 1998). There are cost involved to the mature male parr (often called precocious parr) in terms of growth retardation (Myers et al. 1986) and survival (Myers (1984); Berglund et al. (1992)) but a large proportion of the eggs may get fertilised by male parr, estimated at about 11% by Jordan and Youngson (1992) for the Girnock Burn in Scotland.

During the autumn there are large movements of parr (Calderwood 1906), many of which may be precocious males (Pyefinch and Mills 1963), which are in search of adult females (Buck and Youngson 1982). It has also been suggested that the autumn migrants may be the forerunners of the following spring migration (Mills 1989). At this time, they have yet to undergo the physiological adaptation to seawater (smoltification), and maintain their parr-like appearance.

Smolting occurs during the spring, after the parr have spent a numbers of years in freshwater. The time to smolting generally varies with the latitude, from as little as 1 year for males in France (Bagliniere and Maisse 1985) to up to 10 years for some anadromous salmon in the Ungava river of Northern Quebec (Powers (1969), Robitaille et al. (1986)). In Scotland, parr tend to smolt after between two and four years in freshwater (Buck and Youngson 1982). Once they have left the rivers, they migrate to their feeding grounds as post-smolts, and begin the marine phase of the life.

9.3 The Girnock Burn

Atlantic salmon are widely distributed across Scotland, amongst some 400 salmon rivers. The River Dee is one such river that is particularly productive and has been described as perhaps having the greatest length of first-class salmon fishing in Britain (Ashley-Cooper 1987). The Girnock Burn is a tributary

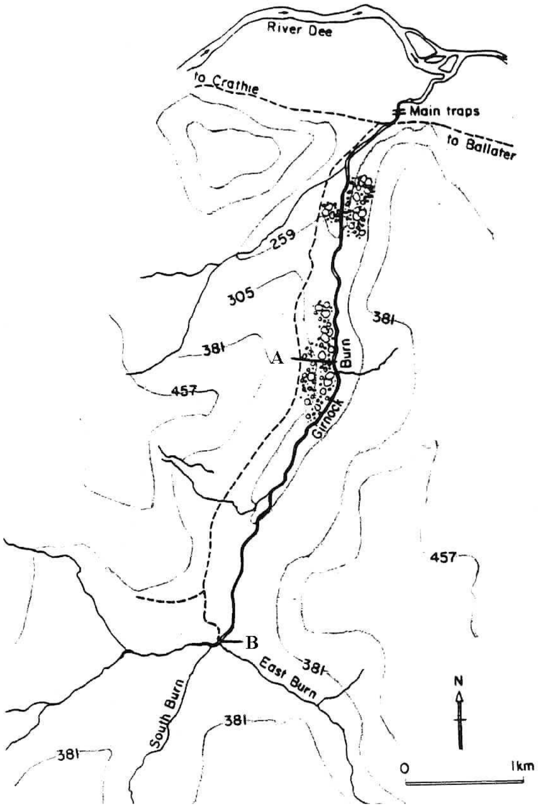

Figure 9.1: *Map of the Girnock Burn* (Buck and Hay 1984).

of the river Dee that has been kept free from fishing and has been extensively monitored since 1966.

This tributary flows from a catchment area of 29.77km^2 and joins the River Dee at an altitude of 230m at about 80km from the sea. The catchment, which rises to an altitude of 570m, contains 32.68km of streams, with an estimated 11.05km to 13.32km being available to wild salmon (Webb and Bacon 1999).

The climate and flow rates in the catchment are highly variable and exhibit strong seasonality. The catchment receives on average 1100mm of precipitation annually, up to 25% of which falls as snow, with the driest months being from May to August (Warren 1985). The river has a mean annual discharge of 0.5m^{3}s^{-1} although flow between June and August rarely exceeds 0.1m^{3}s^{-1} (Moir et al. 1998). The peak flow rates occur during the spawning season (October and November) and the spring due to snow melt, when the smolts are migrating downstream.

9.4 Data Collection at the Girnock Burn

The Girnock Burn was chosen as a study site as it represented what was viewed as a typical spawning stream of the River Dee and has been monitored since 1966. Juveniles emigrate from the Burn in autumn as precocious and immature parr, and during the spring as smolts, the greatest majority of which leave two or three years after hatching (Buck and Youngson (1982); Gani (2000)).

9.4.1 Historical Data Collection and Analysis

Historically, the salmon population has been monitored in the Girnock using three methods. The first was by conducting annual fishing surveys in different parts of the Burn to assess the resident parr population. Samples of the resident parr population were collected each summer by using the electro-fishing method. This involves using an electric device to stun fish so that they can be caught with ease and without permanent injury (Jones 1959). Annual electro-fishing surveys have been conducted in this manner from 1969 to 1986 (with the exception of 1980).

The age of the young salmon can be determined by examining scale samples. As the salmon grow, a ringed pattern is produced on the scales. The distance between the rings depends on the rate of growth. Periods where the spaces between the rings are relatively large indicate summer growth, and the converse for winter growth. Scale samples can accurately determine which particular cohort an individual fish belongs to. The age of the parr is defined by the number of periods when the rings are close together (i.e. the number of winters), so a fish born in April and sampled in the next February would be defined as a one year old fish. If there is summer growth on the youngest part of the scale then a '+' is added to the age. Thus, a fish born in April and sampled the following September would be defined as a '0+' fish.

The two other methods involve collecting data from fish traps which capture returning adults before ascending the Burn and also descending smolts leaving the Burn. A description of both fish traps are given in Buck and Hay (1984) and Gani (2000). Temperature recordings have also been taken from the Burn from May 1968 to December 1996.

This historical data set has been analysed in detail, using a variety of different modelling techniques by Gani (2000). The main emphasis of this work was to investigate annual variability in the growth accomplished by resident parr and also differences in growth rates between different sections of the Burn. However, with the resident parr being censused only once annually the resolution of data to investigate detailed patterns of growth was not available.

9.4.2 Data from Individual Salmon Parr

In June 1998 a new project, conducted by researchers from FRS[1], began. The work involved censusing (by the method of electro-fishing) resident parr from the middle section of the Burn at a much finer resolution than once per year. On each survey, captured salmon were anesthetized, weighed (to the nearest 0.1g) and measured (fork length to the nearest mm). Individuals caught with a length greater than 70mm were tagged interperitonally with a PIT (passive integrated transponder) tag (Prentice et al. 1990) or had their tag number identified if previously tagged. PIT tags were inserted through a small incision between the pectoral fins. Individuals previously recaptured and subsequently captured in the smolt trap, when leaving the Burn, were both weighed and measured.

Table(9.1) displays the number of recaptures for each cohort. It can be seen that individuals were often recaptured. (The greatest number of recaptures was recorded for three individuals from the 1997 cohort who each managed to be caught a total of twelve times!) Data from the 1997 cohort is the most detailed, with by far the greatest number of recorded recaptures.

---

[1] The Fisheries Research Services, The Freshwater Fisheries Laboratory, Faskally, Pitlochry, Perthshire, PH16 5LB

Table 9.1: *Records of recaptures for each cohort.*

	Cohort Year of Birth			
No of captures	1996	1997	1998	1999
$\geq$10	1	3	0	0
9	0	5	1	0
8	1	8	0	0
7	1	12	4	0
6	5	12	7	0
5	7	21	12	1
4	12	36	20	8
3	16	51	19	21
2	30	63	22	29
Total	73	211	85	59

Hourly temperature was recorded by an electronic temperature recorder located at the smolt trap. Figure(9.2) displays the daily average temperature over a three year period. It can be seen that there exists a very strong seasonal trend. Water temperature is usually at its lowest in January or February and rises to an annual maximum in a period lasting from July to September. Following this, temperatures begin to decline back to winter levels, which can often be as low as 0^oC.

9.5 Growth Analysis

Our aim in this section is to elucidate the major growth characteristics of parr in the Girnock Burn. We will investigate when and to what magnitude significant rates of growth (weight and length) are achieved and how these relate to the changes in the physical environment.

There is a substantial body of evidence reporting a strong correlation between

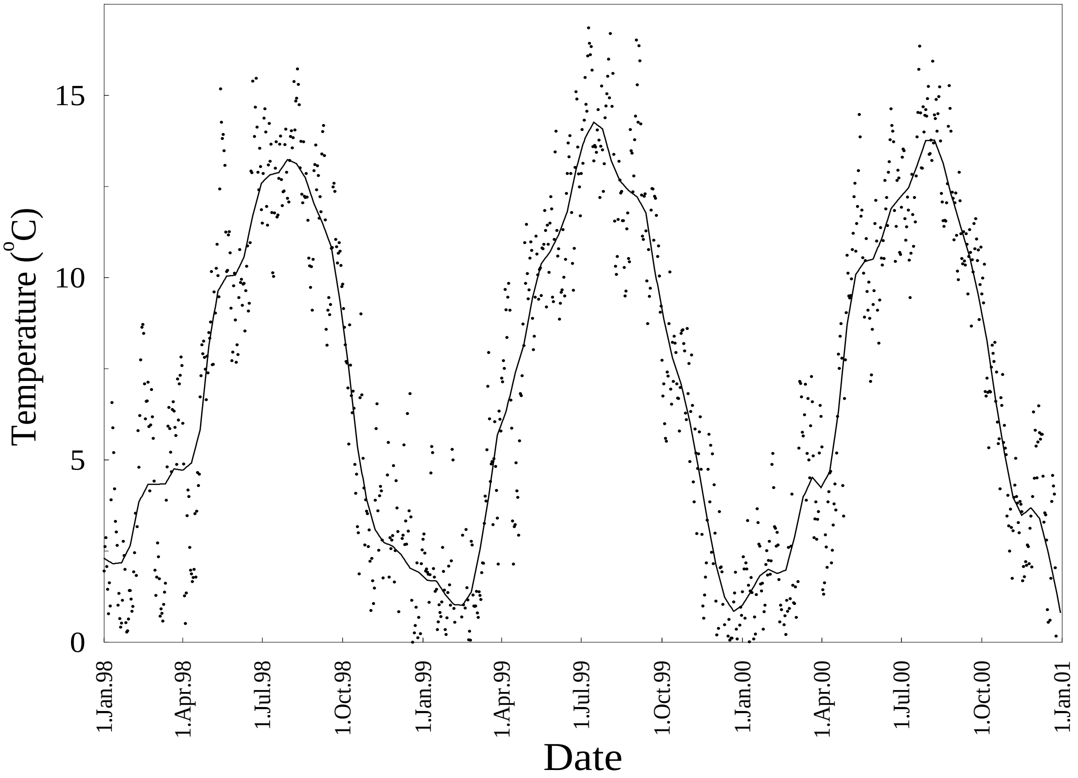

Figure 9.2: *Mean daily temperature recordings at the Girnock Burn. The solid line is a smoothing function of the temperature data.*

fat content and condition factor in wild Atlantic salmon parr (e.g. Pinder and Eales (1969); Herbinger and Friars (1991); Sutton et al. (2000)). Therefore, we shall also investigate temporal changes in condition factor values, which will illustrate the changes in nutritional condition with the changing seasons.

As an illustrative example of the growth in the Burn we shall first investigate the growth of an averaged cohort. The 1997 cohort is the most obvious candidate, since it constitutes the most detailed cohort data set. Figure(9.3) displays mean wet weight and length electro-fishing measurements and also mean values of condition factor ($K = \frac{100W}{L^3}$) for 1997 cohort individuals spanning from Oct 1998 to April 2000. It can be seen that over the winter period there appears to be only a small amount of weight loss and length essentially remains constant. Growth in weight and length begins in March and is sustained until approximately the middle of August. Condition factor reduces over the winter period until the

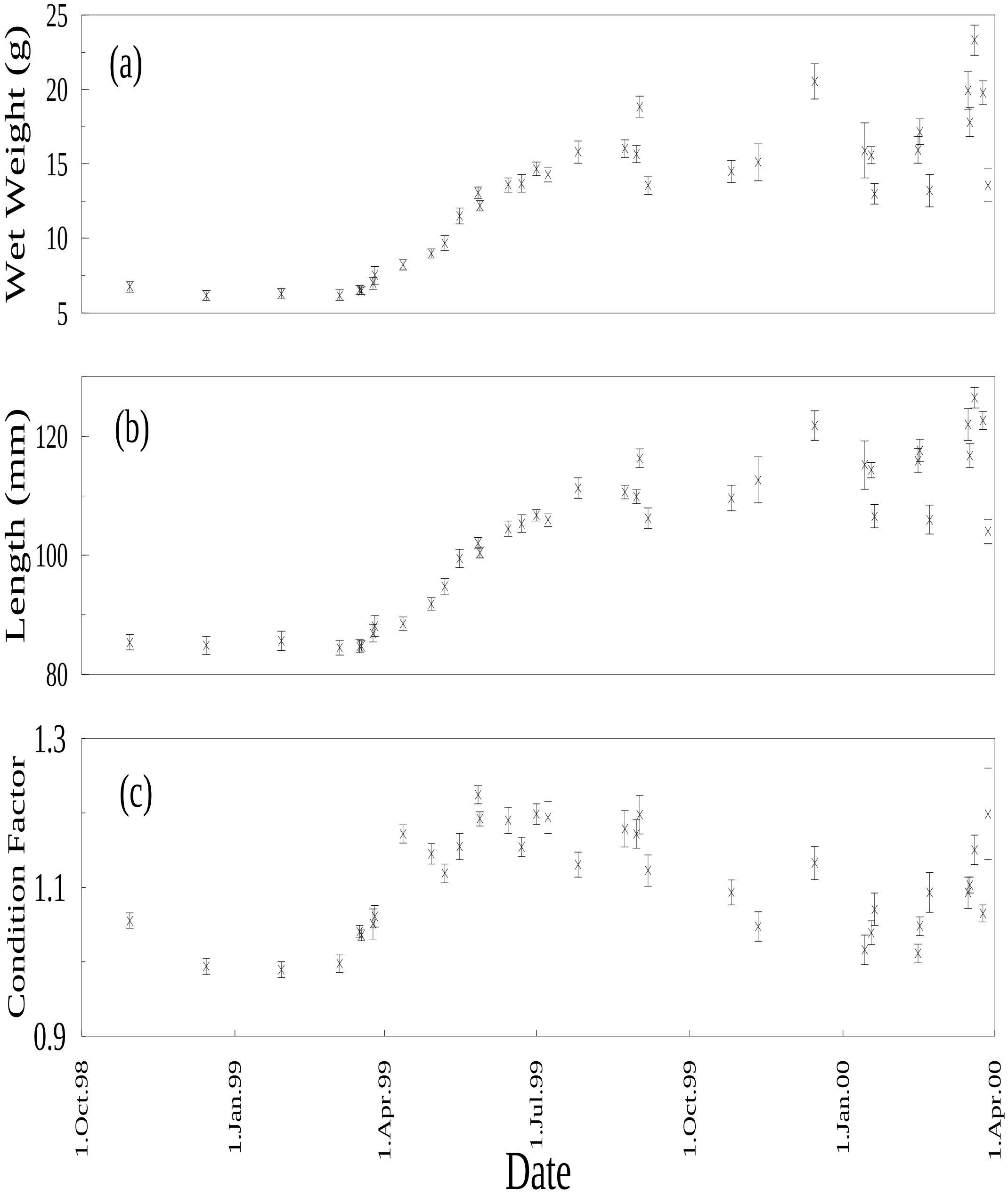

Figure 9.3: *Averaged electro-fishing measurements of a) weight , b) length and c) condition factor for the 1997 cohort. Bars denote 1 standard error.*

onset of spring. Following this, condition factor begins to increase and levels out towards late summer. Following the next winter, condition factor begins to fall and there is evidence of an increase in values with the onset of spring in the year 2000. Towards the end of the study period the electro-fishing data becomes noisier. This is probably due to the number of 1997 cohort individuals resident in the Burn reducing through mortality and also emigrants leaving in Autumn.

9.5.1 Applying the Elliott and Hurley Model

The most obvious factors that will influence growth rates are temperature and food abundance. To aid in the analysis we shall apply the Elliott and Hurley model for maximal growth (explained in section(2.2.2)), which will serve as useful analytical tools to asses the growth of parr in relation to changes in environmental temperatures.

We will begin the analysis by comparing the simulated growth trajectories with mean electro-fishing weight of 1997 cohort. Simulations of maximal growth trajectories were produced from the E&H model for juvenile Atlantic salmon using the parameter values given in table(2.2). Figure(9.4) displays two such growth trajectories having been started off at the observed mean weight of the cohort near the onset of winter and at the beginning of spring period.

Clearly, there are large differences between both growth predictions and the mean weight estimates from the electro-fishing data. Since the model has been parameterised from well-fed fish then it should reasonably be expected to provide an upper bound for growth rates in the Girnock Burn. However, this is not the case since the predicted growth trajectory started from 30 Oct 98 has significantly under-predicted the growth for all but the first mean electro-fishing weight estimate. One reason for this is that the over winter weight loss predicted by the model is grossly over predicted and is almost equivalent to the summer weight gain.

An additional observation is that the model cannot predict the high growth rate observed in the spring at relatively low temperatures (approx. 6^{o}C). The model in the spring of 1999 predicts the fish to be losing weight, whereas in actual fact, they are growing rapidly.

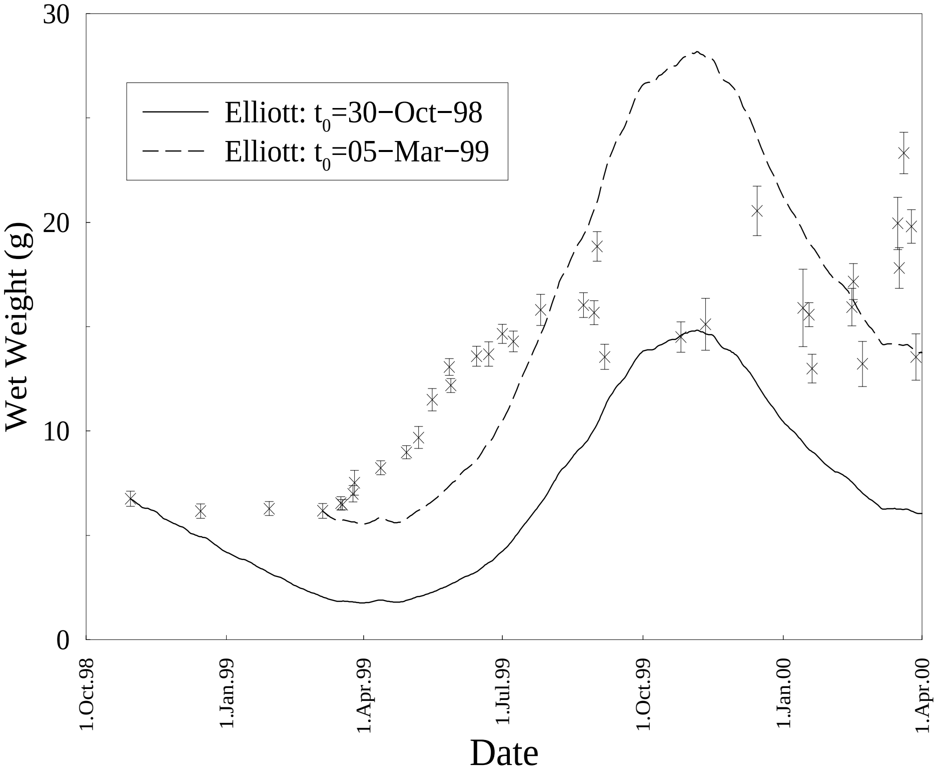

Figure 9.4: *Predicted weight trajectories for the E&H functional model for maximum growth. Data points are the mean electro-fishing weights for the 1997 cohort. Bars denote one standard error.*

The final observation is that the model predicts growth rates to be high within the mid-summer period where the water temperature is more conducive to rapid growth (approx. 10-15^{o}C). Despite these favourable temperature conditions, our averaged data indicates that growth within the Girnock Burn has essentially ceased by this period. In the next stage of our analysis we shall show that this to be also true for individual growth trajectories.

An alternative (and more rigorous) strategy to investigate patterns of growth in the Girnock Burn is to calculate values of specific growth rate for all individuals (in all years) which were captured more than once. Following Ricker (1979) we used the following expression to calculate the specific growth rate (expressed in terms of % weight change/day)

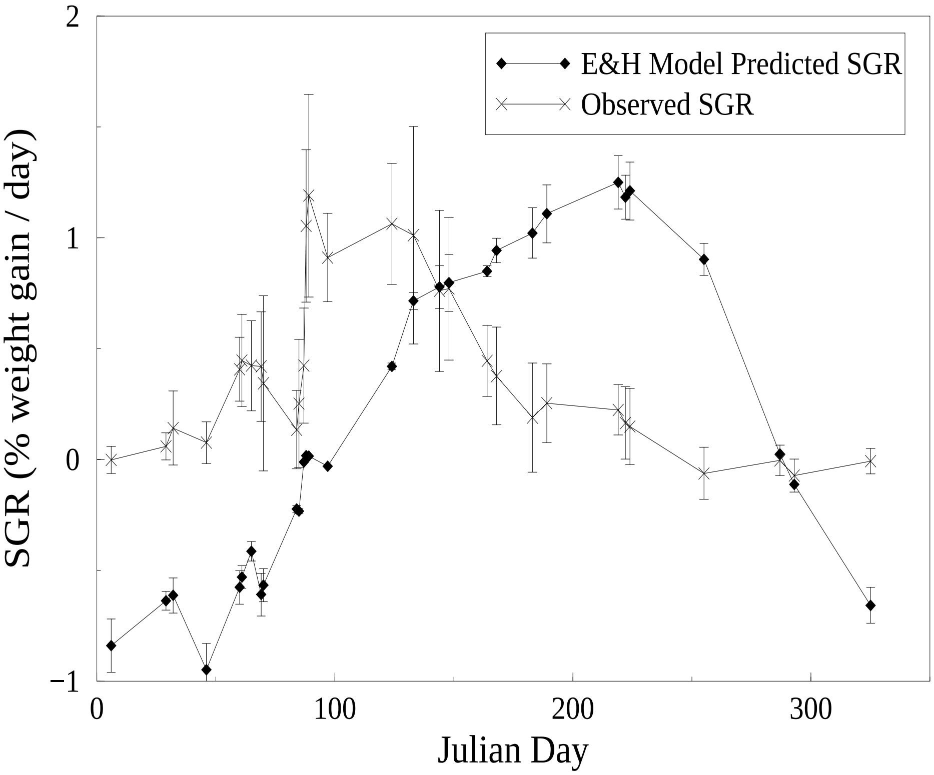

Figure 9.5: *Observed and E&H model predicted values of specific growth rate (SGR) for individual parr at different times of the year. Bars denote 1 standard error.*

$$\text{SGR} = 100\frac{\ln(W_1) - \ln(W_0)}{t_1 - t_0} \tag{9.1}$$

where, W_0 and W_1 are the wet weight observations at times t_0 and t_1, respectively. Figure(9.5) displays the mean SGR values (positioned at the midpoint of each consecutive pair of observations), expressed as a function of the time of year, for individuals recaptured more than once from the Burn. Also plotted in figure(9.5) is the predicted mean SGR values from the E&H model for the same group of individuals.

At the onset of the year, the specific growth rate of parr is low, until spring, where there is a sharp increase. Following this, the values of SGR steadily decline and settle down towards the end of the year. The E&H model predictions are very different to the observed patterns of growth in the Burn. At the beginning of the year the model very much under predicts SGR values and steadily increases to a maximum in late summer, which is over predicting parr SGR. As the water temperature declines with the onset of autumn the model predicted values of SGR also begin to decline but still over predicts growth rate until the very end of the year.

9.6 Budget Analysis

The fact that the E&H model is over predicting mid-summer growth almost certainly means that the natural food abundance is playing a major part in the growth dynamics of parr in the Girnock Burn. To investigate this in further detail we shall carry out a simple energetics budget analysis.

9.6.1 Budget Modelling Approach

Perhaps, surprisingly, there exists no detailed study of the energetics of juvenile Atlantic salmon which investigates the combined effects of ration size, temperature and size. Such comparable studies with brown trout (*Salmo trutta*) conducted by Elliott (1975 a,b; 1976 a,b,c) have served as excellent model parameterisation data sets for a number of different studies (e.g Hayes et al. (2000); Kitchell et al. (1977)). In the absence of a detailed energy budget model for Atlantic salmon parr we will move to a different approach.

The simplest possible statement of growth is encapsulated in the following

$$\text{Growth} = \text{In} - \text{Out} \tag{9.2}$$

or in our more mathematical terms

$$\frac{dW_c}{dt} = A - M, \tag{9.3}$$

which, essentially states that growth is the difference in anabolic (assimilation) and catabolic (maintenance) processes. We can rearrange this equation such that

$$A = \frac{dW_c}{dt} + M. \tag{9.4}$$

A great number of experimental observations have consistently described maintenance rates as being exponentially dependent upon temperature and scaling allometrically with weight (e.g. Elliott (1976b); Brett et al. (1969); Van Winkle et al. (1998) Lantry and Stewart (1993); Rand et al. (1993)) which we describe as follows

$$M = M_{H0} W_c^v \exp(T/T_M) \tag{9.5}$$

where, $W_c = R + S$ is the total carbon weight.

With the high resolution of individual growth data we pretty much know the patterns of growth, that is, we can calculate $\frac{dW_c}{dt}$ in equation(9.4). Consequently, if we can independently parameterise the consistent relationship for maintenance given by equation(9.5) then we can, using equation(9.4), estimate the way assimilation rates change with the changing seasons.

9.6.2 Parameterising Maintenance

Surprisingly, there are very few published data sets concerning the metabolic rates of juvenile Atlantic salmon, an observation recently commented upon by Berg and Bremset (1998). Data of energy losses during starvation are sparse, and where available, only concern a single constant temperature. In such circumstances we shall make the best use of what data is available and compare the final result to the maintenance rates of other salmonid species.

Remarkably, we could only find two parameterisation data sets which we summarise in tables(9.2) and (9.3). Carter et al. (1992) supplies initial and final carbon weight which will allow us to fit directly to the carbon weights. Waiwood et al. (1992) supplies initial and final weight and length measurements. If we

Table 9.2: *Maintenance parameterisation data set from Carter et al. (1992). Values in parentheses denote one standard deviation.*

Dur. of Exp. (days)	Initial Carbon Weight (mg)	Final Carbon Weight (mg)	Temp °C
30	1489.0 (246)	1268.0 (242)	6.2(1.0)

can estimate the carbon initial and final carbon weight for the Waiwood et al. (1992) data then we could fit directly to the carbon weights for both studies. In the absence of any other statistical models that estimate the energy content from a combination of weight and length we shall use the Elliott (1976a) statistical representation parameterised for brown trout (*salmo trutta*). If we then divide these values by our carbon to energy conversion ratio of 12 cal/mg C (see section(8.3)) then we can estimate the initial and final total carbon weights for the Waiwood et al. (1992) study. By rearranging Elliott's statistical representation given by equation(3.4) we can express the predicted total carbon weight W_c (mg C) as follows

$$W_c = \frac{a(100)^{b_1} W^{(1+b_1+b_2)}}{12.0 L^{3b_1}} \tag{9.6}$$

where, W is wet weight (g), L is fish length (cm) and the parameter values of a, b_1 and b_2 are given in table(3.4). The estimated observed initial and final carbon weights for the Waiwood et al. (1992) study are displayed in table(9.4).

Assuming no structural growth during starvation (which is justified given the results of Waiwood et al. (1992) displayed in table(9.3)), total carbon weight

Table 9.3: *Maintenance parameterisation data set from Waiwood et al. (1992). Values in parentheses denote one standard deviation.*

Dur. of Exp. (days)	Initial Wet Weight (g)	Initial Len. (cm)	Final Wet Weight (g)	Final Len. (cm)	Temp °C
42	20.2 (0.7)	12.6 (0.4)	16.9 (1.0)	12.6 (0.4)	13(1.0)

Table 9.4: *Initial observed (Obs.) and final (Fin.) observed and best fit predicted carbon weights.*

Study	Obs. Initial Carbon Weight (mg)	Obs. Final Carbon Weight (mg)	Fin. Predicted Carbon Weight (mg)
Carter et al. (1992)	1489	1268	1329
Waiwood et al. (1992)	2187	1707	1686

changes according to

$$\frac{dW_c}{dt} = -M = -M_{H0} W_c^v \exp(T/T_M) \tag{9.7}$$

which means we require the knowledge of three parameter values. However, it is not feasible to estimate all three parameter values from this very small data set. Therefore, we decided to derive two parameters from the literature, namely, the maintenance allometric index v and the characteristic temperature scaling T_M. With no real evidence to the contrary we decided to use the same values as those established in section(4.2) of 0.75 for v and $12.0^o C$ for T_M.

Following this it was a simple procedure to find the value of the maintenance cost rate scale M_{H0} which minimised the least squares error between the final predicted and observed carbon weights in both studies. Simulations were conducted by numerically integrating equation(9.7) with the initial carbon weight being set at the observed initial value. The best fit parameter value of M_{H0} was found to be 0.014 and the predicted final carbon weights for both studies are given in table(9.4).

The value 0.014 is somewhat less than the value of 0.020, the fitted value for rainbow trout and charr we found in chapter 8. However, given the lower intrinsic growth rates of juvenile Atlantic salmon parr in comparison to rainbow trout (Austreng et al. 1987) and charr (see table(2.2)) then perhaps we should not be surprised. We summarise the maintenance parameter values for Atlantic salmon parr in table(9.5).

Table 9.5: *Independently determined maintenance parameters.*

Parameter	Interpretation	Value	Units	Source
M_{H0}	Maintenance cost rate scale	0.014	$\mathrm{d}^{-1}\mathrm{mgC}^{1-v}$	see section(9.6.2)
T_M	Maintenance characteristic temperature	12.0	^{o}C	Elliott (1976b) Brett (1979) From et. al. (1984)
v	Maintenance cost allometric index	0.75	—	From et. al. (1984) Elliott (1976b)

9.6.3 The Temporal Pattern of Assimilation

Consider an individual captured at time t_0 whom is subsequently recaptured later on at time t_1. Given that both weight and length have been measured on both occasions we can from equation(9.6), estimate the total carbon weight of this individual at time t_0 and t_1, which we denote as $W_c(t_0)$ and $W_c(t_1)$, respectively.

For this individual the balance of carbon is satisfied by the following equation

$$\int_{t_0}^{t_1} dW_c(t) = \int_{t_0}^{t_1} A(t)dt - \int_{t_0}^{t_1} M(t)dt \tag{9.8}$$

which states that the net gain in carbon weight between time t_0 and t_1 is the difference in the total assimilated carbon and total carbon expended on maintenance over this time period. With some rearrangement we can recast this equation as follows

$$\int_{t_0}^{t_1} A(t)dt = W_c(t_1) - W_c(t_0) + \int_{t_0}^{t_1} M(t)dt. \tag{9.9}$$

We have already independently parameterised maintenance and we know the Girnock water temperature history. Therefore, if we assume that the total car-

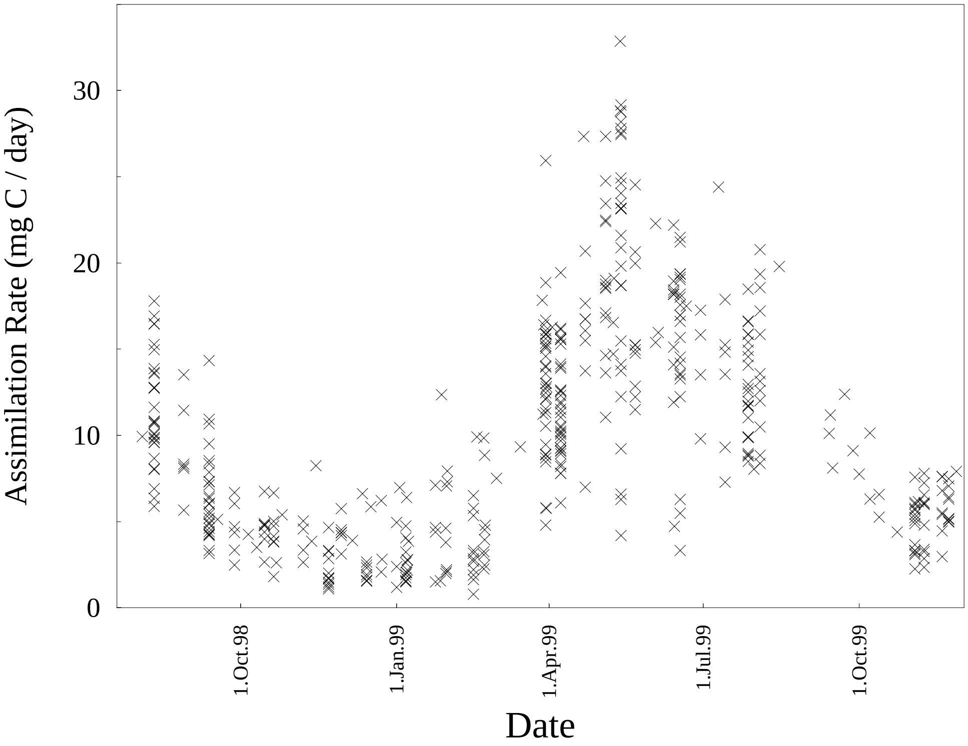

Figure 9.6: *Estimated values of average daily assimilation for individuals from the 1997 cohort. Values have been positioned at the midpoint between successive recapture dates.*

bon weight changes linearly between successive sampling points we can estimate the total maintenance expenditure of carbon between time t_0 and t_1 by summing up the estimated daily maintenance expenditure.

Hence, from equation(9.9), we can estimate the total assimilated carbon between times t_0 and t_1. Following this, it is a simple procedure to calculate the average daily assimilation rate.

Figure(9.6) displays the estimated daily average assimilation for individuals from the 1997 cohort spanning from autumn 1998 to winter 1999. It can be seen that assimilation reduces to a minimum in January and increases to a maximum in May/June. Following this, assimilation decreases over the remaining summer and autumn period.

9.7 Conclusions

We have carried out an exploratory analysis to isolate the major growth characteristics of parr in the Girnock Burn. The analysis has shown us that rates of growth are highest in the spring period of the year and reduce over the summer period. The E&H model for maximal growth could not reproduce this pattern of growth and under predicted spring growth and over predicted summer/autumn growth.

Elliott and Hurley (1997) used their model to simulate growth trajectories of wild parr in the R. Eden, a stream in Northwest England. These simulations did not produce the large winter weight losses exhibited when the model was applied using the temperatures in the Girnock Burn and produced a much more realistic representation of the growth of resident parr. This is probably because the temperatures did not descend below the lower temperature limit for growth of 6^oC for as long and also not as low as in the Girnock during the winter (Gani 2000). However, in concordance with this study investigating Girnock growth, Elliott and Hurley (1997) also noted that the model under predicted growth in the spring and also over predicted growth in the late summer/autumn for the R. Eden. Studies by Allan (1995) and Jensen (1990) have revealed growth rates of young salmonids in spring to be around the theoretical maximum predicted by the growth models of Elliott et al. (1995) and Elliott and Hurley (1997).

The E&H model has also been parameterised from tank based experiments conducted with Atlantic salmon from Norway (Forseth et al. 2001). The water temperatures in Norwegian rivers are both substantially lower and for a longer period than typical U.K. rivers (e.g. see Berg and Bremset (1998)). Surprisingly, the parameter value for the lower temperature limit for growth (T_L) was still found to be approximately 6^oC. Forseth et al. (2001) used this model (parameterised from Norwegian parr) to simulate the growth of wild parr in a Norwegian river. In applying the model they assumed that during the winter period when water temperatures fell below 6^oC that specific growth rate did not fall below zero. Thus, they essentially truncated the model so that the large predicted winter weight loss was not exhibited.

The fact that the E&H model has not been successful shows us that patterns of seasonal growth cannot be simply explained by seasonal changes in temperature. Nevertheless, the model has still served as a useful analytical tool in investigating the yearly growth patterns of parr in the Girnock Burn. We have recorded that growth rates in the spring are very high even though the temperatures are quite low (approx. $4 - 8^{o}C$) but yet low in the mid-summer period when water temperatures (approx. $10 - 15^{o}C$) would allow for high growth rates.

To further investigate the dynamics of growth in the Burn we carried out a simple energetics budget analysis. Using an independently parameterised relationship for maintenance we estimated the yearly pattern of assimilation for all individuals from the 1997 cohort. In the next chapter we shall use what we have learnt about the temporal pattern of assimilation to investigate the resource allocation strategies adopted by parr in the Burn.

Chapter 10

Seasonal Allocation in the Girnock Burn

10.1 Introduction

In this chapter we shall study the production dynamics and the allocation patterns of juvenile Atlantic salmon parr residing in the Girnock Burn. As an essential analytical tool, we shall derive a simple growth and allocation model. This model will allow us to estimate how the rate of energy assimilation and also the rate of energy expenditure changes with the changing seasons. Moreover, we will also investigate how surplus energy is invested into new biomass. We are particularly interested in whether allocation to the different biomass components changes with the changing seasons.

Describing seasonal patterns of growth and allocation poses some particularly interesting challenges to the growth modeller. One has to contend with seasonally changing abiotic factors, such as temperature, coupled with changing biotic factors, such as food availability. However, with access to the high resolution of individual growth data we have an unique opportunity to investigate in fine detail the temporal patterns of assimilation, metabolic expenditure and energy allocation of Atlantic salmon parr in their natural environment.

10.2 Deriving a Model

To drive a resource allocation model we first require an understanding about the Girnock temporal pattern of maintenance and assimilation. We have already parameterised a functional form for maintenance in the previous chapter. Furthermore, we also investigated the temporal pattern of assimilation. If we can characterise this yearly pattern of assimilation with a suitable functional form then we will have a simple model framework which encapsulates the major energy losses and energy gains as a function of the time of year.

To investigate the resource allocation dynamics of parr in the Burn we shall assume a particular allocation scheme (which we assume is independent of season) and then attempt to fit the model (using our predicted temporal assimilation function and our fully parameterised maintenance relationship) to the individual electro-fishing data, both in terms of weight and length. If our model predictions deviate away from observations in a systematic manner, then based on our good understanding of our chosen allocation scheme, we can gain a good understanding of the patterns of allocation adopted by parr residing in the Burn. Furthermore, if significant deviations are found to exist, then our simple allocation model will serve as a platform to which we can make modifications to obtain a better fit to the electro-fishing data, thus gaining an even better understanding of the allocation dynamics of the juvenile parr.

10.2.1 Baseline Allocation Model

Based on its success over its counterparts in predicting the dynamic patterns of growth and allocation in both constant and variable environments we shall use the assimilation allocation scheme. In the absence of any detailed data considering the composition of the fish's prey we shall assume the composition of the prey to be constant and choose the simplified assimilation allocation scheme, described as follows

$$\frac{dR}{dt} = (1-k)A - M \tag{10.1}$$

$$\frac{dS}{dt} = kA \tag{10.2}$$

where, $k = k(X)$ denotes the proportion of assimilate allocated to structure.

To control commitment to structure we choose the same function as described in section(4.6.4) of this thesis, which, is given by

$$k(X) = \min\left\{k_1, \frac{[X-\mu]^+}{a_1}\right\}. \tag{10.3}$$

We have already analysed the behaviour of the assimilation allocation scheme in detail within previous parts of this thesis. Therefore, we shall not re-iterate the properties of this model here. For a recap of the major properties of the assimilation allocation model with respect to temperature, ration level and hyperphagia we refer the reader to sections(4.6), (4.7) and (7.4.3).

10.2.2 Modelling Assimilation

The assimilation rate of parr in the Burn will change with the changing seasons. Our aim here is to develope a simple temporal assimilation function that will allow us to fit the assimilation allocation model to the electro-fishing data. Up to now we have expressed the assimilation term as a series of coefficients in the following manner (see section(2.4.1))

$$A = \lambda(X)\varepsilon U_{H0} S^d \exp\left(\frac{T}{T_H}\right)\phi \tag{10.4}$$

where $\lambda(X)$ is the hyperphagic uptake response function defined in section(7.4.1).

According to the assimilation allocation model, compensatory patterns of growth can be expressed simply by an increase in uptake (see section(7.4.3)). Therefore, in the absence of any detailed energetic studies of juvenile Atlantic salmon necessary to parameterise a number of terms in equation(10.4) we shall group them together into a single fitting parameter such that

$$F(t) = \lambda(X)\varepsilon U_{H0}\phi \tag{10.5}$$

which means that the assimilation rate at time t can be expressed as

$$A(t) = F(t)S^d \exp\left(\frac{T}{T_H}\right). \tag{10.6}$$

We shall refer to $F(t)$ as the scaled annual temporal assimilation function. To investigate the characteristics of $F(t)$ we turn to the individual data and carry out a simple budget analysis.

Selecting a Functional Form for $F(t)$

Displayed in figure(9.6) in the previous chapter is the budget model inferred temporal pattern of assimilation. Before we can select a suitable functional form for $F(t)$ we must scale the above estimated values of daily assimilation to take into account different sizes and temperature ranges. First we must select

Table 10.1: *Independently determined assimilation scaling parameters.*

Parameter	Interpretation	Value	Units	Source
d	Maximum uptake allometric index	0.75	—	Elliott (1976b) From et. al. (1984)
T_H	Uptake rate characteristic temperature	6.0	^{o}C	Elliott (1976b) Brett (1979)

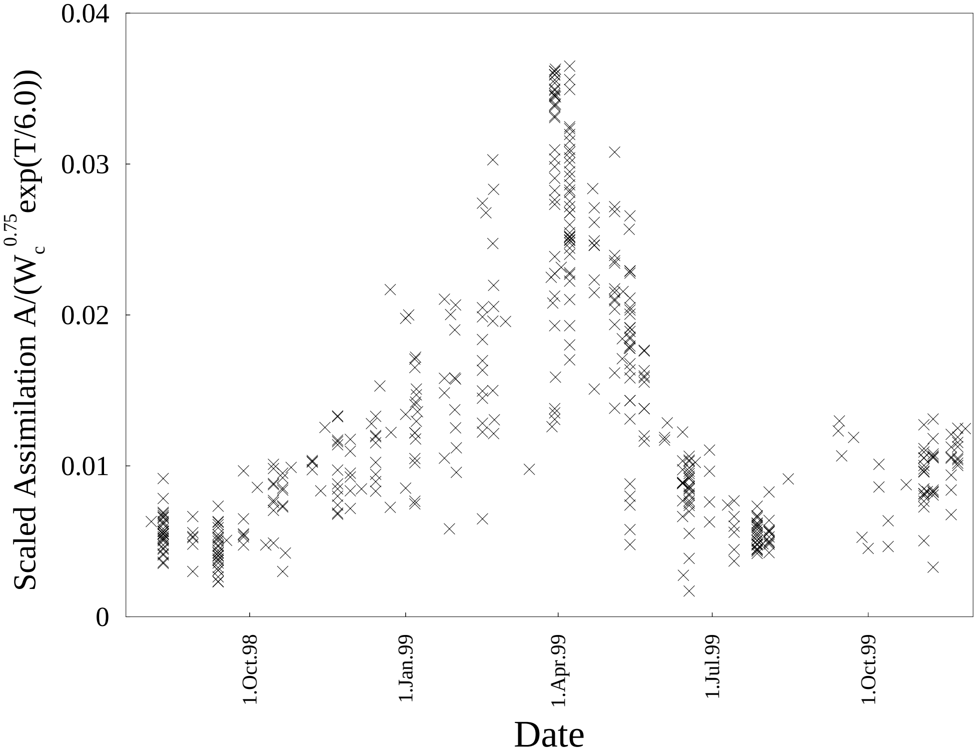

Figure 10.1: *Scaled estimated values of average daily assimilation for individuals from the 1997 cohort. Values are positioned at the midpoint between successive recapture dates.*

suitable values for the temperature (T_H) and allometric uptake scalings (d) in equation(10.6). With no real evidence to the contrary we decided to use the same values as those established in section(4.2) of 6.0^oC for T_H and 0.75 for d. To scale the calculated values of daily assimilation with temperature we divided the estimated daily assimilation values by the exponential temperature scaling of $\exp\left(\frac{T}{6.0}\right)$ using the average temperature value between successive recapture dates. To estimate the effect of size we divided by the quantity W_c^d.

The results of the size and temperature transformation is displayed in figure(10.1). It can be seen that the scaled assimilation values have a prominent seasonal trend with an almost triangular shape. Based upon this trend we decided to use the functional form depicted in figure(10.2). The choice of scaled temporal assimilation function $F(t)$ is a truncated triangular function which requires a total of five parameters to describe its exact dimensions.

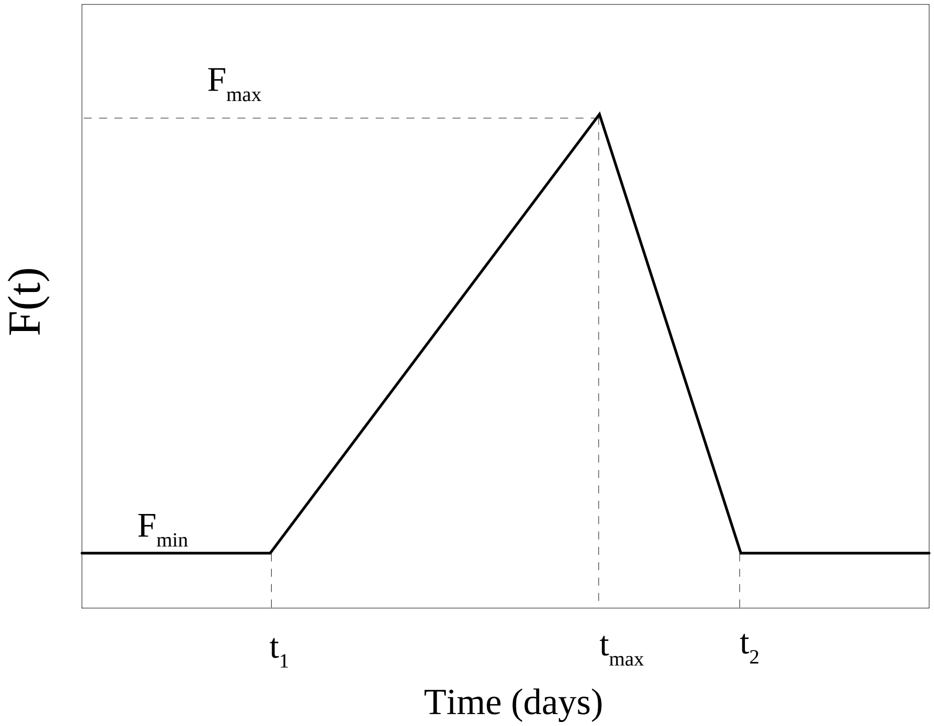

Figure 10.2: *The functional form of the scaled annual food function $F(t)$ is described by 5 parameters.*

10.3 Applying the Model

Having derived a set functional of relationships which describe temporal assimilation, maintenance and seasonally independent allocation we are now in the possession of a baseline model that can predict a particular dynamic pattern of growth and allocation. Our next step will be to compare the growth and allocation patterns of this model with the growth and allocation patterns of parr in the Burn. We shall test the model predictions by fitting simulated growth trajectories to the individual data collected from the Burn. Therefore, we dedicate this section to explaining how this model will be applied to the individual growth data.

10.3.1 The Test Data

We shall concentrate our efforts on the more detailed and high resolution 1997 cohort individual data set. Indeed, for the individual based modelling, rather than trying to factor in annual variation in food abundance (or any other differences between years) we shall mainly concentrate our efforts on a subset of this data stretching over one full annual seasonal cycle.

We truncated the 1997 cohort data to include only one seasonal cycle as a precautionary approach, so that if we do observe any allocation trends then we can be sure that these have arrived from seasonal effects rather than being disrupted in some way by any inter-annual effects. An alternative approach would have been to use the extended 1997 cohort data set but use two free fitting annual scaled assimilation functions for the two consecutive years. This would have entailed increasing the number of global fitting parameters by five but would have only increased the number of individuals we could model by approximately 15%. This was another reason why we adopted the former rather than the latter approach.

Our individual study data will include all 1997 cohort individuals who were captured more than once between autumn 1998 and autumn 1999. This allows us to follow the growth of a 180 individuals, which were each caught an average of 3.5 times during this full annual cycle. Because the first weight and length observation measurements will be used to the calculate the model state variable initial conditions (see below) then this leaves a total of 437 free fitting data points in length and the same number in wet weight.

10.3.2 Modelling Individuals

Quite obviously, the growth and perhaps allocation patterns of individuals will differ from one another. Therefore, our model must be capable of coping and capturing this variability in growth. It is highly likely that there exists inter-individual variability in both maintenance rates as well as assimilation rates (Priede (1985); Hochachka and Mommsen (1995); McCarthy (2000); O'Connor et al. (2000)). However, without any information regarding individual metabolic rates and food consumption it is not feasible to take both these variability factors into consideration because the effect on net production $(A - M)$ will be mutually confounded. Therefore, we shall assume the parameterised relationship for daily maintenance costs (section(9.6.2)) is the same for each and every individual and assume that variability in growth is manifested through inter-individual differences in assimilation.

The next question to arise is how to model inter-individual variability in assimilation. Seeing as the major patterns of growth in the Burn are dominated by seasonal effects we shall attempt to model the growth of individuals by multiplying a global scaled annual food function $F(t)$ by a scalar value which is uniquely assigned to a particular individual. This means that the assimilation rate of individual j at time t is expressed as follows

$$A_j(t) = \Psi_j F(t) S^d \exp(T/T_H) \tag{10.7}$$

where, Ψ_j is a scalar value assigned to individual j. Since the relationship for maintenance has been assumed to be the same for each and every individual then Ψ_j can be interpreted as a relative performance index. This means that individuals with higher values of Ψ_j will grow faster than individuals with lower values of Ψ_j.

The assimilation allocation model was specifically derived to encapsulate the changes in nutritional condition with varying growth performance. Since variability in Ψ_j will change growth performance then changes in nutritional condition will respond accordingly. Therefore, it seems reasonable to assume that the assimilation allocation function given by equation(10.3) is global, i.e. $k(X)$ is an identical function for all individuals.

10.3.3 Energetic Considerations

With the exception of the first weight and length observation, for each individual, all remaining simultaneous measurements of weight and length will be free fitting data points. Once again, following Broekhuizen et al. (1994), fish length will be predicted from structural carbon weight by using the allometric relationship as follows

$$L = \alpha S^{\beta}. \tag{10.8}$$

In a similar manner to that undertaken in chapter 8 (see section(8.3)) we shall estimate the fish's wet weight from a combination of reserve and structural carbon weight using the following expression derived from the statistical representation given by Elliott (1976a)

$$W = \left(\frac{12.0 L^{3b_1} W_c}{a 100^{b_1}} \right)^{\frac{1}{(1+b_1+b_2)}} \tag{10.9}$$

where, L (cm) is fish length (which will be predicted from equation(10.8)), W_c (mg C) is the total carbon weight and W is wet weight (g).

10.3.4 Parameterisation

We can essentially group the parameters into two component sets, namely, global and local parameters. The local parameters are the set of values for Ψ_j which require a value for each individual and will thus be treated as fitting parameters. The global parameters refer to the parameter values that are assumed to be common to each and every individual. The global parameters can be further subdivided into sets which control assimilation, maintenance, allocation and the length to structural weight allometric relationship. We have already parameterised maintenance and independently derived suitable allometric and temperature scalings for assimilation. The values and sources of these parameters values are summarised in tables(9.5) and (10.1). The scaled annual food function requires a total of five parameter values and we treat these as free fitting parameters.

For allocation we require a total of three parameter values, namely, k_1, a_1 and μ in equation(10.3). These three parameters are treated as global free fitting parameters which we assume to be independent of time. Finally, we shall also treat the values of α and β in equation(10.8) relating the length to structural carbon weight as global free fitting parameters. This leaves a total of eleven free fitting global parameters, which, relate to temporal assimilation, seasonally independent allocation and structural allometry.

10.3.5 Initial Conditions

To move the model forward we first require the knowledge of the two initial state variable values, namely, reserve carbon weight R and structural carbon weight S. We use the first recorded length observation (for both average and individual data) to calculate the initial structural carbon weight by using the allometric relationship given in equation(10.8). Seeing as both weight and length measurements were recorded for each fish we could estimate the total carbon weight from equation(9.6) and therefore subsequently calculate the initial reserve carbon weight. Hence the initial values of R and S were chosen such that they satisfied the initial observed weight and length.

10.3.6 Error Measure

We shall use a proportional point error to assess the difference between observed and predicted length and weight observations. The advantage of using the proportional error is that it is far less susceptible to corruption from outliers than, say, a least squares error – a highly desirable property when fitting to potentially noisy individual data.

For reasons that will soon become clear we need to assign an error function (minimising objective function) for each and every individual and also a grand error function which takes into consideration the total error over all individuals. For any individual j which has been recaptured N_j^{R} times within our study period we shall use the sum of proportional error (SPE) defined as

$$\mathrm{SPE}_j = \sum_{i=1}^{N_j^{\mathrm{R}}} \frac{|O_{i,j}^{\mathrm{L}} - P_{i,j}^{\mathrm{L}}|}{O_{i,j}^{\mathrm{L}}} + \sum_{i=1}^{N_j^{\mathrm{R}}} \frac{|O_{i,j}^{\mathrm{W}} - P_{i,j}^{\mathrm{W}}|}{O_{i,j}^{\mathrm{W}}} \tag{10.10}$$

where, $O_{i,j}$ denotes the i'th observed weight or length (superscript denotes which) fitting point for individual j. In a similar manner, $P_{i,j}$ denotes the i'th predicted weight or length (superscript denotes which) fitting point for individual j.

If we now sum up this error function over all individuals then we obtain the grand sum of proportional error (GSPE), defined as follows

$$\mathrm{GSPE} = \sum_{\text{all } j} \mathrm{SPE}_j = \sum_{\text{all } j} \sum_{i=1}^{N_j^{\mathrm{R}}} \frac{|O_{i,j}^{\mathrm{L}} - P_{i,j}^{\mathrm{L}}|}{O_{i,j}^{\mathrm{L}}} + \sum_{\text{all } j} \sum_{i=1}^{N_j^{\mathrm{R}}} \frac{|O_{i,j}^{\mathrm{W}} - P_{i,j}^{\mathrm{W}}|}{O_{i,j}^{\mathrm{W}}}. \tag{10.11}$$

If we now recognise that the first term on the right hand side of equation(10.11) is the sum of proportional errors in all length observations for all individuals (and similarly for weight) then we can express this grand error function as follows

$$\mathrm{GSPE} = \sum_{h=1}^{N} \frac{|O_h^{\mathrm{L}} - P_h^{\mathrm{L}}|}{O_h^{\mathrm{L}}} + \sum_{h=1}^{N} \frac{|O_h^{\mathrm{W}} - P_h^{\mathrm{W}}|}{O_h^{\mathrm{W}}} \tag{10.12}$$

where, N defined by

$$N = \sum_{\text{all } j} N_j^{\mathrm{R}} \tag{10.13}$$

is the total number of free fitting points in weight and (since all individuals had both length and weight measured simultaneously) thus length.

Definitions

For future analytical purposes it is useful to make some definitions so that we can isolate the composition of the grand error (GSPE) in terms of weight and length errors. Hence, we define the following expressions

$$\mathrm{SPE}_{\mathrm{L}} = \sum_{i=1}^{N} \frac{|O^{\mathrm{L}}_{i,j} - P^{\mathrm{L}}_{i,j}|}{O^{\mathrm{L}}_{i,j}}, \qquad \mathrm{SPE}_{\mathrm{W}} = \sum_{h=1}^{N} \frac{|O^{\mathrm{W}}_{h} - P^{\mathrm{W}}_{h}|}{O^{\mathrm{W}}_{h}} \tag{10.14}$$

where, $\mathrm{SPE}_{\mathrm{L}}$ is the sum of proportional errors in length over all individuals. In a similar manner, $\mathrm{SPE}_{\mathrm{W}}$ is the sum of proportional errors in weight over all individuals. Thus the grand error is the sum of these two errors such that

$$\mathrm{GSPE} = SPE_L + SPE_W \tag{10.15}$$

For a more intuitive measure of errors in weight and length we shall define the mean proportional errors

$$\mathrm{MPE}_{\mathrm{L}} = \frac{\mathrm{SPE}_{\mathrm{L}}}{N}, \qquad \mathrm{MPE}_{\mathrm{W}} = \frac{\mathrm{SPE}_{\mathrm{W}}}{N}. \tag{10.16}$$

where, N is the number of free fitting points in length and thus weight. These values can be interpreted as the mean proportional error in predicting a typical data point in weight or length. If these values are further multiplied by 100 then these proportional errors are expressed as percentages.

10.3.7 Simulation

To fit the model to the complete data set we need to fit 180 individual values of Ψ_j and also 11 global fitting parameters which account for temporal assimilation, allocation and structural allometry. Therefore, our total parameter set consists of a total of 191 free fitting parameters. Because of the extremely large number of free fitting parameters it was simply not feasible to attempt to parameterise all 191 values simultaneously using a single downhill simplex method of optimisation (appendix A). However, there are some special properties of the minimising objective function that we took advantage of to employ a nested minimisation procedure. For a rigorous mathematical explanation of this technique the reader is referred to appendix C.

Growth trajectories were predicted for each individual by integrating the model equations (10.1) and (10.2) using the smoothed temperature data as displayed in figure(9.2). We used a fourth order Runge-Kutta algorithm (Press et al. 1989) using a fixed time step of 1 day.

10.4 Results

10.4.1 Fit to Average 1997 cohort data

As an illustration of the goodness of fit we received from our basic model assumptions we display the best fit trajectories to the averaged 1997 cohort data in length and wet weight in figure(10.3). Simulations were conducted by treating the average data as a single individual by choosing a single value of $\Psi_1 = 1.0$ in equation(10.7), thus, only minimising the global free fitting parameters. For the purposes of this illustratory example we assumed the global annual scaled assimilation function to be the same for each annual seasonal cycle.

It can be seen from figure(10.3) that our model captures the major dynamic patterns of temporal growth, both in terms of weight and length. Although the model was only fitted to weight and length observations we can easily produce the models predicted trajectory in condition factor ($K = 100W/L^3$) by using the combination of the best fit weight and length trajectories. Figure(10.3,c) displays the model predicted condition factor trajectory together with the observed values of average condition factor for each sampling date. On first inspection, the predicted trend in condition factor appears to be very good. Condition factor and thus nutritional status quickly increases with the spring growth spurt (as predicted by the assimilation allocation model), peaks in approximately May and reduces steadily until the onset of the next spring growth period. There is, however, a rather uncomfortable pattern of residuals, where, the averaged values are consistently over predicted during the first six months and following this there is a tendency for the averaged condition factor values to be under-

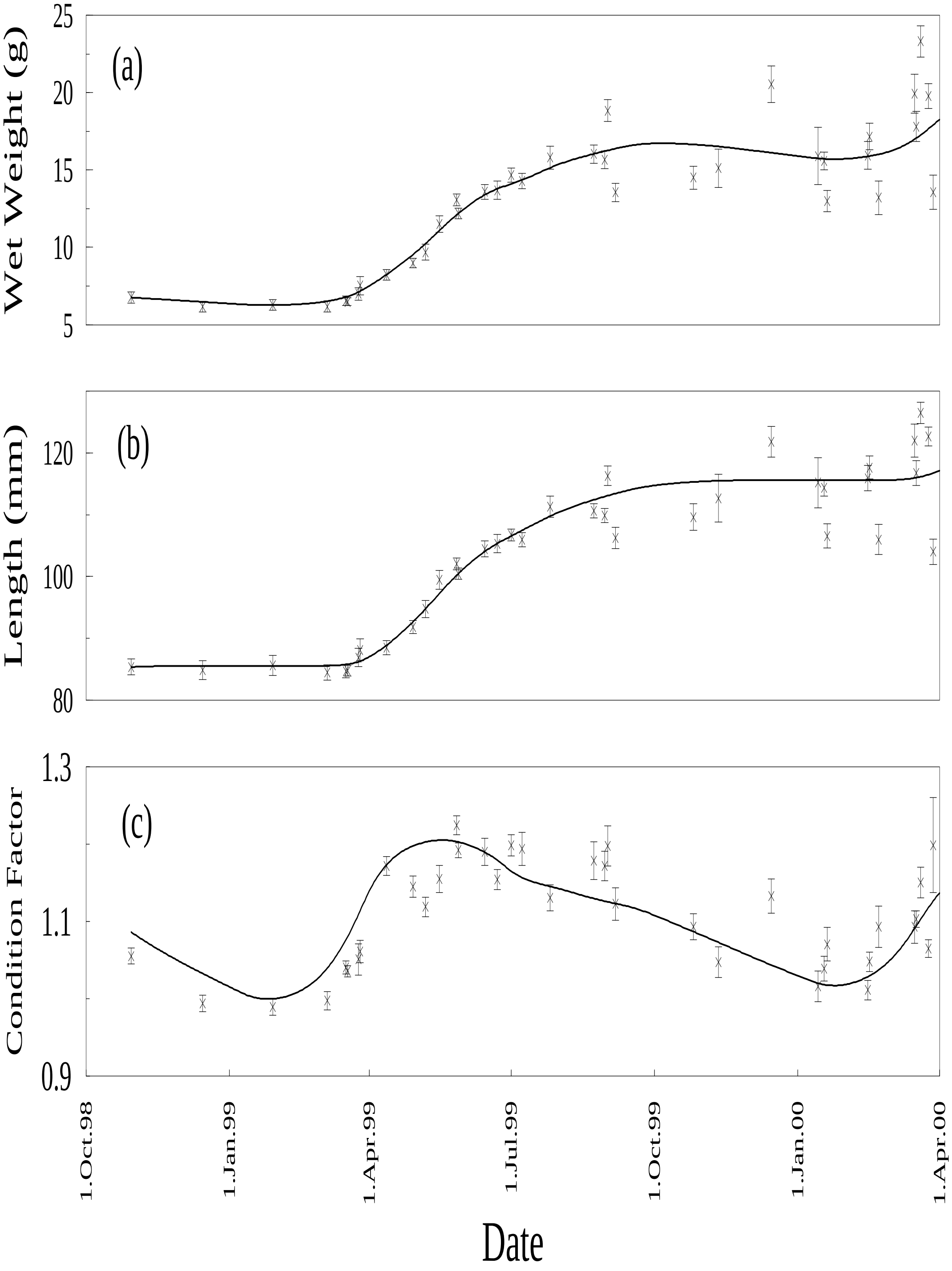

Figure 10.3: *The best fit model growth trajectories in a) wet weight, b) length and model predictions in c) condition factor for the averaged 1997 cohort electro-fishing data. The error bars denote 1 standard error.*

predicted.

Another clear observation is that there exists bias within the averaged data. The model has been started off with the state variable chosen such that the initial averaged weight and length observations are predicted. However, it is clear from figure(10.3,c) that the initial condition factor value predicted from the initial average weight and average length is not equal to the average condition factor calculated from individual condition factor values.

In conclusion, we have obtained a good fit to the averaged 1997 cohort data, allowing us to gain confidence in the ability of the model to reproduce the major dynamic pattern of seasonal growth in the Burn. The predicted allocation behaviour is reasonable, but we have isolated an uncomfortable trend in predicted condition factor values. However, we cannot take our analysis any further because there exists a clear bias in the averaged data. This highlights the dangers of investigating averaged growth, which are manifested through an associated loss of variability data (Sharp 1987). Therefore, the averaged properties of the fish population may not necessarily reflect the properties of the individuals within the population (Juanes et al. 2000). To overcome this problem we need to apply our model to the individual data.

10.4.2 Fit to Individual 1997 cohort data

We fitted the model to individuals caught more than once between autumn 1998 to autumn 1999, as fully explained in section(10.3). Tables(10.2) and (10.3) display the best fit global parameter values and the best fit model error measure values, respectively. Plotted in figure(10.4) is the fitted model predictions against observed values in weight and length. It can be seen that the model gives a very good fit, with over 95% of the variablity being explained in both weight and length. However, closer inspection of figure(10.4,a) reveals a rather disturbing trend, where, the smaller length observations are being under-predicted and the larger length observations are being over-predicted. To investigate this

Table 10.2: *Best fit global parameter values.*

Parameter	Value	Units
Structural Allometry (see equation(10.8))		
α	1.57	cm mgC$^{-\beta}$
β	0.32	–
Allocation Function (see equation(10.3))		
k_1	0.53	–
μ	2.29	–
a_1	4.00	–
Temporal Assimilation $F(t)$(see figure(10.2))		
t_1	314	days from 1/Jan/98
t_2	539	days from 1/Jan/98
$t_{\max}$	476	days from 1/Jan/98
$F_{\max}$	0.0622	mgC^{1-d}day^{-1}
$F_{\min}$	0.0124	mgC^{1-d}day^{-1}

pattern in greater detail we shall investigate the individual fitted model residual values.

Figure(10.5) displays the weight and length proportional residuals ($\frac{Obs-Pred}{Obs}$) summarised into means and plotted by electro fishing sampling date. Although we only fitted to weight and length observations our model is quite capable of predicting a condition factor value for each individual free fitting data point. Therefore, also plotted in figure(10.5) are the proportional condition factor residuals summarised into means for each sampling date.

It is immediately clear that there exists a systematic pattern of residuals in length. Length observations are under-predicted in the spring period, are acceptable in the early to mid summer period, over-predict in the late summer period and then once again become acceptable with the onset of winter. Although the weight residuals are noisier, no such systematic pattern exists. Indeed, there

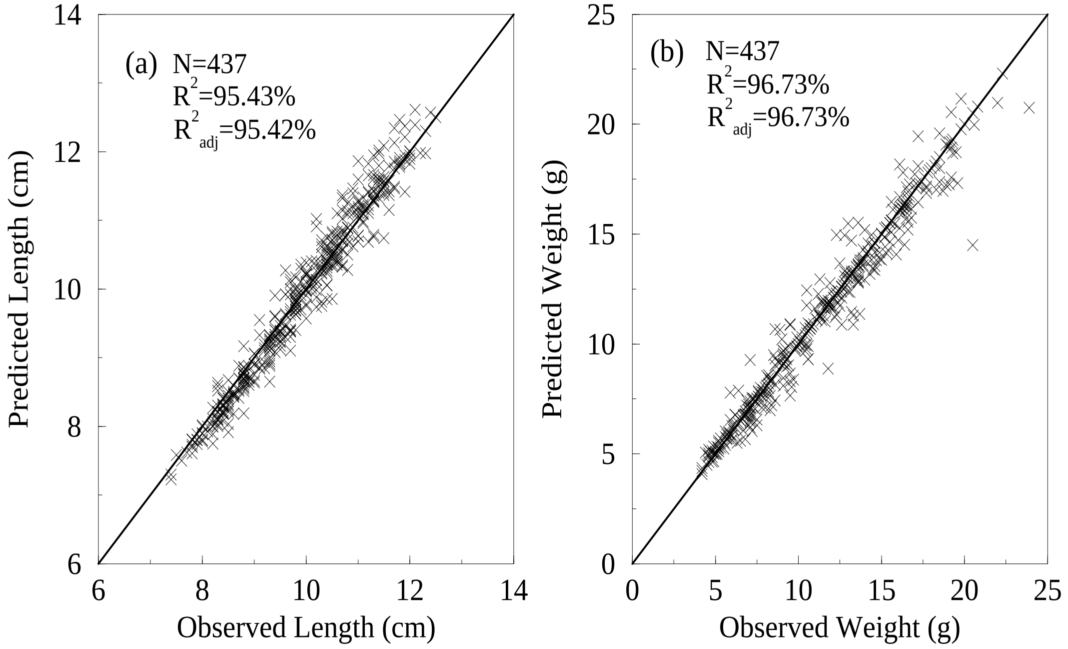

Figure 10.4: *Model predicted versus observed individual values of a) length and b) weight for individually marked 1997 cohort fish caught more than once between autumn 1998 and autumn 1999. The solid lines are straight lines passing through the origin with a 1:1 gradient. Displayed data points do not include first length or weight observations from the study period.*

are periods of the year, such as spring and autumn, where length is being under or over predicted, whereas the weight observations are either being acceptably predicted or even exhibiting opposite prediction trends to length. Because of these conflicting predictions in weight and length the condition factor residuals also exhibit a strong systematic trend, but in the opposite manner to length residuals.

Table 10.3: *Best fit model error measure values. The definitions of each non-dimensional error measure is given in section(10.3.6).*

Error Definition	SPE_L	MPE_L (%)	SPE_W	MPE_W(%)	GSPE
Value	8.30	1.90	17.49	4.00	25.79

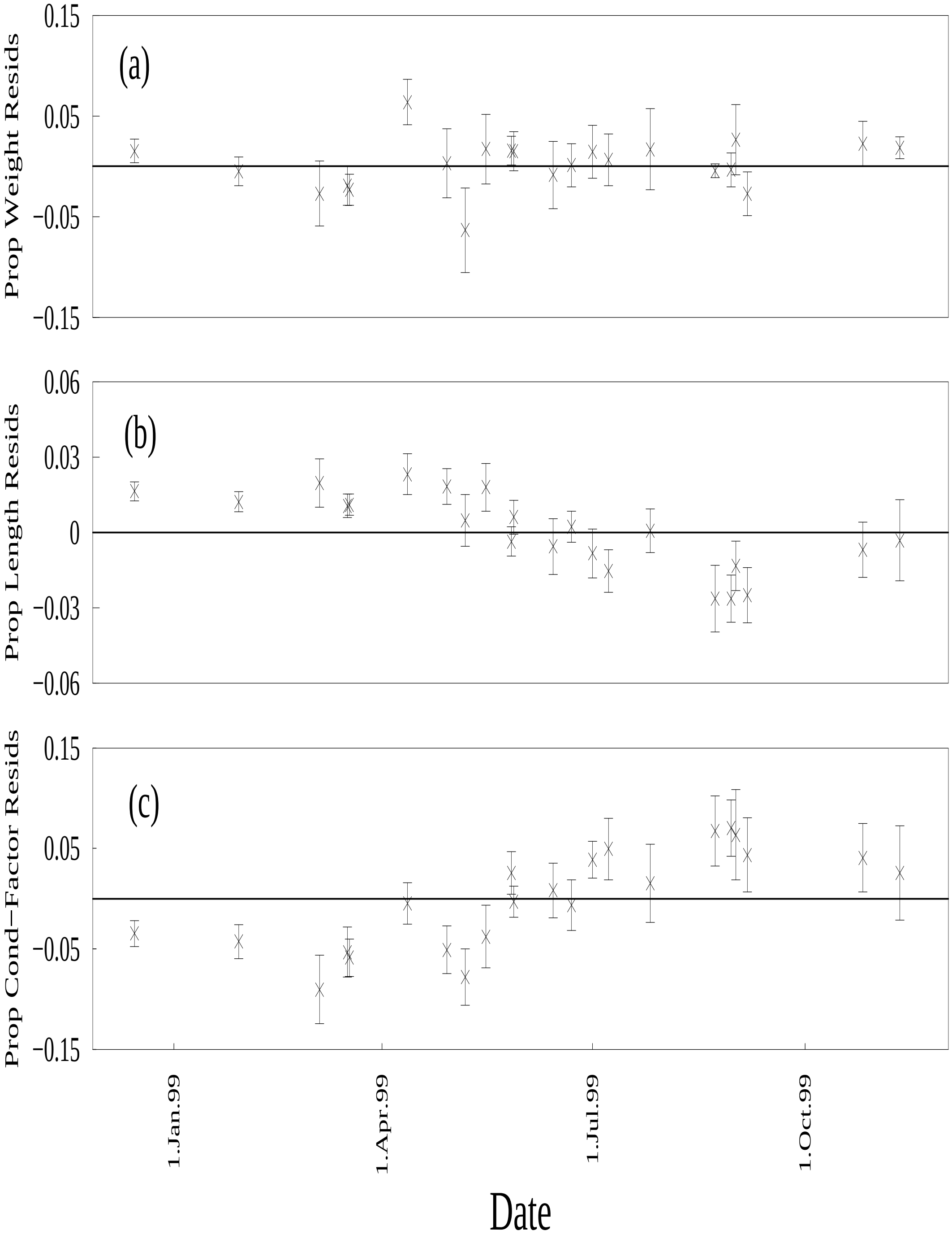

Figure 10.5: *Proportional residuals* ($\frac{Obs-Pred}{Obs}$) *plotted against sampling date from fitting the model to individuals from the 1997 cohort caught more than once between autumn 1998 and autumn 1999. Residuals summarised into means for a) weight, b) length and c) condition factor. Bars denote 95% confidence intervals for the sample mean for each electro-fishing sampling date.*

Summary

Our accuracy in fitting the model to individual weight and length observations is very good (see figure(10.4)), which instills confidence in our approach to modelling individuals (see section(10.3.2)). There is, however, a systematic temporal pattern of length residuals, which is not exhibited in the weight residuals. At certain times of the year we are acceptably predicting weight but unacceptably predicting length. We can deduce from this that our model is, in some way, misrepresenting allocation. Further investigation of the condition factor residuals pretty much confirms this.

Despite the systematic residual pattern in length, the model is still predicting length more accurately than weight (see table(10.3)). One reason for this may be the effect of fish gut fullness. A fuller gut would increase fish weight but would not change fish length. Therefore, the fish's recent feeding history may cause greater variability in weight than in length. However, this also brings in to question the accuracy of the condition factor (a measure of weight for length) as an indicator of nutritional status and therefore our deductions we have made from the results of our model fit. Gani (2000) estimates weight of a juvenile Atlantic salmon with a full gut of food to be between 3-6% percent heavier than a conspecific of equal size with an empty gut. Because condition factor is directly proportional to wet weight then this proportional error would directly translate into an error in condition factor.

The rate of gut evacuation in fish increases exponentially with temperature (Elliott (1972); Talbot et al. (1984); Higgins and Talbot (1985); Jensen (1993); He and Wurtsbaugh (1993)). Given that the parr are feeding more in spring at a low temperature (see figures(9.6), (10.1) and (9.2)) then we should pretty much expect the fish to have a fuller gut than in late summer where consumption rates are lower but water temperature is higher. This means the associated error in condition factor resulting for an increased weight for length will be high in spring but lower in summer. Yet, despite this, our model over predicts condition factor in spring (when gut fullness will be high) and under predicts condition factor in late summer (when gut fullness will be lower). This further corroborates our original deduction that our model is misrepresenting the energy allocation dynamics of juvenile parr resident in the Burn. Therefore, our next step is to modify our model to incorporate this seasonal pattern of allocation.

10.5 Seasonal Allocation Model

10.5.1 Incorporating a Seasonal Allocation Function

We have assumed that the resource allocation dynamics of juvenile Atlantic salmon living in their natural environment can be adequately described by the assimilation allocation model. The model, under the current rules of allocation (see section(10.2.1)), predicts that nutritional condition should always be correlated with a combination of temperature and ration level and thus growth rate (see section(4.6)). However, we have found systematic differences between electro-fishing observations and our model predictions. The model is under predicting length in spring and over predicting length in autumn. In order to improve the model predictions we must, in some way, account for these seasonal changes in allocation by modifying equation(10.3).

From the simple budget analysis we conducted in section(10.2.2) we predicted that the rate of assimilation (and thus growth rate) reduces down over the late summer period. Based on the assimilation allocation model there should also be a concomitant reduction in nutritional condition with this reduced growth rate (see section(4.6)). However, our model under-predicts nutritional condition, principally through over-predicting length in autumn (see figure(10.5)). The most influential parameter in equation(10.3) which defends a good nutritional condition, especially when food consumption is low (see section(4.6.4)), is the defended reserve ratio threshold μ. Therefore, we shall argue, that over the late summer period, the defended reserve ratio value μ may be greater than at other times of the year.

On the other hand, length is being under predicted in spring, even though the juveniles are initially in poor condition following winter. If the value of μ was lower at the onset of spring then individuals would begin committing to structure earlier and also proportionally more (see equation(10.3)) than is presently predicted by assuming a constant value of μ throughout the year.

Our above arguments forecast a time dependent change in the value of μ over a seasonal cycle. In order to model this phenomena we shall modify μ such that it is a function of time. The next question to arise is in what way does μ change, i.e. is it a sudden change alternating from one extreme value to another or is it a gradual change occurring with the changing seasons? There is, however, evidence to suggest that this change in the defended reserve ratio level may be of a more gradual nature than anything else (Metcalfe and Thorpe (1992); Bull et al. (1996)). We shall discuss this in more detail within the discussion section of this chapter.

As a modification to our model we shall replace the constant value of μ in equation(10.3) with a continuous sinusoidal temporal function (with a period of one year) given by

$$\mu = \bar{\mu} + B \sin\left(\frac{2\pi(t-\theta)}{365}\right) \tag{10.17}$$

where, t, represents time in days from 1 January 1998, $\bar{\mu}$ is the mean value of the annual defended reserve ratio threshold function, B is the amplitude of the annual sine curve and θ (days) is a phase lag constant which controls the temporal longitudinal displacement of the curve. We shall refer to this new modified model as the seasonal allocation model.

We shall fit the seasonal allocation model in exactly the same manner as we fitted the original model, as explained in section(10.3), except the number of global fitting parameters has increased to 13 because our original single constant

Table 10.4: *Best fit global parameter values for seasonal allocation model.*

Parameter	Value	Units
Structural Allometry (see equation(10.8))		
α	1.66	cm $\mathrm{mgC}^{-\beta}$
β	0.31	–
Seasonal Allocation (see equ.(10.3) and (10.17))		
k_1	0.79	–
a_1	3.12	–
$\bar{\mu}$	2.12	–
B	0.41	–
θ	113	days
Temporal Assimilation $F(t)$(see figure(10.2))		
t_1	360	days from 1/Jan/98
t_2	549	days from 1/Jan/98
$t_{\max}$	451	days from 1/Jan/98
$F_{\max}$	0.0664	$\mathrm{mgC}^{1-d}\mathrm{day}^{-1}$
$F_{\min}$	0.0116	$\mathrm{mgC}^{1-d}\mathrm{day}^{-1}$

time independent value of μ has been replaced by the above temporal function. It is well worth noting that if our hypothesis is incorrect and the defended reserve ratio value does not change with the changing seasons then the seasonal allocation model can still represent our original model by simply setting $B = 0$ in equation(10.17).

10.5.2 Results

Table(10.4) displays the best fit global parameter values for the seasonal allocation model. The seasonal allocation model predicted versus observed lengths and weights are displayed in figure(10.6). Whilst the new seasonal allocation model has explained no significant extra variance in the individual

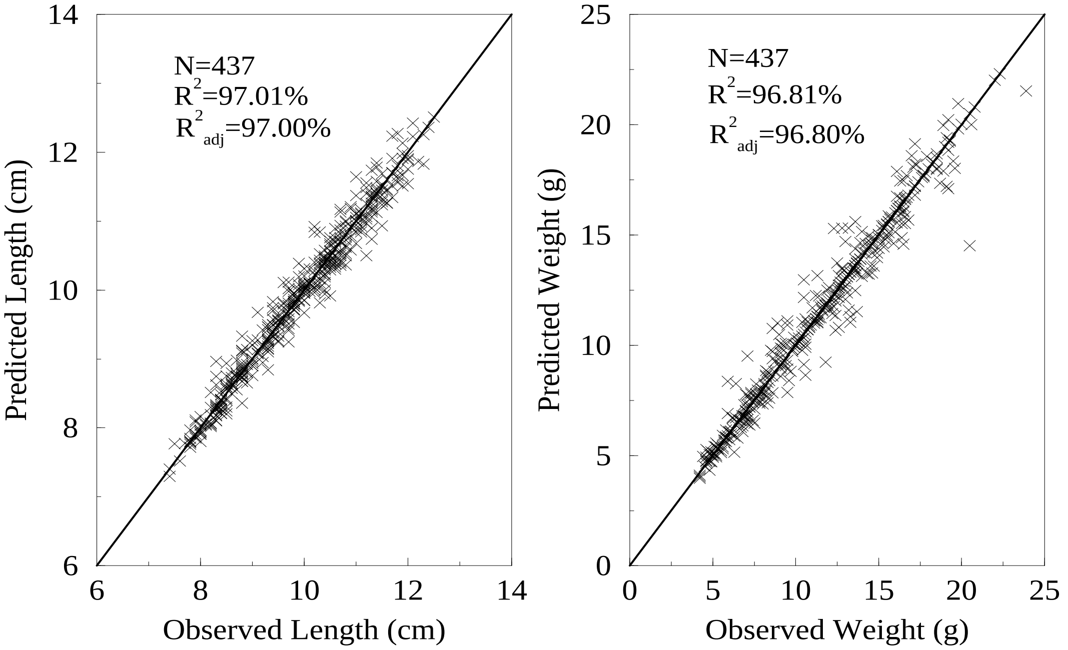

Figure 10.6: *Seasonal allocation model: predicted versus observed individual values of a) length and b) weight for individually marked 1997 cohort fish caught more than once between autumn 1998 and autumn 1999. The solid lines are straight lines passing through the origin with a 1:1 gradient. Displayed data points do not include first length or weight observations from the study period.*

weight observations, there is, however, an increase in the explained variance in length (compare figures(10.4) and (10.6)). Furthermore, the model predictions do not appear to be biased as in the original model (see figure(10.4)).

The error measure values displayed in table(10.5) further corroborate this initial conclusion. The reduction in the grand error value (GSPE) is solely as a conse-

Table 10.5: *Best fit seasonal allocation model error measure values. The definitions of each non-dimensional error measure are given in section(10.3.6).*

Error Definition	$\mathrm{SPE_L}$	$\mathrm{MPE_L}$ (%)	$\mathrm{SPE_W}$	$\mathrm{MPE_W}$(%)	GSPE
Value	6.47	1.48	17.43	3.99	23.91

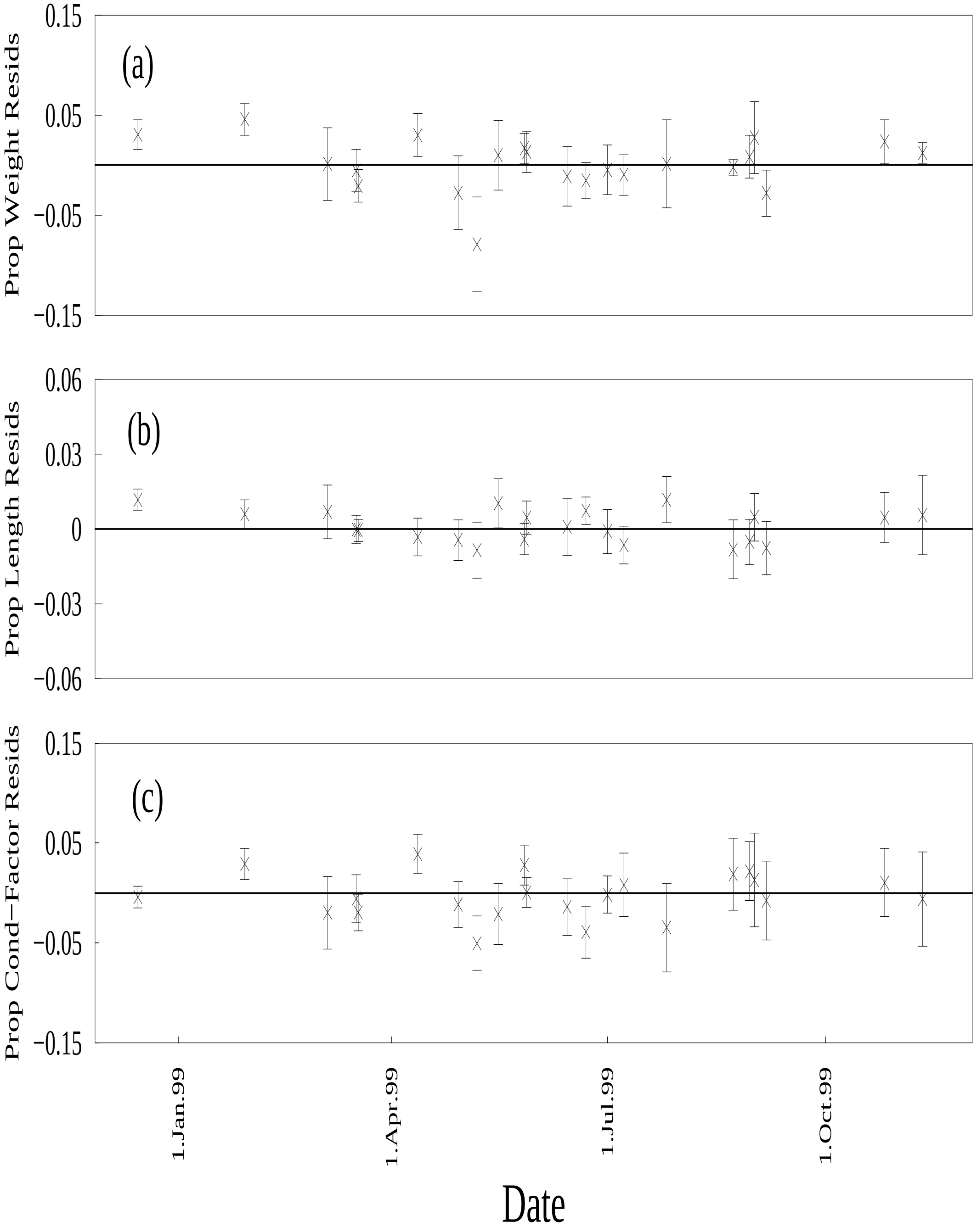

Figure 10.7: *Proportional residuals* ($\frac{Obs-Pred}{Obs}$) *plotted against sampling date from fitting the seasonal allocation model to individuals from the 1997 cohort caught more than once between autumn 1998 and autumn 1999. Residuals summarised into means for a) weight, b) length and c) condition factor. Bars denote 95% confidence intervals for the sample mean for each electro-fishing sampling date.*

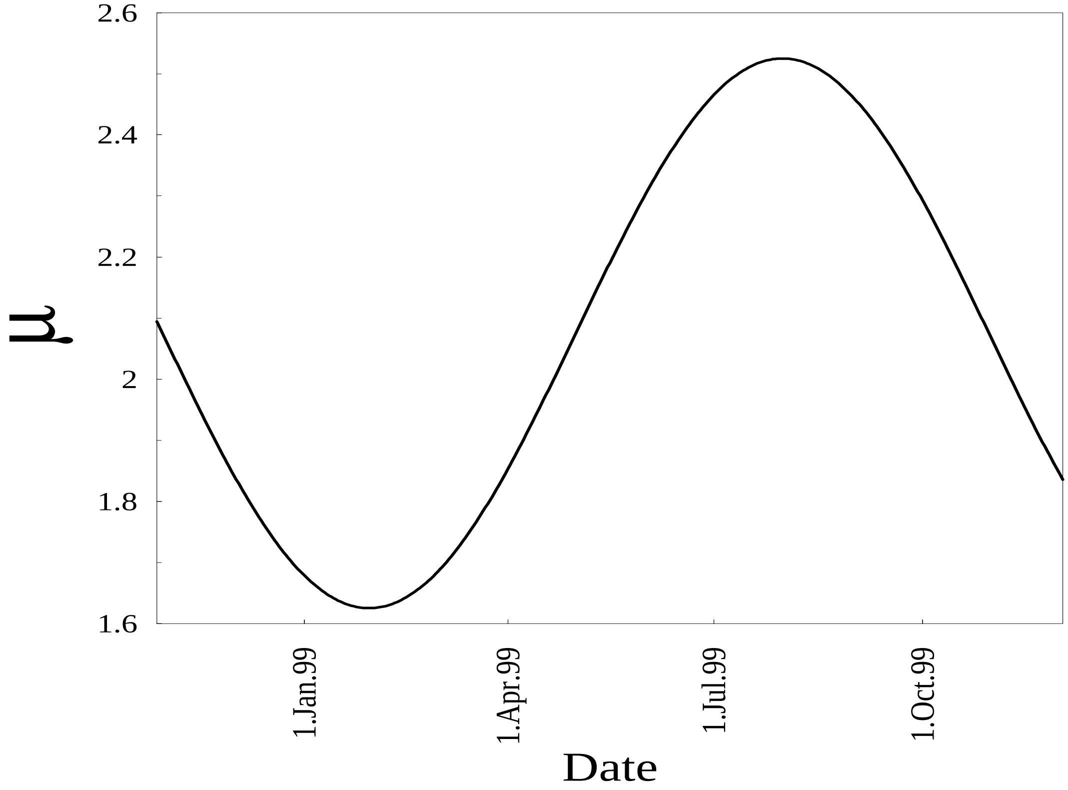

Figure 10.8: *The best fit defended reserve ratio threshold function* μ *for the seasonal allocation model. See equation(10.17).*

quence of an approximate 25% decrease in the proportional error in predicting length (compare tables(10.3) and (10.5)).

Figure(10.7) displays the seasonal allocation model proportional residuals in length and weight and also model predicted condition factor residuals. It can be seen that the seasonal modification in allocation has eradicated the systematic trend in length residuals exhibited by the original model fit (compare figures(10.5) and (10.7)). Since length is now being more accurately predicted then so also are the predicted condition factor values, leading to the eradication of the systematic pattern of residuals also manifested by the original model. Hence, our seasonal allocation model is more accurately predicting the seasonal changes in nutritional condition.

Figure(10.8) displays the best fit functional form for the seasonally changing reserve ratio threshold for maintaining structural growth μ (see equation(10.17)).

As we have forecasted, the reserve ratio threshold is lowest in early spring and rises to a maximum in late summer. We can deduce from this, that during spring, juveniles from the Girnock Burn are primarily directing their resources to structural growth rather than accumulating high levels of reserves. As the growing season progresses and the onset of late autumn becomes nearer, μ increases, indicating that accumulating or maintaining high levels of reserves becomes of more importance than maintaining structural growth.

10.6 Analysis

Following a modification to cope with the seasonal patterns of allocation we have obtained an excellent fit to our individual data with over 96% of the variance being explained in weight and length. This section is dedicated to analysing and drawing inferences from the results of our seasonal allocation model.

10.6.1 Analysis of Ψ_j

The best fit values of Ψ_j, the individual assimilation fitting parameters (see equation(10.7)), for the seasonal allocation model are displayed in figure(10.9). Each histogram represents a subsample of the 1997 cohort parr, defined by the minimum number of recaptures between autumn 1998 and autumn 1999. The distribution of Ψ_j does not appear to be of a standard normal distribution and, indeed, all four displayed distributions failed the Shapiro and Wilk's test for normality (Royston 1982). The values of all Ψ_j (figure(10.9,a)) appear to be tightly grouped with a small number of outliers. As the resolution of data increases (i.e. the greater number of recaptures) the variability in Ψ_j decreases. This indicates that the values of Ψ_j are more reliable with increasing numbers of recaptures. The values of Ψ_j derived from individuals who have only been recaptured once in the experimental period are probably more prone to experimental error. This was mostly found to be the case when an individual was caught only twice but

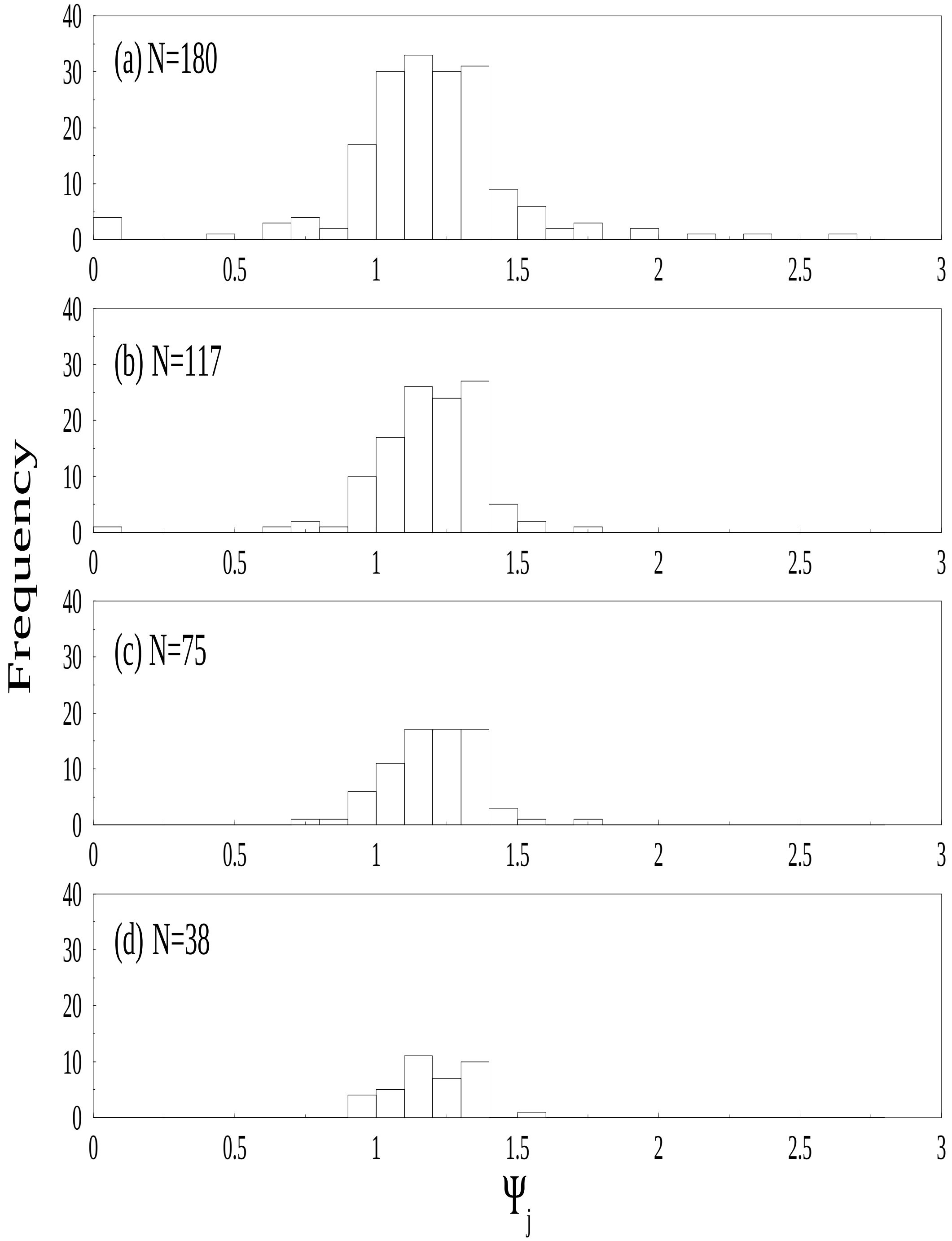

Figure 10.9: *Histograms displaying the distribution of the individual assimilation fitting parameters* Ψ_j *(see equation(10.7)). a)* Ψ_j *for all individuals, b)* Ψ_j *for individuals recaptured more than once, c)* Ψ_j *for individuals recaptured more than twice, d)* Ψ_j *for individuals recaptured more than three times.*

recaptured shortly after the first capture.

In figures(10.9,b and c) the distribution of Ψ_j appears to be skewed with a longer tail to the left. At first, this would seem to be a surprising result since mortality has commonly been shown to be inversely correlated with growth rate for many species of fish (for review see Sogard (1997)). Therefore, one would intuitively expect a truncation of the distribution at the left hand tail. However, it must be noted that the greatest majority of individuals within our study consisted of juveniles who would have migrated in their third year of life. Since the decision to smolt and subsequently migrate is mainly dependent upon achieved size (Elson 1957), then the faster growing remainder of the 1997 cohort, with the highest values of Ψ_j, would have migrated from the Burn as two year olds in April 1999. Only a very few of these individuals were successfully recaptured, principally, because of the shorter time interval they were available above the 70mm length threshold necessary to tag juveniles.

No significant relationship was found between the values of Ψ_j and the number of recaptures ($P > 0.05$ and see figure(10.9)). This may indicate that individually tagging and using the method of electro-fishing for capturing fish did not have any significant detrimental effect on the magnitude of achieved growth. No significant relationship was found between the weight at first tagging and the values of Ψ_j ($P > 0.05$).

Twenty three individuals were positively identified as being male precocious parr in autumn 1999. We took the opportunity to investigate whether there was any difference in these values of Ψ_j and thus growth with the remainder of the population. We could find no significant differences in these values. Indeed, with the exception of one outlier value (derived for an individual only recaptured once), the values of Ψ_j for precocious parr were distrbuted around the mean of the population.

Simpson et al. (1996), based on a series of tank based experiments, found that precocious males did not differ in appetite in comparison with non-maturing conspecifics. Simpson et al. (1996) suggest that the decision to mature was as a consequence of maturing males already being larger and having higher fat contents than non-maturing parr almost a year before spawning. We carried out a brief exploratory analysis to investigate this hypothesis. Using a series of t-tests, we could find no significant size differences between non-precocious and precocious approximately one year before autumn 1999. However, the investigation and comparison of the patterns of growth adopted by non-precocious and precocious parr would benefit from a more thorough analysis. This would be an interesting avenue for future research.

10.6.2 Production Dynamics

In this subsection we shall discuss the major seasonal patterns of energy assimilation and expenditure. Given that we have obtained an excellent model fit then we can reproduce the predicted model trajectories in temporal assimilation and maintenance rates for each and every individual within our study period. Figure(10.10) displays the predicted daily rates of assimilation and maintenance for all individuals between the period of first capture and last capture who fall within our study period. Also displayed in figure(10.10) is the calculated values of net production per unit of assimilate.

Daily assimilation is very low in winter and begins to rise in early spring, quickly reaching a maximum in the middle of May. Following this, daily assimilation gradually declines throughout the summer months, reaching very low values by the onset of autumn 1999. Daily maintenance rates are initially very low over the cold winter months but increase gradually with warming water temperature, reaching a maximum in mid July. As the water temperature begins to decrease, maintenance rates also begin to fall.

The seasonal patterns of assimilation (anabolic) and maintenance (catabolic) rates are very much out of phase with one another. Net production per unit assimilate (a good indicator of growth efficiency) peaks in early April because

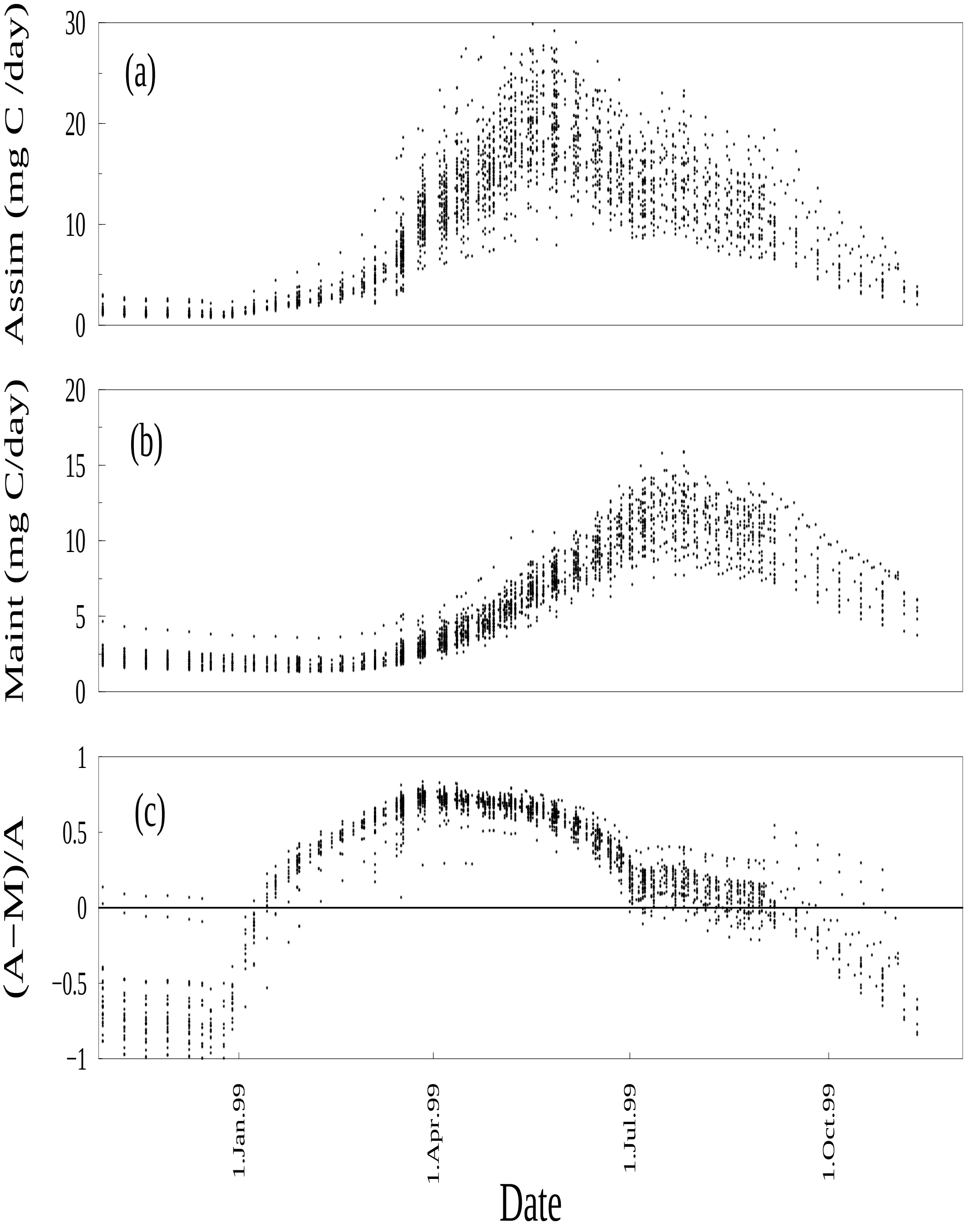

Figure 10.10: *Seasonal allocation model predicted individual temporal values of a) daily assimilation, b) daily maintenance and c) daily net production per unit of assimilate. Values have been displayed for each individual from the 1997 cohort between the period of first capture and last capture between autumn 1998 and autumn 1999.*

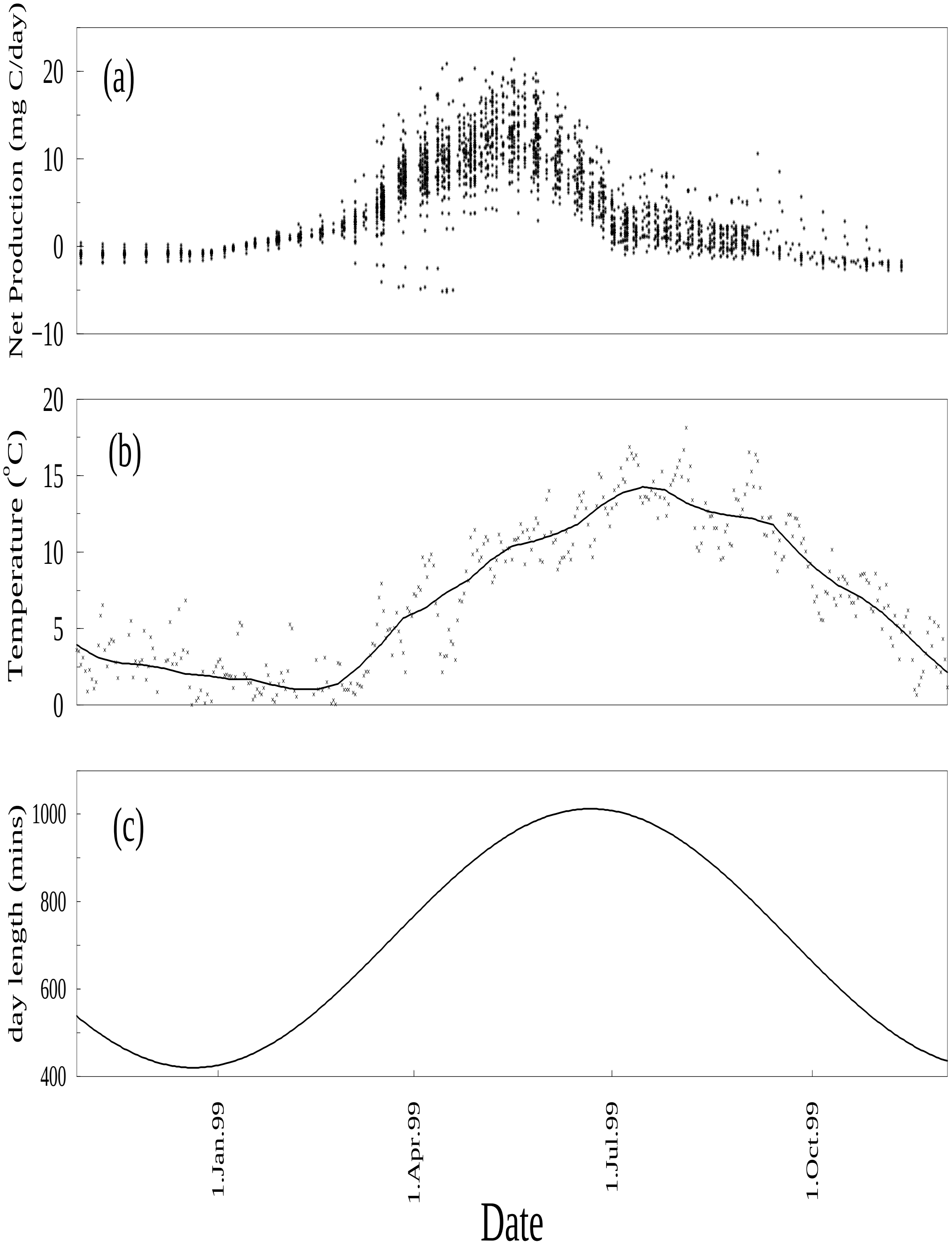

Figure 10.11: *a) Seasonal allocation model predicted individual temporal values of net production* $(A - M)$*, b) daily average water temperature recordings (the solid line is a smoother), c) daylength (taken from Higgins and Talbot (1985)).*

daily assimilation has initially risen faster than daily maintenance. This leads to the interesting hypothesis that the spring growth spurt exhibited by parr may well be partially facilitated by an increased growth efficiency. That is, low rates of maintenance energy expenditure coupled with an ability to still process food at low temperatures would leave a high percentage of the assimilable energy available for growth. This mechanism is similar to the interactive effects of ration level and temperature on growth efficiency which we have discussed in section(4.3).

As the summer progresses the net production per unit assimilate begins to decrease. In particular, the value of net production per unit assimilate is very low in early July, despite the rate of assimilation being almost equal (if not slightly higher) than in early April. This low growth efficiency is a direct consequence of the fish having high summer maintenance rates. This leads to the equally interesting hypothesis that warm summer water temperatures may well be more of a disadvantage than an advantage to wild fish, for the exact opposite reasons to that explained above.

Figure(10.11) displays the model predicted individual values of seasonal net production $(A - M)$, together with water temperature and daylength. It can be seen that the growing season in the Burn is very short. Substantial, positive net production (i.e. growth) only occurs in approximately three months of the whole annual cycle. Moreover, this pattern of growth is distinctly out of phase with water temperature. This pattern of growth seems also to be out of phase with the absolute daylength.

10.7 Discussion

In this chapter we have derived a simple growth and allocation model and applied this model to a detailed, high resolution yearly portion of the individual Girnock Burn growth data. Our model is based on the principle of conservation. We first parameterised a functional form for maintenance which captures how energy expenditure has very consistently been shown to change with water temperature and size. Although the detail and expanse of the maintenance parameterisation data set is relatively poor, we should not expect a change in maintenance parameters to alter the dynamics of our results, since it is the functional form of this relationship which is of the greatest importance and not the values themselves.

An estimate of daily metabolic expenditure allowed us to directly estimate daily rates of energy assimilation in order to satisfy the observed patterns of growth. The strong trend in temporal assimilation rates was clear enough to be characterised by a simple functional form. Our approach to individuals was to assume that each individual's temporal assimilation followed this same global pattern but multiplied by an individually unique scalar value. The goodness of fit we obtained by adopting this approach is surprisingly good. This signifies that not only is the population growth being dominated by strong seasonal factors but so also are all the individual growth trajectories.

The pattern of net production within the Burn is distinctly out of phase with water temperature (see figure(10.11)) and this is the principal reason why the E&H functional model for maximum growth fails so miserably (see section(9.5.1)). Therefore, it is clear that the seasonal growth of parr in their natural environment cannot simply be explained by seasonal fluctuations in water temperature. Surprisingly, the results of tank based experiments conducted with Scottish juvenile Atlantic salmon, supplied with food in excess under ambient photo period and temperatures, are in agreement with this observation. For example, Higgins and Talbot (1985) followed the growth of juveniles from late September to early June in the laboratory under ambient photo period and temperature. Even under the provision of excess rations they found conflicting results in the temperature/growth association. Temperature were generally higher (2^oC to 7^oC) between 25 October and 10 December than in two subsequent intervals (10 December to 25 January, around 3.5^oC; and 25 January to 1 March, around 1^oC), yet specific growth rates were higher during the coldest period (25 January to 1 March) than in the preceding intervals. Furthermore, the average temperature during early spring (1 March 5 April) was 5^oC whereas during autumn (22 September to 25 October) the average temperature was 8^C. The specific growth rates of fish in spring were approximately twice those found in autumn. Higgins and Talbot (1985) concluded that the change in photoperiod was one of the most influential environmental factor in initiating this high growth rate (see figure(10.11)).

It is also well worth noting that as in the Higgins and Talbot (1985) experiment, other workers (Nicieza and Metcalfe (1997); Koskela et al. (1997a); Koskela et al. (1997b); Bremset (2000)) have also documented that juveniles (when properly acclimated) are more than capable of feeding and growing at very low temperatures (as low as 1^oC), which, is in contrast to a lower temperature limit for consumption and growth of approximately 6^oC reported by Elliott and Hurley (1997) and Forseth et al. (2001).

The strong seasonal patterns of growth exhibited by parr in ambient tank based experiments has been reported to be as a direct consequence of seasonal changes in appetite and therefore consumption. Simpson et al. (1996) reports on the appetite changes of Scottish juvenile Atlantic salmon parr reared under ambient photoperiod and temperature over a full annual cycle. In three consecutive yearly experiments, parr exhibited a sharp increase in appetite during early spring. Food consumption peaked in May on rising ambient temperature. However, despite the excess ration supply and the favorable summer temperatures for rapid growth, food consumption declined over the remaining summer months.

Such fine detailed estimates of parr food consumption within their natural environments are very rare. However, Allen (1940) found that the amount of food present in the stomachs of 1+ parr in the River Eden, England rose rapidly with the onset of spring and peaked in May, after which time it declined over the summer months. Similar results have been reported by Huru (1986).

Our model makes some predictions about the temporal changes in rates of assimilation, which we can mostly ascribe to changes in the rates of food consumption. As in the studies we have reported above, there is a marked increase in assimilation with the onset of spring (see figure(10.10,a)). Assimilation peaks in the middle of May and thereafter decreases over the summer period. Thus, our model inferred pattern of assimilation is in good agreement with experimental observations of seasonal patterns of consumption.

The strong seasonal pattern of appetite exhibited by parr (in tank based experiments) has lead workers to suggest that it is a pre-adaption to seasonal fluctuations in prey abundance in their natural habitat (Simpson and Thorpe 1997). In spring/summer 2000 a series of drift netting experiments were conducted to investigate if such a seasonal trend in prey abundance existed for the Girnock Burn. Drift samples were collected using 20x20cm fine mesh nets placed at five different locations. Nine censuses were conducted over a period of time stretching from early March to early July. Each census involved collecting the drift for a 24 hour period. Figure(10.12) displays the average rate of drift biomass caught in the nets over the study period. It can be seen that the drift biomass increases very sharply in spring and in this year seems to have peaked in early May. Following this, there is a dramatic decrease in drift biomass. A number of other studies of invertebrate drift also report that prey abundance is greatest in the spring period and decreases over the summer period (Hynes (1970); Müller (1978); Errikson and Alanårå (1992); Simpson and Thorpe (1997)).

In spring, many aquatic insects are growing rapidly and frequently available as drift food, whereas these same species in autumn are small larvae in the early stages of the life cycle and are rare in the drift (Elliott (1967); Elliott (1970)). Since juvenile Atlantic salmon parr principally prey on invertebrates from the drift then these seasonal changes in drift abundance further corroborates the hypothesis of a seasonal appetite rhythm in sync with the natural prey abundance. Because a high abundance of prey biomass in the drift may only be available for a short time period then a pre-adaptive appetite change in anticipation of this natural food supply would allow parr to make the best use of this valuable

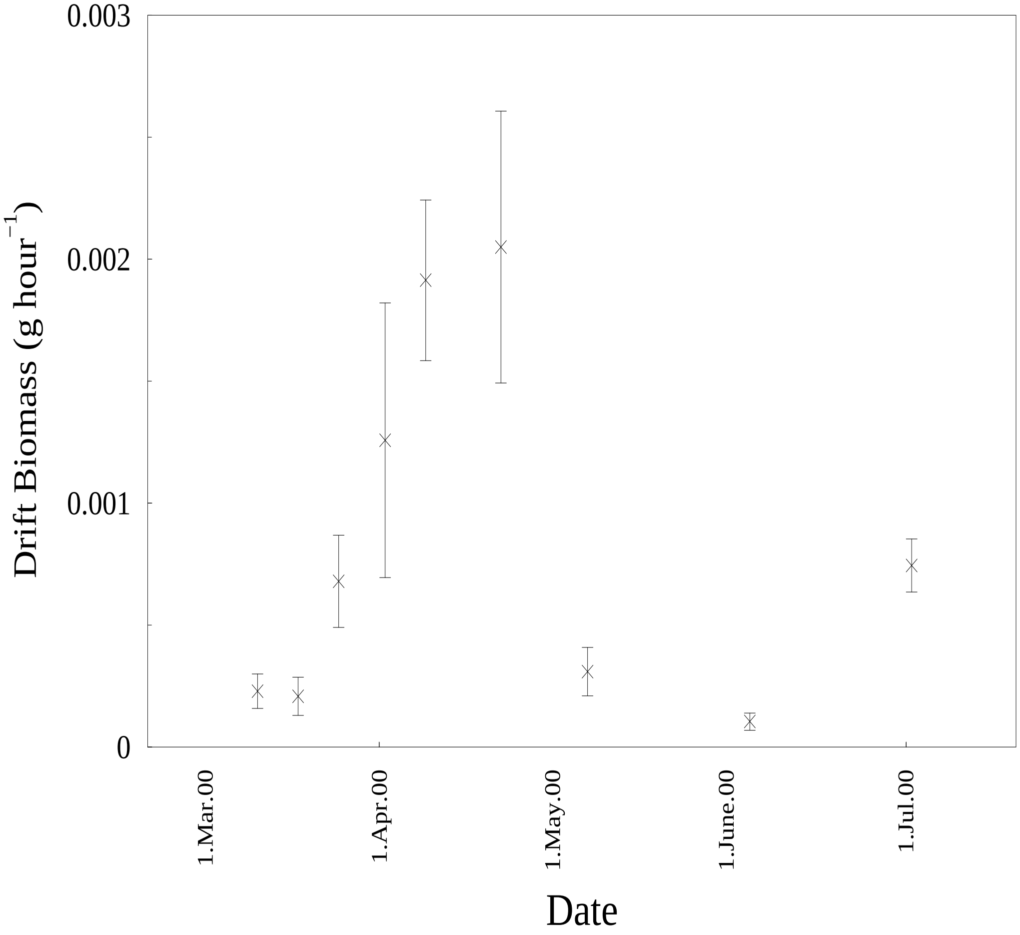

Figure 10.12: *The average catch of drift biomass caught in 20*x*20cm nets from early March to early July in the Girnock Burn. Bars denote one standard error.*

energy source.

Seasonal changes in body composition and therefore allocation have also been reported for parr in tank based environments, but there is also more information with regards to changes in allocation within their natural habitat. For example, despite the reduction in growth rate over the late summer months reported by Higgins and Talbot (1985) (see above), fat levels continued to increase, reaching a maximum in September. In contrast to the majority of experimental results we reviewed in chapter 3, in this scenario, nutritional condition cannot be considered to be correlated with growth rate. We can therefore consider this energy allocation strategy as a strong seasonal pattern. Following this, and despite the provision of excess ration, fat levels decreased gradually over the winter months.

Gardiner and Geddes (1980) report on the changes in body composition of young juvenile Atlantic salmon in their first year of life from the Shelligan Burn, a tributary of the River Almond (Tay river system) in Perthshire, Scotland. Fat levels(% body weight) increased over the late summer months and peaked in September. Over the ensuing winter months, there was a gradual decline in reserves, reaching a minimum in April. With the onset of the growing season in early April the fat reserves of surviving fish began to be replenished.

Berg and Bremset (1998) report on the seasonal changes in body composition of three age classes of juvenile Atlantic salmon from the River Humla, in middle Norway. All three age classes displayed the same seasonal trends in body composition. Fat content (% body weight) was reported to be at a minimum at the onset of the growing season in early April. Fat levels increased gradually over the spring and summer months and reached a maximum in September. Following this, fat levels declined gradually over the winter months, reaching a minimum in April, whereby, the seasonal cycle was repeated. The same seasonal cycle of body composition was observed for juvenile brown trout, *Salmo trutta*, resident in the River Humla.

Our first model, which assumed a time independent assimilation allocation scheme, produced a good fit but misrepresented the within year allocation patterns adopted by the Girnock parr in their natural habitat. In response to this we modified our model by allowing a seasonal change in the the defended reserve ratio threshold value for maintaining structural growth μ, to account for this seasonal trend in allocation. The resultant seasonal allocation model produced a better fit to the individual data by virtue of increased accuracy in predicting patterns of structural growth (i.e. length) and therefore better predicted the nutritional condition of the parr as a function of the time of year. The best fit defended reserve ratio function predicts a reduction in the defended reserve ratio over the winter months, reaching a minimum in early spring and increasing to a maximum in late summer (see figure(10.17)). Thus, our defended reserve ratio function tracks the same patterns of allocation as those reported for other populations of juvenile Atlantic salmon in their natural habitat.

Our defended reserve ratio threshold is conceptually akin to the principle of a defended energy level proposed by Mrosovosky and Sherry (1980) and reported for overwintering juvenile Atlantic salmon parr by Metcalfe and Thorpe (1992). In tank based experiments, juveniles have been shown to express a decrease in appetite with the onset of late autumn/early winter and exhibit a gradual decrease in lipid reserves over the winter months (Gardiner and Geddes (1980); Higgins and Talbot (1985); Metcalfe et al. (1986); Metcalfe et al. (1988); Cunjak (1988)). To investigate this phenomena in more detail, Metcalfe and Thorpe (1992) deprived experimental fish of food for three weeks in November, thus accelerating the depletion in energy reserves. Experimental fish responded by increasing appetite. Appetite was negatively correlated with the estimated energy reserves but the hyperphagic reaction was reported to be controlled by length of increased appetite as opposed to intensity (Bull and Metcalfe 1996). Fish previously deprived of food regained their appetite and made up the lost fat reserves in 4 weeks of resuming refeeding. Metcalfe and Thorpe (1992) concluded that the degree and duration of suppressed appetite is regulated by energy reserves, the salmon effectively having a “defended energy level” below which appetite is increased until lost energy reserves have been restored. The fact that appetite and fat reserves declined in control fish over the winter period lead Metcalfe and Thorpe (1992) to state that the defended energy level was also decreasing over the winter months. This has also been found to be the case in other examples of natural anorexias (Mrosovosky and Sherry 1980).

Further experiments conducted by Bull et al. (1996) have revealed that the appetite responses to winter periods of food deprivation were dependent upon the time of winter in which they were imposed. Fish that were deprived of food in early winter foraged harder to restore lipid levels despite having greater reserves at the time. Fish that were deprived near the end of the winter period did not forage as hard to restore lipid levels even though lipid levels were very low. To investigate this initially counter intuitive experimental result, Bull et al. (1996) derived a strategic model which took into consideration the expected mortality threats from starvation and predation. From this model they could predict the optimal foraging effort which maximises expected overwinter survival. Their model predicted that foraging effort should increase as lipid levels decline but should also decrease as the end of the winter approaches. Bull et al. (1996) concluded that the fish were following seasonal trajectories towards a low target level of lipid early in spring.

The above investigations of overwintering behaviour of salmon parr have mostly been centered around changes in appetite observed in tank based experiments. Our seasonal allocation model illustrates the concomitant changes in allocation strategy. We can further extend the hypothesis of an overwintering "defended energy level" and state that the observed winter changes in lipid depletion are part of a regulated seasonal cycle of energy allocation and usage. With the onset of spring, juvenile parr do not exhibit a quick recovery of reserves to a maximum level and then maintain this high level until late autumn. In contrast, there is a regulated gradual increase in lipid reserves over the growing season. At the very beginning of the growing season allocation to structural tissues is of prime concern. The accumulation of reserves becomes more important as the winter period nears. Levels of reserves peak in autumn and these reserves are drawn upon in a regulated manner over the food scarce winter months. The complete annual cycle of energy allocation and usage leads to a continuous but gradual change in reserve levels throughout the annual cycle. We shall discuss the major ecological benefits that juveniles take advantage of by adopting this strategy in more detail within the next chapter.

For obvious practical reasons, the majority of investigations into the seasonal rhythms of growth, appetite, food consumption and allocation have mostly been conducted under laboratory conditions. Even under these conditions juvenile Atlantic salmon exhibit very strong seasonal trends in growth, allocation and behaviour. However, it has been very much assumed that the observed growth and behavioural strategies are identical to that undertaken by wild parr. With access to fine detailed, high resolution growth data of individually tagged parr, we have, with the help of a simple model, been able to asses whether the same patterns of energy consumption, allocation and expenditure are exhibited by parr in their natural habitat. Our results are in very good agreement with the results of tank based experiments conducted under ambient photoperiods and water temperatures. This further corroborates the conclusions of a great many workers that the major natural stimuli for regulating appetite, allocation and behaviour is the natural changes in photoperiod and water temperature (e.g. Higgins and Talbot (1985); Metcalfe and Thorpe (1992); Heggenes et al. (1993); Bull et al. (1996); Simpson et al. (1996); Skilbrei et al. (1997); Bremset (2000)).

The absence of these naturally changing stimuli may therefore give misleading experimental results. This may be one possible reason why the experimental results of Elliott and Hurley (1997) and Forseth et al. (2001) conducted under constant temperature and photoperiod regimes predict that parr have a minimum temperature threshold for maintaining growth of approximately 6^oC. The models which have been calibrated from these experiments predict that the fastest growth will be achieved when water temperatures are relatively high, which occurs in late summer. However, the natural food abundance is low in this period of the year. This actually means that warm summer temperatures are more a disadvantage than an advantage to wild fish. Since metabolic expenditure increases exponentially with temperature then fish may be required to maintain a high foraging effort, increasing the threat of predation, solely to meet the cost of living and maintain a high level of reserves for the winter period. The exponential increase in maintenance rates with temperature means that a relatively small increase in summer temperature could therefore have a very serious detrimental impact on wild stocks of fish. With the occurrence of global warming this scenario could well become a reality, which may be especially detrimental to the salmonid family of fish, who often fight for survival in seasonally harsh, energy limiting environments.

Part V

Discussion & Overview

Chapter 11

The Ecological Implications of Resource Allocation

Life-history strategies are means by which animals solve the problem of successful reproduction in a wide range of different and often variable environments (Thorpe 1994). One classic problem in life-history theory is to determine the strategies for allocating energy between growth, storage and reproduction that will be favoured by natural selection (Lika and Nisbet 2000). For pre-reproductive organisms this problem reduces down to strategies for allocating to growth and storage which simultaneously optimise survival and growth. High mortality rates during the early stages of salmonid fish ensure the likelihood of survival to adulthood is extremely low (Sogard 1997). Consequently, selection pressures are very high.

Within this thesis we have reviewed a broad body of literature which report on the energy allocation strategies of different species of juvenile salmonids in a range of different environmental conditions. Rather than identifying major inconsistencies between species we have, in general, identified more consistent patterns of resource allocation. In this chapter we take the opportunity to discuss why juveniles adopt these (often initially perplexing) strategies of resource allocation.

11.1 Size Selective Mortality

One of the major observations that were noted from part II (chapter 3) of this thesis was the degree of importance salmonids place on maintaining structural growth. When faced with a growth restriction not only will salmonids reduce the rate of lipid accumulation but will even burn current lipid reserves to maintain a degree of structural growth (Miglavs and Jobling (1989a,b); see table(3.5)). Our modelling analysis showed that slow growing smaller individuals most certainly increase the risk of starvation by partaking of this strategy (see section(4.7)).

Most of the experiments we reviewed in chapter 3 were conducted under laboratory conditions with constant photoperiods and constant temperatures. Therefore, it could be argued that in their natural environments fish may allocate their resources differently. However, such patterns of allocation, namely, slower growing smaller individuals maintaining lower levels of reserves than faster growing conspecifics have also been noted in their natural habitats (Post and Parkinson 2001). With the increased risk of death from starvation incurred by this strategy, one must ask why have such allocation patterns evolved? and what is this constant pressure to grow? There are, however, a whole number of different reasons why such allocation patterns may exist for salmonids, which mostly (we argue) occur as an ecological implication of body size.

Lipids are a highly concentrated energy source which do not contribute to any increase in fish length. This means that high levels of lipid may increase the weight for a given length but do not increase fish size in proportion to the energy investment. For instance, consider again the results of Miglavs and Jobling (1989a,b) (see table(3.5)). Even though the wet weight of feed restricted fish had increased there was no change in the total energy content. Therefore, it is clear that the accretion of leaner body masses results in an increased fish wet weight combined with length per unit of stored energy. That is, allocating to structure increases fish size in much greater proportions than allocating to reserves.

Stream dwelling salmonids are territorial creatures (Puckett and Dill (1985); Elliott (1990); Grant and Kramer (1990); Titus (1990); Youngson and Hay (1996)). Each individual seeks to locate a desirable territory that will provide adequate shelter from predators and supply enough food to grow. Failure to secure such a site will end in death either from starvation or predation (Youngson and Hay 1996). Competition for suitable sites is fierce and once individuals have secured a territory they will vehemently defend it against potential competitors. Territory size increases allometrically with fish length, and the profitability of a territory to its resident is related to its size (Elliott (1990); Grant and Kramer (1990); Keeley and Grant (1994)).

Physical dimensions are important in the competitive interactions of young salmonids (Allen 1969), where, larger bodied individuals have a competitive advantage over smaller conspecifics. As individuals grow they need a larger territory size. Consequently, there is continuous and strong competition for territory space. Therefore, slower growing, smaller less competitive individuals may be forced to allocate more to structural growth to increase body size in an effort to sustain site attachment and/or increase territory size.

Competitive interactions for space and therefore food become particularly strong when the natural food supply is low. Periods of resource scarcity reinforce feeding hierarchies. There is a large body of literature reporting that larger individuals are able to dominate the already scarce food supply leading to a disproportionate distribution of nutritional resources (Davis and Olla (1987); McCarthy et al. (1992); Thorpe and Huntingford (1992); Grant (1993); Jobling (1995); Jobling and Koskela (1996)). Individuals who adopt a more careful strategy to the threat of starvation by continuing a relatively high proportional rate of allocation to reserves during periods of food scarcity will do so at the cost of maintaining structural growth. Conspecifics allocating more to structural growth would gain a competitive edge over these more careful individuals, allowing them to dominate the food supply, further reducing the food consumption of reserve careful individuals.

Another factor that will exaggerate competitive interactions is the effect of population density. The general observation in stream systems is that growth is not density dependent but that density dependent emigration or mortality is common (see reviews in Newman (1993) and Keeley and Grant (1994) but see also Jenkins et al. (1999)). This means that rather than fish reducing territory size they each seek an area which will suit there own individual needs (Youngson and Hay 1996). These processes are equivalent to the principle of "self thinning" as developed in the botanic literature (Norberg (1988); Elliott (1993); Bohlin et al. (1994)). In contrast to streams, lake-dwelling salmonids cannot emigrate when subjected to size-dependent aggressive interactions and therefore may be subjected to stronger density-dependent growth and size dependent mortality (Post et al. 1999). Nevertheless, in both situations, larger individuals posses an advantage over smaller conspecifics.

Predation is one of the major mortality agents within juvenile salmonids. Predation is often size-biased which can usually be attributed to gape limitation, behavioural selection by the predator, or variation in escape ability with prey size (Sogard 1997). Under size-spectrum theory (Sheldon et al. (1997); Platt and Denman (1978)) the abundance of predators progressively decreases as predator size increases. Thus, smaller prey will continually have a larger suite of potential predators compared to larger prey. In such situations, allocation to more structural masses will increase size (and growth rate) and therefore decrease the range of potential predators earlier than a more reserve careful strategy.

It must also not be forgotten that salmonids are themselves predators whose selection of prey is also restricted by their own gape limitation and retentive capabilities. Salmonids feed by sucking water and then squeezing the water out through the gills. Food particles too small will be expelled with the water. The gill rakers, which sift the food items, scale with fish length. Upper limits imposed by the internal breadth of the mouth on prey size consumption also scale linearly with length. Wankowski (1979) estimated the morphological upper and lower limitations to range from 0.0083 to 0.068 body lengths for juvenile

Atlantic salmon parr ranging from 4 to 20cm in length. This means that as fish length increases the range of potential prey items also increases. Although tank based experiments have shown that salmonids exhibit prey size selectivity (Wankowski and Thorpe 1979), observations of salmonid behaviour in the wild do not always agree (Stradmeyer and Thorpe 1987). Dill (1983) suggests that many fish broaden their diet as an adaptive response, including less acceptable prey as the availability of preferred types declines, if this increases their net energy gain. Consequently, preferential allocation to structure, increasing fish length leads to an increase in the number of potential prey items, which may be highly beneficial in periods of low food availability.

All the above factors contribute to size selective mortality effects, where, larger bodied individuals have an advantage over smaller conspecifics. Sogard (1997) has recently reviewed the effects and mechanisms of size selective mortality in the juvenile stage of teleost fish. She points out that the occurrence of size selective mortality requires three conditions: 1) size variation in the population, 2) non-random mortality, and 3) relatively high mortality rates. These three factors are all highly prevalent in the population dynamics of juvenile salmonids. There is a large body of literature reporting the inverse relationship between size and growth rate with survival in wild fish (see Sogard (1997) and references therein). Studies report that even relatively small size differences can cause large differences in selective mortality rates (e.g. Healey (1982)).

Therefore, in the face of low potential growth rates, the benefits of maintaining structural growth and getting larger can often override the increased risk of starvation. The importance of physical dimensions to juveniles has even lead a number of authors to suggest that the uptake in water exhibited by salmonids utilising their lipid stores is an attempt to maintain an appreciable size (Gardiner and Geddes (1980); Post and Parkinson (2001)).

As an illustrative example of the ecological trade-offs juveniles face between allocating to growth or storage within their natural environment we shall consider the study conducted by Post and Parkinson (2001). They observed substantial variation in seasonal growth rates, autumn body size, and growing season survival among eight experimental cohorts of young rainbow trout (*Oncorhynchus mykiss*). Growing season survival was negatively correlated with growing season growth rate. Lipid concentration varied with growth rate such that faster growing cohorts had higher lipid concentrations. By using independent assessments of the allometry of growing season survival and winter metabolism they assessed the benefits of different energy allocation strategies. For cohorts with low growth rates they estimated a somatic growth rate maximisation strategy to produce a 5% survival advantage over an energy storage maximisation strategy. For fast growing cohorts the benefits of adopting an energy storage maximisation strategy was estimated to give a net survival advantage of 7%.

It was important to point out the above example in order to illustrate that the high degree of importance placed on maintaining structural growth (when faced with low potential growth rates) over allocation to storage is not simply a phenomena of tank based experiments. Size selective (and therefore growth rate selective) mortality has very important implications for salmonids in their natural habitat. Individuals who grow fast reduce the time they are susceptible to a large number of predators, have a wider range of possible prey and dominate over smaller subordinate conspecifics. Although such larger individuals have higher metabolic costs, on a unit weight basis these costs are lower than for smaller conspecifics.

11.2 Trade-offs in Rapid Growth

In the natural environment, individuals of many species are subjected to periods of high food availability inter-dispersed with periods of near or actual famine. Salmonids being aquatic ectotherms need pay no heating costs to maintain a constant body temperature. Coupled with the ability to store high levels of reserves, salmonids can survive for long periods of time with no externally derived nutritional sustenance. When the food supply is re-introduced, not only can salmonids fully recover from extremely harsh periods of nutritional restriction but also show higher rates of growth than continually excess fed conspecifics. This phenomena of growth restricted fish being able to make up growth losses is referred to as "catch-up", "recovery" or "compensatory" growth.

Our modelling investigations showed us that compensatory growth is a genuine compensation in structural growth (although full recovery is rare) as well as a recovery of nutritional status (chapters 6 and 8). Thus, the compensatory response would allow fish to buffer the effects of variation in food availability on growth and levels of reserves (Wootton 1990). However, the existence of compensatory growth illustrates that rates of growth (even in fish fed to excess) are often sub-maximal. Why do individuals adopt this apparently sub-optimal strategy?

In the previous section we explained a whole number of reasons why high rates of growth should benefit juvenile survival and therefore fitness. If bigger is generally better, we should expect a continual directional selection toward large body size and fast growth rates. Obviously there must be constraints or trade-offs that place boundaries on such selection (Sogard 1997). We dedicate this section to discussing what the most likely physiological and behavioural restraints cause trade-offs in rapid growth.

Conover and Schultz (1997) provide a compelling argument suggesting that physiological constraints prevent southern populations of Atlantic silverside (*Menidia menidia*) from attaining maximum growth potential, despite demonstrated advantages of large size for avoiding predation and surviving over the winter. Because of the shorter growing season, northern populations grow faster than their southern counterparts allowing them to reach the same size at the onset of winter (Conover and Present 1990). Why, if large body size is beneficial do southern individuals not attain the growth rates as that of their northern population?

Conover and Schultz (1997) have demonstrated through laboratory studies of performance that there is a cost to rapid growth: fish that grow rapidly, and consume large meals to do so, have lower size-specific swimming ability (both burst and sustained swimming) and they are more susceptible to predators. Hence, rapid growth trades-off with defensive capabilities. Southern populations, with their extended growing season, can readily attain sufficient winter size with a moderate growth rate and maintain an energy reservoir for other activities.

It has been known for some time that endocrine manipulation can induce faster than normal growth in fish (reviewed in Tytler and Calow (1985)). For example, growth hormone injections have been shown to increase growth rate, appetite and competitive ability under laboratory conditions (Johnsson and Björnsson 1994). To investigate why endogenous secretion of growth hormone is not higher in wild fish, Johnsson et al. (1999) studied the performance of growth hormone treated juvenile brown trout (*Salmo trutta*) and control (placebo) trout in an enclosed stream section subjected to natural predation. Four experiments were conducted during all four seasons of the year.

Growth hormone treated fish did not have significantly different mortality rates than control fish. However, there was an overall tendency for higher mortality in growth hormone treated trout (33.5%) than in control trout (28.7%). The major differences in experimental groups were in the levels in energy reserves present with the faster growing growth hormone treated trout possessing lower levels of storage energy. Their results support the hypothesis the growth hormone promotes growth (particularly in length) at the expense of energy storage (Sibly and Calow 1986). Johnsson et al. (1999) further suggest that growth hormone promotes growth at the expense of investment in maintenance.

Fast rates of growth have also been related to high rates of resting metabolism (Priede (1985); Metcalfe et al. (1995); Yamamoto et al. (1998); Cook et al. (2000); O'Connor et al. (2000)). Priede (1985) reviews and highlights the trade-offs in metabolic scope (maximum metabolic power-min metabolic power) in fish. It would seem that a high value of metabolic power necessary to process large amounts of food whilst still being able to remain active (to avoid predators and fend off or dominate competitors) comes at a price of high rates of resting metabolism. Such individuals may well be more prone to starvation when enduring nutritional scarcity. On the other hand, low rates of resting metabolism may come at a price of a low maximum metabolic power output.

In reviewing the literature it becomes clear that there are essentially two physiological strategies that can be employed to increase growth rates, both of which have there prices. A decrease in maintenance expenditure will increase growth efficiency but will incur the costs to tissue repair and therefore most probably increase the threat of disease infection.The ability to increase consumption rates may require a greater metabolic scope which means higher rates of resting metabolic rates, therefore, increasing the susceptibility of individuals to starvation (Cook et al. 2000). In addition, the metabolic requirement to process high rates of food intake may encompass much of the available metabolic scope reducing the energy available to other metabolic processes such as locomotor activity which is essential to escape from predators and/or compete with conspecifics.

Aside from purely physiological effects there are also behavioural considerations. Houston and McNamara (1992) showed that the avoidance of risk is frequently of paramount consideration in foraging strategy. It seem plausible that animals whose behaviour is determined by physiological signals will have hunger responses designed to produce foraging behaviour which minimises long term risk rather than short or medium term realised growth rates. There are numerous reports of fish preferentially residing in less rewarding habitats in the presence of predators (see Sogard (1997) and references therein). For example, L'Abée-Lund et al. (1993) report that juvenile Arctic charr (*Salvelinus alpinus*) forage preferentially in the more rewarding pelagic zone, but remain restricted to the benthic zone where growth rates are lower when they share a lake with (predatory) brown trout (*Salmo trutta*).

Clearly, there are trade-offs in realised rates of growth both on an evolutionary and an ecological scale. When food is in relative abundance and despite the advantages of growing fast, individuals may adopt this apparently sub-maximal growth strategy in an effort to maximise the benefits of maintaining a balanced physiological functioning and decreasing potential predator contacts. However, when such a balance is upset then the benefits in growing fast and recovering lost reserves may override the associated costs leading to what we refer to as "compensatory growth".

Very rarely do workers report on the long term well-being of groups of fish subjected to growth manipulation experiments. However, very recent studies suggest that there may be substantial physiological costs in accelerated rates of recovery growth. Morgan and Metcalfe (2001) report that following an autumnal period of food shortage juvenile Atlantic salmon rapidly regained lost reserve status by becoming hyperphagic. However, several months later they entered a prolonged phase of poorer growth performance (despite excess food provision), so that by the following spring they were substantially lower than controls and had lower lipid reserves for their body size. In a follow up paper, entitled "Compensation for a bad start: grow now, pay later?", Metcalfe and Monaghan (2001) review and discuss the physiological costs (ranging from short to long term) which are often displayed by a wide range of taxa who have undergone compensatory growth.

The observations that have recently come to light concerning associated physiological costs leads us to question the potential utility of compensatory growth to the aquaculture industry. Given that the general mechanism for increased growth rates seems to be an increase in food consumption and not increased growth efficiency, coupled with the fact that incidences of over-compensation are extremely rare leads us to draw the conclusion that there is no practical (and certainly no consistent) benefit of feed cycling to the aquaculture industry. Indeed, feed cycling would probably be more likely to lead to a decrease in production with no added benefit of cost savings.

11.3 Coping with a Seasonal Environment

One of the most impressive characteristics of the salmonid family of fish is their ability to adapt to a large range of different environmental conditions – the most immediately obvious and most celebrated, being their ability to traverse between marine and freshwater environments. However, for obvious practical reasons, very little is known about the life history strategies adopted by anadromous salmonids within their ocean going phase. Arguably, however, it is in the freshwater phase of life where juveniles may have to cope with a larger array of different environmental extremes, which not only change with the seasons but also vary on an annual and daily basis. To survive, grow and flourish in such variable and precarious environments necessitates a specialised life history strategy that is not only adapted to the geographical location but also to the local environment.

Our study of the seasonal growth and allocation strategy of juvenile Atlantic salmon parr from the Girnock burn is a very good illustration of how salmonids make the best of seasonally harsh, energy limiting environments (Part IV). Experimental observations illustrate that juvenile salmonids have seasonal rhythms of appetite which are in anticipation of the natural food supply (Metcalfe et al. (1986); Metcalfe and Thorpe (1992); Errikson and Alanårå (1992); Bull et al. (1996); Simpson et al. (1996); Simpson and Thorpe (1997)). Our modelling analysis (chapter 10) highlights the less noted concomitant seasonal changes in energy allocation strategy.

At the onset of spring, reserve levels of juveniles in the Burn are at their lowest levels of the year. However, when the food supply becomes more abundant, juveniles are principally allocating their resources to building structure. This would make sense because there is simply no need for high levels of reserves when individuals are pretty much guaranteed a meal, if not today, tomorrow. Zonneveld and Kooijman (1989) point out a similar prudent seasonal energy allocation strategy in pond snails (*Lymnaea stagnalis*), concerning energy allocation to reproduction (Bohlen and Joose 1982). In simulated summer conditions (long photoperiod) starved snails continue allocation to (energetically expensive) reproduction in the (misguided) anticipation of an abundant food supply. Under simulated autumn conditions (shorter photoperiod) starved snails cease allocation to reproduction in an effort to increase survival time when the food supply is of lower abundance.

There is evidence to suggest that high levels of reserves may increase predation among juveniles in their natural environment. Johnsson et al. (1999) (see previous section) found that hatchery-raised trout with higher initial condition factor values suffered higher rates of mortality than more slender fish. Several studies suggest that birds reduce their fat reserves when predation risk increases, as high levels may inhibit escape ability (e.g. Gosler et al. (1995)). Johnsson et al. (1999) tentatively point out that fish nutritional condition could also be a factor in governing the escape ability of salmonids and also predator preferences. Since risk-taking behaviour may well be increased during the spring period (as a result of an increased appetite) then it would be important that fish maintain the best morphological condition necessary to avoid predation. In other words, leaner more slender fish may well have a reduced risk of predation.

If there is one property that all three of our different allocation schemes have in common is that individuals who allocate more to structure in an environment with a plentiful supply of food grow appreciably faster than conspecifics allocating less to structure. The reason, of course, being that the increased investment in structure allows individuals to consume more of the plentiful food supply. This may be an especially prudent strategy for the Girnock parr, since high food abundance may only be available for a very short period of time. In such a scenario, an increased investment to structural tissues in anticipation of the natural food supply would allow individuals to capitalise on this valuable energy source.

It is also important to note that during spring, older, larger parr are leaving the Burn and beginning their seaward migration. Therefore, prime territory sites (previously dominated by larger fish) will become available to the parr that will remain in the burn for at least another year. Consequently, we should expect a high degree of jostling and antagonistic behaviour through competition for these vacated territories. As noted in the previous section, an increased commitment to structure will increase size and therefore increase individual competitive performance.

There is a substantial body of literature reporting that larger bodied fish, and those with enhanced energy stores are more able to survive intense periods of resource scarcity (see review in Shuter and Post (1990)). As spring turns into summer the natural food supply becomes less abundant and already individuals from the Burn are beginning to accumulate reserve provisions for the ensuing winter period. The seasonal change in energy allocation seems to be a gradual change over the summer period, probably as an insurance against unpredictable inter-annual environmental fluctuations, which may leave less careful individuals leaving reserve accumulation until very late in the growing season facing the winter with low lipid stores. Reserve levels among stream dwelling salmonids usually peaks in late summer (Gardiner and Geddes (1980); Higgins and Talbot (1985); Berg and Bremset (1998)) and for the Girnock individuals there seems to be no exception (see figure(10.8)).

As winter approaches, studies have illustrated that juveniles appear to undergo a decrease in appetite which coincides with a shift in habitat preference (Metcalfe et al. (1986); Metcalfe et al. (1988)). Juveniles leave the relatively shallow fast flowing riffles preferring to spend long periods beneath the substrate (Rimmer et al. (1983); Cunjak (1988); Valdimarsson and Metcalfe (1998)). Feeding may continue over the winter but juveniles have been reported to change from a diel to a less profitable nocturnal feeding pattern. This may be in response to a lower burst swimming capacity at lower temperatures (Webb 1978) increasing the threat of predation in daylight hours (e.g. see Heggenes et al. (1993)). During the winter period, the low rates of food consumption are not sufficient to meet metabolic expenditure. Therefore, no significant resource is directed to structure and lipid reserves are drawn upon in a gradual and regulated manner over the winter period, in an effort to simultaneously minimise the risk of starvation and predation (Metcalfe and Thorpe (1992); Bull et al. (1996)).

The seasonal pattern of energy allocation exhibited by Girnock parr has evolved in such a way to make the very best of a seasonally harsh, energy limiting environment. This seasonal cycle of energy allocation leads to a continuous but gradual change in reserve levels throughout the year. Such seasonal patterns of energy allocation are widespread amongst other species of fish, as well as the salmonids, whom also face the same mortality threats (e.g. Griffiths and Kirkwood (1995); Hurst et al. (2000)).

Chapter 12

Modelling Overview

12.1 Thesis Modelling Objectives

Whether an individual chooses to allocate its (often limited) resources to growth or storage has some enormous implications for its survival and therefore fitness. Nevertheless, most fish growth modellers have adopted sub-classes of models which are simply not capable of expressing this choice in energy investment (see section(2.2)). On the other hand, workers whom are interested in energy allocation have mostly concentrated their efforts on the problems associated with allocation to reproduction (Kooijman (1993); Noonburg et al. (1998); Lika and Nisbet (2000)). As a consequence of this, the (potentially less complicated) resource allocation modelling of juveniles has received very little attention, even bordering on neglect. Most surprisingly, there is a distinct lack of a standardised dynamic modelling framework which can be used to investigate the patterns of energy allocation adopted by the life-history diverse and enormously researched juvenile salmonids. The main aim of this thesis has been to address and make progress in this relatively unexplored modelling research area.

12.2 The Modelling Framework

To investigate the resource partitioning strategies of juveniles we decided upon using the modelling framework initiated by Broekhuizen et al. (1994). The state of an organism is described by two state variables; structural carbon weight S, mainly in the form of proteins and inorganic minerals, and reserve carbon weight R, mainly in the form of lipids and carbohydrates (see section(2.3)). By definition structural carbon weight S is non-decreasing (i.e. commitment to structure is irrecoverable) and is therefore a useful surrogate for length, which also does not decrease with either short or prolonged periods of food deprivation. As a useful measure of nutritional status we used the ratio of reserve to structural carbon weight given by $X \equiv R/S$. In this modelling framework an organism dies when it cannot meet the cost of living, which corresponds to X falling to zero.

Having presented the modelling framework we then went on to derive functional forms which related the model state variables and the environmental conditions of the juvenile to the rate at which carbon is lost from the body (maintenance), together with the rate at which carbon can possibly be (under normal healthy conditions) assimilated into the body (see section(2.4)). By far the most influential environmental factor which affects the processes of maintenance and maximum uptake is water temperature. Ignoring thermal extremes, which eventually reduces uptake capacity, we modelled the processes of maintenance and maximum uptake as both being exponentially dependent upon temperature.

Both maintenance and maximum uptake exhibit a negative allometric relationship with size. However, whereas all tissues require maintenance not all tissues are involved in the processes of gathering and processing of food. Therefore, maintenance was described as being a function of total carbon weight, but in recognition that structure includes such body constituents as the gut and mouth parts, uptake capability was modelled as being solely a function of structural carbon weight. Thus we derived a functional form for maintenance M, standing for the collection of processes necessary to remain alive but independent of the processes of growth. To obtain the realised assimilation rate A we multiplied the fish's uptake of carbon U by an assimilation efficiency constant ε, which represented losses incurred by incomplete absorption and specific dynamic action.

At this stage we were in possession of an intuitive modelling framework, together with equations for describing the physiological processes of assimilation and maintenance. The next stage was to present three different modes of resource allocation which could all be applied to the same modelling framework, rendering all subsequent analysis to be mathematically consistent (see section(2.5)). The one overriding constraint placed on all these allocation schemes was that, wherever possible (i.e. $X > 0$), maintenance costs must be met. This meant that the total change in carbon weight of the organism was equal to the difference in current assimilation and maintenance rates. The net production, reserve and assimilation allocation schemes differ in their assumptions concerning the way juveniles allocate their resources to the processes of maintenance, growth (structure) and storage (reserves). We shall now, in turn, discuss the success of each of these three different allocation schemes to model the resource allocation dynamics of juvenile salmonids subjected to a range of different environmental conditions.

12.3 Net Production Allocation

The principle assumption of the net production allocation scheme we presented in section(2.5.1) is that maintenance always has first and complete call on assimilate. By assuming that a constant proportion of net production is allocated to structure we arrive at a scheme which predicts that individuals who can sustain growth head towards a constant steady state reserve ratio that is independent of both ration and temperature (see section(4.4)). This means that a reduced opportunity for positive growth is met with a reduction in structural growth rate but no reduction in reserve status. When the organism cannot maintain a positive energy balance then commitment to structure ceases, immediately and independently of reserve status.

From the above, it is clear that the net production scheme is a a careful growth strategy in which structural accumulation is only maintained when the conditions for growth are good. Such an allocation scheme may well be applicable to other species of animals who consistently adopt a more careful strategy to periods of nutritional restriction than that of the often reserve risking juvenile salmonid.

One of the major implications of choosing this scheme is that an organism maintaining a stationary or even negative energy balance cannot accrete any new structural tissues, which is in contrast to literature reports. The assumption that maintenance always has first call on assimilate is almost considered to be sacrosanct amongst many growth modellers, although, the exact reasons why are rarely discussed. There is no refuting that, wherever possible, maintenance costs must be met. This means that the change in the total energy content within an organism predicted by any model must reflect this – as all our different allocation schemes do. Most growth models that have been applied to fish use a single state variable such as weight or energy. Since these models are based on the principles of conservation, all single state variable models must, by definition, be net production models. There is no intrinsic reason why the collection of metabolic processes known under the guise of maintenance must have first and complete call on the immediate assimilate when an organism's body constituents are modelled using more than one state variable.

12.4 Reserve Allocation

The reserve allocation model, first presented in section(2.5.2), was derived to test the hypothesis that salmonids principally control the rate and degree of commitment to irrecoverable structural tissues through a monitoring of nutritional status. Individuals in a poorer nutritional state would consider committing less to structure than individuals in a better nutritional status. In principal, this hypothesis could have automatically explained why experimental observations of growth rate and nutritional condition are correlated with one another (chapter 3).

Using the reserve allocation scheme we derived a candidate model in which the steady state reserve ratio was a function of net production (see section(4.5)). This model was capable of exhibiting the qualitative features of how growth rate and nutritional condition are correlated with one another, as elicited by a constant growth regime. However, it was the response to changes in the environment that this model gave poor predictions, particularly with regards to starvation.

When salmonids are starved of food, structural growth is for all intents and purposes, immediately cessated, even in initially reserve rich individuals. The reserve allocation scheme predicts a continued deposition of structural tissues at the onset of the starvation period (see section(4.7)). Indeed, at the very beginning of the starvation period the instantaneous structural growth rate is exactly equal to that elicited by the previous growth regime. This continued growth in starving fish essentially negates any nutritional advantage possessed at the onset of starvation period. This results in initially reserve rich only increasing their survival time by a very small amount compared to initially reserve poorer individuals of similar size (see figure(4.39)).

The fact that salmonids do not exhibit any significant structural growth during starvation hints at only a weak ability for the propensity of reserve tissues to be directly converted into structural body constituents. The effects of different diet formulations on growth and nutrient partitioning gives further credence this hypothesis. If structural growth was solely a function of reserve status then why do diet manipulation experiments consistently show conspecifics (fed feeds differing in lipid concentrations) to maintain identical structural growth rates yet posses significantly different reserve levels (see for example figures(3.5) and (3.6)). In such a situation, the reserve allocation model would predict the individual with the highest reserve status to be growing more rapidly.

The reserve allocation model assumes that all assimilable carbon can be converted into structural body constituents, which basically assumes that lipids can be freely converted into protein. The reserve allocation model is therefore based purely on energetic assumptions and does not consider in any shape or form the physiological constraints imposed by the possible routes of nutrient allocation in fish. For this reason, the reserve allocation model cannot hope to explain the effects of different diet formulations on growth and allocation.

We argued in our review in chapter 6 that compensatory growth was principally motivated by an increased uptake of food as opposed to an increase in growth efficiency. In chapter 7 we incorporated a compensatory growth response by stating that individuals became hyperphagic when reserve status fell below the steady state reserve ratio value maintained when food was in relative abundance (see section(7.4)). Individuals would remain hyperphagic until they had recovered their previous nutritional condition.

With the reserve allocation scheme, the rate and degree of commitment to structure is governed by reserve status. This means that an increase in uptake, triggered by a poor nutritional condition, first results in a recovery of nutritional condition and only then does commitment to structural body masses begin to increase (see section(7.4.2)). This quickly ablates the hyperphagic response resulting in no genuine structural compensation, in contrast to literature reports. Attempts to fit the reserve allocation model (incorporating a hyperphagic response) to the compensatory growth tank-based data, proved unsuccessful (unpublished data). The model consistently and grossly over predicted length gains in starving fish. Furthermore, the model consistently under predicted recovery growth responses, both in weight and length, principally because recovery of nutritional condition was extremely quick.

The reserve allocation scheme is a very poor reflection of the growth and allocation dynamics of juvenile salmonids, particularly with regards to abrupt changes in environmental conditions. It is clear that salmonids have a structural growth dynamic which is very much more related to the immediate food supply and not to stored internal reserves.

12.5 Assimilation Allocation

The net production model proved unsatisfactory because it is a restrictive and careful growth allocation scheme which does not comply with the often reserve risking growth strategy adopted by juvenile salmonids. The reserve allocation scheme was unsatisfactory because of its predictions to changes in the environment which we mostly attribute to its poor nutritional principles. Faced with the inadequacies of these tried and tested allocation schemes, and also the lack of any other (pre-reproductive) allocation models that could be applied to our modelling framework, we were forced to derive a new allocation model. The final result is a simple and novel allocation scheme which has some highly desirable properties.

The assimilation allocation model was derived purely on the simple principle that some nutrients can act as both an energy source and a nutrient source (proteins) whilst others (lipids and carbohydrates) can only mainly act as energy sources. This hypothesis immediately places strong constraints on the possible routes of allocation. It implies that there exists strong and non-reversible nutritional pathways.

Up until now, we have asked the reader to believe the above hypothesis. The strongest pieces of evidence for this hypothesis was gleaned from the effects of different diet formulations on growth and allocation. Furthermore, by turning this hypothesis into a working assumption in chapter 5 our resulting model predictions were in good qualitative agreement with experimental results. We shall now offer biochemical evidence to further support this hypothesis of strong nutritional constraints on the possible routes of resource allocation in fish.

The major structural body constituent of fish are proteins and various minerals necessary to build the skelature (Morgan et al. (2000); Post and Parkinson (2001)). Proteins are large organic molecules that contain carbon, hydrogen, oxygen, nitrogen and sulphur. The elementary composition of most proteins is very similar, approximate percentages being C = 50-55%, H = 6-8%, N = 15-18%, S = 0-4% (Jobling 1994). The fundamental structural unit of the protein molecule is the amino acid of which there are twenty naturally occurring forms that are incorporated into protein. Fish are able to synthesise and inter-convert some of the amino acids, but are incapable of *de novo* synthesis of ten others. Thus, from a nutritional standpoint amino acids can be divided into essential and nonessential (indispensable) groups. Certain amino acids seem to be essential because the fish lack the biochemical machinery required to manufacture the chemical configurations of the carbon chain skeletons of these amino acids (Jobling 1994).

Figure(12.1) displays the various processes involved in the amino acid metabolism of fish. The supply of proteins in the diet is first digested into its amino acid component forms and added into the total free amino acid pool. From this pool there are two routes which the amino acids can take. The amino acids can either be synthesised into body proteins or be converted into a class of compounds known as keto acids. These keto acids can be burnt directly to fuel metabolic processes or be converted into reserves in the form of lipid and carbohydrate. The process of converting amino acids into keto acids requires the removal of nitrogen from the nitrogen rich amino acids.

The most important point to note here is that the total free amino acid pool in fish is very small (equivalent to 2% of the protein pool). The dietary amino acids supplied by a normal sized meal is approximately double the size of the total free amino acid pool in fish (Hochachka and Mommsen 1995). Furthermore, it has been noted that the accumulation of essential amino acids is harmful to the fish, and are therefore maintained at low levels (Millward and Rivers 1988).

Considering the elemental composition of the fish as a whole, the amount of

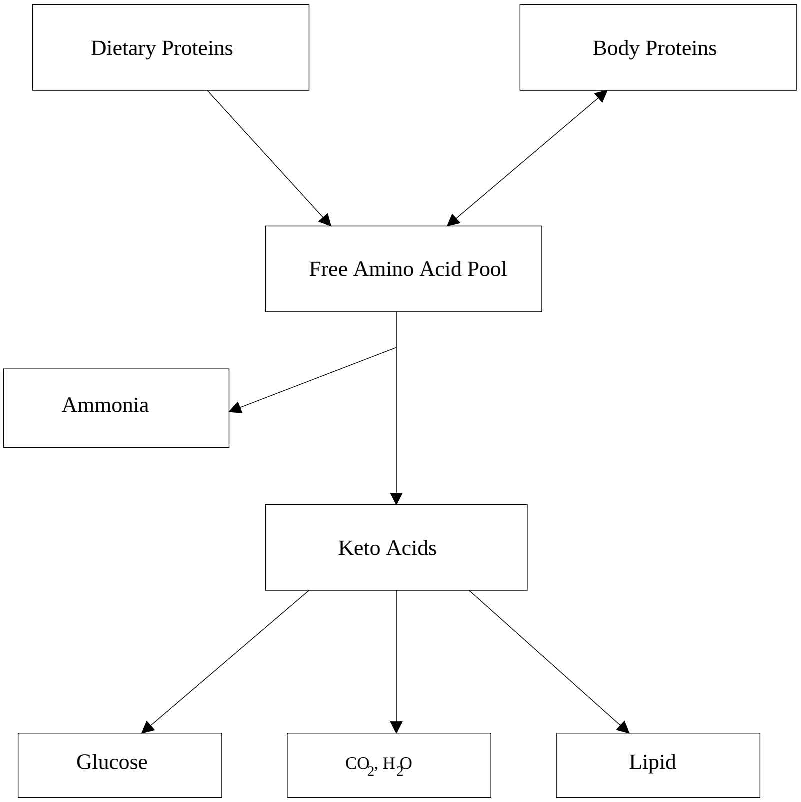

Figure 12.1: *Amino acid metabolism in Fish. Taken from Hochachka and Mommsen (1995).*

non-protein nitrogen is very small, approximately 0.12% of wet body weight (Niimi (1972); From and Rasmussen (1984); Brett et al. (1969)).

From the above biochemical facts we can make a surprising number of quite powerful deductions:

1. The combination of the fish's inability to synthesise 10 essential amino acids from a total of 20, coupled with the fact that the non-protein nitrogen present in the body is very small means that the ability of lipids and carbohydrates to be directly converted into protein is, for all intents and purposes, negligible (pers. comm. Kim Jauncey [1]). This is one reason why we don't see any significant structural growth during starvation, even in initially reserve rich fish. The fish simply lack the nitrogen to accrete any significant amounts of new proteins.

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2. From the above, it is clear that salmonids who manage to maintain protein growth (positive nitrogen balance) whilst remaining in a stationary energy balance (e.g. Miglavs and Jobling (1989b); see table(3.5)) must be using the amino acids in the "maintenance" ration to build new protein and using reserves to meet metabolic costs. This has already been noted by Jobling et al. (1993).

3. The fact that the total free amino acid pool is very small, means that the fish's ability to store amino acids is very small. This implies that protein growth is a "fast" process (pers. comm. Kim Jauncey). That is, when the food supply is withdrawn, protein growth is almost immediately cessated (give or take the remaining food in the gut). In a similar manner, when food is re-introduced, amino acid concentrations can be very quickly recovered, which means that protein growth can almost immediately be restarted.

How do we emulate these strong structural growth characteristics? We make allocation to structure within our modelling framework a function of the immediate assimilate.

The assimilation allocation model was first presented in section(2.5.3). We partitioned the fish's assimilate into two different nutrient classes; structural nutrients, mainly in the form of proteins and inorganic minerals, and reserve nutrients, mainly in the form of lipids and carbohydrates. Structural nutrients can be used to build structure but can also be converted into reserves and/or meet maintenance. On the other hand, reserve nutrients can only be used to meet maintenance and be stored in reserves.

In part II (section(4.6)) we introduced a particular case of the assimilation allocation model in which we assumed a healthy well-fed individual allocates a constant proportion of the structural nutrients in the assimilate to building structure. For a constant diet formulation this means that a constant proportion of the total assimilate is directed to building structure. The resultant steady state reserve ratio behaviour was negatively related to the ratio of maintenance to assimilation. This meant that fish managing to maintain growth sustain a nutritional condition which is a function of ration level and temperature and thus growth rate, as described by the literature.

When a healthy well-fed organism is supplied with a maintenance ration, structural growth continues because allocation is made in proportion to the immediate assimilate. However, the rate of structural growth is relatively slow in comparison to the reserve allocation model because commitment to structure is being constrained by the already low ration of food. Nevertheless, for biological realism we recognised that the assimilation allocation model required a mechanism to reduce and eventually cease any further allocation to structure. In the absence of any evidence to the contrary we decided upon a function which varied linearly with reserve ratio between zero and the nominal proportion of the total assimilate directed to structure. Hence, when a maintenance ration is supplied, structural growth continues slowly until the reserve ratio falls to the defended value μ_S, at which point any further commitment to structure ceases.

In an identical fashion to the net production model the absence of a food supply ceases structural growth, immediately and independently of reserve status. The resultant model dynamics allowed us to derive an analytic solution for the time to death from starvation. From this we predicted that low temperatures, high initial nutritional condition and more interestingly size all lengthened the time to starvation. All these predictions are supported by the literature.

In chapter 5 we investigated the predictions of the assimilation allocation model with regards to changes in the formulation of the diet. We manipulated the composition of the diet by changing a small number of exogenous parameters which controlled the proportions of structural and reserve nutrients in the fish's uptake. As a first approximation we assumed that the conversion of reserve and structural nutrients to their respective assimilate components incurred equal processing costs. In recognition that protein growth can reach a reasonably well defined maximum rate we imposed an upper limit on structural growth rate which we assumed to be proportional to the fish's maximum uptake. Following this, we demonstrated that the addition of lipids in the diet serves only to increase the rate of reserve accumulation. We also demonstrated the importance of supplying enough structural nutrients in the diet to maintain a fast growth rate.

To add more realism we incorporated differential processing costs for reserve and structural nutrient processing. An analysis of this modification revealed the major affects of adjusting the formulation of the diet to to remain very similar, except, however, that equal processing costs under predicts the rate at which the more easily synthesised reserves are accumulated. In addition, we also identified a mechanism which could explain how high lipid levels could increase structural nutrient retention efficiency, commonly referred to as protein 'sparing'. The easier to synthesise reserve nutrients help the fish maintain a good nutritional condition thus avoiding any extraneous catabolism of structural nutrients which may be necessary to meet energetic requirements or defend a nutritional condition.

In the final section of this chapter we outlined the major goals aquaculturists are seeking to maximise when studying the effects of diet formulation. Our model homed in on an optimal diet formulation and ration level. The optimal ration and feed formulation supplies enough structural nutrients to keep structural growth near maximum whilst simultaneously supplying enough energy in the form of the more digestible reserve nutrients (primarily in the form of lipids) to meet energetic requirements and maintain a healthy reserve status, thus avoiding any extraneous catabolism of proteins.

In section(7.4.3) we investigated the dynamics of the assimilation allocation model with the inclusion of a hyperphagic compensatory response function following periods of growth restriction (see section(7.4)). Because commitment to structure is made from the immediate assimilate, an increased uptake serves to increase the structural growth rate beyond normal control levels. This increased commitment to structure prolonged the hyperphagic response in comparison to the reserve allocation model and therefore resulted in a much stronger compensatory growth response.

Based upon the qualitative success of the assimilation allocation model, we went on to fit a number of feed cycling tank-based experimental data sets. For all studies, the model fitted the control portions of the data in an excellent manner. Forward extrapolation of these growth trajectories to include the re-feeding portion of the data revealed that, with the exception of one study, cohorts had undergone an accelerated growth response, both in wet weight and length. By simply stating that individuals were hyperphagic until the previous nutritional condition was recovered, we obtained an excellent fit to the remaining portion of the data sets, both in wet weight and length.

Based upon its qualitative and now quantitative success, the assimilation allocation model was the most natural choice to investigate the growth and energy allocation dynamics of juvenile salmonids in their natural habitat. We first carried out a simple budget analysis to identify the major temporal pattern of assimilation exhibited by juvenile Atlantic salmon parr from the Girnock Burn. The inferred temporal pattern of assimilation was clear enough to be characterised by a simple functional form. The scaled annual assimilation function, together with the independently parameterised maintenance function was used to drive a simple individual based model which assumed non-seasonal assimilation allocation to structure. Although the fit was good, there was a clear and systematic trend in the model length and condition factor residuals, but not weight residuals. This signified that the within year pattern of allocation was being misrepresented. A simple modification, which allowed allocation to change with the changing seasons, eradicated the systematic pattern of residuals in length and condition factor. The best fit seasonal defended reserve ratio μ_S was ecologically sensible and illustrated how salmonids make the best of seasonally harsh energy limiting environments.

12.6 Suggestions for Future Research

One of the most obvious suggestions for future research is to incorporate energy allocation to reproduction within our modelling framework. The reproductive dynamics of the net production model and a cousin of our reserve allocation model have been analysed in detail within Kooijman's dynamic energy budget (DEB) modelling framework. Indeed, Kooijman's energy allocation scheme (commonly referred to as the κ-rule for allocation) analogous to our reserve allocation scheme was specifically derived to explain how individuals allocate energy allocation to reproduction but also still maintain growth. The DEB framework uses the analogous state variables of reserves and biovolume, therefore we should not expect any major differing modelling conclusions concerning these allocation schemes. However, the assimilation allocation model is original and as such no reproductive modelling investigations have been conducted based on its assumptions concerning allocation to growth and storage. Given the success of the assimilation allocation scheme over its counterparts in predicting the energy allocation dynamics of juvenile salmonids then it would also be the natural choice.

Reproduction is energetically very expensive and the greatest demand in spawning salmonids is for lipids (Sedgwick 1988). Therefore, energy allocation to reproduction could reasonably be expected to be made from reserves. Fecundity is related to body size in fish (Wootton 1990), however, diets high in lipid have been shown to increase the incidence of early maturity (Silverstein et al. 1997). This implies that size and nutritional status are both important factors in governing when it is advantageous to become fully sexually mature. As mentioned at the very beginning of this thesis in section(1.2), it is now clear why it is hard to identify between fish size, growth rate and nutritional condition as being the major determinants of sexual maturation, principally because these factors all covary with one another.

The assimilation allocation model encapsulates the relationship between growth rate and nutritional condition. Furthermore, the assimilation allocation model can model the effects of different diet formulations making it a highly desirable mathematical tool for investigating what factors or indeed, combination of factors which mostly govern the onset of sexual maturity. A careful set of experiments noting the incidences of sexual maturity in fish subjected to different growth regimes and diet formulations could be carefully analysed using the assimilation allocation model. Such an experimental protocol, coupled with the aid of our model could lead to a more accurate estimate of what combination of size and nutritional condition initiates sexual maturity. This may be especially useful for the aquaculture industry because the biochemical changes during spawning render fish useless to farmers (Sedgwick 1988). The formulation of the diet could possibly be modified to delay the onset of sexual maturity and therefore increase yield.

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Part VI

Appendices

Appendix A

The Downhill Simplex Method of Optimisation

The downhill method of optimisation (DSO) was developed by Nelder and Mead (1965). The method is a multidimensional procedure to minimise any prescribed error function which can evaluated by a vector of real parameters. There is no requirement for function derivatives to be evaluated, making it especially suitable in cases when the first order derivatives are difficult to calculate or discontinuous.

The DSO algorithm that will be used is from Press et al. (1989) and is best described from a geometric perspective. Consider a fitting objective $f(\mathbf{P}, \mathbf{Y})$ which is a function of the data $\mathbf{Y} = (Y_1, Y_2, ...Y_M)'$ and parameters $\mathbf{P} = (P_1, P_2, ...P_N)'$. The user must initially specify $N + 1$ different trial parameter vectors $\mathbf{P}$. Since each of the $N + 1$ trial parameter vectors $\mathbf{P}$ has a corresponding function value then they are best viewed as being the vertices of a simplex in an $N + 1$ dimensional error space, where, the "highest point" of the simplex exists at the largest function value. The downhill simplex method then takes a series of steps, which include reflections, expansions and contractions of the simplex designed to move the simplex downhill, thus, minimising the objective function. This process is continued until the vertices of the simplex have converged to within a user supplied tolerance resulting in the best fit parameter vector $\hat{\mathbf{P}}$.

In a smooth and well behaved error space the DSO will discover the global minimum in the majority of cases. However, with increasing error space complexity and a greater number of fitting parameters global minimisation occurs less frequently. In such situations it is necessary to utilise the method of bootstrap restarting.

Appendix B

Bootstrap Restarting

The bootstrap restarting method is a technique very recently developed by Wood (2001). Bootstrap restarting can be used in conjunction with most minimisation techniques to help avoid converging in spurious local minima. The trick is to stochastically perturb the objective function by taking bootstrap resamples from the fitting data.

Bootstrap resampling is a process of randomly resampling from the original data with replacement. For example, consider the data $\mathbf{Y} = (2, 6, 9, 3, 7, 0, 6)'$, a bootstrap resample would look something like $\mathbf{Y}^* = (2, 2, 9, 3, 0, 0, 6)'$. The bootstrap resample has the same sample size but the same data point can occur once, more than once or not at all. Bootstrapping methodology is covered extensively in Efron and Tibshirani (1993) and Davidson and Hinkley (1997).

Consider a fitting objective $f(\mathbf{P}, \mathbf{Y})$ which is a function of the data $\mathbf{Y} = (Y_1, Y_2, ...Y_M)'$ and parameters $\mathbf{P} = (P_1, P_2, ...P_N)'$. The boostrap restarting approach is an iterative method which is summarised as follows:

1. Given a starting vector $\mathbf{P}_0$, find the parameters which are at a minimum of $f(\mathbf{P}, \mathbf{Y}) : \hat{\mathbf{P}}_0$.

2. Repeat steps 2-5 for $i = 1, ..., k$.

3. Create a bootstrap resample $\mathbf{Y}_i^*$. From starting parameters $\hat{\mathbf{P}}_{i-1}$ find the parameters which are at a minimum of $f(\mathbf{P}, \mathbf{Y}_i^*) : \hat{\mathbf{P}}_i^*$.

4. From starting parameters $\hat{\mathbf{P}}_i^*$, find parameters that are at a minimum of $f(\mathbf{P}, \mathbf{Y}) : \mathbf{P}_i$.

5. If $f(\mathbf{P}_i, \mathbf{Y}) \leq f(\mathbf{P}_{i-1}, \mathbf{Y})$ set $\hat{\mathbf{P}}_i = \mathbf{P}_i$ otherwise set $\hat{\mathbf{P}}_i = \hat{\mathbf{P}}_{i-1}$

$\hat{\mathbf{P}}_k$ contains the best fit parameters after k iterations. The idea is that although $f(\mathbf{P}, \mathbf{Y}^*)$ will usually preserve the large scale features of $f(\mathbf{P}, \mathbf{Y})$ small scale detail capable of trapping minimisation will differ. Hence the method provides a way of escaping spurious local minima in a way that automatically takes account of the large scale structure of the objective.

The downhill simplex method of optimisation (appendix A) uses $N + 1$ trial parameter vectors ($\mathbf{P}$) which all converge to a single parameter vector $\hat{\mathbf{P}}$ when a minimum has been located. Bootstrap restarting requires that minimisation proceeds from a parameter vector specified by either step 3 or 4. This is easily accomplished with the downhill simplex method by ensuring that one of the initial $N + 1$ parameter vectors is set equal to parameter vector specified by either step 3 or 4.

Appendix C

Nested Minimisation

In this appendix we describe the method we developed to fit our individual based growth and allocation model to the individual electro-fishing data as described in chapter 9. The grand minimising objective function included a large total number of free fitting parameters (> 190), which meant it was simply not feasible to attempt to minimise all parameters simultaneously using a single minimisation procedure. However, the parameters could be partitioned into global parameters (which are common to all individuals) and local parameters (with each being unique to a particular individual and independent of any other individual). This special property of the free fitting parameter set, together with a clever choice of error measure (see equations(10.10) and (10.11)) allowed us to break-up the grand minimisation scheme into a series of smaller minimisation schemes, which meant we could find a much more reliable estimate of the best-fit parameter values. The following is a rigorous mathematical explanation of this technique.

Consider the fitting objective $F(\mathbf{P}, \mathbf{Y})$ which is a function of all the individual salmon parr data $\mathbf{Y}$ within our study period and parameters $\mathbf{P}$ which include global and local parameters. We can express the vector of individual data $\mathbf{Y}$ as consisting of subsets of data which correspond to each individual. Therefore, we can write

$$\mathbf{Y} = (\mathbf{y_1}, \mathbf{y_2}, ..., \mathbf{y_m})' \tag{C.1}$$

where, $\mathbf{y_j}$ denotes the combined length and weight free fitting data for individual j. We can also subset the vector of parameters $\mathbf{P}$ into global parameters (which are common to all individuals) and local parameters (with each being unique to a particular individual) as follows

$$\mathbf{P} = (\mathbf{P_G}, \mathbf{\Psi}) = (P_1, P_2, ..., P_g, \Psi_1, \Psi_2, ..., \Psi_m)' \tag{C.2}$$

where, $\mathbf{P_G}$ denotes the vector of global parameters and $\mathbf{\Psi}$ denotes the vector of individual parameters (see equation(10.7)).

The best fit parameter values $\hat{\mathbf{P}}$ are the set of parameters values which minimise $F(\mathbf{P}, \mathbf{Y})$, that is

$$F(\hat{\mathbf{P}}, \mathbf{Y}) = \min\{F(\mathbf{P}, \mathbf{Y})\} \tag{C.3}$$

The grand objective function $F(\mathbf{P}, \mathbf{Y})$ has been defined such that the best fit parameter values of $\mathbf{P}$ minimises the error displayed in equation(10.11). This error function is the error function given by equation(10.10) summed over all individuals. This means we can express the grand objective function as a sum of local objective functions as follows

$$F(\mathbf{P}, \mathbf{Y}) = \sum_{\text{all } j} f_j(\mathbf{P}, \mathbf{Y}) \tag{C.4}$$

where, $f_j(\mathbf{P}, \mathbf{Y})$ is the local objective function (see equation(10.10)) associated with individual j.

Each individual shares a common set of global parameters with every other individual. However, each individual also has a local fitting parameter Ψ_j which is unique to itself and independent of any other value of Ψ_j. Furthermore, the local objective function associated with individual j is only a function of the data for that particular individual $\mathbf{y_j}$ (see equation(C.1)). The above observations means that we can write

$$f_j(\mathbf{P}, \mathbf{Y}) = f_j(\mathbf{P_G}, \Psi_j, \mathbf{y_j}), \quad \forall\ j \tag{C.5}$$

that is, each local objective function is a function of all the global fitting parameters $\mathbf{P_G}$, only a single individual fitting parameter Ψ_j and only the data associated with this individual $\mathbf{y_j}$.

Therefore, using equation(C.4) and equation(C.5) we can now express the grand objective function as

$$F(\mathbf{P}(\mathbf{P_G}, \mathbf{\Psi}), \mathbf{Y}) = f_1(\mathbf{P_G}, \Psi_1, \mathbf{y_1}) + f_2(\mathbf{P_G}, \Psi_2, \mathbf{y_2}) + .. + f_m(\mathbf{P_G}, \Psi_m, \mathbf{y_m}). \tag{C.6}$$

Each term on the right hand side of equation(C.6) is a local minimising objective function with a unique local fitting single parameter Ψ_j. This means for any arbitrary set of global trial parameter values $\mathbf{P_G}$ we can independently determine the value of Ψ_j which minimises the local objective function $f_j(\mathbf{P_G}, \Psi_j, \mathbf{y_j})$. Furthermore, since each independent local minimisation only requires we find a single best fit value of Ψ_j then we can almost certainly guarantee that we can find the very best fit value of Ψ_j for any particular values of global fitting parameters $\mathbf{P_G}$.

If we now define a set of new local objective functions $g_j(\mathbf{P_G}, \hat{\Psi}_j, \mathbf{y_j})$ such that each refers to the independent local objective function once the minimisation of parameter Ψ_j has taken place then we can express the grand objective function as follows

$$F(\mathbf{P}(\mathbf{P_G}, \hat{\mathbf{\Psi}}), \mathbf{Y}) = g_1(\mathbf{P_G}, \hat{\Psi}_1, \mathbf{y_1}) + g_2(\mathbf{P_G}, \hat{\Psi}_2, \mathbf{y_2}) + .. + g_m(\mathbf{P_G}, \hat{\Psi}_m, \mathbf{y_m}). \tag{C.7}$$

The grand objective function is now only a function of the global parameters $\mathbf{P_G}$ because the best fit vector of local parameter values $\hat{\mathbf{\Psi}}$ are such that they minimise each local objective function for any given arbitrary choice of global parameter values. By applying a minimisation scheme solely to the global parameters such that they minimise the objective function given by equation(C.7) then we shall find the best fit global parameters $\hat{\mathbf{P}}_\mathbf{G}$. However, because we are guaranteed to find the best fit vector $\hat{\mathbf{\Psi}}$ for any choice of $\mathbf{P_G}$ then we shall also find $F(\mathbf{P}(\hat{\mathbf{P}}_\mathbf{G}, \hat{\mathbf{\Psi}}), \mathbf{Y}) = F(\hat{\mathbf{P}}, \mathbf{Y})$ and thus we minimise the grand objective function.

To evoke this method we applied a downhill simplex minimisation method (DSO, see appendix A) to the global fitting parameters. With each set of trial global fitting parameter values we independently minimised each of the local objective associated with each individual by adjusting Ψ_j, again in each case using the DSO algorithm. Each of the local errors were summed up to obtain a total error which was in turn ascribed to the global fitting parameters minimisation procedure, allowing the global minimisation to proceed with another trial global set of parameter values until a minimum was reached. Therefore, this method involved independent local minimisations for each function evaluation of a single global minimisation procedure. Hence, the reason why we refer to this method as nested minimisation. Very similar iterative methods have been developed to solve this type of nested minimisation problem in the context of B-spline surface fitting by Rogers and Fog (1989) and Hoscheck et al. (1989).