Modelling fish feeding and digestion

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Abstract

By constructing a mathematical model, this thesis aims to infer the feeding behaviour of a population of fish from variations in stomach contents samples taken at intervals throughout the day.

I take a population approach to the problem and consider the dynamics of the distribution of stomach contents of a population. Assuming that the population is closed and consists of identical individuals, chapters two and three illustrate the temporal variation in the stomach contents distribution under particular digestion and feeding behaviour.

The middle section of the thesis explores the possibility of developing a method of automatic solution of the inverse problem of finding the parameters defining the feeding behaviour in the model from a given stomach contents distribution. By comparing the feeding behaviour inferred from noisy, categorised data with the known feeding behaviour from which the data was simulated, I can make conclusions about sample size and sampling frequency requirements in order that the feeding behaviour inferred from such samples adequately predicts the feeding behaviour of the population from which the samples were drawn.

In the final section of this thesis, I consider some data recently collected from Loch Gairloch, Scotland. By fitting the output of my model to this data I have inferred the feeding behaviour of the sampled fish species which is then compared to results found in the literature. A further application of this model is in a calculation of daily ration of each species which is then also compared to other results in an attempt to further validate the model.

Contents

Chapter 1

Introduction and motivation

1.0 Introduction

Ecologists have been studying the behaviour of fish for many years in an attempt to find out how particular species fit into the marine or freshwater ecosystem. Like all animals, their behaviour is controlled by the need to survive and can be classified as feeding, reproduction and time spent avoiding predation. Without sufficient food the fish would be unable to grow (Elliott 1975a) or reproduce properly (Karlsen et al. 1995) or have enough energy to move and would therefore be more susceptible to predation. The quest for food is therefore overriding. If we can establish what and how much fish eat then we will have a clearer picture of how particular species fit into a particular ecosystem. Recent interest in fish feeding habits has been sparked off by the plummeting stocks of exploited marine fish populations (Daan 1989, Hempel 1978). Multispecies stock assessment models (which I shall discuss later) constructed in an attempt to help manage this situation require an understanding of the trophic interactions between species and a knowledge of mortality of particular fish cohorts due to predation. Insights into the requirements of such stock assessment models can clearly be gained from studies of fish feeding behaviour.

Unfortunately, there are many practical difficulties associated with studying the feeding behaviour of fish as it is impossible to carry out direct observations of fish in their natural habitats. Studying the feeding habits of mammals and birds is in general easier, most obviously because, in general, the observations do not need to be carried out underwater, but also due to the fact that after feeding there are often visible remains of a meal; for example, half eaten carcasses, bones, regurgitated pellets and identifiable faeces. Even without tracing the every move of the species we are interested in, it is therefore possible, in many cases, to draw sensible conclusions about their feeding habits. Although fish do regurgitate food remains, associating particular regurgitated food samples with a particular fish species is also likely to be very difficult.

An alternative to direct field observations could be to capture fish and hold them in a tank - recording how much and how often they feed. This was attempted by Elliott (1972). However, it is unlikely that it will be possible to recreate sufficiently the natural conditions of the species in a laboratory in order to be able to make any definite conclusions about their feeding activity. It has been known for many years (Bajkov 1935) that feeding is affected by the temperature of the water, its acidity, turbulence and the light intensity. Although it has been shown that relatively few of these external variables account for the majority of the variation in gastric evacuation rate and consequently feeding rate (Bromley 1990, Temming and Anderson 1992), it would be impossible to include, in a tank, the huge choice of prey both live and dead which would be available in the wild and therefore feeding may not occur as it does in the wild. It is also thought that fish caught and held in captivity become stressed and therefore may not feed as usual (Lockwood 1980, Kster et al. 1990) and consequently it seems unlikely that results from laboratory feeding experiments will give us any meaningful information about the feeding habits of fish in the wild.

So, the only option which remains is to catch samples of fish from the wild, remove their stomachs to see what they have eaten and from this attempt to infer their feeding behaviour.

1.1 Importance of fish feeding habits

Hundreds of years before ecologists became interested in the interaction between animal species and began writing papers about food consumption rates and predation of particular species, the feeding habits of fish were being studied in everyday life. Fish have always been a readily available source of food, so early interest in their feeding habits was motivated by the wish to improve fishing methods. For example, if we know when and on what prey species a fish population feeds, catching them is much easier as we know what time of the day they will be most active (i.e. when they are feeding) and with what food to bait them. These days, however, fishing methods are so efficient that studies of fish feeding habits are becoming increasingly important in attempts to regulate fishing.

In the past few decades there has been a noticeable reduction in the exploited fish populations of the world (Hempel 1978, Daan 1989). Worries that severely depleted stocks may never recover have lead to strict limitations on the harvesting of particular species and attempts at constructing more and more effective stock management models. Fish feeding habits have become more useful in the commercial environment with the realisation that fish stocks may be accurately modelled on a multispecies basis, rather than considering all species individually.

In many cases, the analysis of fish stocks is based on estimates made from the numbers caught commercially. It was Gulland (1965) who first developed a model which could be used to monitor fish populations in this way. His model suggested that given a knowledge of the catch of a species at a particular age (from commercial catch data) and natural mortality, then the fishing mortality and population of the species at a particular age can be calculated, by an iterative procedure. This theory is known as Virtual Population Analysis (VPA). Pope (1972) approximated this model by cohort analysis which simplified the iterative procedure required to solve the difference equations. However, in both these methods it is usual to make the assumption that natural non-fishery mortality is constant for all ages.

Beverton and Holt (1957) realised that the life history parameters of fish must be affected by the fluctuating populations of other species. But, for most of the next twenty years, such interactions were not incorporated into any fish stock management models. Questions as to the validity of the single species models began to be asked in the early 1970's by Daan (1973 and 1975). He made a detailed analysis of the stomach contents of cod and found that they preyed on many different fish species, but the dominant species were young haddock and whiting. This lead to the suggestion that young fish will have a higher natural mortality than old fish and that the constant mortality rate assumption is wrong. Major changes to the structure of fish communities in the late 1960's and early 1970's prompted the work of Andersen and Ursin (1977). Knowing that fish species do not exist independently of each other, they constructed a general, comprehensive model of an exploited marine ecosystem. The model which they constructed illustrated the possibility that over fishing of herring and mackerel in the sixties which lead to stock collapses could have meant that enough food was available to trigger an increase in the stocks of gadoids which corresponds to the increases in the catch of these species at this time. So, although this model was rather impractical with the estimation of thousands of parameters required, it did lead other fisheries scientists to realise that a species could not be treated individually.

Returning to the earlier ideas of VPA and utilising catch at age data in attempts to estimate actual fish stocks (Gulland 1965), Helgason and Gislason (1979) suggested a multispecies virtual population analysis (MSVPA), based on the Andersen and Ursin exploited ecosystem model, in which the analysis for several single species was carried out simultaneously with coupling between them. Pope (1979) also reformulated his single species cohort analysis as a multispecies model. Further developments in the MSVPA are discussed in later works by Pope (1989, 1991) while other multispecies models are summarised in Daan and Sissenwine (1991).

Like the single species VPA, the MSVPA requires a knowledge of mortality. It seems probable, at least for small fish that the most important component of natural (i.e. non-fishing) mortality is piscivory, both by individuals of the same species and of other species. The predation load on a particular age class of a particular species (cohort) is therefore likely to change as the fish grow (Daan 1972 and 1975). Some predators will prey on especially small fish, while others will prefer slightly larger ones. So, in MSVPA the natural mortality is usually split into two parts - a constant background mortality and an age and species dependent predation mortality. Although the constant background mortality still has to be estimated (or guessed) it is assumed to be very small in comparison to the total natural mortality when this is significant, i.e. for small fish and the predation mortality is calculated from studies of fish feeding habits.

Clearly measurements of the predation load on particular cohorts of commercial fish species are impractical and therefore a less direct route to obtaining such values has to be taken. Stomach contents analysis were used by Daan (1972 and 1975) to suggest that predation mortality was not equal for fish of all ages and therefore from careful stomach contents analysis, we should be able to get a quantitative breakdown of the diets of all predator classes involved in the MSVPA.

Such quantitative information must be representative of the total annual population and therefore places high demands on the spatial and temporal collection of stomach contents. Consequently, extensive stomach contents sampling projects were carried out in only two years - 1981 and 1991, each known as 'the year of the stomach'. In each year the stomachs of samples of five predator species in the North Sea were dissected and analysed (Anon 1984, Daan 1983, Anon 1994). The results being illustrated as weight of each prey species (by age) found in the stomach of each predator species (by age). These results can then be used to help estimate the predation mortality of a particular prey species at a particular age.

The total predation load on a particular prey cohort due to predation (which is required by the MSVPA) can be expressed as the sum of the numbers of fish eaten by each predator species of a particular age. These numbers in turn can be expressed in terms of the per capita predator *ration*, the *suitability* of a particular prey type as a food item for the predator, the average mass of each prey species and the average abundances of the predator and prey populations. (All variables are age specific). The definitions of *ration* vary from author to author (see Stokes 1992), but it is usually assumed to be constant between years and can be estimated from feeding studies. If the abundances of each prey cohort were known, then the *suitabilities* could be calculated using the stomach weight matrix. However, the abundances are not known. They are therefore initially guessed and then modified by an iterative procedure until the model estimates of each predators consumption agrees closely with the stomach contents data. A more detailed insight into these calculations can be gained from Magnusson (1995) and Sparre (1991).

Closely linked to the very commercially driven construction of fisheries management models are the studies of food webs and ecosystem model. Knowing how fluctuations in fish populations affect other aquatic species is an important part of community ecology. Food webs have been studied for many years (Ivlev 1945, Steele 1974) and most people realise that trophic interactions play an important part in structuring ecological communities. For example Power (1990) found that the effects of fluctuations in the population of roach in a river community were visible through four trophic levels of the food web, down to the levels of diatoms and bacteria.

Obviously without knowing what fish eat, we do not know what level of the food web they belong to and therefore how population changes affect the community. This can easily be decided by a straightforward stomach contents analysis and classification of prey. However, a more difficult question to answer is what effect the population as a whole has on another species. More recent ecosystem models have been built on the basis of a closed energy system analysing the transfer of energy per unit biomass between species. Estimates of such values can be made from assumptions of energy requirements for growth and reproduction combined with efficiency estimates. (Pauly 1986). Alternative calculations of energy requirements can be made from food consumption estimates. These once again can be made from stomach contents samples, usually by combining the dynamics of stomach contents samples with measurements of gut evacuation rates (Elliott and Persson 1978).

With increased attention being paid to the future well-being of the whole ecosystem of the North Sea and other heavily fished areas, fish quotas have been imposed in an attempt to preserve the marine food chain. Fishermen are therefore increasingly looking elsewhere for employment. Fish farming is becoming ever more popular in countries like Scotland and Norway where communities have previously relied quite heavily on the sea fishing industry. Clearly a knowledge of what the farmed fish need to eat to survive and keep them healthy is of paramount importance to the fish farming industry. Recent experiments into fish feeding have been coupled to growth studies with commercial interest concentrating on how to maximise fish growth with minimum expense to the farmer. Models relating fish growth to instantaneous food uptake have been constructed by Majkowski and Waiwood (1981) and Majkowski and Hearn (1984). As well as being useful in fish growth studies, such calculations can be used in calculations of total biomass consumption of a population to be used in food web models.

In this section I have tried to show that a knowledge of fish feeding behaviour is important to many marine and freshwater studies. The discussion actually describes the complexity of ecological systems and how we cannot really consider the commercial fishery view without considering the ecosystem interactions, with fish feeding behaviour being the connection.

1.2 Stomach contents analysis

The previous section illustrated the variety of information required about the feeding habits of fish, with in some cases very precise prey identification requirements and in others, total food ration. The only practical way of drawing any reliable conclusions about the feeding habits of fish in the wild is by gut contents analysis which has been used in various forms for many years. The type of analysis carried out is dependent on the questions which are being addressed and whether the study is concentrating on 'what?', 'when?' or 'how much?' fish eat.

The first studies which were carried out mainly concentrated on the analysis of the diet of different fish species (e.g. Brooks 1886). The basic studies just consisted of catching fish and dissecting their stomach so that the main prey sources could be classified. Such studies are still being carried out today (Hall et al. 1990) and provide important evidence concerning between species competition for particular prey. For example, more recent prey species analysis have incorporated time dependence (Magnuson 1969, Knust 1986) or habitat dependence (Gibson and Ezzi 1986). Then conclusions can be drawn about whether the food of a particular species changes over the course of a day or year or whether prey type is dependent on where the population lives.

Extremely large scale prey species identification studies of certain North Sea fish species were carried out in the Year of the Stomach in 1981 and 1991. The samples consisted of many thousands of fish, each stomach being dissected and categorised for amount of particular aged prey in a particular aged predators stomach (Daan 1983, Anon 1994). The results of such studies are to be used to give measures of the susceptibility to predation as described in the previous section in co-ordination with multispecies virtual population analysis.

Although providing very detailed information on the prey of particular predators, such large scale studies are very time consuming. There are also problems associated with species identification. If stomach samples are taken infrequently, the remains of some prey may have digested so much that they become unidentifiable. To overcome this problem, many scientists have resorted to simply measuring the total stomach contents of the individuals in a sample of fish (Gordon 1977, Keast 1970). This leads to attempts at modelling the changes in the population average stomach contents and inferring diel cycles of feeding intensity which when combined with evacuation rate estimates can be used to make daily ration calculations (Eggers 1977, Thorpe 1977, Elliott and Persson 1978 and Sainsbury 1986) which can then be utilised by the MSVPA.

1.3 Overview of the thesis

As I suggested in the previous section most models of fish feeding behaviour have been based on average stomach contents samples and have not incorporated any of the between individual variability which clearly must exist unless, of course, every individual in the population feeds on exactly the same sized prey at the same time. This, however, is impossible due to the distribution of the prey population available to the predators and there has been found to be quite a large variability between the stomach contents of individuals of the same population at the same time (Brodeur and Pearcy 1987, Jensen and Berg 1993).

In this thesis I shall construct a model which incorporates this stomach contents variability by describing the variation in the stomach contents distribution of a population which is undergoing simultaneous feeding and digestion. The thesis begins with some detailed discussion about models describing the digestion process and then constructs a digestion only model incorporating the stomach contents distribution idea. I have compared this digestion model to other models and actual evacuation data sets and only when the correct digestion set-up has been found do I incorporate the prey size and time dependent feeding process. The remainder of the first part of this thesis then goes on to investigate how the dynamics of the population stomach contents distribution changes under a variety of feeding and digestion regimes.

The whole aim of constructing a model of stomach contents variation is so that we can infer information about the feeding behaviour of fish from actual stomach contents data collected from the field. In the second part of the thesis I shall attempt to construct a non-linear optimisation method which will solve this 'inverse' problem of fitting the feeding and digestion model to a given stomach contents data set and outputting the inferred feeding behaviour. Obviously, real data sets will be noisy due to sampling error and may be sampled infrequently and categorised into few stomach contents categories rather than illustrated as a stomach contents distribution. So, in chapters four and five I have simulated some noisy data sets to investigate how closely this model predicts the feeding behaviour of a complete population of fish by fitting to a randomly taken sample. More importantly, we can then conclude from this section whether there are sampling conditions (i.e. minimum sample size, frequency) which must be obeyed in order that feeding behaviour inferred from these samples by the model is an adequate description of the population feeding behaviour.

The final section of this thesis then goes on to consider some real data sets and infers the feeding behaviour of a number of fish species in a sea loch off the North West coast of Scotland. These inferences and consequent daily ration calculations are then compared to other results in an attempt to confirm the importance and success of this model as a tool for modelling stomach contents variations.

Chapter 2

Modelling the digestion process

2.0 Introduction

In the past twenty years, discussion on the digestion process has increased dramatically as the importance of such information for understanding marine and freshwater ecosystem dynamics has been realised. In particular it has become apparent how the knowledge of food consumption and feeding rates, when coupled with information on types of prey found during stomach contents analysis elucidates the role of the species in the trophic network by giving us an idea of its effect on a prey population.

Most information about the feeding habits of fish has been obtained via the sampling of stomach contents since direct observations of the behaviour of a population of fish are impracticable in the field. Therefore an accurate knowledge of the dynamics of the digestion process is important, as the relationship between the stomach contents and the feeding rate is highly dependent on the digestion rate. For example, suppose the measured stomach contents of an individual are W_t grams at time t hours and W_{t+1} at t+1 hours, then the amount of food consumed in the hour U is related to the stomach contents by

$$U = W_{t+1} - W_t + D \tag{2.1}$$

where D is the constant digestion rate in grams per hour. So, a prerequisite to learning anything about feeding rates from stomach contents samples is that the evacuation process is understood and a realistic value for the digestion rate has been obtained.

2.1 A review of digestion studies

Most theories about the digestion process have been based on an examination of stomach contents either collected from the field or from experiments conducted in the laboratory. And despite the recent increased interest in this field there is still much disagreement and confusion over the major factors which determine the rate of digestion (see Bromley 1994).

The digestion rate is usually defined as the rate at which the stomach is emptied of food whether it is broken down by enzymes and absorbed through the stomach walls or whether it just passes into the intestine undigested. The digestion or evacuation process as it is sometimes called is said to be complete when the stomach becomes empty of all measurable remains.

The usual method of monitoring the evacuation process is to take a population of similarly sized fish and let them acclimatise to life in a closed tank for several weeks. Before beginning the experiment, the fish are starved for approximately three days and then fed to satiation. This is to ensure that all the individuals have, as near as possible, the same stomach contents at the start of the experiment. Immediately after feeding has taken place a small number of fish are removed and the contents of their stomachs extracted, either by using a small stomach pump or by killing and dissecting them. After their single meal the remainder are left without food. Bajkov (1935), Jobling and Spencer Davies (1979) and Elliott (1991) found that water temperature affected digestion rate, so keeping all external conditions constant, groups of the remaining live fish are then removed every couple of hours and their stomach contents extracted. Using such a procedure, the average stomach contents of a given species (under certain external conditions), at a particular time after feeding can then be calculated by dividing the total amount of food in the stomachs by the number of individuals. The rate of depletion of average gut contents is then defined as the average digestion rate of the population.

Most evacuation curves as they are commonly known have been observed to follow one of the two shapes indicated in figure 2.1.

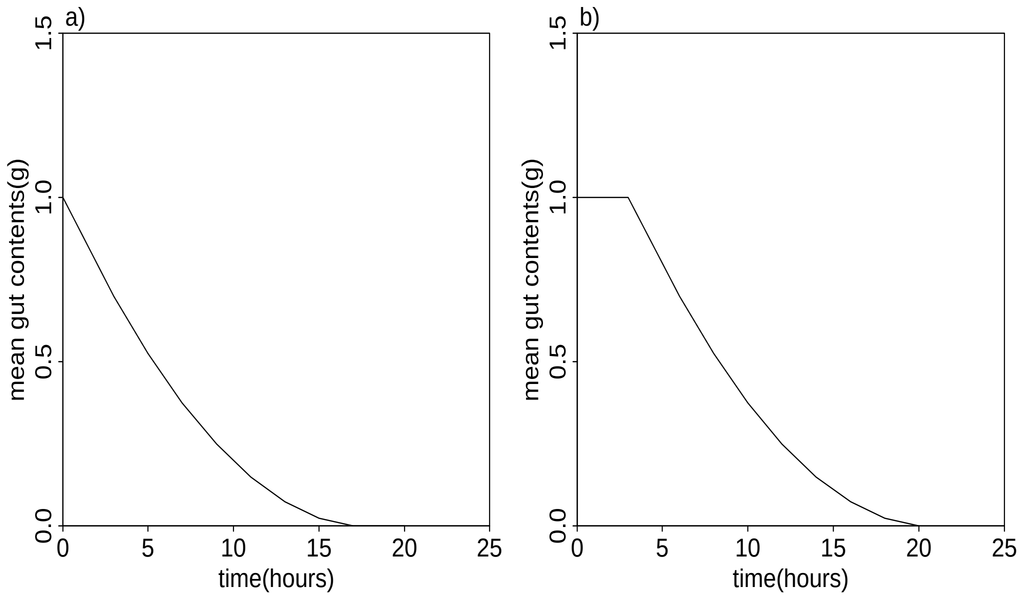


Figure 2.1 Two commonly observed digestion curves.

Looking at the change in stomach contents with time in a non-feeding population of fish, most observers have seen that the average gut contents initially decrease quite rapidly, but as their gut contents decrease, this rate slows down, as seen in figure 2.1a, suggesting a non-linear relationship (Basimi and Grove 1985 and Bromley 1987). However, a number of digestion experiments have yielded depletion curves of the type seen in figure 2.1b (Swenson and Smith 1973 and Grove et al. 1984) where after an initial delay in which there is no reduction in stomach contents, the curve follows the same shape as that in figure 2.1a.

There has been little agreement on the length of the 'delay phase', but it has been suggested that the reason for this delay is due to the time taken for the acids present in the stomach to penetrate the food substance and break it down into pieces of size suitable for passage out of the stomach through the pylorus. A lag of up to thirteen hours was reported of turbot fed especially hardened pellets (Grove et al 1985) whereas Bromley (1987) observed any initial delay to be less than three hours when the same species were fed on frozen fish, and a paper by Elliott (1991) reported that no time lag was apparent when fresh trout fry or sticklebacks were the food source, indicating a dependence of the delay length on the penetrability of food. These results seem to indicate that when fish are feeding on fresh prey, there is little or no delay in gut contents depletion. In most digestion experiments, fish are starved before being fed their single meal. So on feeding their digestive enzymes may be switched off and a delay will occur before digestion commences. In natural conditions it is unlikely that fish will have their digestion switched off (unless there have been severe food shortages) and therefore no delay will occur in the digestion process. So, in this study I have concentrated on single phase digestion models and not attempted to include the delay phase.

The majority of authors have assumed a general model for the depletion of stomach contents to be of the form

$$\frac{dW(t)}{dt} = -KW(t)^c \tag{2.2}$$

where W(t) is the weight (or volume) of stomach contents at time t and c and K are constants. The usual procedure is then to try fitting variations of this model to various data sets and evaluating the goodness of fit by least squares methods.

Despite the many years of digestion studies, there is still much disagreement about the type of model which the digestion process follows. As such a wide variety of fish species have been used in digestion experiments, it is possible that much of this disagreement is due to actual differences in digestion behaviour between different fish species. However, the confusion must also be a consequence of differences in the way the digestion experiments have been conducted and interpreted by different scientists. For example rather than allowing the fish population to initially feed freely and so obtain a range of initial stomach contents, some scientists have unnaturally force fed all individuals so that they initially have exactly the same amount of food in their stomach.

In some cases there has been confusion as to whether the evacuation data obtained from these two experiments is mean stomach contents depletion data or individual stomach contents depletion and as I will show later, the two are not at all interchangeable. Very noisy data may be produced if, for example the fish size range is very broad, which means the fish will be digesting at quite different rates, or if very small samples of fish are taken from a population where there is some variation in initial stomach contents. In which case it is likely that a variety of models will fit the data equally well (or badly) and results obtained in such cases cannot be relied on too greatly. Consistency between studies has also been hampered by inadequacies in actually fitting models to the data, with some authors completely ignoring particular models for no apparent reason. Consequently, the literature on this subject is rather confused (reviewed in Bromley 1994) and so I shall discuss only what I consider to be the most important steps which have been made towards understanding the dynamics of the digestion process.

Early attempts made by Hunt (1960), Daan (1973) and Swenson and Smith (1973) at fitting this general model for various fish species resulted in a linear depletion model, i.e. with c equal to zero. While more recently, a number of scientists have argued that a value of c equal to one, which gives an exponential evacuation model, has been found to best describe the observed stomach contents depletion curve (for example Elliott 1972, Cochran and Adelman 1982, MacDonald et al. 1982 and Persson 1986).

An alternative model has been constructed based on the physiology of the digestion process. The emptying of the gut is regulated by peristaltic contractions which in turn are stimulated by the radial gastric distension. Taking the stomach of a fish to be approximately cylindrical with a constant length, then the tension is proportional to the radius of the cylinder which increases with the square root of the volume (or weight) of stomach contents (Hopkins 1966). Tyler (1970) and Fange and Grove (1979) suggested the constant should be equal to two thirds due to the fact that the food is broken down by enzymes secreted in the stomach which act on the surface of the food bolus whose area is proportional to $(\text{volume})^{2/3}$. Jobling (1981) compared fractional values of a half and two thirds for the constant c with the fit of the exponential model to data from El-Shamy (1976) and showed that the square root option (c equal to a half) gave the best fit to most of the data sets analysed.

Five years later Persson argued that contrary to Jobling (1981), the exponential model generally gave a better approximation of the pattern of food evacuation than the square root model for most fishes studied. He reassessed twenty two data sets and found that in ten cases, taking c equal to one produced a better fit than the others, though this is still not particularly conclusive evidence since he had twelve data sets where one of the other models was the best. He also rejected the biological reasoning behind the square root model. After making stomach size measurements he argued that the stomach could not be approximated by a cylinder of constant length since increasing the amount of food in the stomach increased the length and so the radius will not increase linearly.

It seems possible that since observations of mean stomach contents were not straight lines Persson felt that a linear depletion model was unlikely to be the best fit to the data and chose to ignore this possibility. However, a feasible explanation as to why the gradient of the mean stomach contents depletion curve decreases at low stomach contents levels is given in three much more recent papers by Bromley (1987, 1988, 1991) who supports the case for a linear evacuation model. Even in the type of digestion experiment described earlier where we are dealing with similarly sized fish exposed to the same amount of food , there will be some variability in the stomach contents of the population at the start of the experiment as the individuals will not consume exactly the same amount of food. Some fishes stomachs will therefore contain more than the mean and some will contain less. Supposing that all individuals in the population digest food at the same rate, then those starting with less food in their stomachs will become empty in a much shorter time than those which begin the experiment with a higher stomach content. Bromley (1988) pointed out that due to this initial variation in stomach contents, towards the end of an evacuation experiment the proportion of a population of fish with empty stomachs increases significantly since their gut contents cannot fall below zero. So, the mean stomach contents will decrease more slowly than expected giving the impression that at lower levels of gut fullness the evacuation rate is less. Taking this into consideration Bromley fitted a linear model to his data using the method of maximum likelihood. Just how this censoring in the stomach contents data depends on the variation in the initial stomach contents distribution of the population will be discussed later in this chapter.

The following sections of this chapter go on to look at the relationship between individual and population models and compare the main features of the three plausible models. It then goes on to discuss whether or not digestion data can be easily distinguished as linear, exponential or fractional.

2.2 Digestion models for a non-feeding individual

Section 2.1 highlighted the three main alternative descriptions of the digestion process of an individual as being the linear, exponential and two thirds model. In this section I will compare the shapes of the alternative digestion models which can be used to describe a non-feeding population of fish.

If I first consider the case of linear digestion i.e. c equal to zero in equation 2.2, then

$$W(t) = \begin{cases} W_0 - Kt & \text{if } 0 \le t \le K / W_0 \\ 0 & \text{otherwise} \end{cases} \tag{2.3}$$

describes the reduction in stomach contents with time where W_0 is the stomach contents at t equal to zero. So, while not feeding, the fishes gut weight falls at a constant rate until it reaches zero at time $\frac{W_0}{K}$ which is where it stays, since negative stomach contents are impossible.

When digestion follows the fractional relationship

$$\frac{dW(t)}{dt} = \begin{cases} -KW(t)^{\frac{2}{3}} & w > 0 \\ 0 & \text{otherwise} \end{cases}, \tag{2.4}$$

the reduction of the stomach contents of the non-feeding individual can be expressed as

$$W(t)^{\frac{1}{3}} = \begin{cases} W_0^{\frac{1}{3}} - \frac{Kt}{3} & 0 \le t \le \frac{3W_0^{1/3}}{K} \\ 0 & \text{otherwise} \end{cases}. \tag{2.5}$$

until the individual becomes empty, at time $\frac{3W_0^{\frac{1}{3}}}{K}$, when it stops digesting and the stomach contents remain at zero.

When c is equal to one in equation 2.2, the digestion process follows an exponential relationship and the depletion of stomach contents for a non-feeding individual can be written as

$$W(t) = W_0 e^{-Kt}. \tag{2.6}$$

In contrast to the linear and fractional digestion models, the stomach contents of an individual following an exponential digestion model will not reach zero in finite time, which is illustrated in figure 2.2.

Figure 2.2 shows how different the three models representing the depletion of an individual fishes stomach contents actually are. Suppose I know that a particular fish which initially has ten grams of food in its gut, empties its stomach of all measurable contents in approximately thirty hours, but I do not know what happens in between. Any of the three above models could adequately describe the digestion process by choosing the appropriate value of K, though the shape of the curves they generate is completely different.

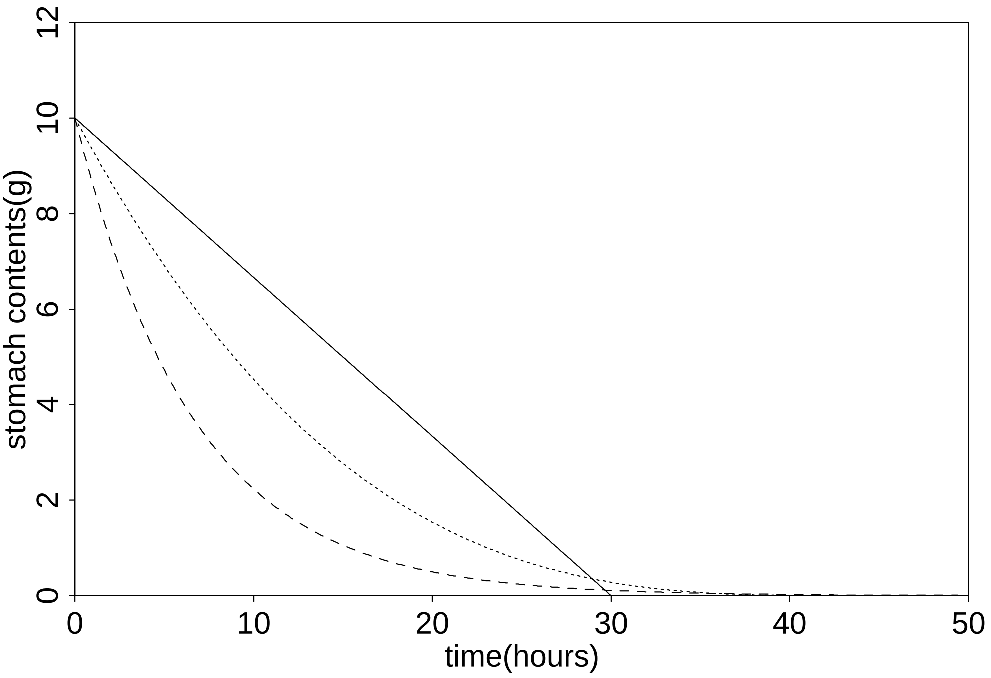


Figure 2.2. Stomach contents depletion curves for an individual fish following a) linear digestion (solid line, K=0.33), b) two thirds (dotted line, K=0.15) and c) the exponential digestion model (dashed line, K=0.15).

Since investigations into digestion are not usually constructed around a single non-feeding fish, but rather a population, I shall show in the next section how population digestion models can be formed and how the shape of the digestion curves is altered.

2.3 Population digestion models

2.3.1 The theory of modelling population digestion

Previous attempts at modelling the digestion process have concentrated on models which consider only the stomach contents of an individual or the average stomach contents of a population. As I have already mentioned, there will be some variation in stomach contents at any one time even in a closed population of similarly sized fish, for example those kept in the tank for use in the digestion experiments described in section 2.1. Much of the detail of this variation in the population is lost when considering only the mean stomach contents, since a particular mean value could result from a variety of distributions of gut fullness.

Clearly the way to overcome this loss of detail is to employ the use of a distribution function in the model to represent the variation in the stomach fullness of a closed population of similarly sized and aged fish. I define a distribution function f(w,t) such that f(w,t)dw represents the proportion of the population who have stomach contents with weights in the range w-dw to w at time t. For mathematical convenience I assume that f(w,t) is defined on the domain w>0 and choose a separate notation, $P_e(t)$, to represent the proportion of empty stomachs at time t. The rationale behind this set-up is that it prevents the build up of a delta function and discontinuities in the distribution function at w=0. An obvious constraint here is that since we are dealing with a closed population, summation of the empties and of f(w,t) over the complete range of stomach weights will include the entire population

$$P_e(t) + \int_0^\infty f(w,t)dw = 1. \tag{2.7}$$

If I assume that an individual whose stomach contains w grams of prey at time t eliminates material continuously from the gut at a rate D(w) grams per hour, then since we are dealing with a closed, non-feeding population, conservation of numbers implies that

$$\frac{\partial f(w,t)}{\partial t} = \frac{\partial}{\partial w}(D(w)f(w,t)) \qquad w > 0 \tag{2.8}$$

and

$$\frac{dP_e(t)}{dt} = D(0^+)f(0^+,t) \tag{2.9}$$

I use the notation 0^+ to denote a place infinitesimally on the positive side of zero.

I now need to decide what form the function D(w) should take by comparing the digestion curves of populations whose individuals follow 1) linear digestion, 2) fractional digestion and 3) the exponential digestion model.

2.3.2 The linear population digestion model

If I follow Bromleys theory about digestion and assume that the digestion rate of all individuals in a closed population of similarly sized and aged fish is a constant K grams per unit time provided that there is food left in the stomach to eliminate, and zero otherwise. Then

$$D(w) = K \qquad w > 0 \qquad (2.10).$$

So, equations (2.8) and (2.9) simplify to become

$$\frac{\partial f(w,t)}{\partial t} = K\frac{\partial f(w,t)}{\partial w} \tag{2.11}$$

which has an absorbing boundary at $w = 0^+$, and

$$\frac{dP_e(t)}{dt} = Kf(0^+,t). \tag{2.12}$$

The above set of differential equations can then easily be solved given a set of initial conditions. Suppose that the population has just been fed a meal and is then prevented from any further feeding. If I suppose that the initial stomach contents distribution is $f_0(w)$ for w>0 and $P_e(0)=0$ then equations (2.11) and (2.12) have the solutions

$$f(w,t)=f_0(w+Kt) \tag{2.13}$$

and

$$P_e(t)=\int_0^{Kt} f_0(x)dx \tag{2.14}$$

which simply corresponds to the initial distribution moving leftwards at a constant rate K with P_e accumulating all the probability which sweeps out into the absorbing boundary at zero.

The stationary solutions, P_e^* and $f^*(w)$, occur as t tends to infinity. So,

$$P_e^* = \lim_{t\to\infty} P_e(t) = \int_0^{\infty} f_0(x)dx \tag{2.15}$$

which is equal to one by definition of the stomach contents distribution function. Substituting this into the conservation condition (2.7) leads us to the solution $f^*(w)$=0 ″w>0. So under conditions of no feeding, there is a steady state solution which occurs when all the fish have empty stomachs, which is as expected.

Supposing that the population has just been fed a meal which leaves them with a normal stomach contents distribution with mean μ_0 and standard deviation σ. Then the position of the peak of the distribution decreases as

$$\mu(t)=\mu_0-Kt \tag{2.16}$$

while the shape of the distribution remains the same (σ is constant) as the distribution is just moving to the left at a constant rate.

Since we are assuming that the weight of stomach contents of an individual can take any positive value, then an expression for the mean stomach contents of the population can be written as

$$\overline{W(t)} = \int_0^\infty \frac{x}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{x-\mu(t)}{\sigma}\right)^2} dx . \tag{2.17}$$

Letting $z = \left(\frac{x - \mu(t)}{\sigma}\right)$, the above equation becomes

$$\overline{W(t)} = \int_{\frac{-\mu(t)}{\sigma}}^{\infty} \frac{(\sigma z + \mu(t))}{\sqrt{2\pi}} e^{-\frac{1}{2}z^2} dz \tag{2.18}$$

which with some manipulation gives a semi-analytic expression for the depletion in average stomach contents with time

$$\overline{W(t)} = \frac{\sigma}{\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{-\mu(t)}{\sigma}\right)^2} + \mu(t)\left(1 - F\left(\frac{-\mu(t)}{\sigma}\right)\right) \tag{2.19}$$

where F is the standardised cumulative normal probability distribution.

It is not obvious from this expression how altering the size of the standard deviation of the initial distribution affects the shape of the average stomach contents depletion curve, as increasing the standard deviation increases the first term, but decreases the second. However, some simple calculations made using expression (2.19) and illustrated in figure 2.3 show that for the broader initial distribution the deviation from the linearity begins earlier than for a narrower distribution which is a straight line until the last few hours of digestion.

Figure 2.3 also illustrates the increase in empty stomachs during the digestion process and shows that in the population which initially has a quite broad initial stomach contents distribution (standard deviation equal to three), the accumulation of the population in the empty stomach category begins quite early and is much more gradual than for the narrow initial distribution case who all become empty over a much shorter period of time.

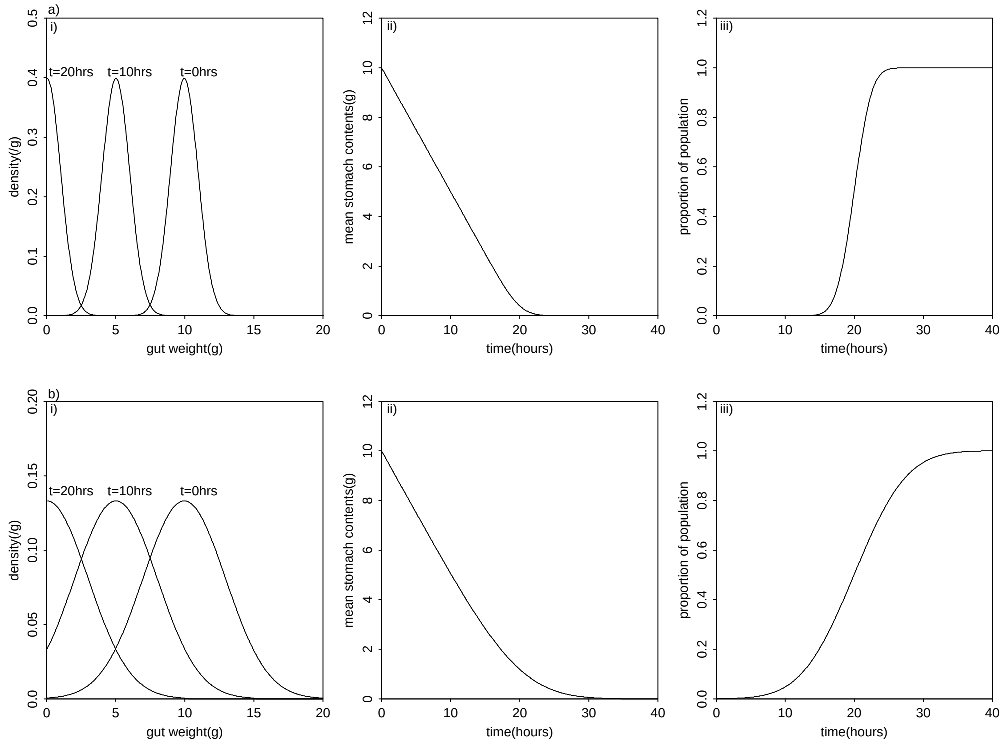


Figure 2.3. The progression of initial stomach contents distributions (i) shown together with their corresponding mean stomach contents depletion curves (ii) and variation in proportion of empty stomachs (iii) for a population whose individuals digest linearly at a rate equal to 0.5. The initial distributions are normal with identical means of ten grams and standard deviations of a) one and b) three.

2.3.3 The fractional population digestion model

When the digestion rate of the individuals in a population is proportional to their stomach contents to the power two thirds, equations (2.8) and (2.9) become

$$\frac{\partial f(w,t)}{\partial t} = Kw^{2/3}\frac{\partial f(w,t)}{\partial w} \tag{2.20}$$

and

$$\frac{dP_e(t)}{dt} = Kw^{2/3}f(0^+,t). \tag{2.21}$$

Although an analytic solution cannot be found to this pair of differential equations, given an initial stomach contents distribution, the progression of the distribution function can be calculated numerically and is pictured in figure 2.4i.

In the fractional digestion model, as the digestion rate is proportional to the stomach contents to the power two thirds, those individuals with large amounts in their stomachs will digest faster than those with lower stomach contents. So, the shape of the stomach contents distribution narrows during the digestion process and this is illustrated in figure 2.4i. It was shown in section 2.2 though, that individuals digesting in such a way do become empty and so there will be some censoring observed in the mean stomach contents curve, as some individuals become empty faster than others and consequently the mean stomach contents decreases slower than expected. However, the censoring which takes place in this model is much less obvious than that which occurs in the linear model, as the distribution function has narrowed considerably and majority of the population have stomach contents quite tightly packed around the mean value as they approach zero. As a consequence, the mean stomach contents depletion curves generated from two very different initial distributions are quite similar (figure 2.4ii).

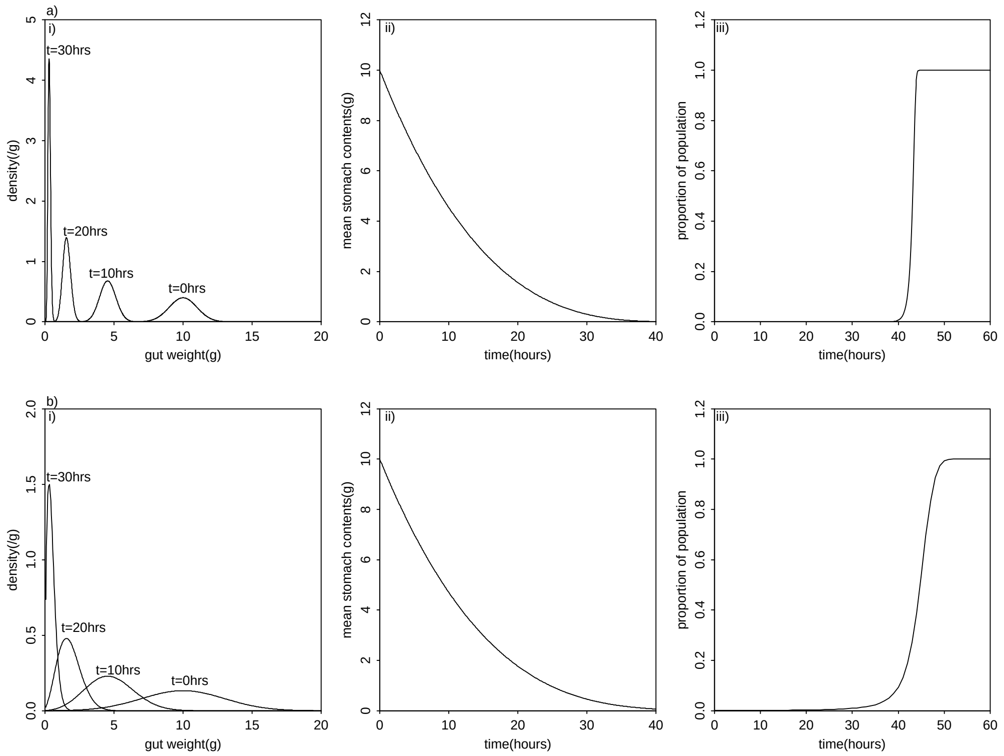


Figure 2.4. The progression of two different initial stomach contents distributions (i) together with their corresponding mean stomach contents curves (ii) and variation in the proportion of empty stomachs (iii) for a population whose individuals follow a fractional digestion model with rate constant 0.15. The initial distributions have mean ten grams and s.d. of a) one and b) three.

The effects of the narrowing stomach contents distribution are also seen in the variation in the proportion of the population with zero stomach contents. Initially this proportion increases quite gradually (figure 2.4bii) as the stomach contents distribution is quite broad and so there are some individuals with relatively low stomach contents. By the time the peak of the distribution reaches zero, it has become so narrow that the remainder of the population become empty over a very short period of time. So, the sharp increase in the proportion of fish with empty stomachs is followed by a fairly sudden halt as all the population have become empty.

2.3.4 The exponential population digestion model

Looking now at the model in which the individuals of a population follow the exponential digestion model i.e. D(w)=Kw for all w. Then equations (2.8) and (2.9) become

$$\frac{\partial f(w,t)}{\partial t} = Kw\frac{\partial f(w,t)}{\partial w} \tag{2.22}$$

and

$$\frac{dP_e(t)}{dt} = Kwf(0^+,t) \tag{2.23}$$

which again can only be solved numerically.

As in the fractional digestion model, the digestion rate is dependent on the current stomach contents of the individual concerned, so the stomach contents distribution will likewise narrow as the digestion process continues which is shown in figure 2.5i. In this case however, an individuals stomach contents never actually reach zero so the narrowing distribution continues to narrow and builds up as a delta function at $w = 0^+$. To overcome the problems caused by the delta function at zero, the numerical solution of the problem is halted before much significant build up occurs.

In the exponential model an individuals stomach contents never actually reach zero, they only tend to zero as time tends to infinity, so if there are initially zero fish with empty stomachs, then this is true for all time (figure 2.5iii), and there is no censoring of the mean stomach contents depletion curve as illustrated in figure 2.5ii. This is shown analytically in the following section.

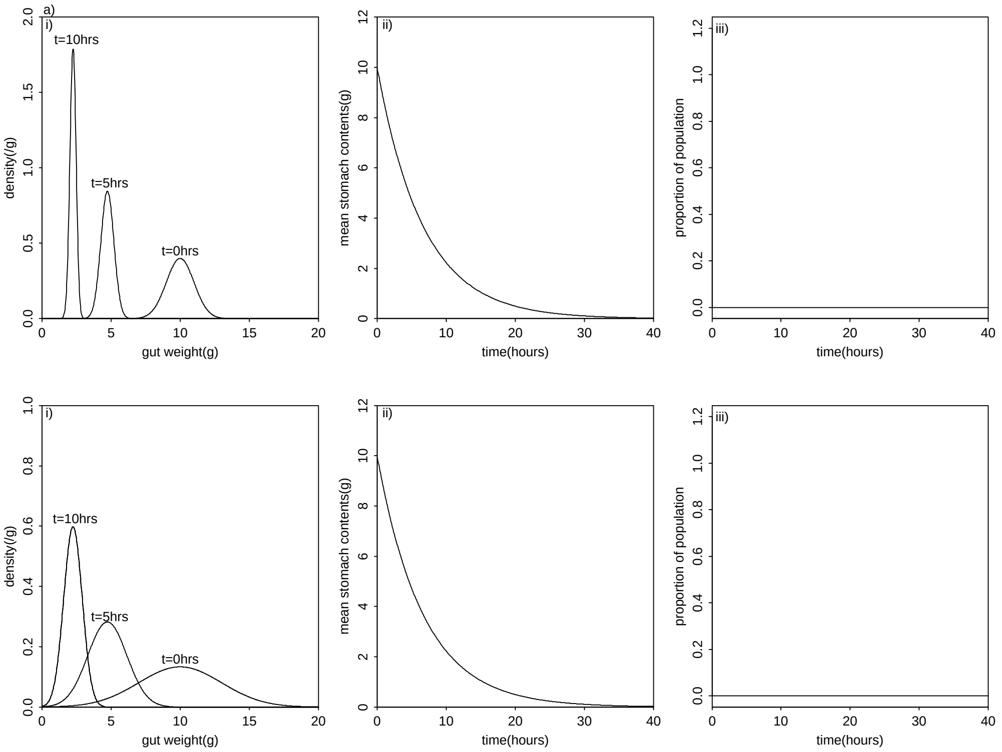


Figure 2.5. The progression of two different initial stomach contents distributions (i) together with their corresponding mean stomach contents curves (ii) and variation in the proportion of empty stomachs (iii) for a population whose individuals digest exponentially with rate 0.15. The initial distributions have mean ten grams and s.d. of a) one and b) three.

Consider a population of N fish each following the individual exponential digestion model with an identical digestion rate constant (K) and individual stomach contents W_i (i=1..N)

$$\frac{dW_i}{dt} = -KW_i \qquad i = 1..N \tag{2.24}$$

Then, summing all the individual stomach contents and dividing the total by the number of fish in the population gives the average gut contents

$$\overline{W(t)} = \frac{1}{N}\sum_{i=1}^{N} W_i(t). \tag{2.25}$$

Differentiating this expression for the mean gut contents of the population gives

$$\frac{d\overline{W}}{dt} = \frac{1}{N}\sum_{i=1}^{N}\frac{dW_i}{dt} \tag{2.26}$$

and substituting from equation (2.24) we get

$$\frac{d\overline{W}}{dt} = -\frac{K}{N}\sum_{i=1}^{N} W_i \tag{2.27}$$

$$= -K\overline{W}.$$

which shows that in the case of exponential individual stomach contents depletion, the mean stomach contents follow exactly the same curve as that of an individual whose initial stomach contents are equal to the population mean i.e.

$$\overline{W(t)} = \overline{W_0}e^{-Kt} \tag{2.28}$$

where $\overline{W_0}$ is the initial mean stomach contents.

2.3.5 Comparison of models

All the initial distributions observed so far have been normal with mean ten grams and standard deviations small enough so that the shape of the distribution is not initially truncated at zero. However, if the standard deviation is much larger than about three grams, then the initial mean will be censored for all digestion models. For example, if the initial distribution has a standard deviation of eight and a mean of ten grams, then there will be some individuals who start off with empty stomachs and the calculated initial mean stomach content will be larger then expected for all three digestion models.

This initial distribution produces greatly censored linear and fractional digestion curves since the effects of empty stomachs is already taking effect at zero time.

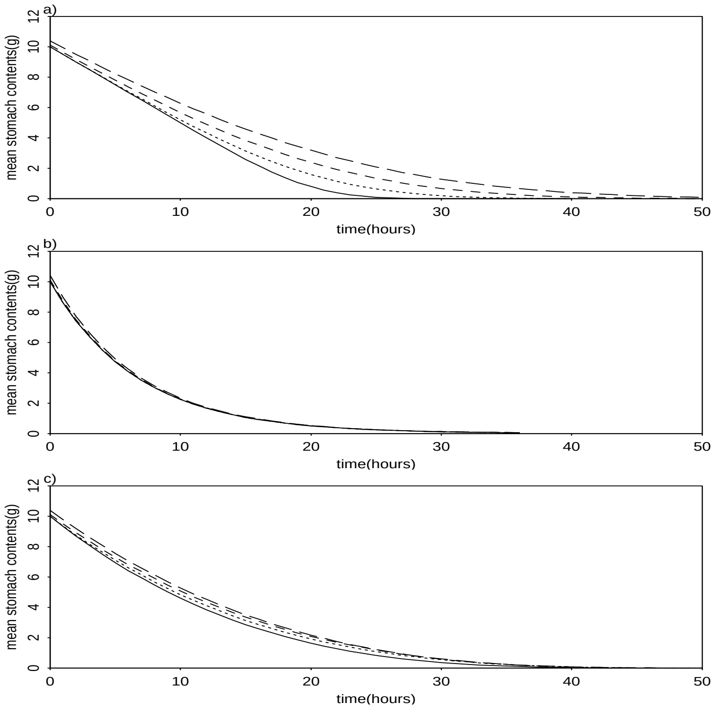


Figure 2.6 Depletion of mean stomach contents with time for populations whose individuals follow a) a linear digestion model (K=0.5), b) an exponential digestion model (K=0.15) and c) a fractional digestion model (K=0.15) having a normal initial distribution with mean ten and standard deviations two (solid), four (dotted), six (dashed) and eight (long-dashed).

However, the effect of this very broad initial stomach contents distribution on the exponential digestion curve (shown in figure 2.6b) is just to raise the curve by a fixed proportion at each point without changing its shape, since no more fish become empty during digestion. The use of this initial distribution in the case of the exponential model is unnecessary as I showed analytically in the previous section and these raised curves could just as easily have been produced by increasing the initial mean stomach contents in equation (2.28).

2.4 Uniqueness of digestion curves

The previous section illustrated the great difference in the shapes of the population digestion curves produced from different digestion models with identical initial stomach contents distribution and showed the extent of the effect of different initial stomach contents distributions on a population following a particular digestion model. The question which now needs to be considered is whether a mean stomach contents depletion curve obtained from one model and set of parameters, can be replicated using one of the other models and a different set of parameters (i.e. a different initial distribution and digestion constant). I shall approach this problem by generating a set of digestion data from one of the models and then attempting to fit the other models to this data by varying the model parameters and minimising the mean of the sum of the squared errors. The data set can be generated by sampling the mean stomach contents at hourly intervals. As my optimisation routine I have chosen a version of the simplex method (Nelder and Mead (1965)) which although rather inefficient in the number of function evaluations required for convergence, works quite quickly when the computational burden is not too big. (Chapter 4 describes in more detail the variety of available optimisation routines.)

Calculations of the mean stomach contents depletion curves for the exponential and linear models are fairly straightforward due to the expressions (2.20) and (2.28). The expression which generates the linear population digestion curve involves the calculation of standardised cumulative normal probabilities which are easily accomplished using the appropriate NAG routine, while expression (2.28) which describes the depletion of mean stomach contents for a population with exponential digestion is just a simple negative exponential function. However, to gain the corresponding curve from the fractional digestion model is decidedly more time consuming as the problem must be solved numerically. The speed of solution is further hampered by the need for very fine discretisation in the space dimension which is required to avoid problems in the numerical solution as the stomach contents distribution narrows and reaches zero.

Initially, I shall regard the mean stomach contents sampled at hourly intervals from the fractional model with a particular set of parameters as my set of data.

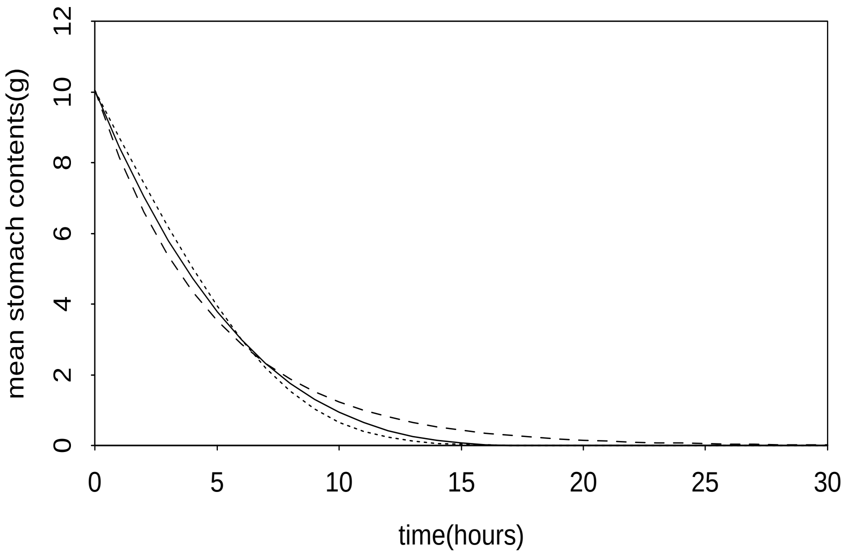


Figure 2.7. Mean stomach contents depletion curve for a population of fish with normal initial stomach contents distribution (mean 10 grams and standard deviation 5) whose individuals follow a fractional digestion model with rate constant 0.4 (solid line), with the most closely fitting linear digestion (dotted) and exponential digestion (dashed) curves.

Keeping the initial stomach contents distributions identical to that used in the fractional depletion curve data set, I shall initially attempt to fit the exponential and linear models by varying only the digestion rate constant K. The initial stomach weight distribution is normal with mean ten and standard deviation five and the population digestion rate constant is 0.4. The exponential and linear depletion curves which most closely fit the fractional digestion model curve are shown in figure 2.7.

Although the linear model produces a curve which is quite similar to that of the fractional model, it is still easily distinguished as it is much straighter. The identifying feature of the exponential model is its very long tail which, combined with the initial quite fast mean stomach contents depletion, gives a less adequate fit to the data than the linear model. The fitted digestion rates of the linear and exponential models are given in table 2.1 along with their mean squared errors.

Model	Digestion rate	Mean square error
Linear	1.37	0.02
Exponential	0.21	0.04

Table 2.1. Digestion rates and mean square error values of the best linear and exponential fits to the data generated by a population with a normal initial stomach contents distribution with μ equal to 10 grams and σ equal to 5 following a fractional digestion model with rate constant 0.4.

An improvement to the fit of the two models could be made by allowing the parameters defining the shape of the initial stomach contents distribution to vary, in addition to the digestion rate constant K. The initial distributions are truncated at zero and the remaining proportion of individuals are put into the empty stomach category. So, when fitting the linear model, there are three fitting parameters - K (digestion rate constant), μ (position of the peak in the initial stomach contents distribution) and σ (the initial standard deviation), while for the exponential model there are only two - the digestion rate constant K and the initial mean stomach contents, $\overline{W_0}$.

The new curves fitted to the same fractional digestion data are illustrated in figure 2.8 and the best fit parameters are shown in table 2.2. Predictably the fit of both models has improved. The nearest fitting mean stomach contents curve produced by the linear model is very close to being indistinguishable from the fractional data with a mean squared error of 0.0007. This implies that we can only distinguish between the two if the initial distribution of the stomach contents is known.

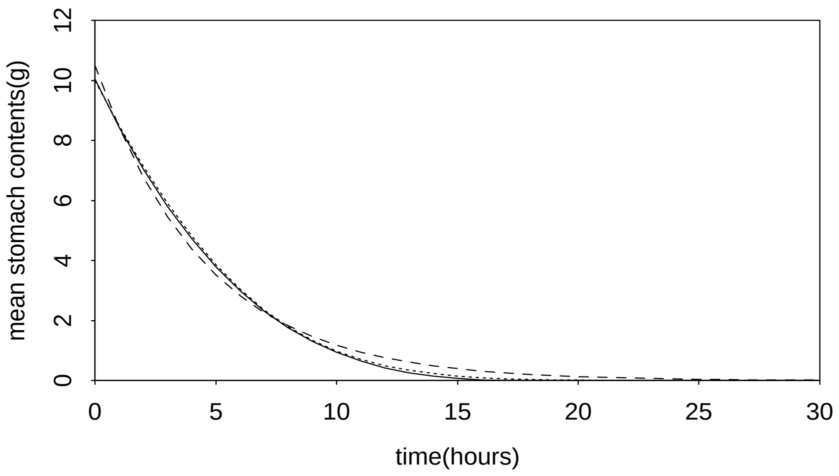


Figure 2.8. The linear digestion (dotted) and exponential digestion (dashed) curves which best fit the fractional digestion curve (initial mean 10 grams, standard deviation 5 and rate constant 0.4, solid line) when all three parameters are allowed to vary.

In this case, the initial stomach contents distributions are quite different with the linear initial distribution being much broader and positioned nearer to zero. The higher standard deviation produces the early deviation from linear stomach contents depletion which is required if the fractional shape is to be imitated closely, while the lower value of μ prevents the initial mean stomach contents from being too high.

The high digestion rate is required as there are many individuals in the population with very high stomach contents which would otherwise take a very long time to empty their stomachs. The exponential model once again proves to be a less accurate fit to the fractionally generated data due mainly to the very long tail.

Model	Initial conditions	K	Mean sq. error
Linear	μ=7.88, σ=12.81	2.12	0.0007
Fractional	μ=10, σ=5	0.4	0 (actual data)
Exponential	$\overline{W_0}$ =10.5	0.22	0.03

Table 2.2. Parameter values for the best fitting linear and exponential models along with those from which the fractional data was generated.

I have shown that for a particular set of data generated using the fractional digestion model an almost indistinguishable set can be produced by linear digestion while the exponential mean stomach contents depletion curve decreases too slowly for very low stomach contents. The question which now arises is whether a set of data generated from a linear digestion model can be fitted as well by the fractional model.

In this example I shall reverse the fitting procedure and take the mean stomach contents sampled at hourly intervals from an evacuation curve produced by a population with linear digestion as the data set and attempt to fit the fractional and exponential models by varying both the digestion rate and initial stomach contents distribution. The stomach contents of the population which follows a linear digestion model with rate 0.25 grams per hour are initially normally distributed with μ equal to ten grams and the standard deviation five. This broad initial distribution will produce a mean stomach contents depletion curve which very early on becomes censored, deviates away from the straight line and is therefore likely to be quite closely copied by the other two models. The best fitting exponential and fractional curves are shown in figure 2.9.

It appears from this illustration that most of the error in the exponential model is due to the height of the tail as the stomach contents approach zero. Extending the fit to 160 hours in an attempt to pull the exponential tail down towards zero does not significantly change the shape of the curve as even very small changes to the height of the tail are associated with very large changes earlier on. To significantly reduce the tail would require the exponential to be initially very much steeper which would provide a worse fit to the first half of the linear digestion curve.

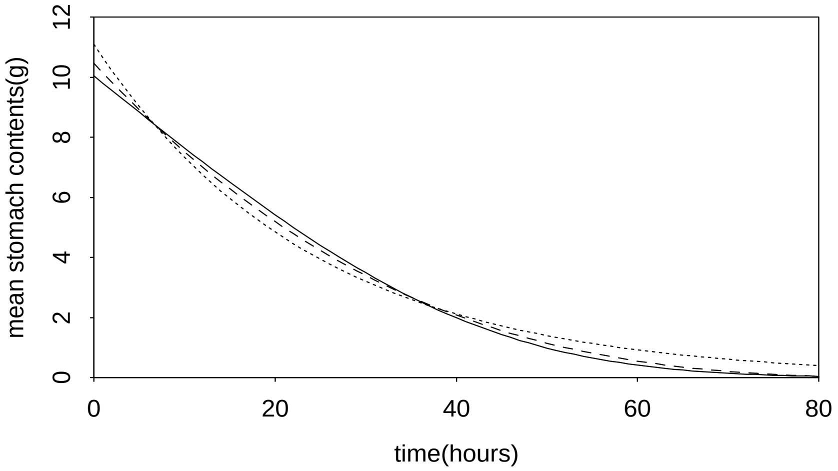


Figure 2.9. Stomach contents depletion curve of a population with normal initial gut contents distribution (mean 10, standard deviation 5) whose individuals follow a linear digestion scheme with digestion rate 0.25 grams per hour, together with its closest fitting exponential (dotted) and fractional (dashed) digestion curves.

Predictably, the fractional model most closely fits the linear digestion data, but the minimum mean squared error value is surprisingly large when compared to that which occurred when the reverse fitting procedure was carried out in the previous example.

The mean squared deviation of the fractional model from the linear data in this example is in fact almost thirty times that which resulted when the reverse fitting was carried out in the previous example (tables 2.2 and 2.3). This could either be due to the particular example which has been chosen or it could be that for some reason we can get a closer fit to fractional data using the linear model than the other way around.

Model	Initial conditions	K	Mean sq. error
Linear	μ=10, σ=5	0.25	0 (actual data)
Fractional	μ=10.46, σ=0.28	0.07	0.02
Exponential	$\overline{W_0} = 11.10$	0.04	0.19

Table 2.3. Parameter values of the best fitting fractional and exponential models, together with linear model parameters from which the data set was generated.

To investigate this possibility, I shall now take the resulting best fit fractional model parameters to generate a new set of data and refit the linear digestion model to it. The resulting fit is a great improvement and the best fit parameters are shown in table 2.4, together with the minimum mean squared error.

Model	Initial conditions	K	Mean sq. error
Linear	μ=7.64, σ=9.83	2.10	0.0014
Fractional	μ=10.46, σ=0.28	0.07	0 (actual data)

Table 2.4. Parameter values of the refitted linear digestion model.

When the fractional model was fitted to the linear data, the resulting parameters indicated that a very narrow initial stomach contents distribution was required to produce this 'best fit', although the actual data had been generated from a linear digestion model where the population started with quite a broad initial distribution. However fitting the other way round indicated that the linear model must have an extremely broad and truncated initial distribution to fit the fractional data, even when this data had been generated by a population whose initial stomach contents distribution was very narrow. As the fractional model is fitted to the linear data, it reduces the initial standard deviation, thereby removing any censoring. The fractional curve though, even with a delta function as its initial stomach contents distribution and therefore no censoring, will always be curved and hence may not be able to get very close to fitting a linear data set. On the other hand, the initial distribution is able to get broader and broader, so that the censoring in the digestion curve begins as soon as the digestion process starts and consequently linear digestion curves can be forced to deviate far from linearity and produce very good fits to data generated from fractional digestion models.

These results show how similar digestion curves produced by populations following different digestion schemes can be. In particular, the fractional and linear digestion models are sometimes visually indistinguishable and we can only conclude which model the data came from if we also have some knowledge of the initial stomach contents distribution of the population. The exponential model is generally quite easily recognisable due to the very long tail in the digestion curve as stomach contents get low. However, if very accurate methods and instruments are unavailable when collecting experimental data, this tail in unlikely to be apparent and the digestion data could possibly be indistinguishable from the fractional or linear model. Experimental data is always going to be noisy as the samples of fish used are never going to be very large. It is possible therefore, that even with just a small amount of noise in the data all three models may become indistinguishable, which is what I shall investigate in the following section.

2.5 Simulated data

So far the digestion curves have been produced by assuming that the distribution of fish stomach contents follows a perfect normal distribution. However, in practice, digestion curves will not be so exact. Experimental mean stomach contents depletion curves are constructed by sampling a particular number of individuals from a non-feeding population of fish at fixed time intervals.

In an attempt to simulate typical experimental data I have solved the digestion models numerically, outputting the exact solution at fixed time intervals. The stomach contents range is divided into many small equal categories and the proportion of the population in each interval at each time step is recorded. The unit interval is then divided into intervals each of width equal to these proportions. At each sample point, a simulated data sample is produced by generating a set of pseudo-random numbers between zero and one and counting the proportion which fall into each interval. This gives the noisy numerical distribution from which the mean stomach contents are calculated.

Figure 2.10 shows some examples of noisy initial distributions where the sample has been taken from a population whose initial distribution is normal with m equal to ten and a standard deviation of three grams. Although all three distributions appear to be quite noisy, we can establish just by looking that the mean stomach contents in each case is not far from ten grams.

Given that the digestion curve is noisy, there will be no exact fit by any set of parameters and digestion model, even the one from which it was generated. The closeness of the fit will depend on the size of the sample i.e. on the number of random numbers which are generated. The question that I wish to answer is how easily can we distinguish the fit of the 'wrong' model from that of the 'right' digestion model, when the digestion curve becomes noisy.

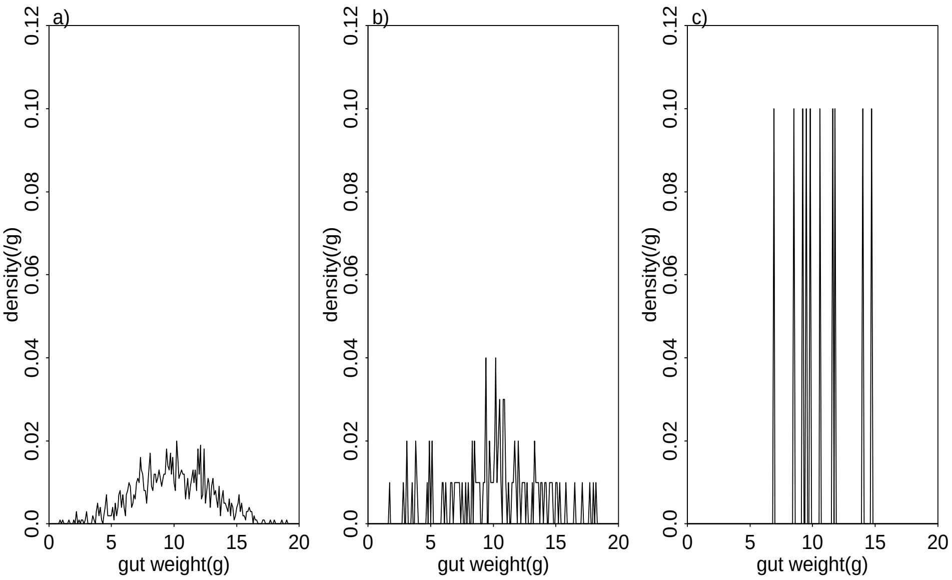


Figure 2.10. Noisy distribution simulated by taking samples of a) 1000, b) 100, and c) 10 individuals from a normal distribution with μ equal to ten grams and σ equal to three. The actual mean values are a) 9.92 grams, b) 10.09 grams and c) 10.66 grams.

I have chosen three examples to answer this question, in which both the parameters defining the populations initial stomach contents distribution and the digestion rate constant are varied. The first example is of data sampled from a population whose initial stomach contents distribution is normal with mean 10 grams and standard deviation 5 whose individuals follow the linear digestion model with a digestion rate of 0.25 grams per hour. When the digestion curve is free of noise, obviously the minimum mean squared error of the fitted linear model is zero. Predictably, when a digestion curve is obtained via population samples this mean squared error increases, but this is true of the error measure of all three models. (Compare table 2.5 to table 2.3 in section 2.4). For a large sample of 1000 individuals the digestion curve which is shown in figure 2.11a does not look very noisy. The minimum mean squared error of the fractional model is five times that of the linear and the exponential over twenty times greater, so the data set is still distinguishable as linear.

Sample size	Model	Initial conditions	K	Mean sq. error
1000	Linear	m=9.93, s=4.71	0.24	0.01
	Fractional	m=10.45, s=5.7	0.08	0.05
	Exponential	$\overline{W_0} = 11.03$	0.04	0.21
100	Linear	m=9.93, s=4.31	0.23	0.09
	Fractional	m=10.43, s=9.3	0.08	0.12
	Exponential	$\overline{W_0} = 11.06$	0.04	0.30
10	Linear	m=9.62, s=3.94	0.21	0.95
	Fractional	m=10.07, s=0.8	0.06	1.00
	Exponential	$\overline{W_0} = 10.70$	0.04	1.19

Table 2.5. Fitted parameters and minimum mean squared errors of the three models fitted to noisy digestion curves generated by taking samples from a population of fish with a normal initial stomach contents distribution with μ equal to ten grams and σ equal to five whose individuals all digest linearly at a rate of 0.25 grams per hour.

However, as the sample size is decreased, the error measures all become much larger and it becomes less obvious by which model the data has been produced. For a sample size of ten individuals which is comparable to the numbers of fish used in actual digestion experiments, the digestion curve which is shown in figure 2.11b has become quite noisy. Although the best fitting linear model still gives an error measure which is slightly lower than the other two models, the three minimum mean squared errors are almost equal and the data can only be distinguished as linear or fractional if we know what the initial stomach contents distribution looked like. Table 2.5 shows the initial conditions which are required to produce the best fits for each of the three models. The fractional model requires an extremely narrow distribution to fit the data, while the exponential model achieves its best fit to the data by pushing $\overline{W_0}$ well above its observed value. The narrowness of this distribution is perhaps a little unrealistic, which could be a reason for ruling out the fractional model which leaves the linear model as a slightly better fit than the exponential model to the data.

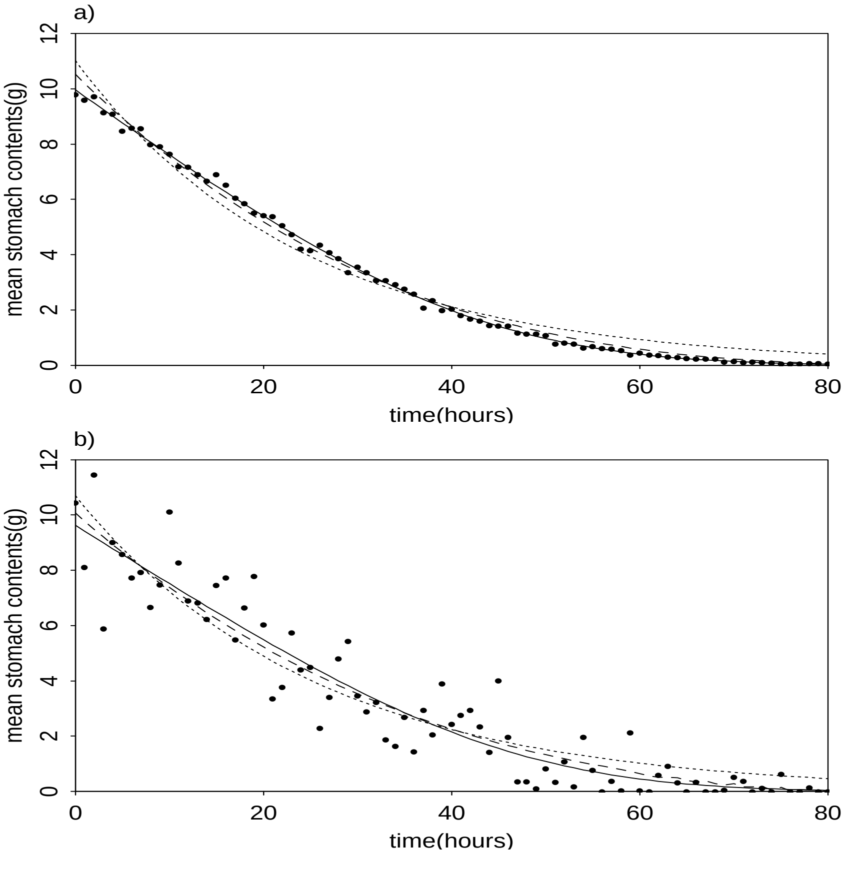


Figure 2.11. Noisy linear data (points) generated by taking samples of size a) 1000 and b) 10 with their closest fitting exact linear (solid), exponential (dotted) and fractional (dashed) digestion curves .

My second set of examples are generated using the fractional digestion model. The population initially has a normally shaped stomach contents distribution with mean 10 grams and standard deviation 1.5 and the individuals all follow the fractional digestion model with rate constant 0.2. In section 2.4 I showed how well the linear model could be fitted to fractional data and that the two models could only be distinguished if their initial stomach contents distributions are known. When the same fitting procedure is carried out on data which has been simulated by sampling from stomach contents distributions generated by the fractional model, similar confusion arises.

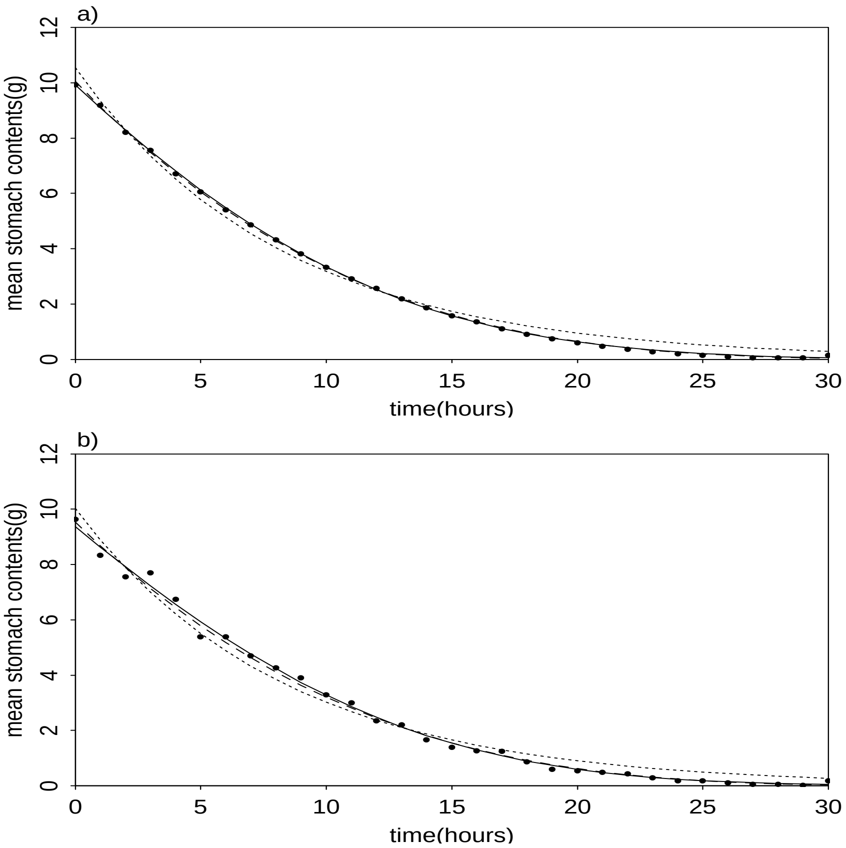


Figure 2.12. Noisy fractional data (points) generated by taking samples of size a) 1000 and b) 10 with their closest fitting exact linear (solid), fractional (dashed) and exponential (dotted) digestion curves. ((b) appears less noisy when compared to 2.11b as σ is much smaller and therefore the occurrence of extreme values is less likely and consequently the mean more like its expected value).

The resulting parameters and minimum mean squared errors for the three models with differing sample sizes are shown in table 2.6 and the corresponding digestion curves are illustrated in figure 2.12.

For all sample sizes, the fitted exponential curve gives a minimum mean squared error which is much larger than the other two models and therefore even when these fractional data are quite noisy, it is quite clear that it has not been sampled from a population which is digesting exponentially.

Sample size	Model	Initial conditions	K	Mean sq. error
1000	Linear	m=8.42,s=11.32	1.10	0.002
	Fractional	m=10.04,s=3.11	0.21	0.003
	Exponential	$\overline{W_0} = 10.54$	0.12	0.080
100	Linear	m=7.7, s=12.94	1.20	0.005
	Fractional	m=9.95, s=2.28	0.20	0.003
	Exponential	$\overline{W_0} = 10.48$	0.12	0.075
10	Linear	m=8.8, s=8.10	0.87	0.033
	Fractional	m=9.53, s=2.35	0.20	0.038
	Exponential	$\overline{W_0} = 10.03$	0.12	0.122

Table 2.6. Mean squared errors of the three models fitted to noisy digestion curves generated by taking samples from a population of fish whose initial gut contents distribution is normal with mean 10 and standard deviation 1.5 whose individuals follow the fractional digestion model with rate constant 0.2.

However, once again the linear and fractional models give very similar least mean square errors for all sample sizes. In fact for a sample size of ten, the linear model gives a slightly better fit to the fractionally generated data than the fractional model itself. The only way to distinguish which model the data is generated by, is to consider how realistic the initial stomach contents distributions are. For all sample sizes the initial stomach contents distributions required by the two models are very different with the linear model requiring a very broad normal distribution. So, if we know that the initial distribution is not particularly broad then we could conclude that the data came from a population whose individuals follow a fractional digestion model.

The final set of digestion curves which are to be studied are those produced by a population which has a normal initial stomach contents distribution with mean 10 grams and standard deviation 2.5 and whose individuals digestion exponentially with rate constant 0.15. Table 2.7 shows the resulting best fit parameters and minimum mean squared errors.

The fractional model gives a much worse fit to the data than the other two models even for very small sample sizes, but the linear minimum mean squared errors are of approximately the same size as those of the exponential model. Looking at the parameters resulting from the fitting procedure, our attention is instantly drawn to those predicted by the linear model. The initial distribution requires a massive width and a large negative value for μ, while the digestion rate is also predicted as being extremely large. These values are obviously exceedingly unlikely and we can safely conclude that the data was sampled from a population following the exponential digestion model. The 'best fit' curves for samples of size 1000 and 10 are illustrated in figure 2.13.

Sample size	Model	Initial conditions	K	Mean sq. error
1000	Linear	$\mu = -3.9\times10^{10}$, $\sigma = 6.9\times10^{9}$	1.7×10^{8}	0.003
	Fractional	m=9.46, s=3.45	0.26	0.057
	Exponential	$\overline{W_0} = 9.98$	0.15	0.002
100	Linear	$\mu = -7.0\times10^{8}$, $\sigma = 1.4\times10^{8}$	3.9×10^{6}	0.004
	Fractional	m=9.63, s=3.50	0.26	0.046
	Exponential	$\overline{W_0} = 10.14$	0.15	0.005
10	Linear	$\mu = -2.3\times10^{6}$, $\sigma = 6.1\times10^{6}$	1.9×10^{4}	0.041
	Fractional	m=8.96, s=3.32	0.24	0.072
	Exponential	$\overline{W_0} = 9.46$	0.14	0.042

Table 2.7. Fitted parameter and least mean squares of the three models fitted to noisy digestion curves generated by taking samples from a population of fish with normally distributed initial stomach contents with μ equal to ten grams, σ equal to 2.5 grams, digesting exponentially with a rate constant of 0.15.

The extremely odd values predicted by the linear model can be explained by considering how the linear model changes shape to fit the exponential shaped data. The exponential is far from linear and the linearity in the digestion curve produced by the linear digestion model decreases as the standard deviation of the initial stomach contents distribution increases. So, obviously a very large standard deviation is required for a linear digestion curve to look anywhere near exponential. To maintain the correct value of the initial mean stomach contents ($\overline{W_0}$), the value of μ must decrease as the standard deviation increases. In this case, the standard deviation is so large that a very large negative value of μ is predicted. Finally, since there are some individuals in the sample with extremely high stomach contents, an unfeasibly high digestion rate is required to obtain the correct gradient for the digestion curve.

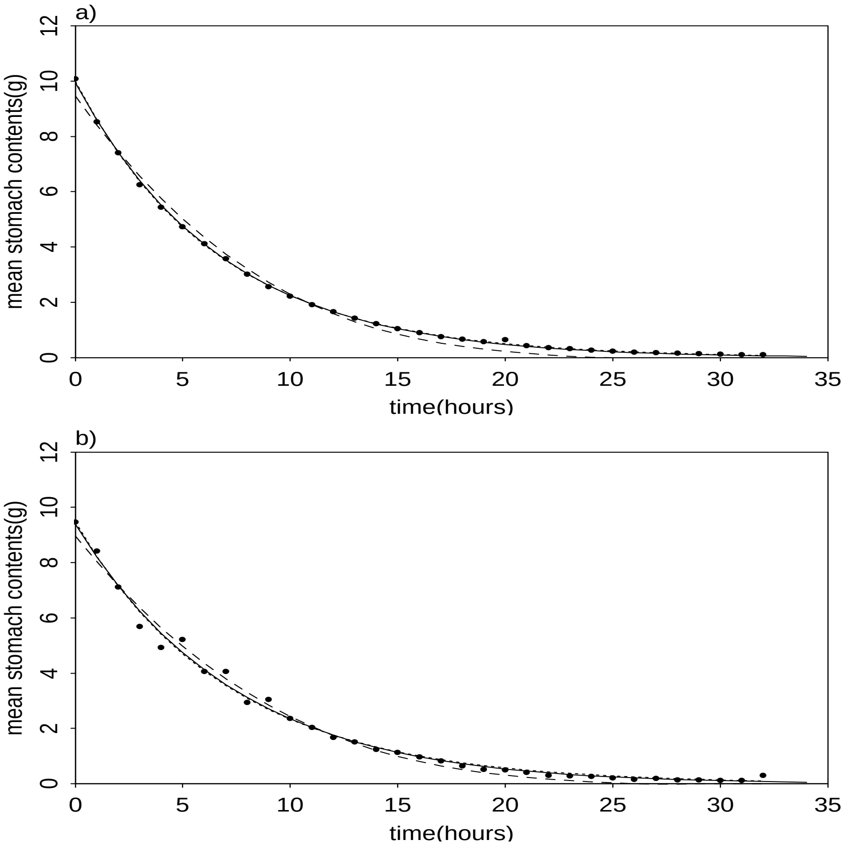


Figure 2.13. Noisy exponential data (points) generated by taking samples of size a) 1000 and b) 10 with their closest fitting exact linear (solid), fractional (dashed) and exponential (dotted) digestion curves.

These sets of examples show how digestion curves produced by taking even very large samples can often be indistinguishable as being generated from a particular model and when sample sizes as low as ten are used it is possible that all three models may give equally good fits to the data. Most experimental digestion curves are constructed by taking samples of around ten fish at each time interval and calculating their mean stomach contents. So given the above results it seems unlikely that when considering experimental data, it will be possible to make definite conclusions about the digestion model which the population follows. In this case the only option is to look at the predicted initial stomach contents distribution and hope that one model gives a more sensible prediction than the other two.

2.6 A comparison with real data

The previous sections have shown how difficult it can be to distinguish between digestion curves even when sample sizes are still quite large. In this section I shall re-examine some sets of experimental data, which in general are produced by taking quite small samples, and attempt to decide what digestion model the population is following. Extensive digestion experiments have been carried out by Elliott (throughout the 1970's), Jobling (during the 1970's and 80's) and Bromley (more recently), so I shall take some of their data sets for re-examination. However, the three authors carried out their experiments differently and the resulting data sets therefore have to be treated differently.

Elliott (1972) investigated gastric evacuation of brown trout. In his experiments he fed exactly twenty prey items (*Gammus pulex*) of similar size (approximately 9 mm in length) to all individuals in his initial population of fish, so there would only be a very slight variation (if any) in initial stomach contents across the population. By sampling ten trout every three hours he calculated the mean dried stomach contents and constructed the digestion curve. The data appears to be exponential and is illustrated in figure 2.14.

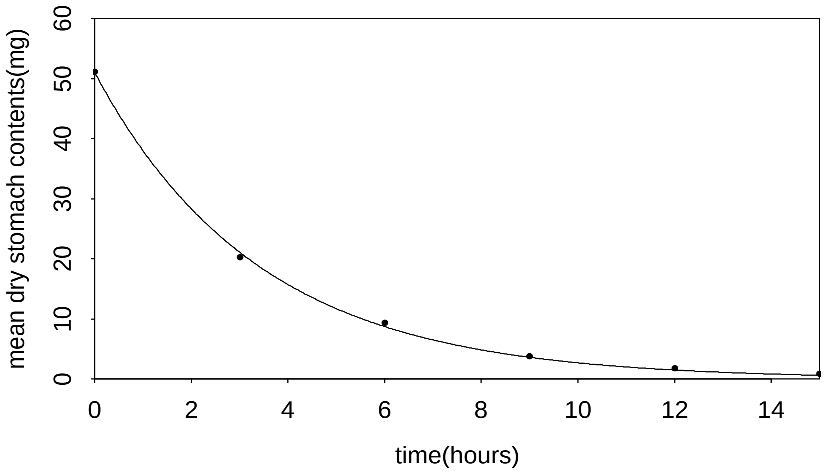


Figure 2.14. Elliotts evacuation data for trout (points) together with the fitted exponential digestion curve.

I attempted to fit the three models and as expected the exponential was the one to give the most sensible results. Both the linear and fractional models required very broad initial distributions to generate a curve which anywhere fitted the data, contrary to the actual initial stomach contents distribution which as I have already concluded will be very narrow. The digestion curve produced by the exponential model is independent of the width of the initial distribution and is only regulated by the initial mean stomach contents and digestion rate constant. The exponential model in fact provides a very accurate fit to the data with a minimum mean squared error of 0.26 which is quite small compared to the magnitude of the data and so there can be no doubt that these fish are digesting exponentially.

Work on digestion in plaice was carried out by Jobling and Spencer Davies (1979). Their digestion experiments consisted of force feeding groups of fish with exact volumes of food and then weighing the dried stomach contents of pairs of fish sampled from the population at approximately two hourly intervals. The fish in these experiments all initially contained the same amount of food as they had been fed precisely the same amounts via an intra-gastric tube. In this case it would be foolish to attempt to fit curves generated by models in which the initial stomach contents distribution is allowed to vary, as the initial stomach contents of all fish in the population is equal and known. Instead I fitted the individual digestion curves given in section 2.2 by varying only the digestion rate constant K and holding W_0 fixed at the measured value. The results of the four experiments in which the initial amount of food differs, are shown in figure 2.15.

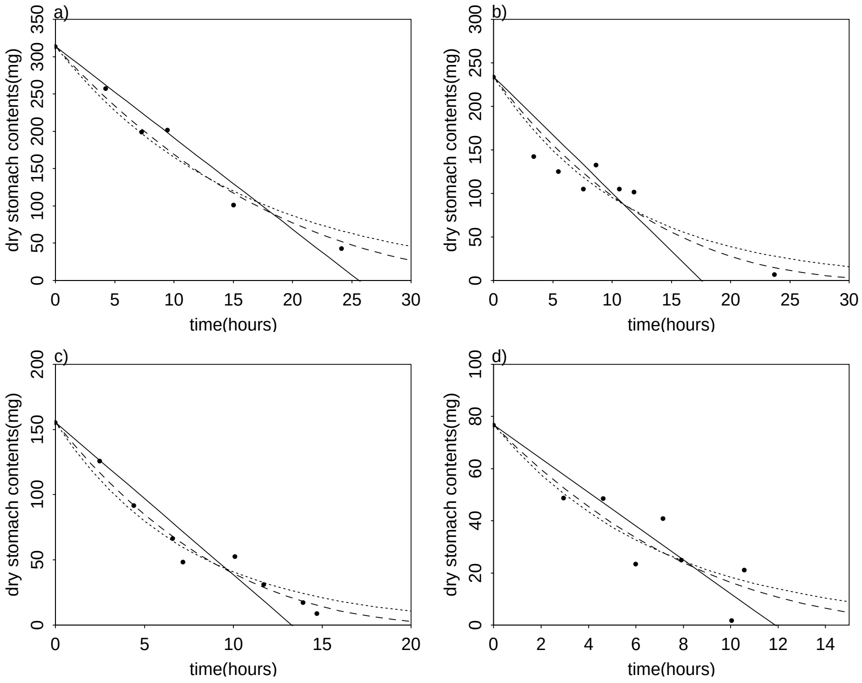


Figure 2.15. Joblings evacuation data (points) with its fitted individual linear (solid), fractional (dashed) and exponential (dotted) digestion curves for meals of approximately a) 315 mg, b) 234 mg, c) 155 mg and d) 77 mg.

Since all the individuals in these experiments initially have equal stomach contents, then if the individuals in the population were identical, they should all be digesting identically and the data should lie perfectly on a curve generated by a particular individual digestion model. The data from all four experiments though is very noisy. The most likely explanation for this seems to be the very broad range of fish sizes being used (15g-33g). Fishes of different sizes digest at different rates, so since some of the fish in this population are twice the size of others, the stomach contents of all the individuals will not remain identical over the sampling period and so the samples taken may appear quite noisy. Fitting the model to the data is also hampered by the limited number of data points towards the lower end of the evacuation curve. In none of the four examples is there a clear indication of whether the stomach contents have reached zero or whether there is a tail present. No further stomach samples were taken later on to confirm what was happening. The noisiness of the data is reflected in the large values of the minimum mean squared errors compared to the average dry stomach contents over the time period and are shown in table 2.8.

	Model	K	Mean sq. error
Set a	Linear	12.3	356
	Fractional	0.38	201
	Exponential	0.06	368
Set b	Linear	13.4	659
	Fractional	0.47	425
	Exponential	0.09	390
Set c	Linear	11.7	177
	Fractional	0.59	56
	Exponential	0.13	80
Set d	Linear	6.5	83
	Fractional	0.51	75
	Exponential	0.14	79

Table 2.8. The 'best fit' values of K and the minimum mean squared errors for the three individual models fitted to Joblings plaice data.

This combination of noisy data and scarcity of data points during parts of the evacuation period implies that any conclusions that have been drawn from this data may be very unreliable. For example in data set a, the two-thirds digestion model seems to best fit the data points, but this is one of the cases in which it would be helpful to have some later data points. The fractional model predicts a tail in the evacuation curve which goes on past the last available data point and since we have no idea of what is going on here we do not know if this prediction is valid. If the sampling had gone on longer and revealed that the stomachs had already all reached zero, then the fit of the fractional model would worsen and that of the linear would improve. The results for set b seem to indicate that the linear model is a much worse fit to the data than the other two. This result however may not be correct as once again it is impossible to decide from the data points what is happening towards the end of the digestion period. The last two data samples are taken so far apart that we cannot tell whether the stomach contents have been zero for long (which would favour the linear digestion model) or whether they have been gradually tailing off.

Looking at all the data sets together, my results seem to indicate that the fractional model is on average the best fit to the data. However, due to the noise and scarcity of the data points, this conclusion cannot be regarded as particularly reliable.

The final sets of data have been taken from a paper by Bromley (1988) on evacuation in whiting. Although Bromley claims that linear digestion model is appropriate for whiting feeding on meals of frozen sand-eels, he does not consider any of the other options. His digestion experiments consisted of batches of similarly sized whiting freely feeding to satiation, two-thirds satiation and one fifth satiation. Groups of ten fish were sampled at intervals after feeding and their mean stomach contents measured. Since the fish in these experiments have been allowed to feed of their own accord, some individuals will have managed to consume more prey items than others and therefore the population will have an unknown initial stomach contents distribution. So, the population digestion models are fitted to this data by allowing the initial conditions and digestion rate to vary. The resulting parameters are shown in table 2.9 and the data plus best fit curves are illustrated in figure 2.16.

	Model	Initial conditions	K	Mean sq. error
Satiation	Linear	μ=23.99, σ=6.72	0.32	0.80
	Fractional	μ=24.67, σ=8.14	0.05	1.94
	Exponential	$\overline{W_0} = 25.44$	0.02	3.04
2/3 Satiation	Linear	μ=15.61, σ=15.52	0.49	0.05
	Fractional	μ=16.50, σ=0.23	0.07	0.04
	Exponential	$\overline{W_0} = 17.18$	0.03	0.34
1/5 Satiation	Linear	μ=5.50, σ=4.53	0.31	0.32
	Fractional	μ=5.58, σ=1.00	0.09	0.36
	Exponential	$\overline{W_0} = 6.11$	0.07	0.34

Table 2.9. The 'best fit' parameter sets to the Bromley data obtained by the simplex method together with the minimised mean square error.

Comparing the minimum mean squared errors obtained for the three models indicates the linear model as a clear best fit to the satiation data which is not too noisy (see figure 2.16). In the other two examples, the best model is not so obvious. In the two-thirds satiation case, the fractional model also fits the data very well and all three models fit the one-fifth satiation data equally well.

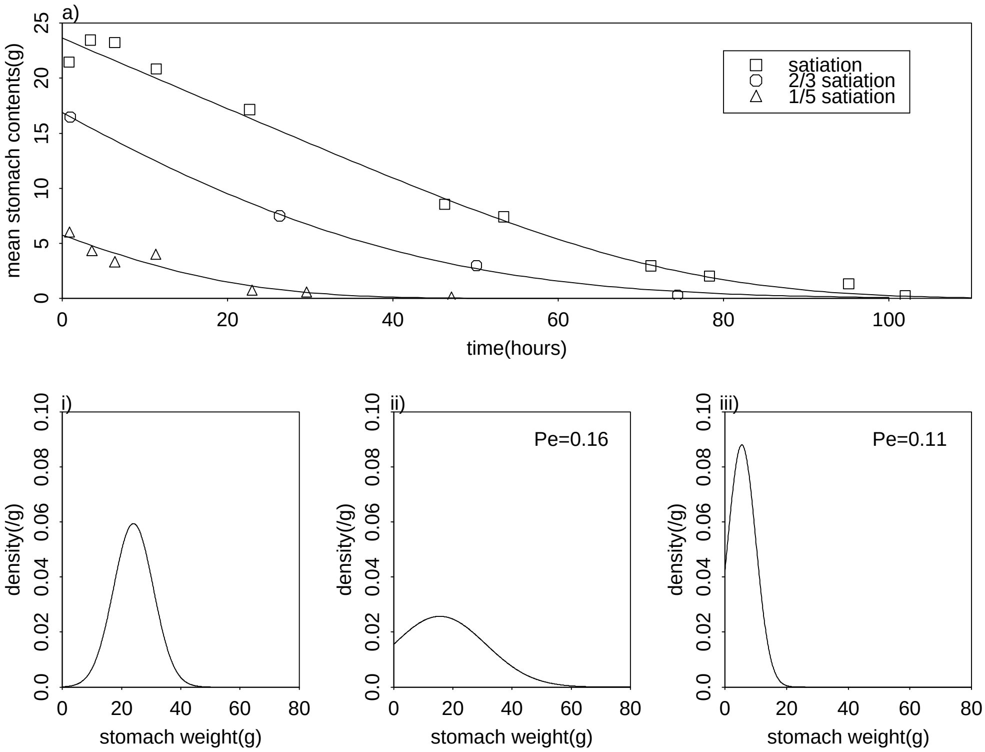


Figure 2.16a. The Bromley digestion data with fitted linear digestion curves and initial stomach contents distributions for i) satiation, ii) 2/3 satiation and iii) 1/5 satiation.

In the second data set the problem can be overcome by looking at the initial stomach contents distributions predicted by the two models. The fractional model predicts an unreasonably narrow initial stomach contents distribution (see table 2.9 and figure 2.16bii) and therefore I can conclude that the linear digestion model is a more reasonable fit. In the final data set, however, the initial conditions required by all three models seem fairly believable, so in this case I am not able to make a similar conclusion. Overall however, these results seem to agree with Bromley that the linear model is most appropriate in the description of his digestion data.

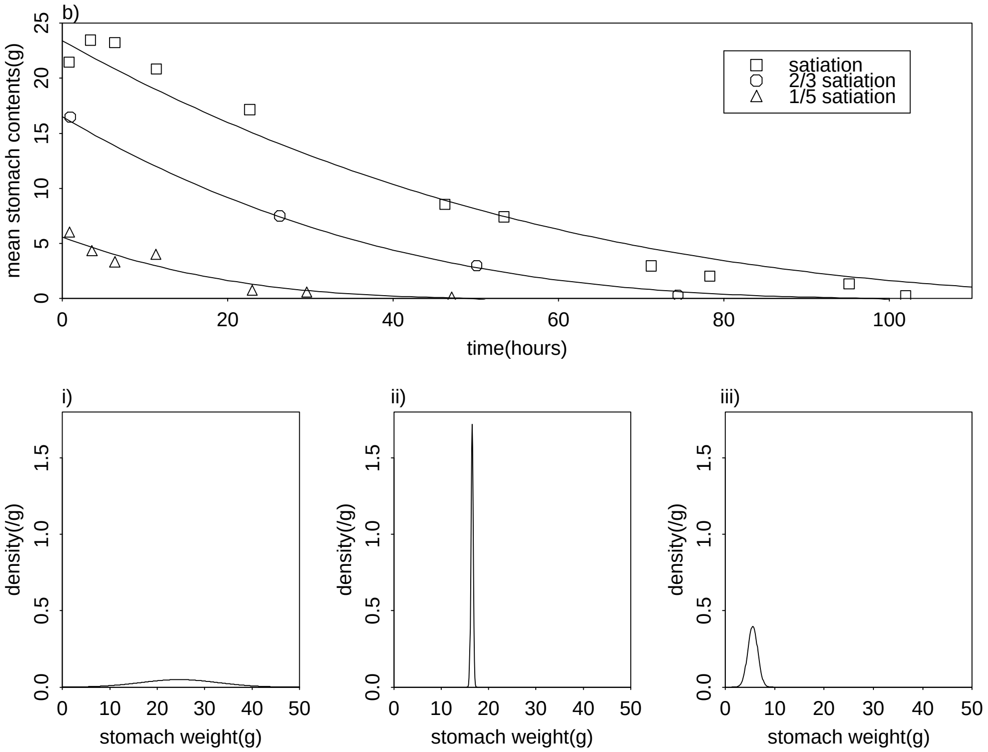


Figure 2.16b. The Bromley digestion data with fitted fractional digestion curves and initial stomach contents distributions for i) satiation, ii) 2/3 satiation and iii) 1/5 satiation

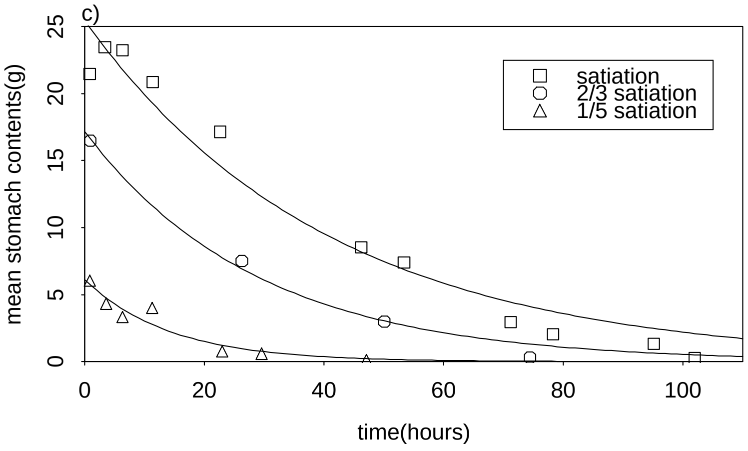


Figure 2.16c. The Bromley digestion data with fitted exponential digestion curves.

In this chapter I have explained the dynamics of the various individual digestion models and shown how the shape of the digestion curves generated by a population of fish depend on the initial distribution of stomach contents of that population. Sections 2.5 and 2.6 have shown how it is often very difficult to distinguish whether evacuation data has been produced by a population digesting linearly, fractionally or even exponentially when the data is quite noisy and the initial stomach contents distribution of the population is unknown.

For the purpose of this thesis I am most interested in the common marine fish species inhabiting the sea lochs of the west coast of Scotland, two of which are whiting and plaice. So, given the quite strong indication that whiting follow a linear digestion model, for the remainder of this thesis I shall assume a linear digestion process. However, one of the advantages of the feeding and digestion model which I shall go on to construct in chapter 3 is that the digestion rule can be quite easily altered by substituting in a different expression for D(w), the digestion rate and the numerical solutions can then be carried out in a similar way.

Chapter 3

A model of feeding and digestion

3.0 Introduction

In chapter two I considered the mechanics of the digestion process and formulated a model to describe the variation in the stomach contents distribution of a non-feeding population of fish after the consumption of a single meal. I shall now attempt to extend the model to include feeding and thus form a realistic picture of the daily variation in stomach contents. Before deciding how to include feeding into the partial differential equation model which represents the non-feeding case, I shall highlight some of the main factors governing their feeding behaviour.

Most of the theories about the feeding behaviour of marine fish have largely been deduced from calculations based on stomach contents data collected from the field coupled with laboratory feeding experiments. This is due to the huge practical difficulties of observing the fish in their natural habitat. In the wild, the time fish spend actually eating will be interrupted by time spent foraging for food and escaping from predators, but in order to survive a fish must eat enough food to enhance growth and provide the energy required to avoid predation. So, feeding will consist of a series of meals interrupted by the need to find new prey and avoid predators. This being the case, then it is unlikely that the fish will be feeding at a constant rate. Stomach contents samples taken by Brodeur and Pearcy (1987) and Hall et al. (1995) support this view. The paper by Brodeur and Pearcy (1987) also notes that there is a large variability between individual stomach contents at any one time implying that not all fish are feeding synchronously.

The feeding rate itself will be regulated by a number of factors including satiation, the availability of the desired food and the ability of the individual to catch it. Studies by Ivlev (1961), Magnuson (1969) and Elliott (1975) found that food acquisition during a period of feeding decreases as a result of satiation. Obviously if the population was exposed to a plentiful supply of food and food consumption was not regulated, then the fish would carry on feeding indefinitely and consequently the stomach contents would go on increasing without limit. The ability of an animal to catch its chosen prey also must be considered when discussing fish feeding habits and is regulated by prey behaviour and the presence of other competing predators. The concentration and availability of some prey species varies considerably during the day, with some being moved by the tides and others migrating through the water column with changes in light intensity. Many predators largely rely on sight to find and catch their prey, so most of their successful feeding activity will take place during the day, with very sporadic or zero feeding during darkness. A number of authors have found evidence to illustrate these variations. For example, after food consumption calculations made from stomach contents data, MacDonald and Waiwood (1986) argued that pleuronectides are solely daytime feeders, while Hall (1987) concluded from his calculations that dabs were primarily night-time feeders and did not rely on their sight to capture prey.

A population of identical individuals feeding on a source of identical prey will have a range of stomach contents when feeding ceases, due to the distribution of the prey relative to the predator population. However the exposure of a population of fish to a single species of similarly sized prey will only occur in laboratory experiments. In natural conditions, many prey species of a wide variety of sizes will be available to the population. Gut contents sampled from fish in the wild have included the remains of a wide variety of prey types (Hall et al. 1990) implying that fish are not particularly selective in what species they will and will not eat. Therefore, in the wild, a population of identical fish will be feeding on a range of meal sizes at any one time and will consequently have a range of stomach contents.

To build a model which could incorporate a detailed description of all the variations mentioned above would prove very difficult, so before going any further some simplifying assumptions are required.

3.1 Some assumptions about the feeding process

Previous feeding models have considered, like those for digestion, only individual stomach contents or the average stomach contents of a population of fish and have not considered the between fish variability in stomach contents. In fact most feeding models have just been based on the digestion models described in chapter one, but with the addition of an extra term, R(t), to represent the food consumption rate

$$\frac{dW(t)}{dt} = R(t) - KW(t)^c. \tag{3.1}$$

This model was used by Pennington (1985) in its most general form and by Elliott and Persson (1978), with c equal to one, to make estimates of the daily consumption of fish. Both these studies recognised that there was likely to be some variation in the gut weights even amongst individuals from a population of similarly sized and aged fish due to the variety of available meal sizes and in which case used mean feeding rates and mean stomach contents values in their calculations.

Equation (3.1) could quite adequately be used to describe the variation in the stomach contents of a feeding individual or the variation in average stomach contents of a population whose individuals are feeding identically and therefore all contain the same amount of food. However a population of fish in the wild will not have identical stomach contents and an alternative model needs to be formulated. In chapter two, I constructed a model which describes the time variation of the stomach contents distribution for a non-feeding population of fish. In this section I shall explain how this model can be extended to include the feeding process.

I will begin my discussion of the feeding process by considering what happens to the gut contents of a fish when it consumes a single meal. I shall assume that on ingestion of a meal of weight m, the stomach contents of an individual fish are increased from w to w+m grams i.e. the complete weight of the meal reaches the stomach. Since a meal consists of a rapid ingestion of food, it is not irrational to suppose that this increase in stomach contents takes place approximately instantaneously. This implies that unlike digestion, feeding is a discontinuous process as on consumption of a meal, the stomach contents jump immediately from w to w+m without passing through any of the values in between.

If I now return to the description of stomach contents distribution used in the digestion model, I can say that the proportion of fish with gut weights in the range w-dw to w at time t (f(w,t)dw) can only be changed by digestion or feeding. Considering for the moment only the effects of feeding, then an increase in this proportion is produced by feeding activity among individuals with lower gut weights or empty guts who manage to ingest a meal of exactly the right size to take their gut contents into the range w-dw to w, while ingestion of a meal of any size by fish already in this category will reduce this proportion as individuals are moved to a higher gut weight.

I have already mentioned that many fish species have a very varied diet. However, a model which included information about the consumption of particular prey species would be extremely complicated to formulate and would have to include a great many parameters. Instead I shall consider all prey species together and assume that a meal taken by a fish at a particular time is the instantaneous ingestion of a single prey item.

As I discussed earlier, even a population of similarly sized fish feeding from an identical supply of prey will take various sized meals. Assuming that the same distribution of meals is available to the whole population, I will introduce a distribution function $\Phi(w, m, t)$ such that $\Phi(w, m, t)\,dmdt$ represents the probability that between time t and t+dt, an individual with current stomach contents w ingests a meal weighing between m and m+dm grams.

Using this definition, I can now write expressions for the rate at which fish leave and enter a particular stomach contents weight due to feeding. The rate at which individuals arrive at a gut weight of w from one of w-m is dependent on the rate at which they consume meals of size m. Since the rate of increase in category w to w+dw is due to the feeding activity in all lower classes, the total rate of entry from non-empty stomachs is

$$F(w, t) \equiv \int_0^w \Phi(w, m, t) f(w - m, t)\,dm \qquad (3.2).$$

Fish can also arrive at a gut weight of w from the empty stomach state when they eat a meal of exactly w grams in weight.

The fish population is feeding continuously, so that one meal is followed by another and a fish which has just gained a stomach contents of w will immediately move into a higher stomach weight category as another meal of any size is taken. So I can write

$$U(w, t) \equiv \int_0^\infty \Phi(w, m, t)\,dm \qquad (3.3)$$

as the average rate at which an individual with current gut weight w at time t ingests meals of any size, which is equivalent to the per capita rate at which individuals leave this weight due to feeding and move to a higher one.

These feeding terms can now be added to the digestion model (equation 2.11) to give a partial differential equation which describes the variation in the stomach contents distribution of a population of simultaneously feeding and digesting fish.

$$\frac{\partial f(w,t)}{\partial t} = K\frac{\partial f(w,t)}{\partial w} - U(w,t)f(w,t) + \Phi(w,w,t)P_e(t) + F(w,t) \qquad w > 0$$

(3.4)

The first term in the equation is due to the digestion process and describes the continuous constant depletion of the stomach contents of all individuals. The second term is the per capita rate at which individuals leave the stomach weight of w due to feeding multiplied by the proportion of individuals with this weight to give the total decrease in the proportion of the population with stomach weight w due to feeding. The last two terms in equation in the equation represent the rate of entry to stomach weight w due to feeding from lower stomach weights. F(w,t) is defined in equation (3.2) and the third term describes the rate at which individuals with empty stomachs eat meals of size w and so arrive at a stomach weight of w grams.

The feeding process only affects the empty category by removing individuals at a rate U(0,t). So, the rate of change of the proportion of the population with empty stomachs is given by

$$\frac{dP_e(t)}{dt} = Kf(0^+,t) - U(0,t)P_e(t). \qquad (3.5)$$

In its present form the definition of U(w,t) (equation 3.3) is quite general and does not explain the specific dependence on the initial stomach contents. Obviously feeding is reduced by satiation, which is controlled by stomach fullness (Hamilton 1965) and the dietary energy content of the food items consumed (Fletcher 1984). So, the model should include some limitations to the amount of food that can be eaten and the size of prey which the population is able to consume. The simplest way to include a fullness control is to say that an individual fish will refuse any meal which will take its stomach contents above a particular value w_F which represents the maximum stomach contents of all individuals in the population which is being considered. This assumption then implies that fish with empty stomachs will be able to eat meals with a wide variety of weights while fish which are almost full will only be able to eat small meals or will not eat at all. The meal size function can now be written as

$$\Phi(w,m,t)=\begin{cases}A(m,t) & 0<m\le w_F-w\\ 0 & \text{otherwise}\end{cases} \tag{3.6}$$

and the functions (3.2) and (3.3) can be simplified to

$$F(w,t)\equiv\int_0^w A(m,t)f(w-m,t)dm\,. \tag{3.7}$$

and

$$U(w,t)\equiv\int_0^{w_F-w} A(m,t)dm \qquad (3.8).$$

3.2 The constant feeding rate model

If I consider again the equations defining the model dynamics, it looks unlikely that it will be possible to find an analytic solution to the equations in their present form. A simplification can be made by supposing that the meal size distribution (A(m,t)) is a time independent function and can be written as RM(m) where R is a constant uptake rate and M(m) is a distribution function dependent on meal weight only. Although this supposition is made to simplify the mathematics of the problem, it is not a completely irrational assumption to make about the feeding behaviour of some fish species. For example, a population of non-visual feeders whose prey is permanently available i.e. unaffected by the tides or light intensity and who are not prone to predation by other animals may feed for long periods of time at a constant very low rate. The functions F(w,t) and U(w,) can then be rewritten as

$$F(w,t) = R\int_0^w M(m)f(w-m,t)dm, \tag{3.9}$$

and

$$U(w) = R\int_0^{w_F - w} M(m)dm \tag{3.10}$$

and the model equations become

$$\frac{\partial f(w,t)}{\partial t} = K\frac{\partial f(w,t)}{\partial w} - U(w)f(w,t) + RM(w)P_e(t) + F(w,t) \tag{3.11}$$

and

$$\frac{dP_e}{dt} = Kf(0^+,t) - RP_e(t). \tag{3.12}$$

Clearly if the constant feeding rate R is equal to zero, then these equations reduce to those defining the variation in stomach contents of non-feeding population of fish (equations 2.11 and 2.12).

In chapter two I explained how, after an initial transient, the digestion only equations reach a stationary solution in which the entire population have empty stomachs. A steady state solution will occur in this case when the proportion of fish leaving each of the categories due to feeding and digestion is balanced by the proportion entering them by digestion from above and feeding from below. If the stationary solutions of the above equation are denoted as previously, then clearly equation (3.12) implies that

$$P_e^* = \frac{Kf^*(0^+)}{R} \tag{3.13}$$

and equation (3.11) becomes

$$\frac{df^*(w)}{dw} = \frac{1}{K}\left[U(w)f^*(w) - RM(w)P_e^* - F^*(w)\right] \tag{3.14}$$

On substituting the expression for P_e^* into equation (3.14), we observe that $f^*(w)$ must satisfy the following differential equation

$$\begin{gathered} \frac{df^*(w)}{dw} = \frac{1}{K}\left[U(w)f^*(w) - \left(\frac{Kf^*(0^+)}{R}\right)RM(w) - F^*(w)\right]; \\ f^*(0) = f_0 \end{gathered} \tag{3.15}$$

and the condition

$$P_e^* + \int_0^\infty f^*(w)dw = 1 \tag{3.16}$$

where

$$\begin{aligned} F^*(w) &= R\int_0^w M(w-m)f^*(m)dm \\ &= R\int_0^w M(m)f^*(w-m)dm. \end{aligned} \tag{3.17}$$

This problem cannot be solved, however, without knowing the value of the initial condition, $f^*(0^+)$. Suppose I divide through equation (3.15) by $f^*(0^+)$ to give

$$\frac{d}{dw}\left(\frac{f^*(w)}{f^*(0)}\right)=\frac{1}{K}\left[U(w)\left(\frac{f^*(w)}{f^*(0)}\right)-KM(w)-\frac{F^*(w)}{f^*(0)}\right] \tag{3.18}$$

and introduce a new function

$$g^*(w)=\frac{f^*(w)}{f^*(0)}, \tag{3.19}$$

then we obtain the differential equation

$$\frac{dg^*(w)}{dw}=\frac{1}{K}\left[U(w)g^*(w)-KM(w)-G^*(w)\right];\ \ g^*(0)=1 \tag{3.20}$$

where

$$G^*(w)=R\int_0^w M(m)g^*(w-m)dm\,, \tag{3.21}$$

which can be solved for $g^*(w)$ with no dependence on the value of $f^*(0^+)$. If the solution of equation (3.20) is $g_o(w)$ then the solution of (3.15), $f^*(w)$, is just a multiple of this, $f^*(0^+)g_o(w)$. However, the solution of equation (3.15) must also satisfy condition (3.16). Substituting the expressions for $f^*(w)$ and P_e^* into (3.16) gives

$$\frac{Kf^*(0^+)}{R}+\int_0^\infty f^*(0^+)g_o(w)dw=1 \tag{3.22}$$

which on rearranging gives

$$f^*(0^+)=\frac{1}{\dfrac{K}{R}+\displaystyle\int_0^\infty g_o(w)dw}. \tag{3.23}$$

The stomach contents distribution function can then be written as

$$f^*(w) = \left(\frac{1}{\frac{K}{R} + \int_0^\infty g_o(w)dw} \right) g_o(w) \qquad (3.33)$$

and the proportion of the population with empty stomachs in the stationary state is

$$P_e^* = \frac{1}{1 + \frac{R}{K}\int_0^\infty g_o(w)} \qquad (3.34)$$

where $g_o(w)$ is the solution of equation (3.20).

Although the steady state equation (3.14) (or equation 3.20) is much simplified in comparison to the time dependent case, it is still a relatively complicated differential equation due to the term $F^*(w)$ and cannot readily be solved analytically. However, given a particular meal size distribution, the functions U(w) and $F^*(w)$ can easily be calculated using a numerical integration scheme, for example the trapezium or rectangular rule. The ordinary differential equation can then be solved using a fourth order Runge-Kutta method provided that values for the feeding rate, R, the digestion rate and the 'initial' condition $f^*(0^+)$ have been supplied, and P_e^* can be calculated from (3.12). This method is implemented in a standard software package SOLVER (Gurney et al 1992) with adaptive step-size and accuracy control. Initially I have assumed that the meal size distribution is shaped like a normal distribution (truncated at zero and renormalised if necessary), with mean equal to 1 gram, standard deviation 0.5 and feeding rate 0.1 meals per hour. The solutions of equation (3.15) produced by choosing different initial conditions are illustrated in figure 3.1, which confirms that $f^*(0^+)$ in equation (3.15) is just a scaling factor in the solution before normalisation. Hence the solution can be calculated by solving equation 3.15 with any chosen value of f_0 and renormalising the numerical solution.

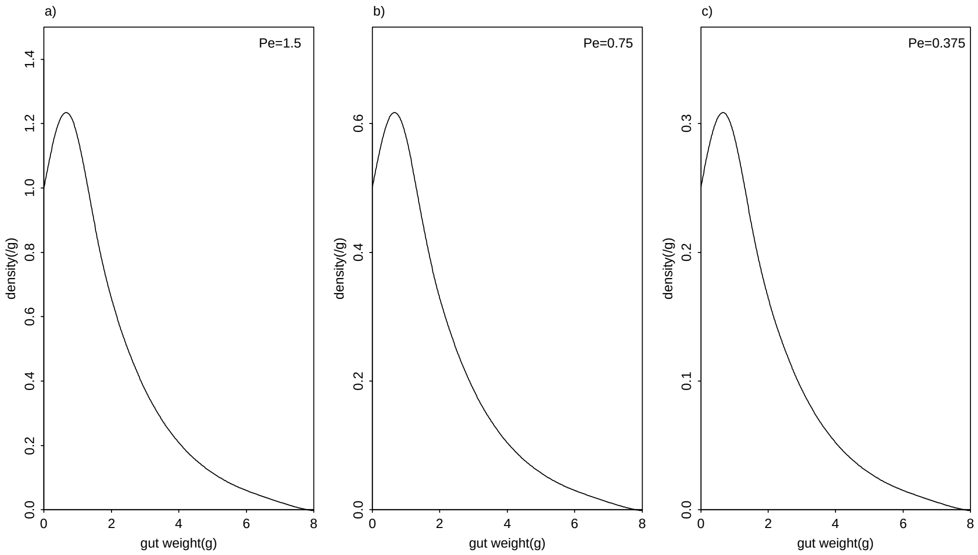


Figure 3.1 Stationary state distributions produced by initial conditions of a) 1.0, b) 0.5 and c) 0.25.

3.3 Variations in stationary state distributions

To help understand how the stomach weight distribution is affected by meal size distribution, I have initially concentrated my efforts on the numerical solution of the stationary state equation and will proceed later to consider the time varying case and the transient stage which is passed through to reach this solution.

Since one of the aims of this work is to help understand the interaction of fish and their prey we would like to be able to obtain information on the meal size distribution of a species of fish from its stomach contents distribution. In order to make specific conclusions from stomach contents distribution observations it is necessary to ascertain that the relationship between the gut weight distribution and meal size function is one to one and that a particular solution cannot be generated by many different feeding regimes. This cannot be proved analytically due to the impossibility of finding an analytic solution, so the only way to proceed is by a series of numerical experiments and trial and error.

In chapter two, I discussed the differences between digestion models, but did not consider how these affected the stomach contents distribution of feeding population of fish. So, before beginning the investigation into how changes in the rate of feeding and mean meal size affect the shape of the stationary state stomach contents distribution, I shall show how important it is that the digestion rate is known. As in the previous section I have initially assumed that the meal size distribution M(m) takes the form of a normal distribution which has been truncated at zero and normalised over the range of the stomach weights.

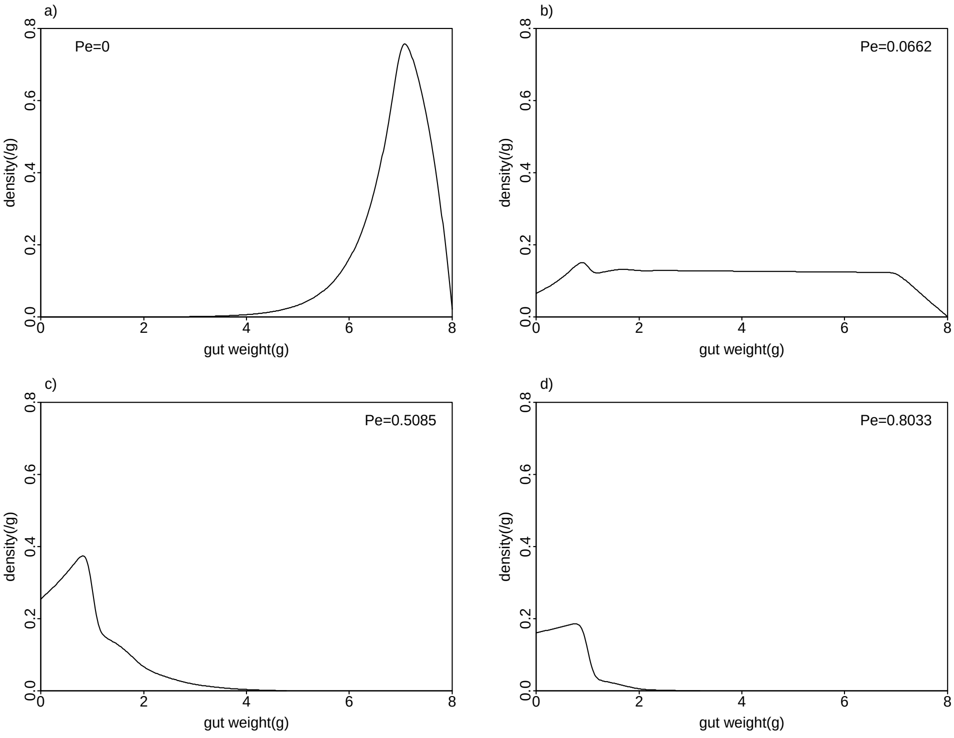


Figure 3.2. Stomach contents distributions for a population feeding a normal meal size distribution with mean one gram, standard deviation 0.1 and at a rate 0.1 meal per hour with digestion rates of a) 0.05, b) 0.1, c) 0.2 and d) 0.5.

Figure 3.2 shows that quite small changes in the linear digestion rate can considerably affect the stationary state stomach contents distribution of a population of fish. The stationary state stomach contents distribution shown in figure 3.2a is that of a population whose individuals are digesting at a very low rate when compared to their feeding rate. This low rate cannot stop the majority of the population from building up in a peak at the top of the stomach contents range. Doubling the digestion rate produces the very level stomach contents distribution illustrated in figure 3.2b while increasing the digestion rate by ten times produces the gut weight distribution shown in figure 3.2d in which most fish have empty stomachs and the remaining few have very low stomach contents.

These results highlight the importance of a known digestion rate and so throughout the feeding experiments in the rest of this chapter I shall keep the digestion rate fixed at a rate of 0.15 grams per hour. This is typical of the values for the digestion rate of marine fish of the size and species whose feeding behaviour will be studied later in this thesis (Robb 1990).

In the first set of experiments I shall hold the meal size function as a constant normal distribution and investigate how the shape of the gut contents distribution changes as the rate of feeding is increased. The maximum gut contents w_F is equal to 8 grams throughout. I have already found an analytic solution to the case when the feeding rate, R, is equal to zero - all the stomachs are empty. As the feeding rate is increased, the proportion of empty stomachs drops and a distribution of non-empty stomachs begins to appear. For low feeding rates there is a peak in the distribution around the mean meal size stomach contents and very few individuals have much food in their stomachs. However, as the feeding rate is increased further, the proportion of fish with high stomach weights increases, as the digestion rate is not high enough to keep this proportion down, reducing the fraction of the population with low stomach contents so that when the population is feeding at a rate equal to 0.35, the stomach contents distribution appears much flatter, as illustrated in figure 3.3d.

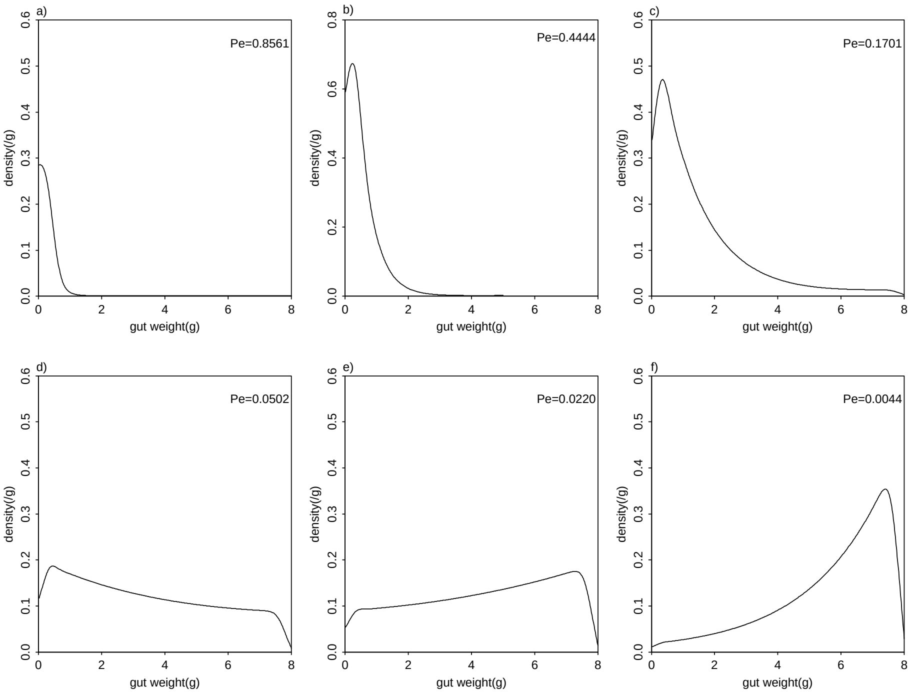


Figure 3.3. Stomach contents distributions of populations feeding on normally shaped meal size distribution with mean meal size 0.4 grams , standard deviation 0.2 and feeding rates a) 0.05, b) 0.2, c) 0.3, d) 0.35, e) 0.37 and f) 0.4. The maximum stomach weight of the individuals is 8 grams.

Further increases in the feeding rate lead to a build up of the population towards the higher end of the stomach contents range. The assumption made about the stomach capacity is that a meal is rejected if by consuming it the stomach contents would have gone over their upper limit, which in this case is 8 grams. Since the mean meal size is quite small (0.4 grams), individuals can go on feeding even when they have fairly large quantities of food in their stomachs. So, this fullness peak builds up quite close to the stomach contents upper limit.

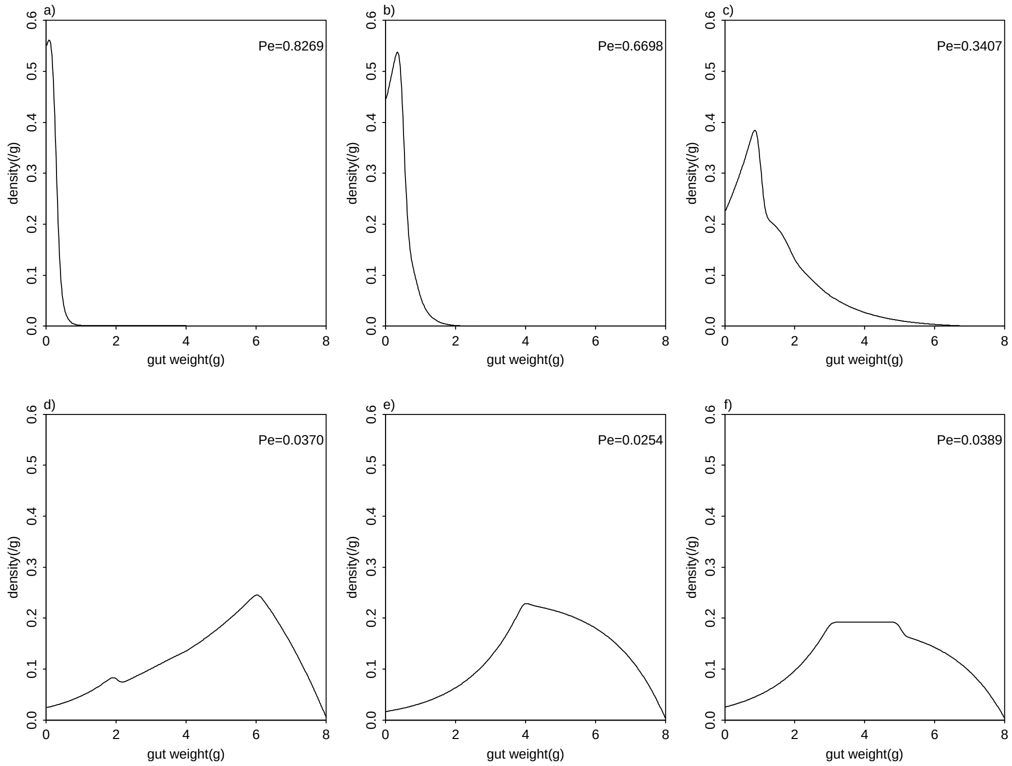


Figure 3.4. Stomach contents distributions for a population feeding at a rate 0.1 grams per hour on a normally shaped meal size distribution with standard deviation 0.1 and mean a) 0.25, b) 0.5, c) 1.0, d) 2.0, e) 4.0, f) 5.0.

Holding the feeding rate and the standard deviation at 0.1, I shall now investigate the effect of changing the mean meal size. The digestion rate and the maximum stomach contents are fixed as before. With a very low mean meal size, the stomach contents distribution is extremely skewed to the lower end of the range with many empty stomachs and a large proportion of the population with gut contents around the mean meal size (figure 3.4a-c). As the mean meal size increases, the peak moves towards the right as expected, but the proportion of fish with large stomach contents also increases as they eat several consecutive meals. The meal size distribution which generates the stomach contents distribution shown in figure 3.4d has a mean of two grams, which accounts for the large proportion of fish with high stomach contents. In this case the proportion of fish with a particular gut content increases with gut weight until a peak at around six grams is reached. Since the meal size distribution is very narrow, most available meals are very close to two grams in weight, so few fish with gut contents above six grams will be able to feed due to the upper stomach contents limit and so the stomach contents distribution drops at this point. This peak occurs at lower gut weights as the mean meal size is increased as shown in figures 3.4e and 3.4f. In fact the mean meal size is so large (5 grams) compared to the maximum stomach contents (8 grams) in figure 3.4f, that one meal pretty much fills the stomach.

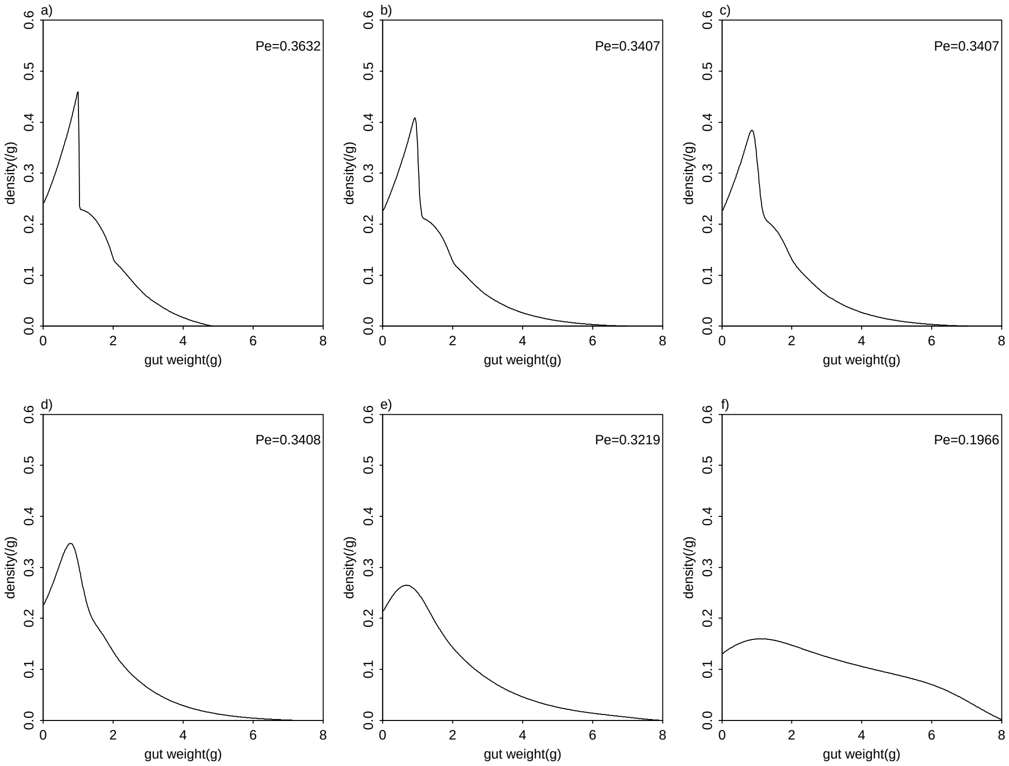


Figure 3.5. Stomach contents distributions of a population feeding at a rate 0.1 on meals whose sizes are normally distributed (truncated at zero and eight grams) with mean one and standard deviations a) 0.01, b) 0.05, c) 0.1, d) 0.2, e) 0.5 and f) 1.0.

The consequences of altering the parameters which have so far been considered have been significant and clearly visible. I now wish to consider the effects of changing the variability of the meal size distribution. Figure 3.5a shows the stomach contents distribution which occurs when the meal size distribution is very narrow (the standard deviation is equal to 0.01), implying a prey population with very little size variation. The narrowness of the meal size distribution is reflected in the stomach contents distribution by very definite peaks at the mean meal size and twice the mean meal size, as empty fish consume two consecutive meals. As the size of the meals becomes more varied i.e. the standard deviation is increased, then the peak at two grams (twice the mean meal size) disappears, the peak at one gram becomes less pronounced and a growing proportion of fish have large stomach contents as larger meals become increasingly available.

So far I have found little evidence to suggest that a particular stomach contents distribution will result from the solution of equation (3.14) with condition (3.16) for more than one set of parameters. However, the meal size distribution which so far has been used has been relatively simple, consisting of only a single normal distribution. The distribution of meal sizes is likely to be more complicated than just one normal distribution, in fact it may have many peaks depending on the variation in size and species of the available prey. For example a population of fish may have two sources of food, one of extremely small but very abundant prey and the other of much rarer, but very large prey. The meal size function will then be made up of two separate normal distributions representing the distribution of meals from each source. The question which needs to be answered here is can the stomach contents distribution from a single peaked normal distribution be reproduced by feeding on more than one food source. Figures 3.6 and 3.7 show some more complicated feeding functions with their corresponding stomach contents distributions.

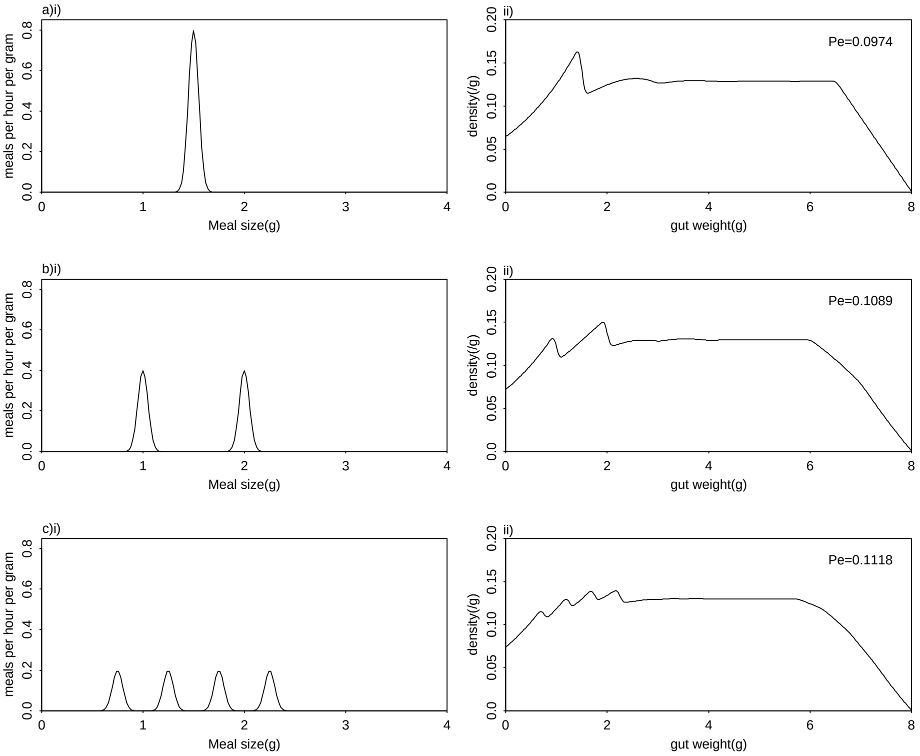


Figure 3.6. Meal size functions (i) with their associated stomach contents distributions (ii), where the meal size functions are as follows: a) single normal distribution with mean 1.5, and feeding rate 0.1; b) two normal distributions with means 1 and 2, and feeding rate 0.05 and c) four normal distributions with means 0.75, 1.25, 1.75 and 2.25, and feeding rate 0.025. All standard deviations are 0.05.

In consecutive distribution functions, the number of food sources doubles, the individual functions having means on either side of the peak in the previous example and feeding rates at half the previous value. In figure 3.6, the meal size distributions are all very narrow and this is reflected in the very clear peaks in the stomach contents distribution. The different gut weight distributions, although as a whole are quite similar in shape, due to their identical overall mean meal size (1.5 grams), are easily distinguished from each other by looking at the details of the distribution. There are a number of small peaks present in each stomach contents distribution, corresponding to the number of separate normal distributions which make up the meal size distribution function.

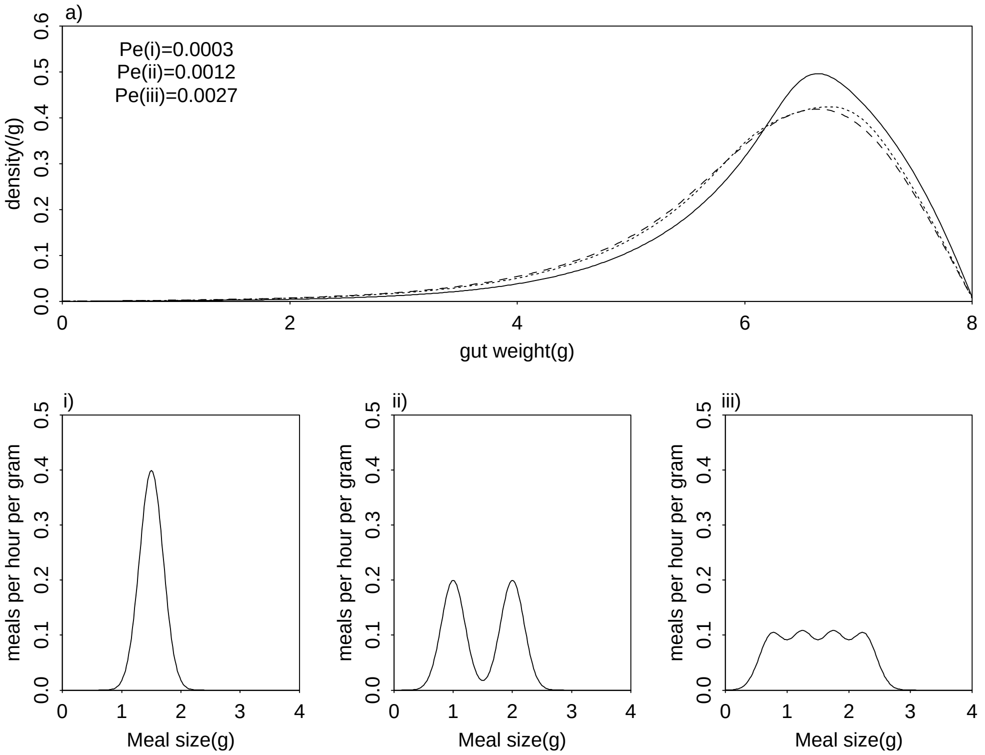


Figure 3.7. Stomach contents distributions (a) with their associated meal size functions as follows: i) single normal distribution with mean 1.5 and rate 0.2 (solid line stomach contents distribution); ii) two normal distributions with means 1 and 2 and feeding rate 0.1 (dotted line) and iii) four normal distributions with mean 0.75, 1.25, 1.75 and 2.25 and feeding rate 0.05 (dashed line). All the standard deviations are equal to 0.2.

The examples in figure 3.7 are identical to 3.6 except for the standard deviations of the meal size distribution which are four times bigger than those shown in figure 3.6. The three stomach contents distributions have quite similar overall shapes and no particular distinguishing features (unlike those in figure 3.6), although the feeding functions are quite different. However, if the three distributions are superimposed on top of one another as in figure 3.7a, they are quite clearly different.

The four normal distributions which make up the feeding function shown in figure 3.7iii have become almost indistinguishable due to the very wide standard deviation of each individual distribution. The shape of this function can be matched quite closely by a single normal distribution of equal mean and much larger standard deviation, as shown in figure 3.8a. The resulting stomach contents are easily distinguished when illustrated on the same set of axes, though we would not be able to guess, seeing the distributions individually, that one had been produced by a population feeding on four prey sources and the other by a meal size distribution consisting of a single much broader normal distribution.

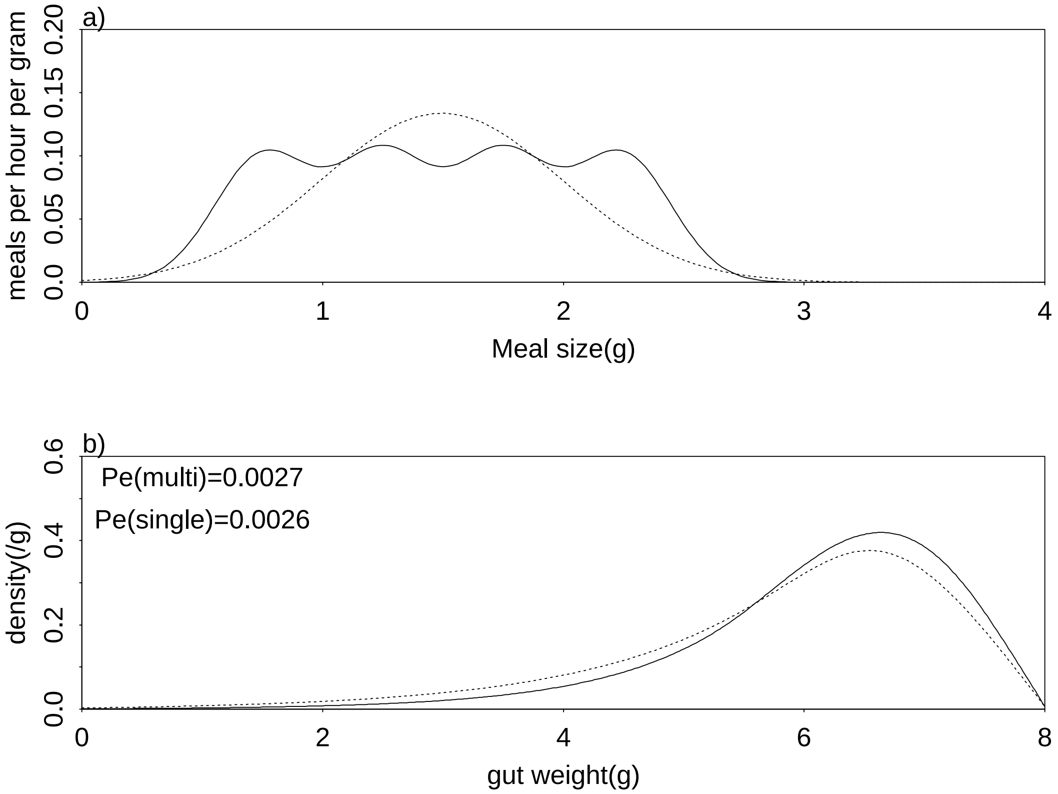


Figure 3.8 Meal size distributions (a) consisting of (solid) four normal distributions with means 0.75, 1.25, 1.75 and 2.25, standard deviation 0.2 and feeding rate 0.05 and (dotted) a single normal distribution with mean 1.5, standard deviation 0.5 and feeding rate 0.17, together with their associated stomach contents distributions (b).

I shall now consider the effect of using an alternatively shaped distribution function. The main features of a normal distribution with a mean of one gram and standard deviation of 0.24 can be reproduced by replacing it with a triangular shaped distribution, centred at one and whose base is of width 1.2. This is illustrated in figure 3.9ai. The corresponding stomach contents distributions are almost identical and virtually impossible to tell apart. However, since the two feeding functions which generate these stomach contents distributions are very similar anyway, it seems unlikely that it will ever be necessary to distinguish between the two.

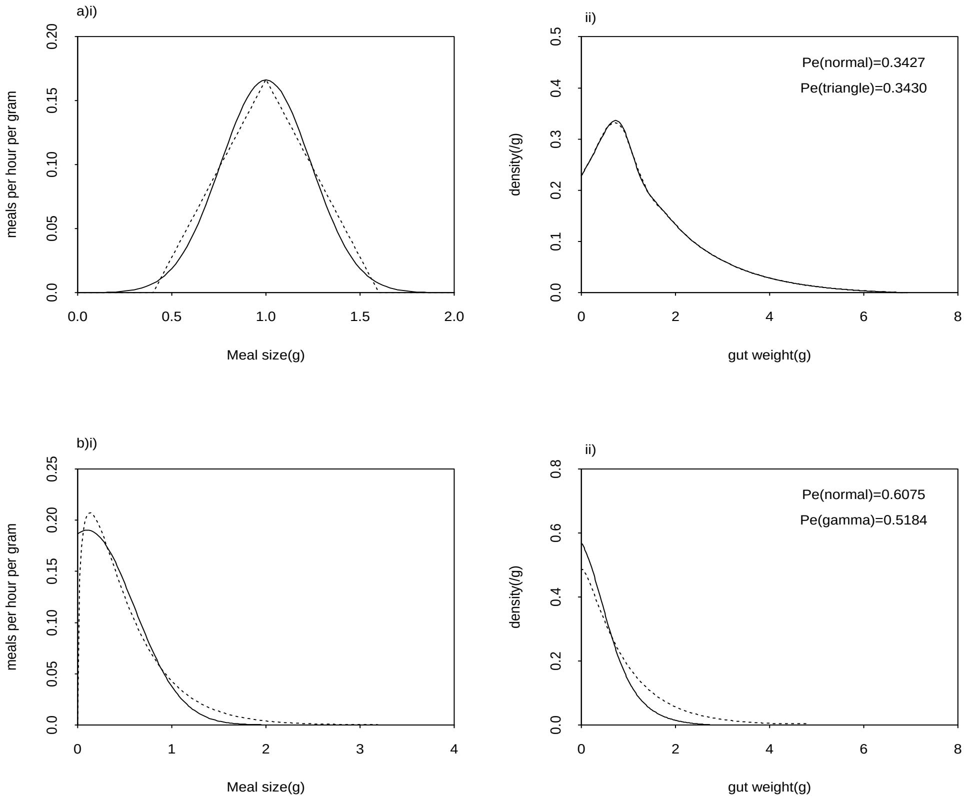


Figure 3.9. Normally distributed meal size functions (solid line) compared to their closest fitting triangular distribution (dotted line (a)) and gamma distribution (dotted line (b)), with their associated stomach contents distributions.

The shape of a feeding function made up of a normal distribution which is very skewed towards zero (mean 0.1) with a larger standard deviation (0.5) and feeding rate 0.14 is similar to that of the gamma distribution

$$\Omega\left(\frac{w}{x_o}\right)^n e^{-\left(\frac{w}{x_o}\right)} \tag{3.35}$$

with n equal to 0.35, W equal to 0.142 and x_o 0.38. The resulting gut weight distributions are illustrated in figure 3.9bii.

The stomach contents distribution generated by the normal feeding function is much more skewed towards the lower end of the stomach fullness range than that produced when feeding on meals which follow the gamma distribution. Although the illustrated gamma and normal distributions are quite similar at low meal sizes (figure 3.9bi), the gamma distribution tales off much slower, so that when a population of fish are feeding on meals whose sizes have a gamma distribution, there will be more larger meals available and consequently a larger proportion of the population will have larger amounts of food in their stomachs.

By looking at these examples of stomach contents distributions generated from a population feeding at a particular rate and on meals with a particular distribution, I have tried to show that the relationship between gut weight distribution and feeding function is one to one. None of the examples have produced identical stomach contents distributions, although some have been quite difficult to distinguish without comparisons made by illustrating all distributions on the same axes. These difficulties arose only when steady state stomach contents distributions were generated by meal size distributions made up of differing numbers of prey sources. So, I can conclude from this section that once a digestion rate has been established, it should be possible, in theory, given a stationary stomach contents distribution and a fixed number of prey sources, to find the unique set of parameters defining the meal size distribution and feeding rate. The parameters are not considered unique in a strict analytic sense, but in the sense that meal size distributions which produce numerically identical stomach contents distributions are themselves numerically indistinguishable. I shall return to the question of uniqueness for differing numbers of prey sources later in the thesis, when I shall also investigate the effect of noisy or incomplete data.

3.4 The time dependent feeding rate problem

Although the previous section gives a good indication of the stomach contents distributions, this has limited value when considering the feeding dynamics of most fish species. As I discussed in section 3.0, the feeding rate has frequently been found to be dependent on light intensity and the tidal cycle, so it is not unreasonable to assume that the consumption rate varies periodically. Returning to the formulation of the model, I shall now rewrite the feeding function as R(t)M(m) where M(m) is a distribution function dependent only on meal weight and R(t) is a cyclic function. The partial differential equation model defining the stomach contents distribution variation can now be written as

$$\frac{\partial f(w,t)}{\partial t} = K\frac{\partial f(w,t)}{\partial w} - U(w,t)f(w,t) + R(t)M(w)P_e(t) + F(w,t) \qquad (3.36)$$

and

$$\frac{dP_e(t)}{dt} = Kf(0^+,t) - R(t)P_e(t) \qquad (3.37)$$

where $$U(w,t) = R(t)\int_0^{w_F - w} M(m)dm \qquad (3.38)$$

and $$F(w,t) = R(t)\int_0^w M(m)f(w-m,t)dm\,. \tag{3.39}$$

It was seen in the previous section that even an analytic solution to the general constant feeding rate problem was an impossibility, so an expression for the variation of the stomach contents distribution in the more realistic varying feeding rate model is likely to be even less feasible. However, there are many reliable numerical difference schemes which can be used to solve partial differential equations of this type. Suppose that I discretise the system in the weight dimension so that $f_i = f(i\Delta w)$ for $i = 1..\frac{w_F}{\Delta w}$ and use a central differencing scheme to approximate the derivatives everywhere except at the edges where one sided differences are used. The partial differential equation then becomes a system of coupled ordinary differential equations which can be solved using the fourth order Runge-Kutta method. (The functions U(w,t) and F(w,t) are obviously dealt with in the same way as they were in the constant feeding rate model). The system of differential equations is shown in appendix A.

This method of solution of a partial differential equation is probably not the method of choice for most numerical analysts as there are many standard numerical methods available for the solution of such equations, for example the Crank-Nicolson and Lax-Wendroff schemes. However, such methods, known as the 'method of lines', have been suggested by Verwer and Dekker (1983). The central differencing scheme produces a stiff system of ordinary differential equations, the solution of which by Runge-Kutta methods is stable (Dekker and Verwer 1984). Before this method can be relied upon completely though, the solution must be tested further to check that the peculiarities at the end points in the discretisation of the weight dimension do not significantly affect the solution. The simplest way of doing this is to set R(t) equal to a constant and let the model run until the stomach contents distribution function remains stationary, at which stage it should be identical to that predicted by the stationary state equation described in the earlier part of this chapter. I shall compare the solutions of these two methods in the next section and at the same time I can consider how the steady state is reached.

3.5 Constant feeding rate dynamics

Before investigating the dynamics of the transient solution in much detail, I shall first check the solution of the time dependent set of equations (3.36 and 3.37), by setting R(t) equal to a constant and comparing the solution to that of the stationary state equation. Figure 3.10 shows the progression of the stomach contents distribution of a population of fish from a normal initial stomach contents distribution with mean 2 grams and standard deviation 0.5, to their stationary state.

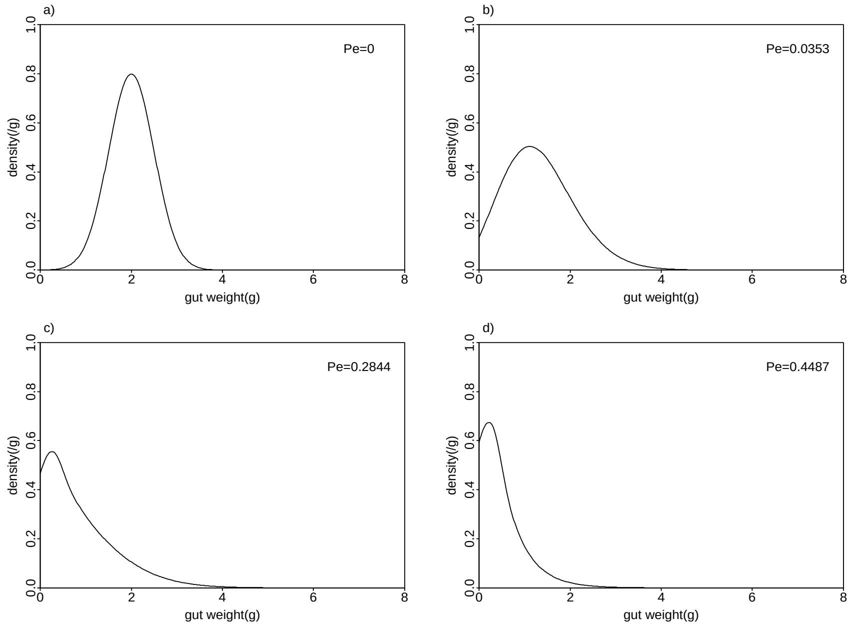


Figure 3.10. Stomach contents distributions of a population of fish with normal initial distribution (a) with mean 2 grams and standard deviation 0.5, at b) 10 hours c) 25 hours and d) stationary state (100 hours), feeding on a meal size distribution with mean 0.4 grams, standard deviation 0.2 and at a rate of 0.2 meals per hour.

When the stationary distribution is compared to that produced by the stationary state equation (see figure 3.3b), the two look the same and numerically, are virtually identical with a difference of less than 0.5%. The small inaccuracies are due to the different numerical methods used for each solution.

Although, information is lost about the stomach contents distribution by considering only the mean stomach contents, this is a much more convenient way of considering how the solution progress with time and does not require the many illustrations of stomach contents distributions. However in certain feeding situations, the dynamics become quite complicated and in which case, a few select illustrations of stomach contents distribution functions will be of help. In this section I aim to show how the progression of an initial stomach contents distribution to its stationary state is affected by changes in the distribution of available meals and the rate of feeding. In all of the following examples the population concerned has a digestion rate of 0.15 grams per hour, an upper stomach contents limit of eight grams and an initial stomach contents distribution which is normal with mean 2 grams and standard deviation 0.5 grams. Most of the equilibrium stomach contents distributions have already been illustrated in section 3.3 when the variation in stationary state distributions was investigated.

In my first set of examples, illustrated in figure 3.11, I have shown the variation in the mean stomach contents with time for a range of feeding rates. When the population has a very low feeding rate of 0.05 meals per hour, the mean stomach contents drop very quickly from two grams and the low stationary state is reached within approximately 25 hours. In this case the feeding rate is so low that very few fish can reach high stomach contents unlike a population feeding at a rate of 0.4 grams per hour. This eight fold increase in the feeding rate causes an increase of over one hundred times in the final stationary mean stomach contents which are not reached until nearer 800 hours.

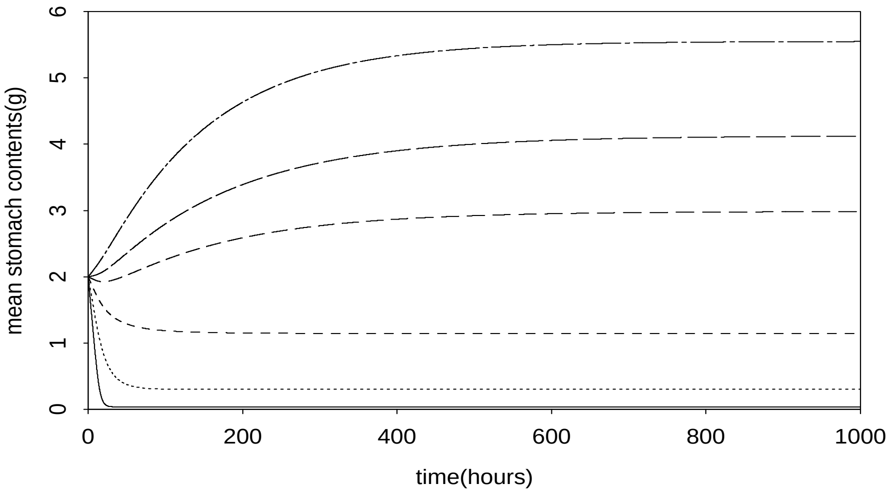


Figure 3.11. Progression to equilibrium for a population of fish with a normal initial stomach contents distribution with mean two grams and standard deviation 0.5 feeding on a meal size distribution with mean 0.4 grams, standard deviation 0.2 and constant rates 0.05 (solid line), 0.2 (dotted line), 0.3 (short dashed), 0.35 (dashed), 0.37 (long dashed) and 0.4 meals per hour (dot-dashed).

Figure 3.12 shows the variation in mean stomach contents for the same initial population when the width of their meal size distribution is varied. The distribution is centred at one gram and the members of the population feed at a rate of 0.1 meals per hour. Clearly for low meal size distribution standard deviations, for example 0.01 and 0.2, very few fish will have high stomach contents, so the mean stomach contents will be quite low - approximately one gram and fall directly to their steady state from the initial condition.

However, when the population feeds on a meal size distribution with standard deviation one gram, the mean stomach contents initially decrease, before increasing to their stationary state value. The stomach contents are initially normally distributed with a mean of two grams and a standard deviation of 0.5, so only a very tiny proportion of the population have high stomach contents to begin with. As the feeding and digestion process begins, this normal distribution starts to move to the left (due to the digestion process) and some individuals become empty, while at the same time the population is feeding at a low rate on a wide variety of meal sizes, so a very small proportion of the population will have a large amount of food in their stomach. Initially, the number of fish with large stomach contents is so small that it does not significantly affect the mean stomach contents which decrease due to the digestion process. However, since these fish have eaten quite large meals, it takes a very long time for them to digest the food and become empty again, and all the while, more fish are eating large meals and the proportion of the population with high stomach contents is increasing. Hence, the mean stomach contents increases until it reaches its stationary state.

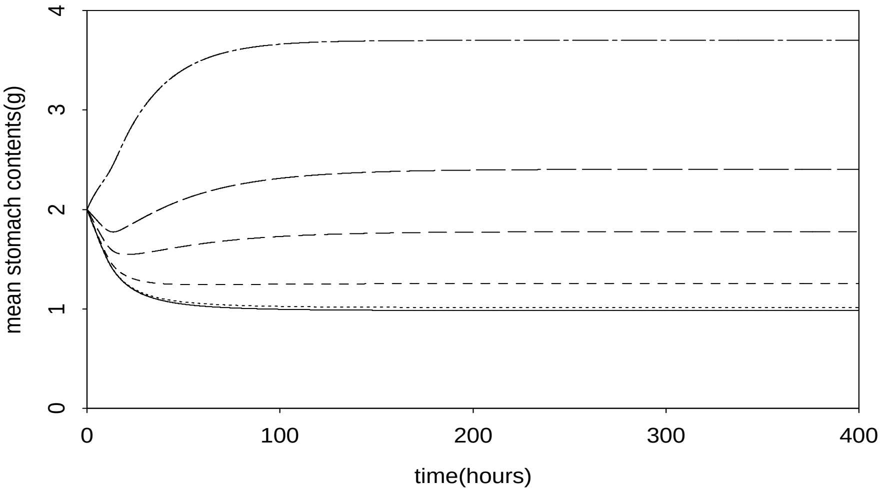


Figure 3.12. Time history of the mean stomach contents of a population whose initial stomach contents distribution is normal with mean two and standard deviation 0.5, feeding at a constant rate of 0.1 meals per hour on normally distributed meals with mean one gram and standard deviations 0.01 (solid line), 0.2 (dotted), 0.5 (short dashed), 0.75 (dashed), 1 (long dashed) and 2 (alternate dot dashed).

The immediate increase in the mean stomach contents curve when the population begins feeding on a meal size distribution with standard deviation 2 grams is due to the availability of extremely large meals. The consumption of very large meals by even just a few individuals, who consequently become very full, is enough to override the initial reduction in mean stomach contents due to the digestion process.

An even more interesting transient to consider is that which occurs in figure 3.13. This illustration shows how the steady state is reached for a population feeding on meal size distributions with different means.

Our attention is quickly drawn, to figures 3.13e and 3.13f which show oscillations in the mean stomach contents before it settles down to its steady state. The mean stomach contents variation illustrated in figure 3.13f was generated by allowing the population to feed on very large meals (mean five grams), but with very little size variation (standard deviation 0.1).

As the fish initially begin to feed, a peak in the stomach contents distribution begins to build up at around the seven gram stomach weight which is where a five gram meal will take them from an original stomach contents of around two grams, so the mean stomach contents initially increases. Once they have taken one meal, of such a size, though, these fish are unable to feed much further as there are very few small meals available and the consumption of a meal of around five grams in weight would take their stomach contents above their upper limit. Therefore these fish will be digesting only. After some time there are very few fish left with low stomach contents and therefore few are able to take a meal (due to their large sizes), so the majority of the population are digesting and hence the mean stomach contents are decreasing. This decrease continues until a substantial amount of the population have digested enough so that their stomach contents are low enough to take another large meal and so the population begin to move to high gut weight levels again and thus the mean stomach contents increase. As this process continues, the population slowly begins to spread out over the gut range due to fish with a broader range of gut contents feeding on meals with a range of sizes. The movement of the population peaks becomes less and less obvious and eventually the equilibrium is reached as the proportion of fish gaining a stomach contents weight due to ingestion from below or digestion from above is balanced out by those leaving this weight due to feeding or digestion.

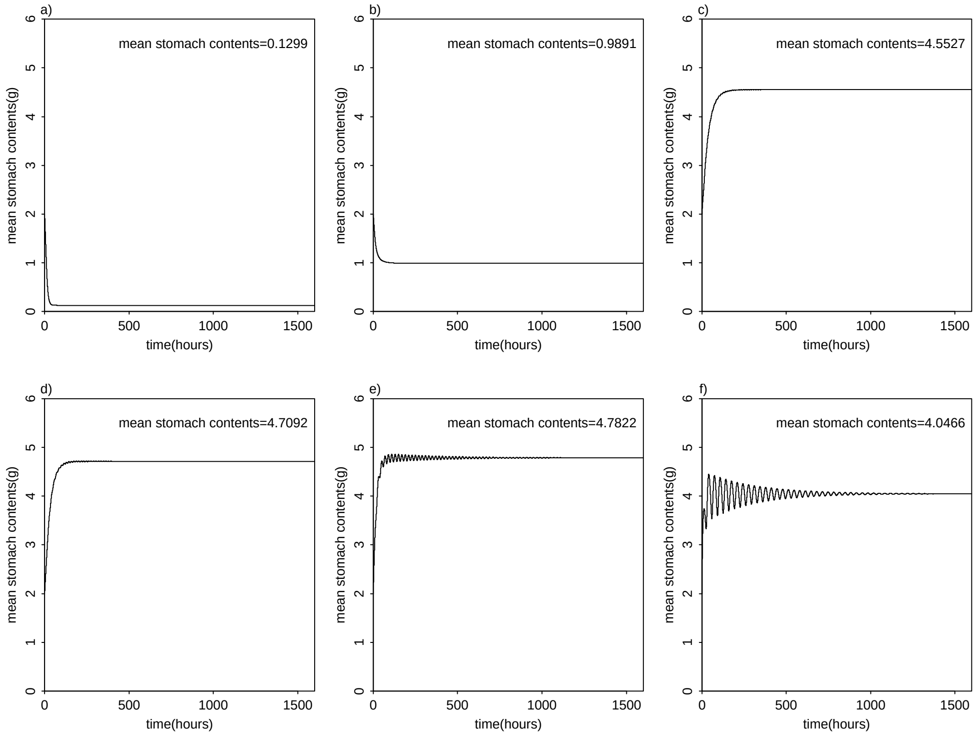


Figure 3.13. Temporal development of the mean stomach contents of a population whose initial gut weight distribution is normal with mean two grams and standard deviation 0.5, feeding at a constant rate of 0.1 meals per hour on a normally distributed meal size distribution with a standard deviation of 0.1 and mean a) 0.5 grams, b) one gram, c) two grams, d) 2.2 grams, e) three grams and f) five grams.

Figures 3.13a-e show that the stationary mean stomach contents increases as the mean meal size increases. However, there is a decrease in the equilibrium average gut weight when the mean meal size increases from three grams to five grams, illustrated in figures 3.13e and 3.13f. This is due to the combined effects of the very large meals and the upper limit to the gut contents. Only fish in the lower end of the gut contents range are able to feed and most other fish will be rejecting food and digesting only, therefore the mean stomach contents will be lower than in those cases where the mean meal size is somewhat smaller and less food is being refused. These equilibrium mean stomach contents show that for such a population feeding at quite a low rate (0.1 meals per hour), they are better off feeding on a meal size distribution with a mean of less than half their stomach contents, rather than trying to feed on very large meals.

In this section I have tried to show that the existence of the equilibrium is dependent on a complicated combination of digestion and unrestricted feeding at low gut weights, together with consumption rate restrictions enforced by the upper stomach contents limit.

3.6 Variable feeding rate dynamics

I shall return my attention now to the case when a population is feeding at a rate which varies throughout the day. It has been suggested that some fish species feed mainly during the day and are much less active during the hours of darkness and vice-versa for other species, in which case it would be sensible to begin by choosing a sinusoidal curve with period twenty four hours to represent the feeding rate function. So, I shall write

$$R(t) = \begin{cases} R_1 + R_2 \sin\dfrac{\pi t}{12} & \text{when } 0 \le R_1 + R_2 \sin\dfrac{\pi t}{12} \\ 0 & \text{otherwise} \end{cases} \qquad (3.40)$$

which is a constant background feeding rate R_1 with the addition of a sinusoid to give the variation. The function is clipped as zero so as to cut out negative feeding rates which would be absurd. I shall refer to the constant R_1 as the underlying feeding rate and the constant R_2 as the feeding rate amplitude. Figure 3.14a shows that for a population feeding at a sinusoidally varying rate, the variation in mean stomach contents reaches a repetitive ‘limit cycle’ with period twenty four hours. The variations in gut weight distribution which are produced by this particular feeding rate fluctuation, are illustrated in figure 3.14b. Although these dynamics are driven by the variations in the feeding rate function, for convenience, I shall call them ‘limit cycles’ as they are stable, independent of the initial stomach contents distribution, and cycle (with period twenty four hours) between an upper and lower limit

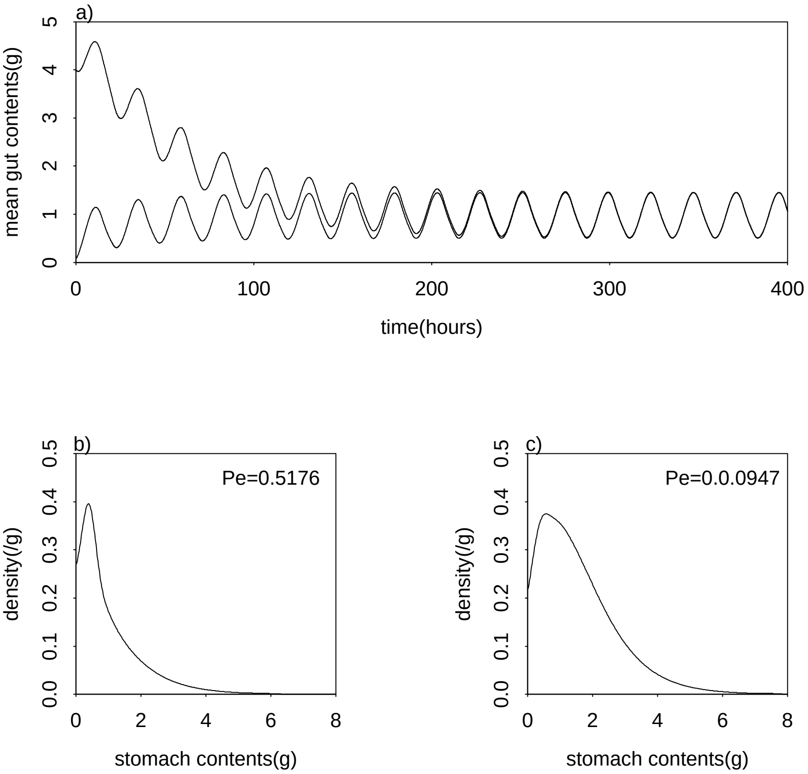


Figure 3.14. a) Progression of mean gut contents of a population of fish feeding on a normal meal size distribution with mean 0.5 and standard deviation 0.2 with a sinusoidal rate function with R_1 equal to 0.2 and R_2 to a limit cycle from two different initial stomach contents distributions. The stomach contents distribution at the trough of the limit cycle is shown in b) and c) illustrates the distribution at the peak of the mean stomach weight cycle.

In the next section I shall attempt to explain the dynamics of the time dependent feeding rate problem in the same way as I did the constant feeding rate problem, by solving the problem for a number of sets of feeding parameters (μ, σ, R_1 and R_2) and looking at how the variation of a particular parameter affects the solution.

Since I have already looked at how the actual meal size distribution affects the stomach contents distribution function I shall initially concentrate on the effects of changes to R_1 and R_2. In the first set of examples, illustrated in figure 3.15, I have kept the amplitude of the feeding rate oscillations constant at 0.2, but chosen different values of R_1. The corresponding feeding rate functions are illustrate in figure 3.16.

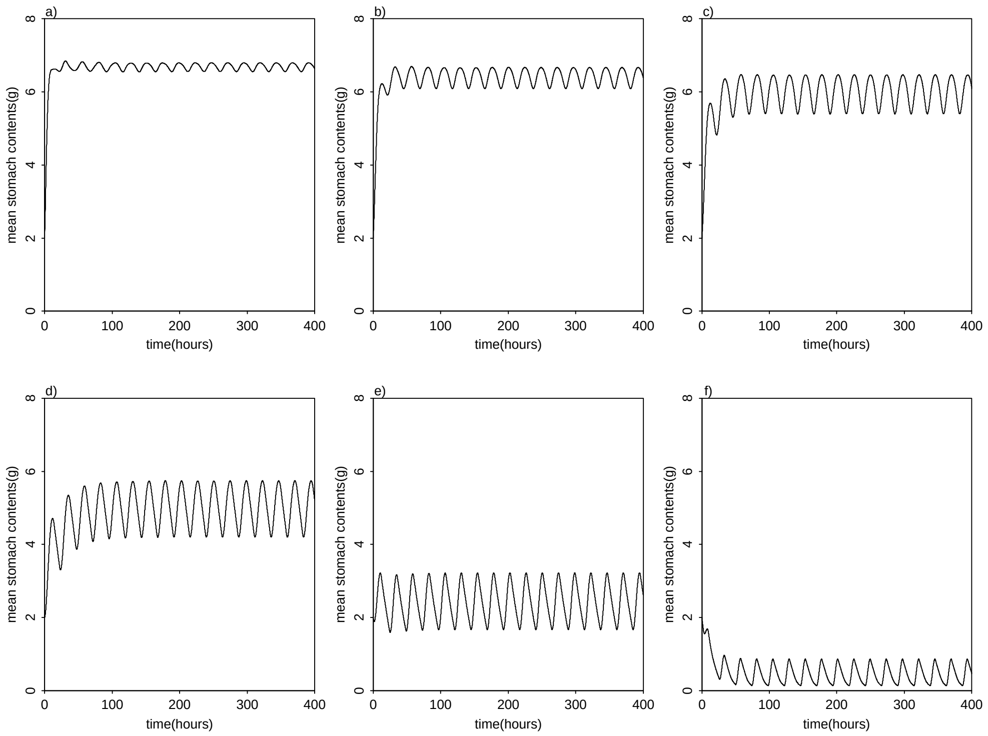


Figure 3.15. Variation in the mean stomach contents of a population whose initial gut contents distribution is normal with mean two grams and standard deviation 0.5, feeding on a meal size distribution with mean two grams, standard deviation 0.2, with a sinusoidal rate function with amplitude 0.2 and R_1 equal to a) 0.5, b) 0.3, c) 0.2, d) 0.1, e) 0 and f) -0.1.

In figure 3.15a, the constant underlying feeding rate of the population is very high at 0.5 meals per hour. Since most of the population have very high stomach contents, even at the trough of the sinusoid, the increase in feeding rate due to the sinusoidal part of the function will have little affect since only a small proportion of the population will be able to feed anyway, due to the upper stomach contents limit. As the underlying rate decreases, a slightly lower proportion of the population have very large stomach contents, more fish will be able to increase their feeding rate as the rate function increases and hence the amplitude of the mean stomach contents oscillations will be greater.

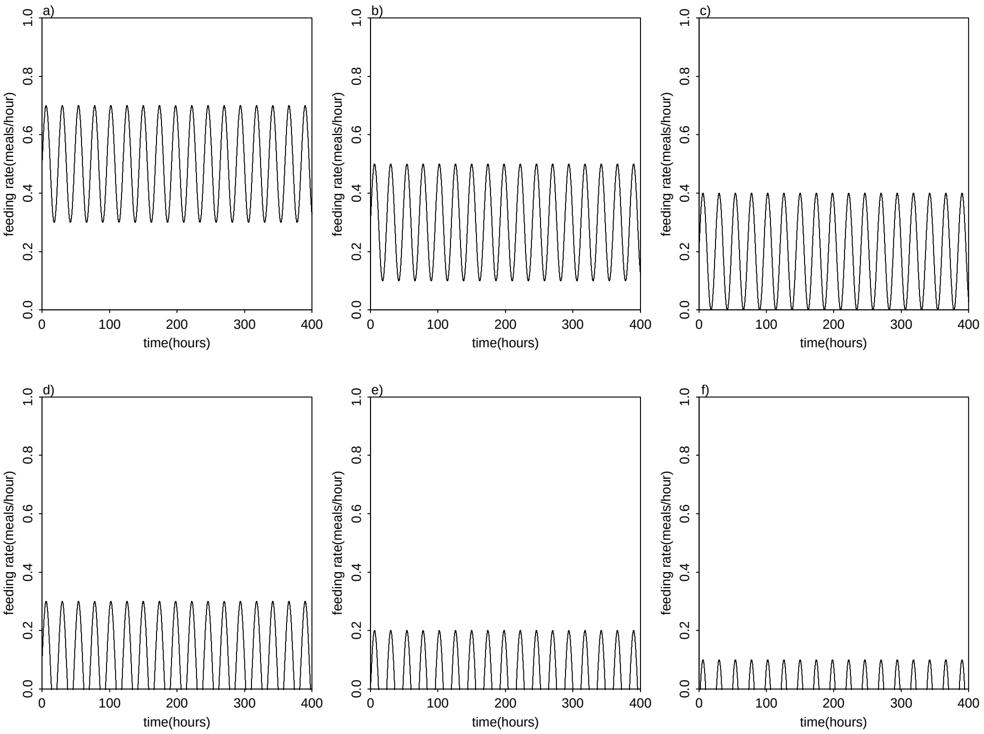


Figure 3.16. Feeding rate functions with amplitude equal to 0.2 and R_1 equal to a) 0.5, b) 0.3, c) 0.2, d) 0.1, e) 0 and f) −0.1, corresponding to the mean stomach contents variations shown in figure 3.15.

I have defined the feeding rate function as a clipped sinusoidal function and consequently if the underlying feeding rate R_1 is less than 0.2 (the amplitude of the rate function), there will be periods of time when the overall feeding rate is zero (see figures 3.16d-f) i.e. the individuals are digesting only. So, due to the complete cessation of feeding during some part of the day, the mean stomach contents of the population will drop more rapidly, causing an even greater amplitude in the mean stomach contents oscillations. By giving R_1 a negative value (figure 3.16d), the feeding rate function has been translated down so far, that most of it has been cut off at zero and hence the population is digesting for most of the time and only has a peak feeding rate of 0.1 grams per hour. Following this feeding regime, only a very small proportion of the population will gain very high stomach contents and therefore the mean stomach contents will never reach very large values. The shape of the limit cycle appears to be deforming with the mean stomach contents decreasing for longer than they are increasing, though they never reach zero as those few individuals whose stomach contents do reach quite high weights will not be able to digest down to zero stomach contents before feeding recommences.

Figure 3.17 compares the mean stomach contents variation curves of populations whose feeding regimes are identical except for the amplitude of the variations. As expected, the amplitude of the oscillations observed in the mean stomach contents curve increase as the amplitude of the feeding rate function oscillations increases.

This illustration also shows that the amplitude of feeding rate oscillation affects the position about which the oscillations occur. As the amplitude decreases, the mid point of the mean stomach contents oscillation increases.

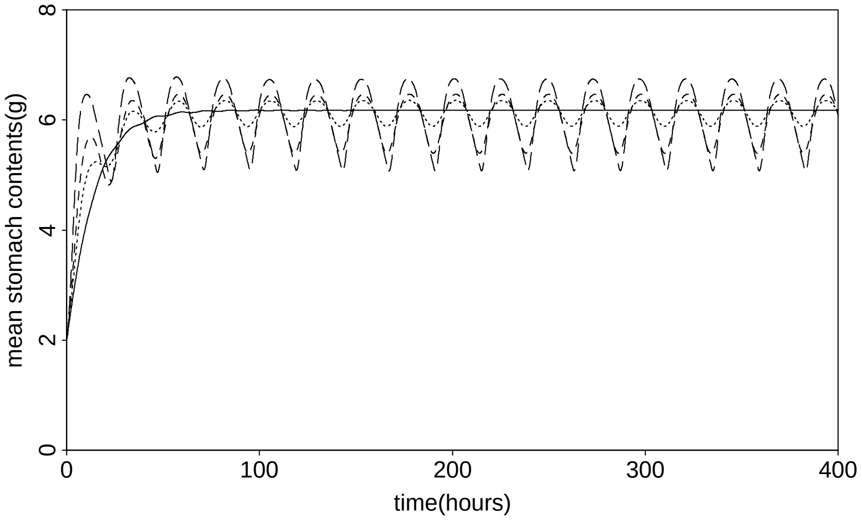


Figure 3.17. Progression with time of the mean stomach contents of a population feeding on meals with mean size two grams and standard deviation 0.2 grams at an underlying feeding rate of 0.2 and a feeding rate amplitude of i) zero (solid line), ii) 0.1 (dotted line) iii) 0.2 (short dashed line) and iv) 0.5 (dashed line).

The limit cycles are also affected by the parameters defining the meal size distribution itself. The mean stomach contents of a population of fish with a meal source which is distributed normally with mean 1 gram and standard deviation 0.2 grams oscillate around a fairly low point (approximately 1 gram) as shown in figure 3.18a. As the mean meal size increases, the mid-point of the oscillations increases until the upper limit to the stomach contents begins to come into affect. When the mean meal size gets very large, there will be virtually no small meals available, as the standard deviation of the meal size distribution is very narrow, so many individuals will be unable to feed. The effects of this restriction become more obvious as the mean meal size gets larger and the position about which the mean stomach contents oscillates drops.

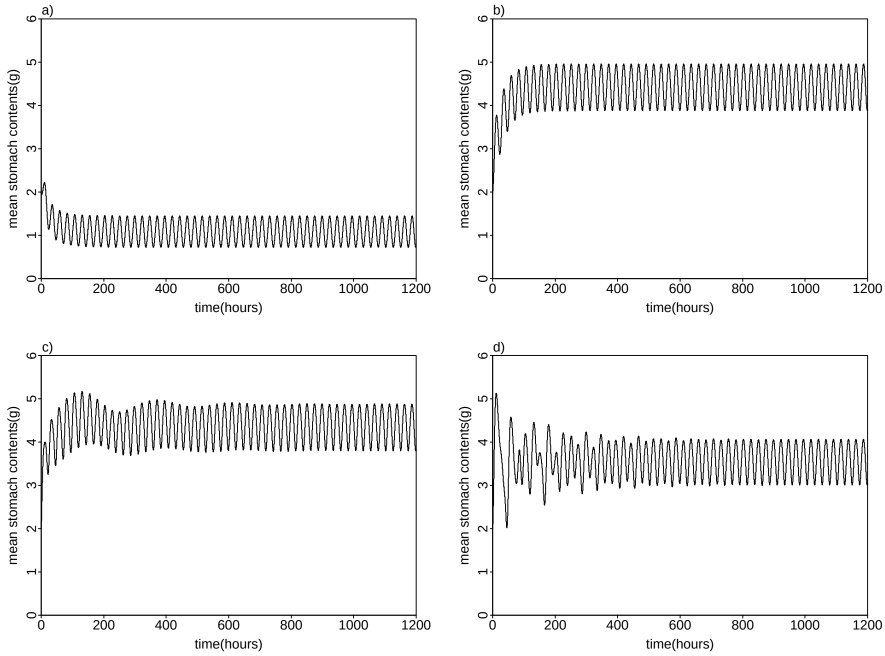


Figure 3.18. Variation in mean stomach contents for a population feeding at a sinusoidally varying rate with R_1 and R_2 both equal to 0.1, on a meal size distribution with standard deviation 0.2 and mean a) 1 gram, b) 2 grams, c) 4 grams and d) 6 grams.

So far, I have considered only very simple feeding behaviour, that the population feeds on only one meal size distribution and at a rate which has one peak and one trough per day. However, it has been suggested that some fish species have two daily feeding peaks, possibly at dawn and dusk. This behaviour could be simulated by doubling the frequency of the sinusoid and translating it in the time direction so that the feeding peaks occur at the right times. It is quite likely though that these feeding peaks may be of different amplitudes with fish populations feeding at a higher rate at dawn than at dusk, due to possible greater energy needs during the day when they may be more susceptible to predation. As such a feeding rate function cannot easily be formed using a sinusoidal curve, the most obvious way to simulate such behaviour seems to be via an ordinary step function. The effect of substituting a step function for a sinusoidal feeding rate function is shown in figure 3.19.

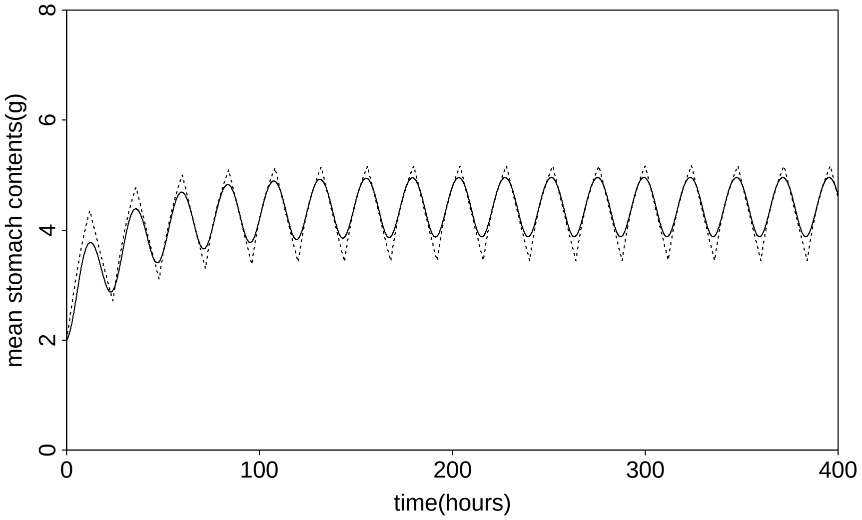


Figure 3.19. Variation in mean stomach contents of two identical populations feeding on normal meal size distributions with mean 2 grams and standard deviation 0.2, with i) a sinusoidal rate function with R_1 and R_2 equal to 0.1 and period 24 hours (solid line) and ii) with a rate function which takes the form of a step function with the value 0.2 for the first half of the day and zero otherwise.

As the step function feeding rate switches between two distinct values discontinuously, the variations in the mean stomach contents curve are much sharper than those observed for a population whose feeding rate varies continuously. Apart from this difference, the two feeding regimes generate very similar mean stomach contents variation curves.

The feeding behaviour of a population of fish could be even more complicated than that described above as the population may be feeding on multiple meal sources each of whose availability varies during the day.

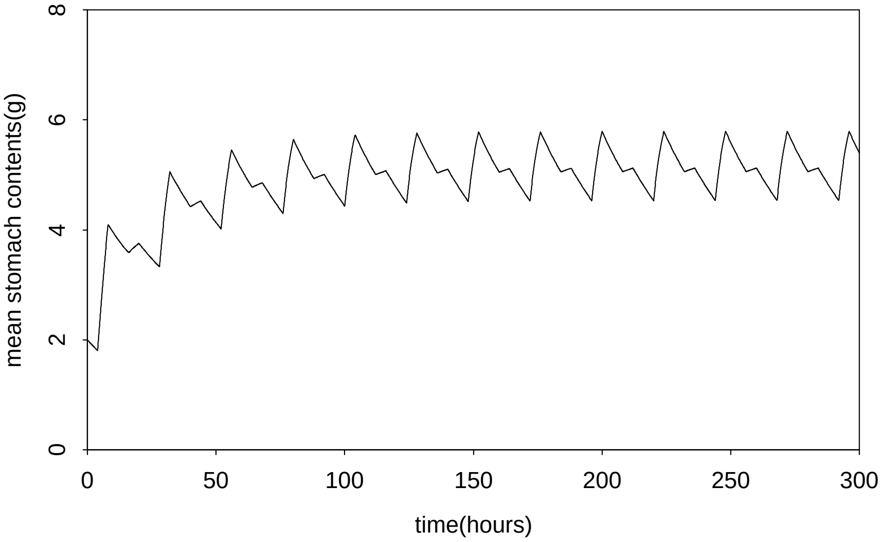


Figure 3.20. Time history of the mean stomach contents distribution of a population of fish feeding on two normally distributed meal sources, one with mean two grams and standard deviation 0.1 at a rate of 0.4 meals per hour between 4am and 8am and 0.05 meals per hour during the rest of the day and the other with mean 0.5 grams and standard deviation 0.1 at a rate 0.2 meals per hour between 4pm and 8pm and zero for the rest of the day.

Figure 3.20 shows the variation in mean stomach contents for a population of fish which has two meal sources, one with a large mean which is most readily available between the hours of four and eight in the morning (around dawn) and the other source which has a lower mean and becomes accessible during the late afternoon and early evening between four and eight. The feeding rate is fairly low at all other times. A consequence of this more complicated feeding regime is that the limit cycle becomes double peaked. The large peak being due to the early morning feeding on mainly quite large meals and the smaller peak due to the evening feeding on a low mean meal size distribution.

3.7 Summary

The previous sections have shown just how complicated the dynamics of both the stationary state solution and time dependent solution can be. In section 3.3 I tried to illustrate the uniqueness of the stationary state solution through a series of examples. I found no evidence to indicate that identical equilibrium stomach contents distributions could occur in identical populations feeding on the same number of prey sources but with different means and standard deviations and at different rates. So in this case we can say that the relationship between feeding parameters and stomach contents distribution is one to one and the inverse problem can, in principle, be solved.

However, some stomach contents distributions generated with different numbers of prey sources appeared quite similar. So, at this stage the possibility that more than one feeding regime can generate a particular distribution cannot be ruled out when the numbers of prey sources is not fixed. Even if such solutions are unique, the stomach contents distributions may be so similar that given only a small amount noise in the data, they may become indistinguishable. In the following chapter I shall attempt to find a suitable method for solving the inverse problem and then go on to investigate how easy it is to infer the feeding behaviour when the stomach contents data are noisy or categorised into stomach weight intervals.

With the introduction of time dependence, the problem becomes much more complicated, with many different feeding regimes being quite feasible and some mean stomach contents oscillations appearing quite similar. However, given the previous result about distinguishability of stationary state stomach contents distributions, given a fixed number of prey sources, it seems likely that development of the time dependent stomach contents distribution of a population feeding in a particular fashion will also be unique. So, if we consider the variation in stomach contents distribution with time instead of the mean stomach contents, and have a complete picture of how the stomach contents distribution of a population varies over a day, then we should be able to find the unique set of parameters and rate function which define its feeding behaviour.

Once again however, if the stomach contents data have been sampled from the field they will be quite noisy and are likely to consist of proportions of the population whose stomach contents lie in quite broad gut weight categories. Furthermore the samples will not have been collected at very fine time intervals. Given such data, it will become more difficult to infer the feeding behaviour of a population and it may be impossible to tell from the stomach contents data whether a population is, for example, feeding with a sinusoidally varying rate or a step function.

The next section of this thesis deals with the solution of these inverse problems. I will attempt to show how well these problems can be solved when a complete description of the time dependent stomach contents distribution is available, and how the information which we can obtain about the feeding behaviour of the population deteriorates due to sampling of the population at infrequent time intervals and categorisation of stomach contents.

Chapter 4

The constant feeding rate inverse problem

4.0 Introduction

In section 3.4, I explained how the stationary state equation could be solved numerically given a particular meal size distribution and feeding rate. I illustrated how variation in the parameters affects the shape of the stationary state distribution and attempted to show that the relationship between the parameters and stomach contents distribution is one to one. Although we have not managed to prove complete uniqueness, the results clearly indicate the likelihood that given that we know the number of prey sources involved in the meal size distribution, then only one biologically sensible set of parameters which generate the stationary state stomach contents distribution can be found. Obviously, given a particular steady state distribution, an attempt can be made to find the appropriate set of parameters by trial and error provided the feeding function type is known. This, however, would be tedious and time consuming. So, it would be more sensible to try to find a suitable automatic method of solution for this inverse problem of finding the feeding parameters from the stationary stomach contents distribution.

The aim of this chapter is to first decide on a suitable method of solution of the inverse problem and to monitor its performance over a variety of problems, looking at whether the results it produces, given data with known feeding functions (generated from the solution of 3.15), are always the expected ones. Our eventual goal is to be able to successfully infer the feeding behaviour of a population of fish from their stationary stomach contents distribution without any prior knowledge of their meal size distribution or feeding rate. However, stomach contents data collected in the field will never take the form of a perfect numerical distribution which is a particular solution of the stationary state equation (3.15). So the rest of this chapter goes on to consider the effect on the results of the automatic fitting procedure, of more realistic simulated data incorporating noise and data which have been categorised into intervals.

4.1 Optimisation techniques

There is no standard method of solution of differential equation inverse problems, the technique used depends greatly on the type of problem and its complexity i.e. on the number of dimensions, whether the parameters exist linearly or non-linearly in the solution and whether derivatives or second derivatives of the solution can be calculated. When an analytic solution can be found to the ordinary differential equation, the inverse problem is just a case of fitting a curve to a set of data points and finding the parameters which give the best fit. This can be done using the general linear least squares method or one of the standard non-linear least squares versions which involve the use of function derivatives or second derivatives.

Unfortunately, in this case we have no explicit form for the function which we wish to fit to our observed stomach contents data. The solution of the stationary state differential equation (equation 3.15) has to be calculated numerically, so any non-linear optimisation method which involves the use of analytic derivatives must be ruled out here, making the task slightly more difficult. However, there are still a number of alternative procedures, the most popular being the downhill simplex method and the derivative-free Gauss-Newton algorithm.

Both of these methods can be used to solve the problem of finding the parameter vector $\mathbf{P} = (P_1, P_2 \ldots, P_N)$ which minimises a suitable error measure Q(**P**) between the observed data points and the components of a vector valued function $\mathbf{f}(\mathbf{P})$.

The simplex or polytope algorithm was suggested by Spendley, Hext and Himsworth (1962) and modified by Nelder and Mead (1965). As the name implies, the method involves the use of a simplex - an N-dimensional figure consisting of N+1 vertices and all their interconnecting line segments and faces. Suppose the problem is N-dimensional (i.e. the problem has N unknown parameters) and the chosen starting point is the N-dimensional vector $\mathbf{P_0}$, then the other N vertices required to define the initial simplex are generated using

$$\mathbf{P_i} = \mathbf{P_0} + \lambda \mathbf{e_i} \tag{4.1}$$

where the $\mathbf{e_i}$'s are N unit vectors and λ is a constant of magnitude relative to the problems characteristic scale length. At each stage of the process, the point giving the highest value of the error measure is replaced by a new point at which the function has a more desirable value. This new point is obtained by a series of reflections, expansions and contractions of the worst point about the centroid of the N best points. At a minimum, whether global or local, the simplex contracts itself around its best point pulling in from all directions. (See appendix B for details).

Box (1966) and Bard (1970) conducted numerical studies which showed that when a sum of squares function was to be minimised, algorithms using the Gauss-Newton approach were generally faster than those that do not. In the Gauss-Newton method $\mathbf{f}(\mathbf{P})$ is approximated by a first order Taylor series about the current value of the parameter vector **P**, giving a linear least squares problem which is then solved to give a new value of **P**. This method, however, requires the function derivatives to be known and so is not suitable for our problem.

Ralston and Jennrich (1978) considered a derivative-free Gauss-Newton algorithm called DUD (doesn't use derivatives) which under normal operations requires one function evaluation for each iteration except for extra evaluations needed to get started. The N-dimensional initial vector must again be chosen by the user and the routine then computes the other N vectors which are required to start by replacing the i'th component (for i=1,...N) by a non-zero number h_i. The suggested value for h_i is 0.1 multiplied by the corresponding component of the initial vector. This alternative method, instead of using a Taylor expansion, now approximates $\mathbf{f(P)}$ at each step by a linear function which matches $\mathbf{f}(\mathbf{P})$ at the N+1 previous values of the parameter vector. This also leads to a linear least squares problem which can be solved to obtain a new value of **P** which replaces the parameter vector giving the largest value of the error function. The new set of parameter vectors are then used in the next iteration and this process continues until a suitable convergence criteria has been met. (See appendix B for details).

The only problem now is to choose which algorithm to use. In the next section I shall conduct a series of trials of the two non-linear optimisation methods described above in order to decide which is most suitable for this problem.

4.2 Difficulties with the optimisation technique

Before attempting implementation of either of these non-linear optimisation techniques, a suitable error measure and convergence criteria had to be decided upon. The most popular error measure is the mean squared deviation, so I initially decided to use this, and Q(**P**) is defined by

$$Q(\mathbf{P}) = \sum_{i=1}^{m} (y_i - f_i(\mathbf{P}))^2 \tag{4.2}$$

where the y_i are the m observed data points and the $\mathbf{f_i}(\mathbf{P})$ are the components of a vector valued function $\mathbf{f}(\mathbf{P})$. In our case the P_i are the parameters defining the meal size distribution and feeding rate, the y_i are the observed numerical stomach contents data and the $\mathbf{f_i}(\mathbf{P})$ are the numerical solution of the stationary state differential equation with feeding governed by the parameter vector **P**.

A more important point of discussion is that of convergence and how to get the routines to stop. The routines should end when the error measure has attained its minimum value and an acceptable solution has been reached. It may also be desirable to terminate the routine if progress becomes unreasonably slow, if a particular number of function evaluations has been exceeded or if the iterative procedure is cycling between values.

As the simplex method converges to a minimum, the simplex pulls itself in around its best point and consequently it becomes smaller and smaller. So, the convergence criteria which is usually used here is that the difference between the function evaluations at the points of the simplex are less than a particular small value. Convergence of the DUD routine can be found by comparing values of the least mean squared error on successive iterations. At the minimum the difference should be zero, so we can say that the optimum has been reached when this difference is less than a particular value.

There are however, problems with these convergence rules resulting in false convergence i.e. converging at the wrong point. The procedure may for some reason be taking very small steps. For example, in the simplex method, the simplex may have become very small without actually reaching its minimum and therefore successive function evaluations may be very close to each other, though not necessarily small. Another problem is that the algorithms will converge at the first minimum which they come across, whether global or local. So, for a very complicated error surface, like the sketched example shown in figure 4.1, this criterion could end up producing very wrong answers.

This problem can be eased by the additional constraint that the error measure itself must also be less than a particular small value at the convergence point. However, this still does not solve all the problems as the value which is chosen may be greater than two minima or it may be lower than all of them, in which case an adequate solution will never be found. In this section, however, I shall be dealing with problems which I know have a minimum least squares value of zero, so I can choose a very small error measure as an extra convergence criteria in this case. One final requirement is that after a certain number of iterations, the routines terminate, whether or not a solution has been found, to prevent them heading off in completely the wrong direction indefinitely.

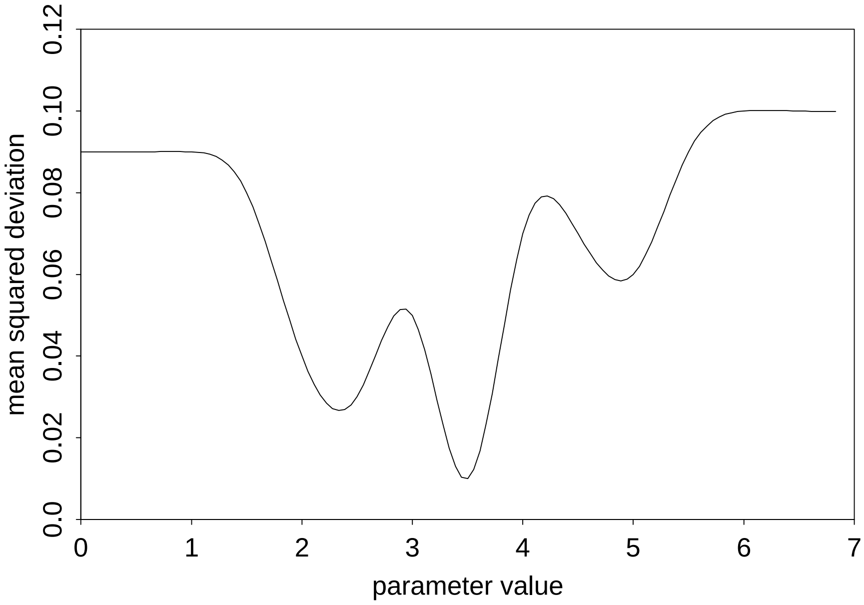


Figure 4.1. An example of a very complicated variation in error with a single parameter.

The rest of this section contains an analysis of how the performance of the two techniques compare over a series of typical problems. In all of the trials I have chosen a set of parameters which define the constant feeding behaviour of a population of fish and calculated the numerical stationary stomach contents distribution. Initially, the solution was calculated at 400 points along the stomach weight interval, to give a numerical density function which is then converted into proportion. The observed data is then a set of values describing the proportion of fish in each of the very small intervals. Since I have calculated this numerical solution from the steady state differential equation (equation 3.15) with known parameter values, I can check that the non-linear least squares procedures are converging to the correct parameter values.

I began my comparison of the two optimisation methods by considering the numerical stationary stomach contents distribution of a population of fish feeding at a relatively low rate on a very narrow truncated normal prey distribution with a low mean. This gives a distribution which is skewed very much to the left with a large proportion of stomachs remaining empty and is illustrated in figure 4.2. The population in this example consists of individuals whose maximum stomach contents are seven grams and digestion rate is 0.13 grams per hour, which are typical values for some of the fish populations which will be studied later in this thesis.

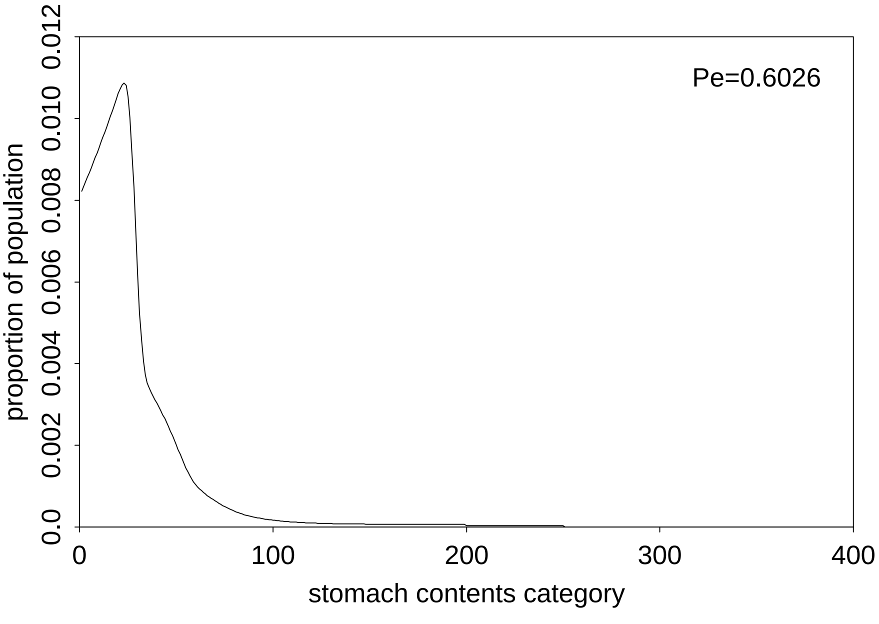


Figure 4.2. Stationary stomach contents distribution of a population of fish feeding at a constant rate of 0.1 meals per hour on a normally shaped meal size distribution with mean 0.5 grams and standard deviation 0.05 grams. The upper limit to the stomach contents is seven grams and the digestion rate is 0.13 grams per hour.

It seems quite obvious that this stomach contents distribution occurs for a population feeding at quite a low rate on relatively small prey with a narrow size distribution since there are hardly any individuals with much food in their stomachs and therefore we would expect that an optimisation routine should converge quite quickly to the solution parameter set. However, as the next section explains, even this relatively easy problem causes some difficulties.

Both algorithms require a 3-dimensional initial vector from which to generate their starting points and in addition the simplex method requires the user to supply the values of the λ_i, which I have initially assumed to be equal to half of the i'th component of the initial vector. The question is how to decide where the routines should be started from. An initial point randomly chosen from a particular domain would be the ideal starting point as this could then be used regardless of whether anything about the meal size distribution function was known. Unfortunately, when this method was used, both methods repeatedly failed to converge to the expected solution, sometimes cycling between values or exceeding the maximum number of iterations without making any progress in the right direction. This failure to converge to any point could be due to the distance of the initial starting point from the actual solution, a very complicated error surface, on the value of the λ_i in the simplex method, or these failures could be due to other inadequacies in the optimisation routines.

It is difficult to get a good idea of how the error measure varies, as in this case it is a four dimensional surface. However, the three cross-sections illustrated in figure 4.3 show a relatively simple error surface and suggest that once the trial parameter vectors lie within the vicinity of the minimum, convergence should be quite rapid, except perhaps for the standard deviation. In this case, the minimum of the mean squared error is very broad indicating that quite a range of standard deviations give mean squared errors almost as low as the minimum value.

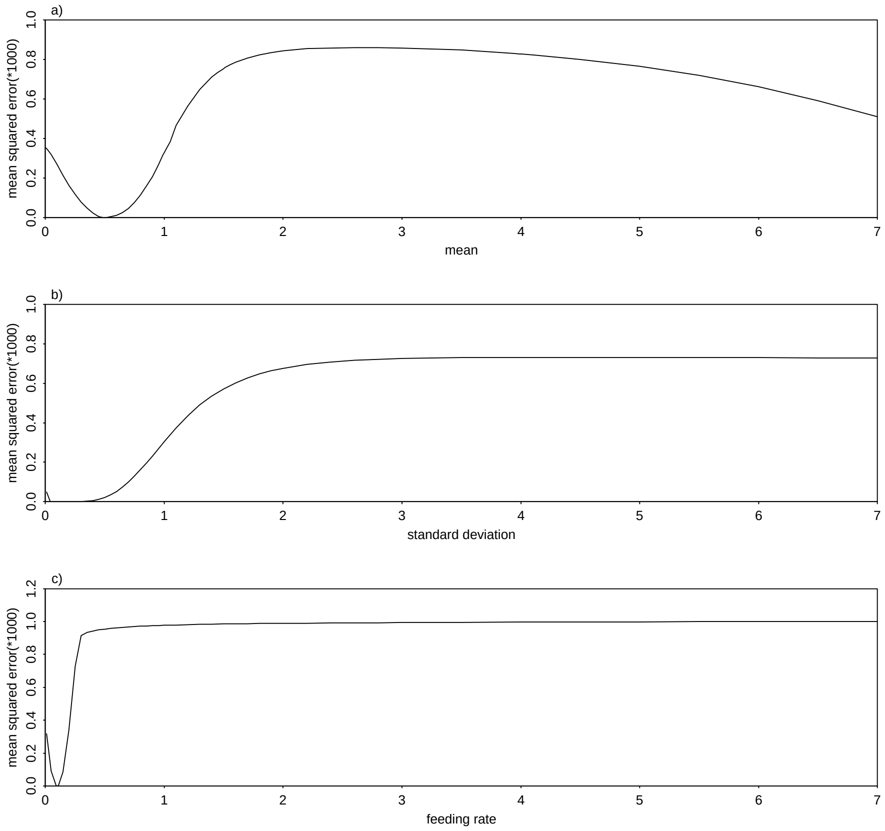


Figure 4.3. Variation in mean squared error between a stomach contents distribution describing the proportion of fish with a particular weight generated by a normal feeding function with mean 0.5, standard deviation 0.05 and feeding rate 0.1 and the solutions of the stationary state differential equation for varying a) mean, b) standard deviation and c) rate.

Figure 4.3 also suggests that convergence from far away initial parameters will be very slow due to the flatness of the error surface in this region. In fact, beginning with the value of the mean of the meal size distribution very far from its optimum may cause the routine to diverge away from the optimum as the mean squared deviation decreases with increasing mean at large distances from the optimum.

The two routines were both altered so that the starting values could be varied and comparisons made of how each procedure converged from particular starting points. I began by starting two of the parameters at their known values and varying the third, noting if the procedure converged and how many iterations (function evaluations) it required for correct convergence. If either routine exceeded 2000 iterations, I chose to halt it anyway, in order to prevent the algorithms running indefinitely without reaching a solution. Even with two of the three parameters being given their known correct values at the beginning of the optimisation process, the procedures still did not always converge. The results of the optimisation procedures for those trials when the initial value of the mean was varied are shown in table 4.1.

	Simplex method		DUD	
Initial mean	Converges	Iterations	Converges	Iterations
0.1	YES	245	YES	286
0.4	YES	209	YES	223
0.5	YES	116	YES	4
0.6	YES	144	YES	213
1.0	YES	190	YES	268
1.5	YES	261	YES	302
2.0	YES	277	NO	cycles
2.5	YES	578	NO	cycles
3.0	YES	1096	YES	230
4.0	NO	too many	YES	204
5.0	NO	too many	YES	5
6.0	NO	too many	YES	147
7.0	NO	too many	YES	230

Table 4.1. Success of the simplex and DUD non-linear optimisation techniques when attempting to fit the solution of the stationary state equation to a stomach contents distribution generated from a meal size of 0.5, standard deviation 0.05, feeding at a rate of 0.1 meals per hour while varying the starting point of the mean meal size.

Similar results occurred for the case when the initial feeding rate of the population was varied, with a few cases where the optimisation routine did not converge to the expected values. However, both processes converged for all the various starting values of the standard deviation. The results indicate that neither algorithm performs consistently worse than the other, though the simplex method seems more likely to make no progress towards an optimum value for the parameters within a reasonable time, while DUD fails more often than not due to a continual cycling of parameter values, which I shall discuss later in this section.

For a moment I shall leave the problem of deciding between the two non-linear least squares processes and look at some ways of improving each method. I first considered the affect of changing the value of the λ_i i.e. the size and shape of the initial simplex.

Start	μ=1		σ=0.2		rate =0.2	
λ_i	Converges	Iterations	Converges	Iterations	Converges	Iterations
0.001 x P_0^i	YES	656	YES	250	YES	325
0.01 x P_0^i	YES	437	YES	242	YES	237
0.1 x P_0^i	YES	329	YES	225	YES	190
0.25 x P_0^i	YES	258	YES	201	YES	165
0.5 x P_0^i	YES	181	YES	183	YES	155
0.75 x P_0^i	YES	297	YES	245	YES	204
1.0 x P_0^i	NO	too many	NO	too many	NO	too many
2.0 x P_0^i	NO	too many	NO	too many	NO	too many

Table 4.2. Success of convergence of simplex method to expected parameters (μ=0.5, σ=0.05 and rate=0.1) when the size of the initial simplex is changed, when the initial parameters are changed only one at a time.

The results shown in table 4.2 indicate that provided the values of the λ_i are not too large compared to the actual initial parameter values, the routine will converge to the expected parameter sets from an initial parameter vector in which the three components have been individually perturbed a short distance away from their optimum. The speed of convergence, however, does appear to depend on the size of the initial simplex. Initial simplexes which are too small make convergence very slow as it is unlikely that the optimum lies within, or near to the initial parameter vector and therefore many small steps have to be taken before the minimum is reached. A very large initial simplex is likely to enclose the optimum parameter set, but the routine requires many more iterations before the simplex becomes small enough around its minimum point to satisfy the convergence criteria.

Looking at the examples I have chosen, it seems that taking the values of the λ_i to be half of the i'th component of the initial parameter vector usually gives the fastest convergence, which is the value I had already guessed at and therefore is used in all further experiments.

If we reconsider the results of the DUD trials shown in table 4.1, we notice immediately that as the initial mean value is increased away from the optimum, convergence gets slower and then fails by going into cycles. However, as the initial mean is increased even further the speed of convergence begins to increase, before once again decreasing. A simple explanation for this can be found if we consider how the convergence routine works. Once the initial parameter vector has been chosen, three other vectors are required to start the process, each of which is generated by replacing the i'th vector component by a non-zero number. In this case this non-zero number is 0.1 multiplied by the corresponding component of the initial vector. So, in the trials conducted here, when the initial parameter vector is (5,0.05,0.1), one of the vectors generated to start the routine will be the optimum and therefore only one more iteration will be required for convergence than when the routine was initiated with the actual optimum vector (see table 4.1).

The problem which occasionally occurs when the DUD optimisation technique is used, is a cycling between parameter values and the routine basically comes to a halt and no further progress is made. The simplest case of this occurs when the new parameter vector which is generated by one step of the optimisation procedure is no better than the four parameter sets which have just been tested and is in fact identical to the worst fitting parameter set. This new parameter vector then replaces the worst one which was used in the previous step (to which it is identical), but since this does not alter any of the vectors, the minimum mean squared error is identical to that which occurred in the previous step. Hence, the difference between consecutive least mean squared errors is zero, although the actual value of the minimum mean squared error will not have reached its required minimum. Consequently, the routine repeats this step over and over again and no progress is made. More complicated cycling problems can occur when the procedure returns to the same set of four parameter vectors after a number of iterations. These problem can be helped by restarting the procedure at a small distance away from the best fitting parameter values when the cycling begins. The routine then usually converges within a couple of restarts. If it does not, then the routine will as usual be stopped when the total number of iterations exceeds the maximum allowable number.

I also experimented with several different values of the difference between consecutive minimum mean squared errors required for convergence. I eventually decided that 1×10^{-14} was a suitable value for this difference and the minimum mean squared error itself had to be less than 1×10^{-12}. The root mean squared error is therefore 1×10^{-6}, which, compared to the mean proportion of the population per stomach weight category, 2.5×10^{-3}, is quite small and gives the parameter values correct to four decimal places.

Returning to the comparison between methods, I increased the complexity of the problem by using a meal size distribution function made up of two normal distributions, which gives a 6-dimensional problem. One of the prey sources is very small while the other has quite a large mean weight and is consumed at a quarter of the rate of the small prey. Once again the values of the maximum stomach contents and digestion rate were typical of some of the marine fish species which will be studied later in this thesis. The resulting stomach contents distribution is shown in figure 4.4.

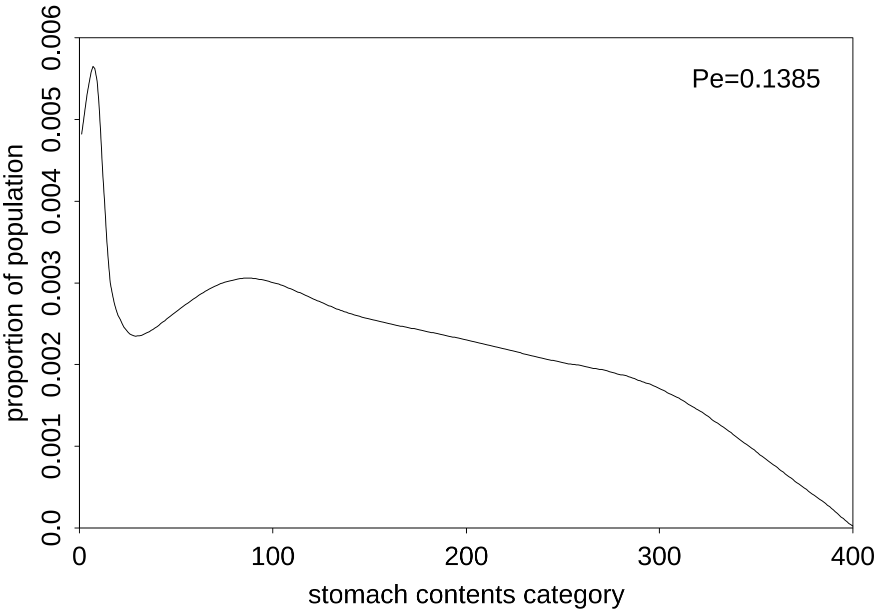


Figure 4.4. a) Meal size distribution made up of two prey sources, one with mean 0.2 grams and standard deviation 0.05, being consumed at a rate of 0.2 meals per hour and the other with mean 1.7 grams, standard deviation 0.5 and being consumed at 0.05 meals per hour., with b) the resulting stationary state distribution of the feeding population whose digestion rate is 0.13 grams per hour and maximum stomach contents are 7 grams.

Once again then, I attempted to fit the model to the data using both methods, assuming that the maximum stomach contents are seven grams and the digestion rate is 0.13 grams per hour. The success of the two routines was again compared by checking over what parameter range and how quickly the two methods converged to the expected parameter set.

(a)	Simplex method		DU D	
Initial rate1	Converges	Iterations	Converges	Iterations
0.05	NO	too many	YES	244
0.10	YES	1119	YES	227
0.25	YES	1186	YES	207
1.0	YES	995	YES	267

(b)	Simplex method		DU D	
Initial mean2	Converges	Iterations	Converges	Iterations
0.5	NO	too many	NO	too many
1.0	YES	1584	YES	255
1.5	YES	818	YES	197
2.0	YES	712	YES	207
2.5	NO	too many	YES	204
3.0	NO	too many	YES	179

Table 4.3. Success of the two routines when attempting to fit the solution of the stationary state equation to a stomach contents distribution generated from the two prey source meal size distribution illustrated in figure 4.4a, when the starting point of the consumption rate of the small prey is varied (a) and (b) when the initial value of the mean of the large prey is varied, while all the other parameter are started at their known values.

In this problem of increased dimensions, the simplex method performed far worse than DUD, taking far longer to converge and quite frequently not converging at all within the maximum number of iterations. Table 4.3 shows the convergence results for two of the six parameters.

On the basis of the results of these experiments I decided to use DUD as my non-linear least squares optimisation technique as it has proved to have a slightly wider range of convergence than the simplex technique and also requires much fewer iterations to converge, particularly for higher dimension problems (though each iteration takes slightly longer due to the matrix inversion involved in the calculation).

4.3 Distinction of solutions

In chapter three, I provided clear evidence that a stationary stomach contents distribution of a population feeding on a fixed number of prey sources is generated by the solution of the stationary state equation with a single set of biologically reasonable feeding parameters. However, it was more difficult to decide if this uniqueness holds for the stomach contents distributions of fish populations feeding on differing numbers of prey sources, or whether in fact identical stationary stomach contents distributions can be produced by a population feeding on four prey sources and one prey source, for example. I have endeavoured to verify this by fitting solutions of the steady state equation generated by feeding functions made up of the wrong number of prey sources or the wrong type of distribution, to a stationary stomach contents distribution with a known set of feeding parameters.

I began by taking a stationary gut contents distribution generated by a single normal meal size distribution as my initial data set. The first question which has to be answered is whether a feeding function which is a combination of two or more prey sources can produce an identical distribution. I have chosen two very different stationary stomach contents distributions as examples - one with many low stomach content individuals and the other very skewed towards the upper end of the stomach contents range.

The first example is illustrated in figure 4.2 (p109) and is generated by a population feeding on a very narrow meal size distribution function centred about a low mean at a rate which is low compared to the digestion rate. In an attempt to fit a solution generated by a bimodal meal size distribution, I began the six dimensional optimisation routine with a variety of parameter vectors defining two narrow food sources, positioned near to the known solution. In all cases, I found that the routine converged to a set of parameters defining the expected feeding function.

When the routine was initialised with two prey source distributions whose means are both quite close to 0.5, then the final set of parameters describes two distributions, identical to the expected meal size distribution, whose feeding rates add up to 0.1, the required feeding rate. But, if the two initial prey source distributions are further apart, then three of the final parameters describe the expected feeding function, while the feeding rate of the second distribution converges to zero and therefore the values of its mean and standard deviation are irrelevant. Table 4.4 shows some typical sets of initial and final parameter values.

Similar results to those explained above occurred when attempts were made to fit a solution generated by a meal size distribution with three or four prey sources.

The fact that this stomach contents distribution cannot be reproduced with multiple prey source meal size distributions could be due to the shape of this particular example. The very definite peak and its narrowness indicate that the population is feeding on a very narrow meal size range which would not occur if there were many prey sources, unless they were all extremely narrow. The lack of individuals with high stomach weights emphasises that there are no large meals available and that the feeding rate is fairly low compared to the digestion rate.

	μ1	σ1	Rate1	μ2	σ2	Rate2
Initial param.	0.4	0.02	0.13	0.45	0.05	0.05
Final param.	0.5000	0.0502	0.0789	0.4999	0.0499	0.0210
Initial param.	0.3	0.03	0.05	0.6	0.1	0.08
Final param.	0.5166	0.0987	0.00001	0.5001	0.0500	0.0998

Table 4.4. Typical initial and final parameter sets which occur when attempting to fit a stomach contents distribution generated by a double prey source meal size distribution to one which is generated by a population feeding on a distribution with mean 0.5 grams and standard deviation 0.05, at a rate of 0.1 meals per hour.

As an alternative distribution, for use as my next example, I returned to the gut contents distribution illustrated in figure 3.7 (p79). All three distributions illustrated here, although not identical have quite similar overall shapes, with the majority of the population having high stomach contents, so it seems possible that they might not be produced by unique feeding functions. I began with the single prey source stomach contents distribution. Once again, for all sets of initial parameters, the optimisation routine converged to a set of parameter values which describe a feeding function identical to the expected one.

I also attempted to fit the distribution generated by a bimodal meal size distribution and illustrated in figure 3.7, with solutions generated by a feeding function which has more than two prey sources. Likewise, the routine always converged to the expected parameter values, giving two normal distributions positioned at one and two grams with standard deviations 0.2 and feeding rates of 0.1 meals per hour.

I shall now consider the reverse question, of whether a stomach contents distribution can be underfitted i.e. whether an identical solution can be found which is generated by a meal size distribution with less prey sources.

As my first example, I have reconsidered the distribution function illustrated in figure 4.4 (p116). I chose a variety of starting parameter vectors and attempted to fit the gut contents distribution using the three dimensional optimisation routine. From all initial sets of parameters the routine failed to find a minimum and halted after too many function evaluations at a point nowhere near to a possible minimum. This is likely to be due to the very peculiar shape of the stomach contents distribution which has quite a definite narrow peak at low stomach contents, but is also quite spread out at higher gut weights. The narrow peak implies a very narrow meal size distribution with a low mean size while the broadness of the upper part of the distribution indicates that there must be some larger meals available, which suggests that a double prey source distribution is likely. Therefore the optimisation routine is unlikely to find a minimum for a single normal meal size distribution.

I next returned to those examples of figure 3.7 which had a large proportion of individuals with high stomach contents and no outstanding features which make them obviously generated by a meal size distribution with a particular number of prey sources. I first attempted to fit the numerical gut contents distribution of a population feeding on a double prey source meal size distribution function with a solution generated by a single normal meal size distribution. An exact solution was still not found. In this case the algorithm does get to a minimum value for the least mean squared error, but does not halt as the fitted solution is not an exact fit and therefore this minimum is not low enough to satisfy the convergence criteria.

Although the optimisation procedure does not find a set of parameters that identically reproduces the solution generated by a double food source meal size distribution, this minimum does occur where we would expect it. The parameter values describe a normal meal size distribution situated approximately midway between the two normal distributions which appear in the actual meal size distribution. The standard deviation has quite a large value so that a wide range of meal sizes are consumed and the feeding rate is approximately equal to the sum of the two rates of the actual feeding function. Figure 4.5 compares the actual and fitted feeding distributions and the associated stomach contents distributions.

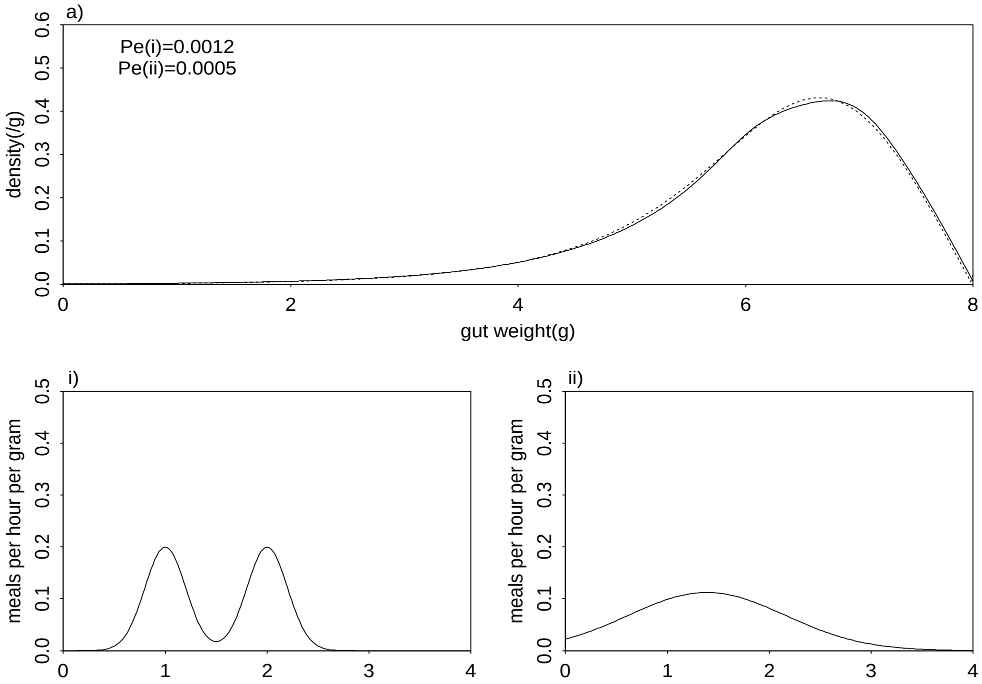


Figure 4.5. (a) Stomach contents distribution (solid) generated by a double prey source meal size function together with the closest fitting stomach contents distribution generated from a single prey source meal size function (dotted). The double prey source distribution is illustrated in i) with means at 1 and 2 grams, standard deviation 0.2 and feeding rate 0.1. The single meal size distribution with mean 1.39 grams, standard deviation 0.77 and feeding rate 0.22 is shown in ii).

I next attempted to 'underfit' a stomach contents distribution generated by a four prey source meal size distribution, similar results occur. The mean squared error did reach a minimum, except not a low enough one for us to accept that an identical fit to the data set has been made. However, if the convergence criterion for the magnitude of the mean squared error was less strict, for example 1×10^{-8} instead of 1×10^{-12}, then the routine would have converged and we would wrongly conclude that the distribution had been reproduced identically.

These results emphasise that even when differing numbers of prey sources are allowed in the meal size distributions, a particular noise free numerical stomach contents distribution can only be generated by a unique feeding regime and the routine converges as expected.

So far this analysis of the inverse problem has been concerned with stomach contents distributions generated by a known type of feeding function (in this case the normal distribution) and I have shown that the optimisation routine does not converge to 'wrong' answers provided that the convergence criteria are very strict. I shall now investigate whether the stomach contents distribution of a population feeding on an alternatively shaped meal size function can be identically reproduced by solutions generated by a normal distribution.

As my first example I have reconsidered the stomach contents distribution generated by the triangular meal size distribution illustrated in figure 3.9. The numerical stomach contents distribution is almost impossible to tell apart from that generated by a normal feeding function, so it would not be surprising if in this case the three dimensional optimisation routine converged and we concluded that the stomach contents distribution had been identically reproduced. Once again however, the strictness of the convergence criteria prevented the routine from ending as the mean squared error is not quite low enough. The minimum value it reaches is 1.5×10^{-10} while our aim is for it to be less than 1×10^{-12}. When attempting to fit a normal feeding distribution to a stomach contents distribution generated by a gamma distribution (see figure 3.9), the optimisation routine again failed to converge, but this time did not make any headway towards a sensible answer and by the time the routine is halted, the value of the mean being a large negative number and the standard deviation also being very large. The algorithm has obviously gone in such a direction in an attempt to reproduce the effects of the long tail of the gamma function, but has not reached a minimum.

The results of this section show that particular numerical stomach contents distributions are generated by a unique feeding function and provided the convergence criteria used in the optimisation method are severe enough, the method will converge to the correct answer, if there is one. For less strict convergence criteria though, the optimisation technique may converge to give an alternative set of parameters that generate a solution which is not exactly identical to the data we are attempting to fit it to. This error in some cases however can be very small, an average of 0.1 per cent.

Real stomach contents data will never be in the form of an exact stomach contents distribution, it will in general be noisy due to sampling. Therefore, the optimisation routine will never be able to find a set of parameters which generates a solution that identically matches the data set and so different feeding regimes will produce equally good fits to a single set of noisy data. In the next section I shall investigate whether we can still clearly conclude the values of the population feeding parameters when the data is sampled and categorised.

4.4 Some experiments with simulated data

The preceding sections of this chapter have dealt with finding sets of parameters which generated a particular known population stomach contents distribution. However, real stomach contents data which are provided for analysis will never be in such an ideal form. In fact the data may be quite noisy depending on the size of the samples which have been taken. A large sample will provide the most clear distribution shape, i.e. it will be less noisy than a small one and more like the population distribution from which it was sampled. But, dissecting the stomachs of many thousands of fish is impracticable, so in general sample sizes are usually of hundreds of fish, rather than thousands. During stomach contents analysis, the gut weight range is divided into intervals and the individual measurements categorised accordingly. The data then consists of the proportion of the sample in each stomach weight category. So, a detailed and accurate description of the stomach contents distribution will be provided when the range is split into very small intervals, but much of this detail will be lost as the intervals become broader. The question which needs to be answered is how well can we infer the feeding behaviour of the actual population of fish from such samples. So, in this section of the chapter I shall investigate the relationship between sample size, interval width and the value of the feeding parameters obtained and compare them to those of the actual population.

To begin this investigation I have simulated some data sets with the same combination of feeding parameters, but different numbers of stomach contents categories and various sample sizes, using a similar method to that used to generate the digestion data in chapter two. First a noise-free distribution, generated by a known feeding function is divided into m categories with the empty stomachs as category m+1. The unit interval is then split into subintervals each of width equal to the proportion of the population held in each of the m+1 distribution categories. A set of r random numbers between 0 and 1 is generated and the proportion falling into each interval is noted. This fraction then represents the proportion of the population contained in each category of the distribution. This method of random sampling is known as the sequential search method (Dagpunar 1988).

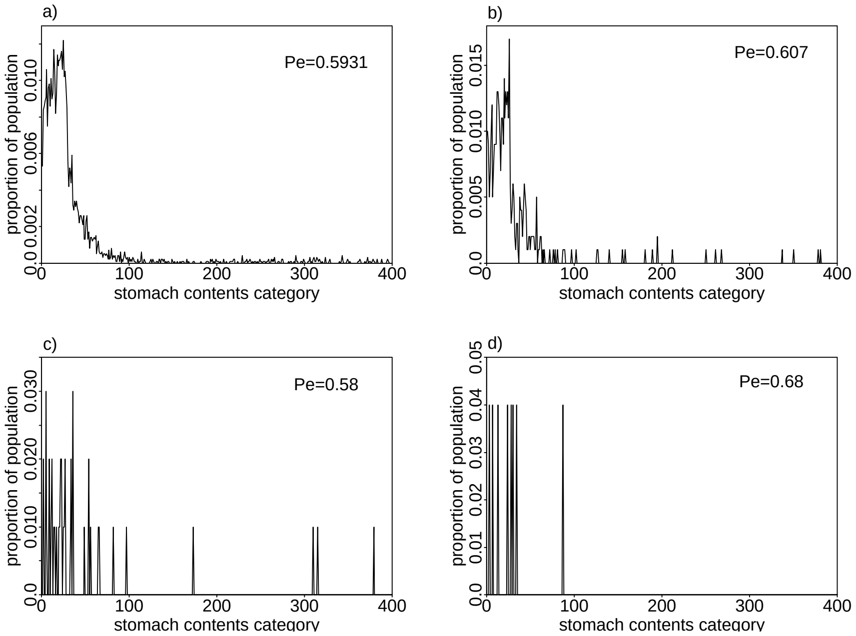


Figure 4.6. Stationary stomach contents distributions illustrating proportions of the sample in 401 stomach categories generated from a feeding function with mean 0.5, standard deviation 0.05 and feeding rate 0.1 for sample sizes of a) 10000, b) 1000, c) 100 and d) 25. The maximum stomach contents is 7 grams and the individuals all digest at 0.13 grams per hour.

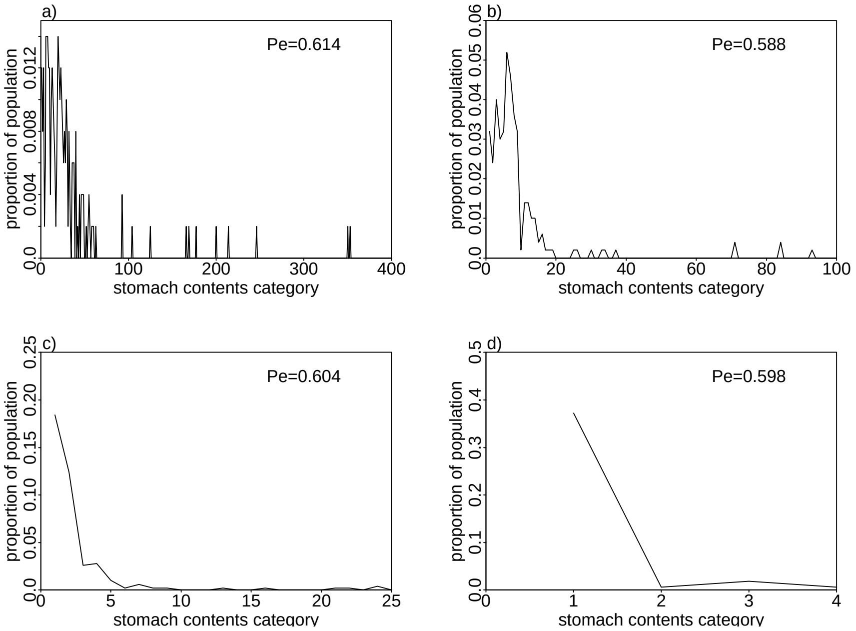


Figure 4.7. Stationary stomach contents distributions illustrating the proportions of a sample of size 500 taken from a population feeding on a meal size distribution with mean 0.5 and standard deviation 0.05 grams at a rate of 0.1 grams per hour when the data is categorised into a) 401, b) 101, c) 26 and d) 5 intervals.

Obviously, if a larger sample of random numbers is taken, then the distribution becomes less noisy and more recognisable as the exact distribution from which it was generated and small samples become more noisy, as is illustrated in the examples shown in figure 4.6.

Decreasing the number of categories, i.e. making each category wider (except for the empties) also causes the noisieness to decrease, but this also reduces the detail seen in the distribution, illustrated in figure 4.7.

As I have already shown in section 4.1, the optimisation algorithms will not converge when the chosen starting value is very far from the actual solution, so there seems little hope of this happening when the distribution is not an exact solution of the differential equation. In this case though, the noisy data which I am using has been generated from known distributions, so there is an obvious parameter vector from which to start the optimisation process. The set of parameters giving the best fit to the noisy distribution should not be too far from those which generated the corresponding exact stomach contents distribution, so the optimisation process should converge quite easily.

At present, the optimisation procedure requires a very low minimum mean squared error value for convergence as previously we had been dealing with stomach contents distributions which had been generated exactly from a particular set of feeding parameters and therefore had a minimum mean squared error of zero. However, now we are dealing with noisy data and the best fit of the model to the data will not give a minimum mean squared error of zero. As a consequence, it is probable that the optimisation routine will not converge with the strict convergence criteria used in the previous sections, even when the minimum has been reached. To rectify this situation I shall discard the restriction that the minimum mean squared error has to be less than 1×10^{-12} for convergence and for us to be able to conclude that the global minimum has been reached. Since data sets are simulated by random number generation, we have no idea of what size the error measure is going to be at its minimum and therefore cannot place any convergence restrictions on it. However, as the optimisation routine is started from near the expected to be the global minimum, it is unlikely to converge to a local minimum and the convergence restrictions placed on the difference between consecutive error measures should be adequate.

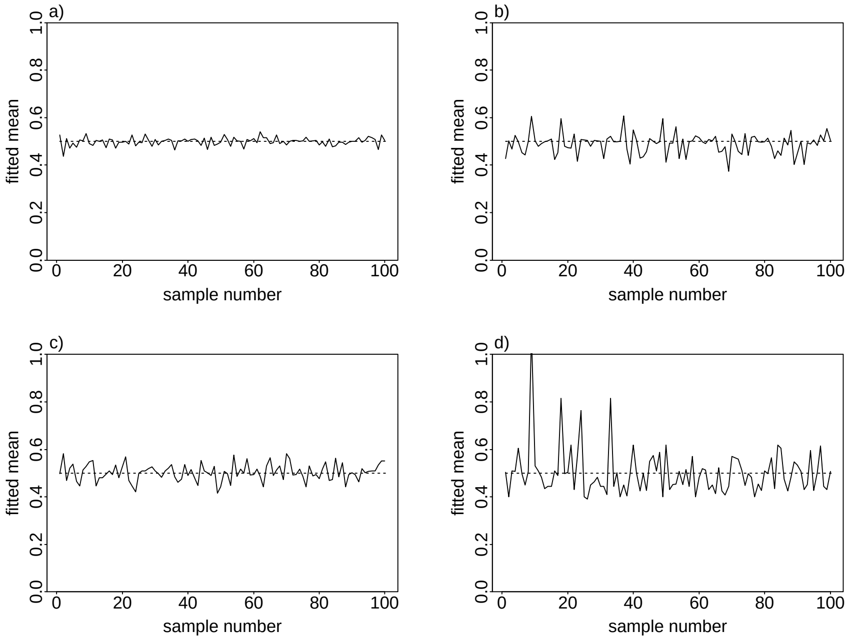


Figure 4.8. Variations in fitted mean of the meal size distribution obtained from the optimisation routine for different random number sets, for a) samples of size 1000 and 101 categories, b) samples of size 100 and 101 categories, c) samples of size 1000 and 5 categories and d) samples of size 100 and 5 categories. The population stomach contents distribution was generated using a feeding function with mean 0.5 grams, standard deviation 0.05 and feeding rate 0.1 meals per hour.

Since the noisy distributions are simulated using sets of random numbers, no two stomach contents distributions will be identical. Therefore, data sets distributions simulated using identical generating parameters and equally sized intervals, but different samples will not give the same fitted parameter values. An example of the variation observed in the fitted values of the mean of the meal size distribution is illustrated in figure 4.8 for a variety of sample sizes and numbers of stomach weight categories.

These illustrations show that the variations between the fitted parameter values depend on the size of the sample and number of stomach contents categories. So, in order to come to a decision about how reliable the results of this inverse problem are when dealing with such data, I shall repeat the optimisation process one hundred times with different samples of the same size for each number of stomach categories and then calculate the appropriate summary statistics. The experiments were conducted for less than twenty-six stomach contents categories and sample sizes of 1000 and below, as these seemed comparable to values used in real stomach contents analysis (e.g. Hall et al. 1995 and De Groot 1964). Once again I have used a very narrow single prey source meal size function with a relatively low feeding rate compared to the digestion rate to generate the population stomach contents distributions from which the noisy and categorised data are simulated.

The variation in the expectation and coefficient of variation over a range of sample sizes and number of categories of each of the three parameters defining the feeding behaviour is illustrated in figures 4.9 to 4.11. The experiments were carried out at twenty points over the category-sample size plane and then interpolated using cubic spline functions to give points on a finer grid over the whole plane.

The first set of illustrations shows the variation in the average of the fitted mean meal size and its coefficient of variation. Although the variation in the expectation appears to be a rather uneven surface with many peaks and troughs, this mean value is never very far away from the population value of 0.5. However, for small sample sizes (less than 50) and more than about ten stomach weight categories, the mean value appears to be increasing away from the population value. The combination of small sample sizes together with quite a number of stomach weight categories will inevitably produce extremely noisy data sets with the average number of individuals per category being very low or less than one. As a consequence the results obtained from fitting a population stomach contents distribution to such data are unlikely to be very reliable.

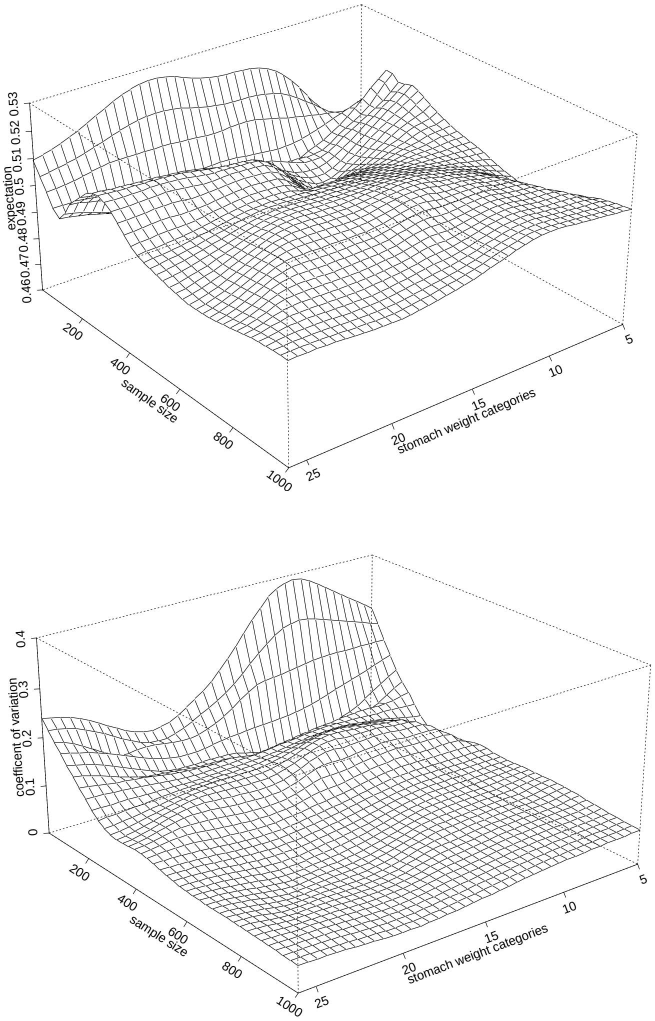


Figure 4.9. Variation in a) the mean and b) the coefficient of variation of the fitted mean of the meal size distribution with sample size and number of categories. The population meal size mean is 0.5.

The coefficient of variation is quite low (less than 0.1) over a large part of the sample size-weight category range and only begins to increase much as samples get down to below 200 in size. And in fact does not increase above 0.2 until sample sizes contain less than about 75 individuals when the coefficient of variation begins to rise quite rapidly, especially for low numbers of stomach weight categories, which is as we would expect.

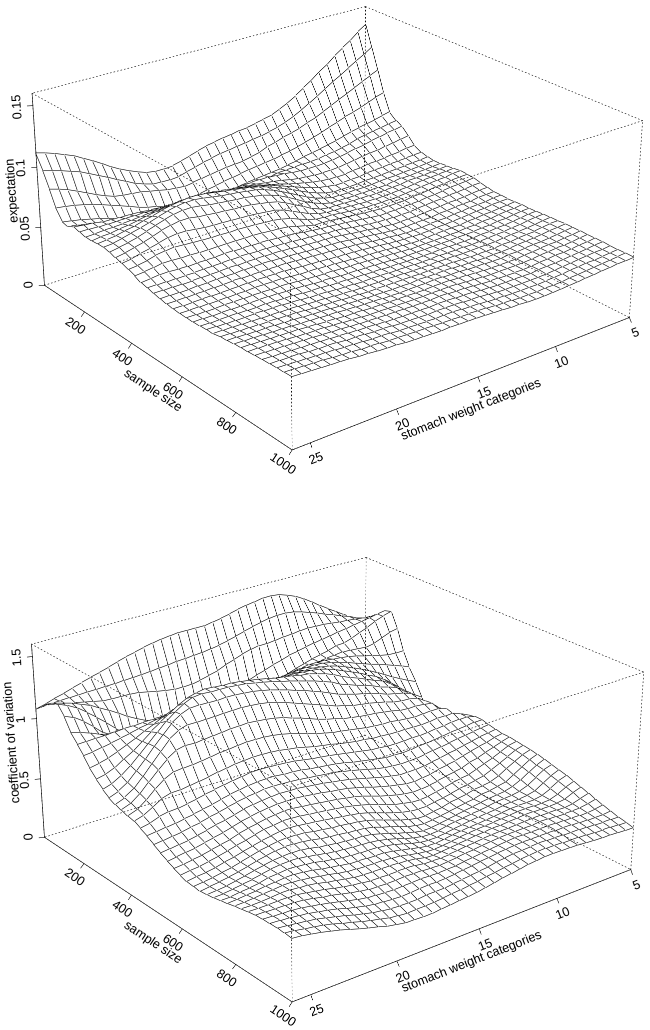


Figure 4.10. Variation in a) the mean and b) the coefficient of variation of the fitted standard deviation of the meal size distribution with sample size and number of categories. The population meal size standard deviation is 0.05.

Moving on now to the average standard deviation of the fitted meal size distribution which is illustrated in figure 4.10a. We can once again see that for large sample sizes the average value is close to the actual population value of 0.05. Over the major part of the range of the variables, the surface of the expectation of the standard deviation remains quite flat and close to 0.05. However, once the sample sizes fall below 100 individuals, the mean standard deviation begins to increase, first quite slowly, but then more rapidly, particularly for low numbers of stomach weight categories. For small samples of 25 individuals, the averages of the fitted standard deviations lie between two and three times that of the population from which the samples were drawn. The most noticeable increase in the expected value of the standard deviation as sample sizes get smaller occurs when the stomach weight range is divided into very few categories. This is most likely to be due to the increasing width of the categories. Since the actual fish population stomach contents distribution is quite narrow and very skewed to the left hand end of the stomach weight range, all of the sampled individuals may have stomach contents contained in the first of four very broad stomach weight categories, except for the empties who are included in a fifth category. We therefore do not know how the individuals are distributed within that interval. They may be as expected or they could be in a much flatter, broader distribution and therefore the standard deviation may be larger.

The coefficient of variation of the standard deviation is relatively high for a large part of the category-sample size range indicating that there is a lot of variation in the values of the fitted standard deviations at each point, even for large samples. This implies that the value of the fitted standard deviation is quite sensitive to the changes in the detail of the distribution produced by taking different random samples. At low standard deviations, the position and overall shape of the stomach contents distribution are affected most by the mean of the feeding function and the feeding rate, while the meal size standard deviation mainly affects the detail of the distribution (reconsider figure 3.5a-d). Since the overall shape and height of the distribution does not change much between samples, only the fine detail, there will be less variation in the fitted values of the mean and feeding rate than there is in the standard deviation. Therefore the coefficient of variation of the standard deviation will be much greater than that of the other two parameters at all sample sizes and numbers of categories.

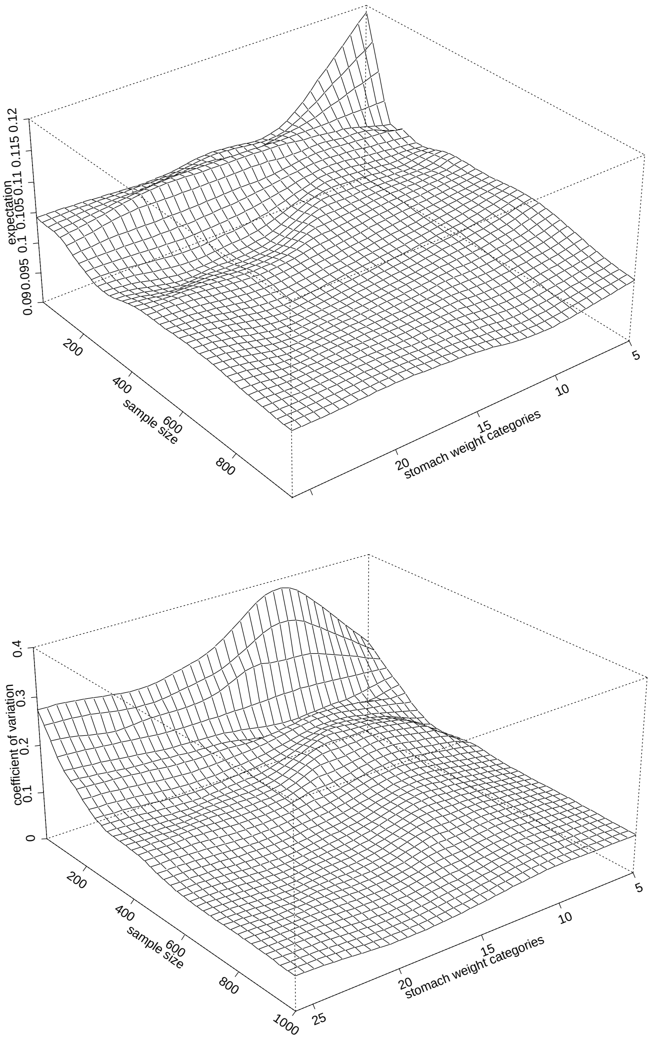


Figure 4.11. Variation in a) the mean and b) the coefficient of variation of the fitted feeding rate with sample size and number of categories. The population feeding rate is 0.1.

For large sample sizes, the average value found for the feeding rate over the hundred samples is quite close to that of the population from which the samples were drawn (0.1). It is not until the sample sizes fall below 200 that this average begins to increase and to a significantly higher value when there are fewer categories. Due to the fewer stomach weight categories, the width of each becomes wider and therefore samples taken from fish populations feeding at slightly higher rates may have the same proportion of fish per interval and the routine converges to a higher rate. However, this increase in mean feeding rate is by less than twenty per cent and is therefore incomparable to the huge increases of 200 and 300 per cent seen in the standard deviation values. As the sample sizes become smaller, the distributions become more noisy and so the variability in the fitted feeding rates increases which is seen in the illustration of the coefficient of variation.

From these sets of experiments, I wish to find a combination of sample size and stomach weight categories which gives a reliable description of the feeding behaviour of the population from which it was drawn. Such combinations will have an average of the parameter value being considered close to the population value and will have a low coefficient of variation. In such a case we can be confident that if one such sample is drawn from the population and categorised, then the fitted values obtained from the optimisation technique will adequately describe the feeding behaviour of the whole population.

If I now reconsider figures 4.9-4.11, we can see that the lowest coefficient of variation and expectation nearest the population parameter value occur for very large samples (1000) and a lot of stomach weight categories. However the processing of such data would be very time consuming, so we are really aiming for a lower number of individuals per sample. Taking samples of approximately one hundred individuals categorised into between five and ten stomach weight intervals still gives quite promising results. The coefficient of variation at this point is still quite low (below 0.2) except for the standard deviation where it is about one and the means of all three parameters are close to the population values. Consequently I can conclude from this section that this combination of sample size and stomach categories is a good choice for use in stomach contents analysis, combining practicality with relatively reliable results.

4.5 Conclusion

The aim of this chapter was to find an automatic method of solution of the stationary state inverse problem. In the early sections of the chapter I discussed the suitability of various optimisation methods and eventually decided to use a modified derivative-free Gauss Newton method.

The method worked relatively well for noise free stomach contents distributions which had been generated exactly from a known feeding function and provided the starting parameters were quite close to the actual minimum, the routine did not take too long to converge to the expected parameters. The results did however show that without very strict convergence criteria, if completely wrong meal size distribution shapes are used, the optimisation routine may converge to wrong parameter sets for certain stomach contents distributions. For noisy data the strict convergence criteria have to be relaxed in order for the routine to converge at all, since we will never be able to find a population stomach contents distribution which exactly reproduces the distribution of a sample of individuals. So, in this case convergence with the wrong number of prey sources is quite likely to occur. However, if we assume that the actual number and type of prey sources is known, then this problem should not arise.

In the experiments with simulated noisy and categorised data, I have tried to show how reliable this automatic method is for inferring the stationary feeding behaviour from real data sets. Since we will never have a complete description of the stomach contents distribution of a population of fish, we need to know how accurately the feeding behaviour which is inferred from the stomach contents data of samples of the population, describes that of its parent population. The results indicate that provided the sample which has been taken is not too small (approximately 100) and the number of stomach contents categories is between five and ten, then the feeding behaviour inferred from this sample should reasonably describe the feeding behaviour of the population from which it came.

The example I have used is relatively simple with just a single prey source stomach contents distribution. However, considering the results of sections 4.2 and 4.3, this method should be applicable to higher dimension problems provided that we do actually know how many prey sources the population itself is feeding on.

Since it is unlikely though that a population of fish will be feeding at a permanent constant rate, a more interesting problem is that of time dependent feeding. In the next chapter, I shall investigate how well we can infer the time dependent feeding behaviour of a population with varying stomach contents.

Chapter 5

The time-dependent feeding rate inverse problem

5.0 Introduction

Chapter four made an attempt at solving the inverse problem for the stationary state differential equation. A global optimisation method which converged in a reasonable length of time could not be found due to the laborious calculations required during the numerical solution of the ordinary differential equation. This does not bode well for dealing with the even more complicated and computationally intensive time dependent inverse problem.

The numerical experiments in chapter three demonstrated that the time dependent model required approximately four to five days to reach its stationary cycle, which using the numerical methods described in chapter three takes about 15-20 minutes computing time. All non-linear optimisation techniques require repeated calculations of the solution, so obviously a routine which incorporates this method of calculation of the time varying stomach contents distribution will be extremely time consuming and possibly hardly worth the effort. So, if we wish to find an automatic method of solution of the time dependent inverse problem and carry out any experiments on the effect of noisy and sampled data, we need to be able to calculate the solution considerably faster.

One option is increasing the width of the intervals at which the gut contents distribution is calculated, as is increasing the integration time step. However, as well as increasing the speed of the calculation, the accuracy of the solution is reduced, with some very large errors occurring. So, since there appear to be no quicker methods of solving the partial differential equation which describes the time variation of the stomach contents distribution, another modelling approach must be used. In this chapter I shall reformulate the model using a discrete approach, in the hope of speeding up calculations. Once such calculations have been incorporated into an automatic optimisation procedure, I should then be able to perform experiments similar to those of chapter four to test the reliability of population feeding behaviour results inferred from sampled data, but this time incorporating sampling frequency as we are dealing with a time varying distribution.

5.1 The finite difference approach

A method often used in the modelling of ecological systems is the difference equation approach. It is most often used when modelling populations with age structure which have distinct age classes. In this chapter I shall form a set of difference equations by discretising the stomach contents range and constructing a map which relates the variables at time t to those at time t+1. So, in this case, instead of distinct age classes, we shall be considering distinct stomach contents classes.

I shall consider the stomach contents range $[0, w_F]$, to be divided into an array of N boxes, each of width Δw, such that at time t, $n_{i,t}$ is the number of stomachs with weight between (i-1)Δw and iΔw and $n_{0,t}$ is the number of empty stomachs. The number $n_{i,t}$ obviously depends on how many stomachs came into the interval during the previous time step due to digestion and how many entered this category by eating. This in turn depends on the length of one time interval. For simplicity I shall suppose that during one time step, individuals can either eat a single meal of a particular size or they can digest from category i to category i-1. This assumption about digestion leads to the constraint that

$$\Delta t = \frac{\Delta w}{K} \tag{5.1}$$

where K is the digestion rate. The meal ingested during this time interval can be of any size provided that it does not take the individuals into a category which would be out of the stomach contents range, which is the same satiation rule that was used in the continuous feeding and digestion model.

I shall next define the expression $U_{i,t}$ as the rate at which weight class i individuals eat meals at time t. Then we can write

$$\frac{dn_{i,t}}{dt} = -U_{i,t} n_{i,t} \tag{5.2}$$

as the rate of change of the number of individuals in weight class i due to feeding.

The proportion of weight class i who do not eat a meal in time t to t+Δt, $S_{i,t}$, can then be approximated by

$$S_{i,t} \approx \exp\left\{-U_{i,t} \Delta t\right\}. \tag{5.3}$$

These individuals of weight class i who do not eat a meal within the time interval, therefore must digest, according to the rule stated earlier, unless they are already empty, in which case they remain so. Consequently, this proportion, $S_{i,t}$, of category i individuals will have digested into weight class i-1 by time t+Δt. The digestion part of the difference equations can therefore be written as

$$n_{0,t} = S_{0,t-\Delta t} n_{0,t-\Delta t} + S_{1,t-\Delta t} n_{1,t-\Delta t} \tag{5.4}$$

and for i>0

$$n_{i,t} = S_{i+1,t-\Delta t} n_{i+1,t-\Delta t} \tag{5.5}$$

which basically states that those fish in category i+1 at time t-Δt who do not eat, digest into category i by time t. The difference equation representing the empty fish (5.4) obviously has an extra term representing those individuals already empty which do not eat in the interval t-Δt to t.

Moving on now to the definition of feeding. I shall first define $P_{i,n}$ as the probability that a meal eaten by a weight class i individual weighs between (n-1)Δw and nΔw. However, weight class i individuals will not feed on meals which take them into a category above the upper stomach contents limit, in this case category N, so the probabilities must obey the constraint

$$\sum_{n=1}^{N-j} P_{j,n} = 1 \qquad \forall j, \tag{5.6}$$

i.e. for each weight class j, the sum of the probabilities of all possible meals is equal to one.

As I described in chapter two, the number of individuals moving into a weight class category i, is due to individuals in lower weight classes consuming meals of exactly the right size to take them into this category. I shall first consider the transfer of individuals from weight class j to a higher weight class i, due to feeding. I have already defined $S_{j,t}$ to be the proportion of individuals in weight class j who do not feed at time t, so therefore the number who do eat a meal can be written as

$$\left(1 - S_{j,t}\right) n_{j,t} \qquad (5.7).$$

For the consumption of this meal to take the individuals into weight class i, it must be of the correct size. The probability that this meal consumed by class j individuals is of weight between (i-j-1)Δw and (i-j)Δw is of course equal to $P_{j,i-j}$ and therefore the number of j class individual transferring to class i during the interval t to t+Δt due to feeding can be written as

$$\left(1 - S_{j,t}\right) n_{j,t} P_{j,i-j}. \tag{5.8}$$

All individuals however, are exposed to food and so may be feeding. Therefore, the number of individuals entering weight class i at time t due to feeding from lower weight classes is clearly

$$I_{i,t} = \sum_{j=0}^{i-1} \left(1 - S_{j,t}\right) n_{j,t} P_{j,i-j} . \tag{5.9}$$

The complete feeding and digestion dynamics can then be defined by the following set of difference equations

$$n_{o,t} = S_{o,t-\Delta t} n_{o,t-\Delta t} + S_{1,t-\Delta t} n_{1,t-\Delta t} \tag{5.10}$$

$$n_{i,t} = S_{i+1,t-\Delta t} n_{i+1,t-\Delta t} + I_{i,t-\Delta t} \qquad \text{for } 0 < i < N \tag{5.11}$$

$$n_{N,t} = I_{N,t-\Delta t} . \tag{5.12}$$

Obviously there is no 'I' term in the equation defining the number of empty individuals at time t, as a fish which takes a meal will not become empty. Similarly there is no 'S' term in the equation for the highest weight class as there is no category above N down from which the individuals can digest.

5.2 Solution of finite difference equations

Once we have been provided with a set of initial conditions, i.e. values for $n_{i,0}$ for all i, then it is easy to solve the set of finite difference equations (5.10-5.12). The numbers of fish contained in a particular stomach contents category at time step t can be calculated by a simple map from those at time t-Δt. The solution, however, must be compared to that of the continuous model to verify that the two approaches to modelling this feeding and digestion system do not give radically different answers.

In order to make these comparisons, I calculated the numerical stomach contents distribution with a number of feeding regimes (stationary state solutions as well as varying contents of stomach weight categories) and using a variety of different discretisation widths.

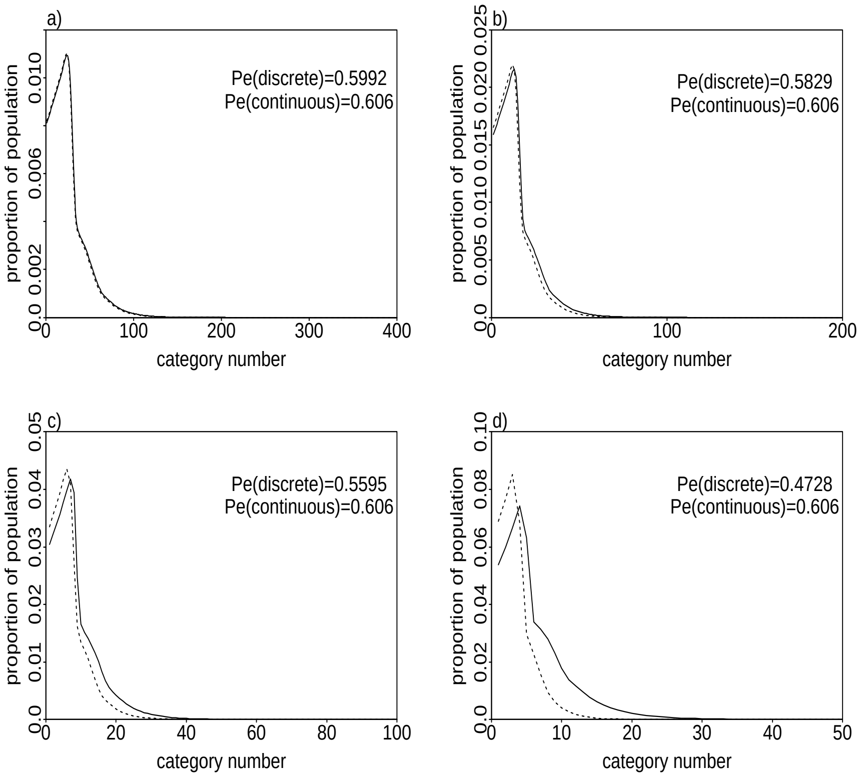


Figure 5.1. Stationary state solution of the continuous model (dotted), compared to that of the discrete formulation (solid), with N equal to a) 400, b) 200, c) 100 and d) 50. The population has digestion rate 0.13 grams per hour and stomach contents limit 7 grams and is feeding on a truncated normal meal size distribution with mean 0.5 grams, standard deviation 0.05 grams at a rate of 0.1 meals per hour.

Figures 5.1 and 5.2 compare the stationary solutions of the two models for populations with very different feeding rate functions. The solutions of the two models show very close agreement for a large number of boxes (figures 5.1a and 5.2a) and are visually almost indistinguishable. However, as the number of sub-intervals decreases the steady state solutions match less well.

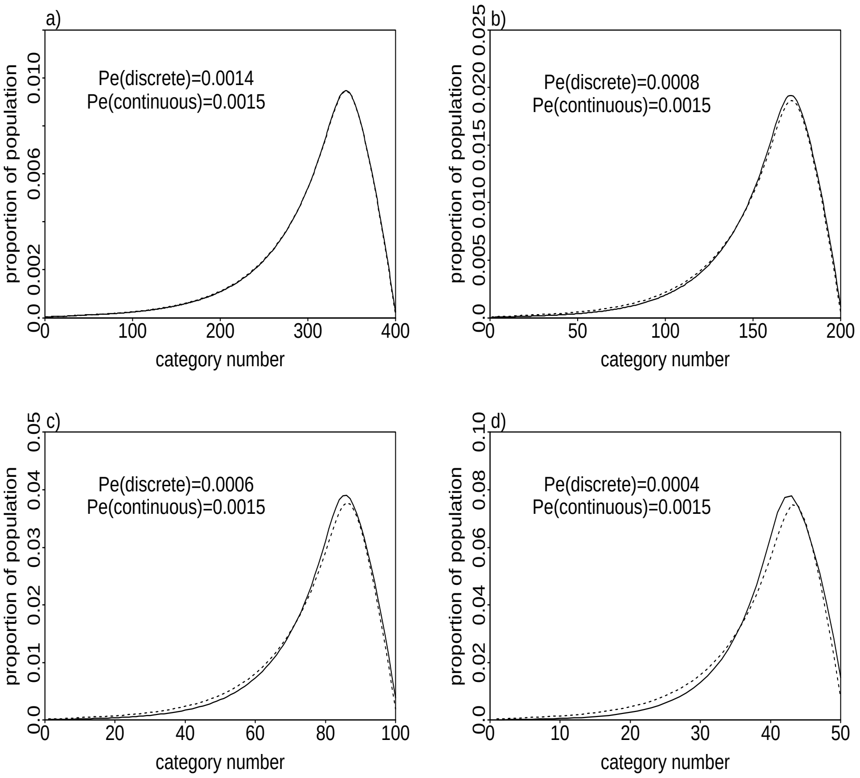


Figure 5.2. Stationary state solution of the continuous model (dotted) compared with that of the discrete model (solid), when N equals a) 400, b) 200, c) 100 and d) 50. The population has a digestion rate of 0.13 grams per hour , a maximum stomach contents of seven grams and is feeding on a meal size distribution with mean one gram, standard deviation 0.2 grams and at a rate of 0.2 meals per hour.

It appears that as the grid becomes less fine the discrete solution begins to overestimate the proportion of the population with high stomach contents, which also seems to be the case when the feeding rate varies with time. The variation of the proportion of fish in a number of stomach weight categories is illustrated in figure 5.3, with 5.3a showing the empty category and 5.3f, the highest weight category.

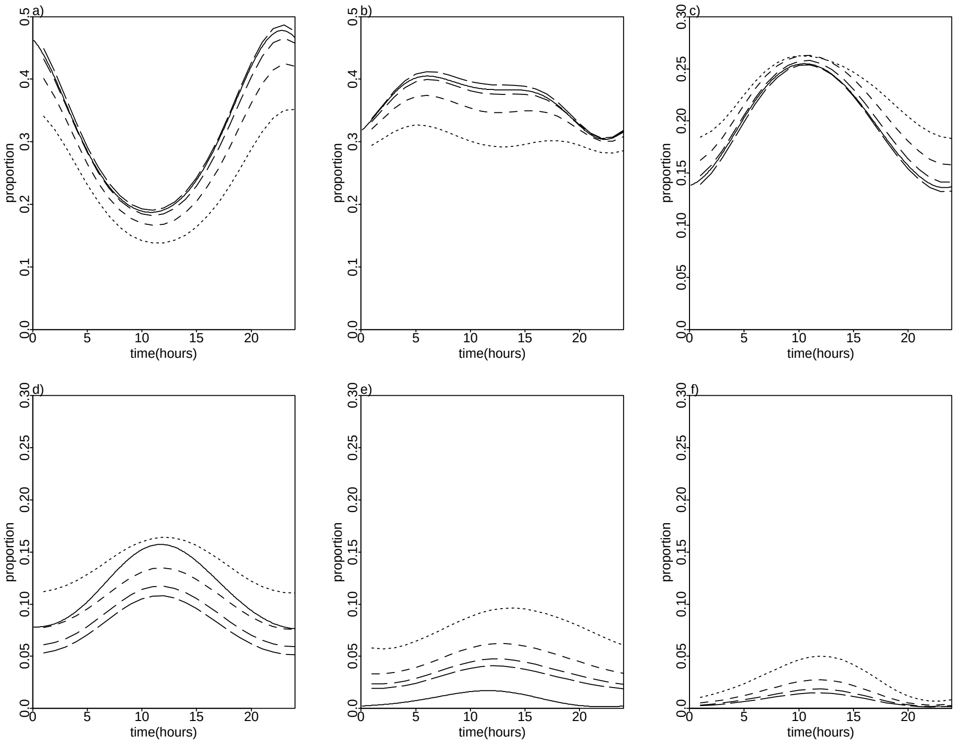


Figure 5.3. Comparison of the solution of the continuous model (solid) with that of the discrete model over a series of stomach weight categories: a) empty, b) 0-1.5 grams, c) 1.5-3 grams, d) 3-4.5 grams, e) 4.5-6 grams and f) 6-7.5 grams, for a population feeding on normally distributed meal size distribution, truncated at zero, with mean 1 gram, standard deviation 0.2 grams and R_1 and R_2 equal to 0.1. In each of the illustrations the solution of the continuous model is solid line, the discrete solutions are broken lines with N equal to 400 shown as long-dashed, 200 as dashed, 100 as short-dashed and 50 as dotted. The digestion rate is 0.13 grams per hour.

Since the whole point of this reformulation of the model is to increase the speed of computation of the varying stomach contents distribution, I must now choose a discretisation which combines a reasonable amount of accuracy with speed. Obviously, considering these illustrations, it would be preferable to calculate the solution of the discrete model with a very fine discretisation. However, the computation time of the discrete solution illustrated here, with 400 sub-intervals, is actually much longer than that of the solution of the continuous problem.

If I half the number of boxes, this halves the computation time for one time step as half the number of variables are involved and therefore the number of calculations is halved. The length of the time interval though, expressed in equation 5.1, is also affected by the stomach weight grid. In fact, halving the number of intervals doubles the length of the time step and therefore the number of time steps required to reach he stationary cycle is also halved. So, the computing time required to reach the stationary cycle is actually proportional to the square of the number of sub-intervals in the stomach weight range.

The computation of the discrete solution with N equal to 200 is still relatively slow and any optimisation technique incorporating such a solution would still be unthinkable. However, when the difference map formulation contains only 100 or 50 difference equations, the stationary stomach contents cycle can be calculated in a matter of seconds rather than minutes. Although some systematic errors are beginning to occur when the number of sub-intervals is reduced, the discrete solution still retains the overall shape of the continuous solution and in general the mean error seems to be less than five per cent. The solutions of the discrete model with 50 boxes are beginning to look quite different from the continuous solution, so the solution with 100 sub-intervals appears to give the best combination of speed and accuracy and therefore I shall use this in all further calculations.

5.3 Some comments on the fitting procedure

This method of calculating the time varying stomach contents distribution can now be incorporated into a non-linear optimisation method. The time dependent inverse problem is a higher dimensional problem than the constant feeding rate problem and therefore it seems safe to say that DUD will be once again be the most suitable optimisation routine as it performed significantly better than the simplex method for high dimension problems. In this section, I shall consider some of the difficulties associated with the time dependent inverse problem in particular.

In all the fitting experiments which were carried out, the data to which the model was fitted consisted of the stationary cycle of the time dependent stomach contents distribution at intervals over the period of twenty four hours. In chapter three I showed that the stationary cycle was reached within approximately five days and therefore the model was allowed to reach this cycle before its output was used in the fitting procedure. The mean squared error is then calculated by summing over all data points at all sample times. I decided to retain the values of the convergence criteria used in chapter four as these once again gave fitted parameters within one per cent of the actual expected values.

In chapter four I found that the optimisation routine does not converge to unexpected parameter sets when dealing with population stomach contents distributions, provided that the convergence criteria are very strict. I shall next discuss whether this applies to the much more complicated time dependent case.

So far in this thesis, when dealing with the time dependent feeding problem, I have used four parameters to define the sinusoidally varying feeding behaviour of a population feeding on a single source meal size distribution - the mean meal size, the standard deviation of the distribution, the underlying feeding rate and the amplitude of the feeding rate oscillations (see equation 3.40). In chapter three, we did not consider the fact that the timing and frequency of the feeding rate oscillations may also affect the resulting time dependent stomach contents distribution. In fact I just assumed that the feeding cycle lasted twenty four hours and the sinusoidally varying rate was not displaced from zero hours. However, for a population feeding on a single prey source, a further two parameters are required for a complete definition of the feeding behaviour as the feeding rate function now takes the form

$$R(t) = R_1 + R_2 \sin \frac{n\pi(t-d)}{12}. \tag{5.13}$$

when R(t) is positive and zero otherwise. The parameter n represents the frequency of the oscillations and d is the position of the sinusoidal feeding rate function over the day, i.e. it defines when the increases in feeding rate begin.

The fitting procedure is now a six dimensional problem which is obviously going to be more difficult to solve than the three dimensional problems of the previous chapter. However, when a detailed description of the stomach contents distribution is available at hourly time intervals, there is sufficient data to solve the inverse problem and the optimisation routine still accurately converges to the six expected parameters provided that their starting values are quite near the optimum.

In this chapter, I again attempted to fit solutions of the feeding and digestion model to data sets using feeding functions made up of the wrong number of meal sources. I generated a data set using a meal size distribution made up of two meal sources, one with a large mean and one small, whose feeding rate oscillations both occur in twenty-four hour cycles and are half a cycle out of phase. Attempting to fit the resulting data using a single peaked meal source distribution proved impossible even when the frequency and timing parameters were allowed to vary. Too many iterations occurred without the optimisation procedure getting anywhere near what appeared to be even a local minimum. The routine appeared to be heading towards a meal size distribution oscillating at twice the rate of the two single ones from which the data was generated, possibly in an attempt to reproduce the timing of the alternate oscillations. However, the changes in the stomach contents distributions which are generated by the two very different meal source distributions could not be reproduced by a single peaked meal source distribution and therefore the routine failed to converge.

Even when the two meal sources which generate the data had much closer means, the optimisation algorithm still did not converge. It did get to a minimum value for the least mean squared error, but did not halt as the fitted solution is not an exact fit to the data and therefore this minimum is not low enough to satisfy the very strict convergence criteria which I have been using.

Similar results occurred when I attempted to overfit the time varying stomach contents data using a feeding function made up of more meal sources than were used to generate the actual data. I generated a data set using a single medium sized prey source distribution. If the frequency and timing of the two fitting prey sources were forced to be equal in the fitting procedures, then the parameters converged to a set which describe the feeding behaviour as feeding on a single meal source at a rate oscillating between the correct values at the expected frequency and timing, provided that none of the parameter values were initially too far away from the optimum. Depending on the positions of the two initially chosen meal source distributions, the optimisation procedure either converged to give two identical distributions whose underlying feeding rates summed to the required value or four of the parameters described the expected feeding behaviour while the feeding rate parameters of the second distribution converged to zero.

When the two sets of timing and frequency parameters were allowed to vary independently of each other in this fitting procedure and they were not initialised with values very close to the optimum, then the procedure failed to converge. In the first instant, the frequency and timing parameters tended to move away from the actual values and then the parameters describing the shape of the meal size distributions began to move away from their optimum values pulling the parameter set even further from its optimum. As a consequence the optimum was not reached within the limit on the number of iterations.

I showed in chapter four that stomach contents distributions generated using differently shaped meal source distributions could not be confused provided that the very strict convergence criteria are adhered to. In this next section I shall show that the wrong shaped feeding rate functions cannot be fitted to a particular data set provided that the minimum value required for the least mean squared error is low enough.

I generated a set stomach contents data using a narrow truncated normal meal size distribution with a fairly large mean. The feeding rate of the population was varied sinusoidally with equal underlying feeding rate and amplitude (0.1) so the truncation at zero has no effect and the function retained its sinusoidal shape. I attempted to fit a single prey source distribution with a step function feeding rate assuming that the timing and number of the discontinuities in the step function are known. The least mean squared error once again reached a minimum value, but the routine failed to halt as the optimum fit did not exactly match the data set and therefore this minimum value was still too high. The parameters at this minimum described the expected meal source distribution, but with alternate twelve hour high feeding (0.2 meals per hour) and twelve hour zero feeding periods.

The reverse experiment of fitting data produced by a sinusoidally varying feeding rate function to data actually produced by a step function gives similar results in that the routine does not halt as the minimum mean squared error is higher than the value required for convergence of our optimisation routine.

All these experiments show that, similarly to the time independent problem, the automatic optimisation method does not converge to unexpected answers provided that the convergence criteria are very strict. Relaxing the convergence criterion for the minimum mean squared error would allow the prediction of wrong parameter sets. However, these predictions would not produce feeding behaviour vastly different to the actual behaviour and therefore the feeding behaviour inferred by the model is still quite an accurate description of the actual behaviour. In the next section the convergence criterion for the minimum mean squared error is relaxed completely as the experiments are concerned with simulated noisy data and whether the population feeding behaviour can be inferred using noisy, categorised samples.

5.4 Simulated time dependent data

Like the approach of chapter four, I shall now go on to discuss the effect of noise, categorisation and sampling frequency on the results of the optimisation process. The results of chapter four indicated that the feeding behaviour inferred from stomach contents samples most reliably predicted that of the population from which they were drawn when samples were large and categorised into many stomach weight intervals, although the results did not deteriorate badly until the samples were much smaller than one hundred individuals and categorised into about five gut weight categories. We would expect similar results to arise from experiments involving a time dependent feeding rate, but we must also now consider that the accuracy of the results may be affected by the frequency at which the samples are taken.

As I showed in the previous section the fitting procedure can become very complicated in the time dependent case with a very large number of parameters which slows down the optimisation routine. So, in this section, as I just wish to compare the accuracy of feeding behaviour inferred from random samples with that of the actual population, I have assumed a relatively simple single meal source feeding regime. However, even this leaves us with the possibility of six unknown parameters.

As the first step in this investigation I have simulated some data sets using the same parameter sets to describe the feeding process, but with differing sample sizes and number of stomach weight categories. The example illustrated in figure 5.4 shows that even when the data is very noisy, by considering the variations in proportion of fish in each stomach weight category, we can infer by observations the approximate frequency and timing of the feeding rate function. There is only one cycle in the dynamics of the stomach weight category contents over the twenty four hour period and therefore we can conclude that only one cycle of the feeding rate function occurs during the day. The contents of the empty stomach category drop over the first half of the day implying that feeding is highest during this period and that the feeding rate function is an undisplaced sinusoid function. This reduces the inverse problem to a four dimensional problem rather than six which speeds up the optimisation method considerably.

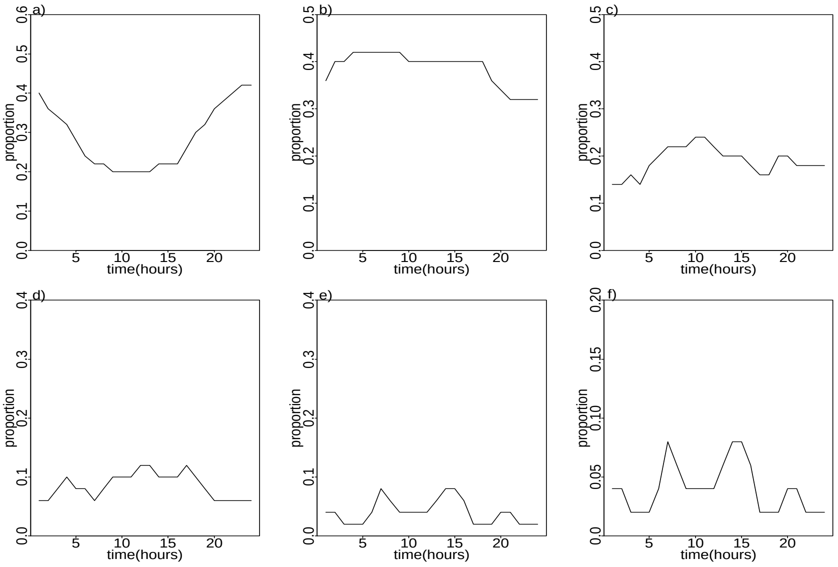


Figure 5.4. Variation in the proportion of a sample in six stomach weight categories a) empty stomachs, b) 0-1.5 grams, c) 1.5-3 grams, d) 3-4.5 grams, e) 4.5-6 grams and f) 6-7.5 grams, for samples of size 50 drawn from a population feeding on a normal meal size distribution, truncated at zero with mean one gram, standard deviation 0.2 grams and R_1 and R_2 equal to 0.1.

As in chapter four, when attempting to fit the model to the noisy sampled data, I began the optimisation routine at the known population parameters from which the data were simulated. The severe convergence criterion for the mean squared error was once again discarded as there will be no exact fit to these noisy data sets. The experiments were carried out in a similar pattern to those in chapter four, except that for each combination of sample size and number of stomach weight categories a number of experiments had to be conducted for data sets sampled at different time intervals. The optimisation routine was carried out for one hundred different random samples of each combination of sample size, sampling frequency and number of categories and then the appropriate summary statistics were calculated. The variation in mean value and absolute coefficient of variation for each of the four parameters are illustrated for a fixed sample size with varying numbers of stomach weight categories and sampling frequency.

The first illustration shows the variation in the average fitted mean meal size and its absolute coefficient of variation for samples of 500 individuals. The value of the average appears to remain relatively constant and close to the population value of 0.5 for all sampling intervals and stomach weight category widths until the number of stomach weight categories is less than about twelve. At this point, for very infrequent sampling, the average value decreases away from the population value. As the number of stomach weight categories is reduced, the decrease in the mean value becomes greater and is apparent even in more frequently taken samples. The deviation of the expected value of the mean meal size away from the population value appears to be quite systematic, with the prediction getting much smaller for very infrequently taken samples categorised into a small number of stomach weight categories.

The coefficient of variation, for all combinations of stomach weight categories and sampling interval is quite small. However, as the sampling interval increases, the reliability of the prediction decreases, i.e. the coefficient of variation increases, particularly at low numbers of stomach weight categories.

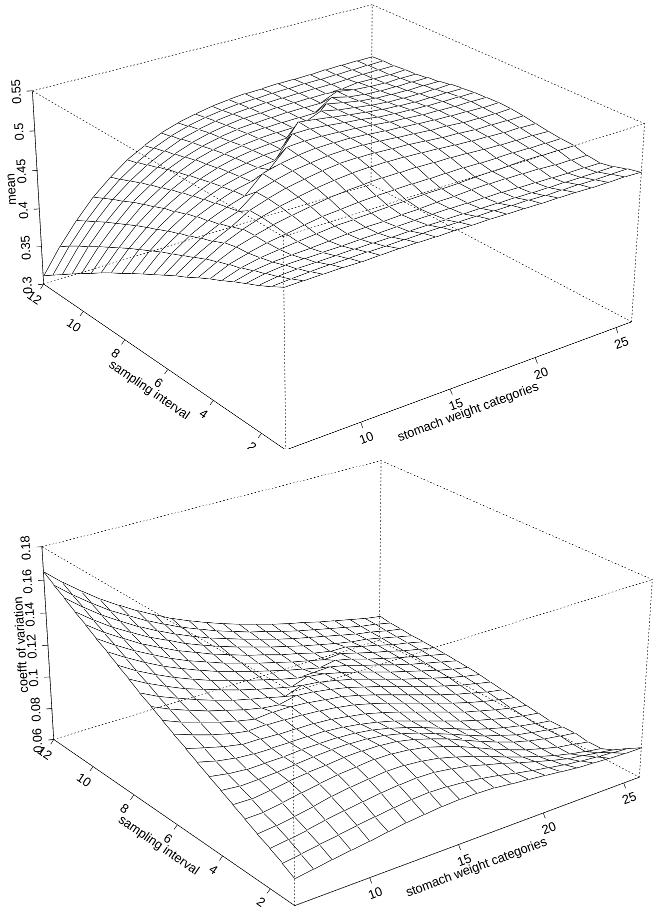


Figure 5.5. Variation in the average (a) of the fitted mean meal size and its coefficient of variation (b) with number of stomach weight intervals and sampling frequency for samples of 500 individuals. The population mean meal size is 0.5.

The corresponding illustrations of the variations in average standard deviation of the meal size distribution and its coefficient of variation are shown in figure 5.6. Once again for most of the range, the average standard deviation surface is quite flat and close to the population value of 0.05, but for large sample intervals and a small number of stomach weight categories, the average value increases by approximately eight times. There is also a corresponding increase in the coefficient of variation, although this is quite high over the whole range when compared to that of the mean of the meal size distribution.

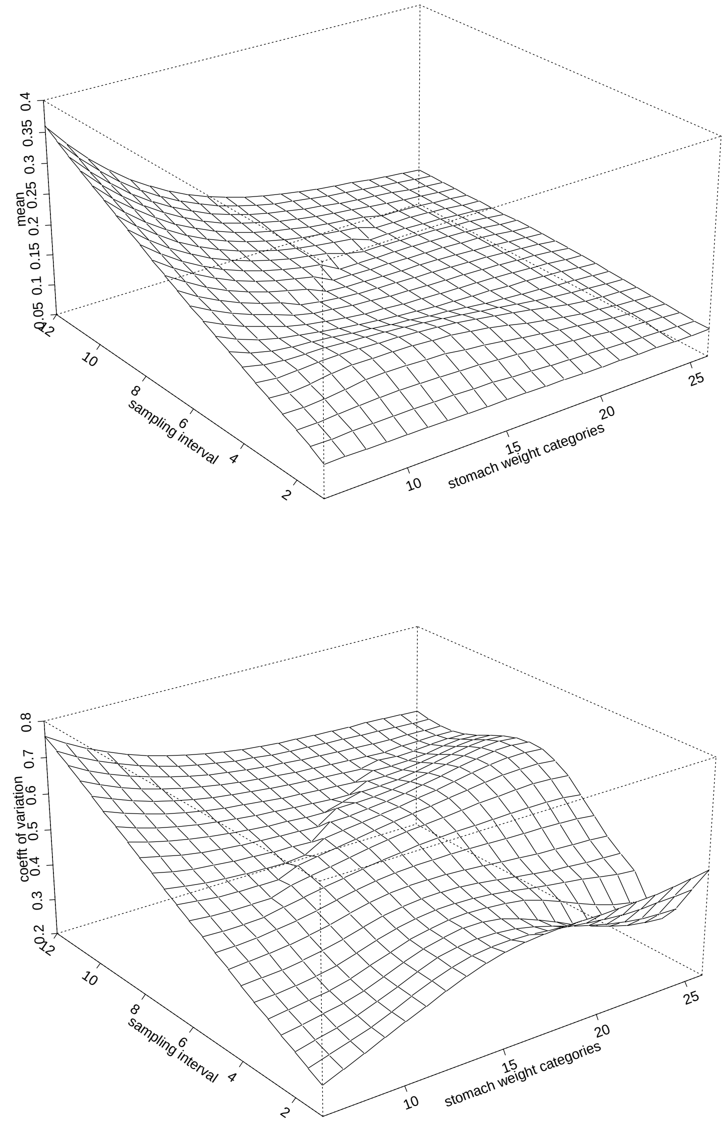
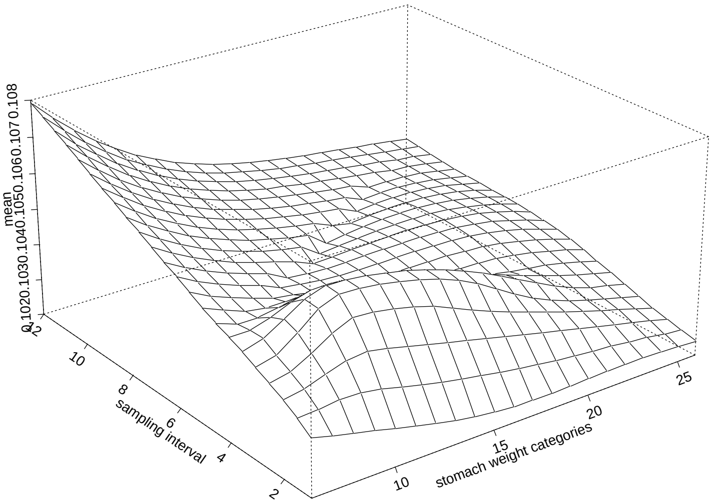


Figure 5.6. Variation in a) average and b) coefficient of variation of the standard deviation of the meal size distribution with number of stomach weight categories and sampling interval for samples of size 500. The population meal size distribution standard deviation is 0.05.



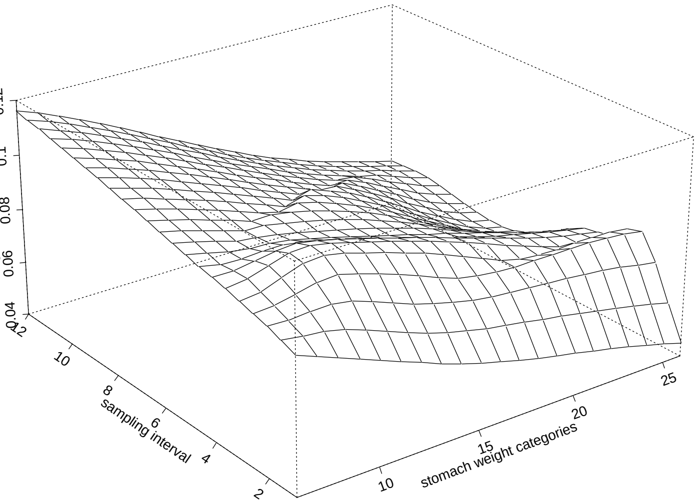


Figure 5.7. Variation with sampling interval and number of stomach weight categories in a) average and b) coefficient of variation of the underlying feeding rate of samples of size 500. The population value is 0.1.

Both illustrations of the variation in the average values of R_1 and R_2 (the parameters defining the feeding rate function), show that the sample predictions are closest to the population values for a large number of stomach weight categories and very frequent sampling and worst for infrequent sampling and a small number of stomach contents intervals. The total deviation from the population values over the whole range, however, are quite small (10%) when compared with the change in the other two parameters (40% for the mean and 600% for the standard deviation) at their worst points. Correspondingly, the coefficient of variation is very low for most combinations of sampling interval and number of stomach weight categories, but does increase towards the large sampling interval/small number of stomach weight categories corner.

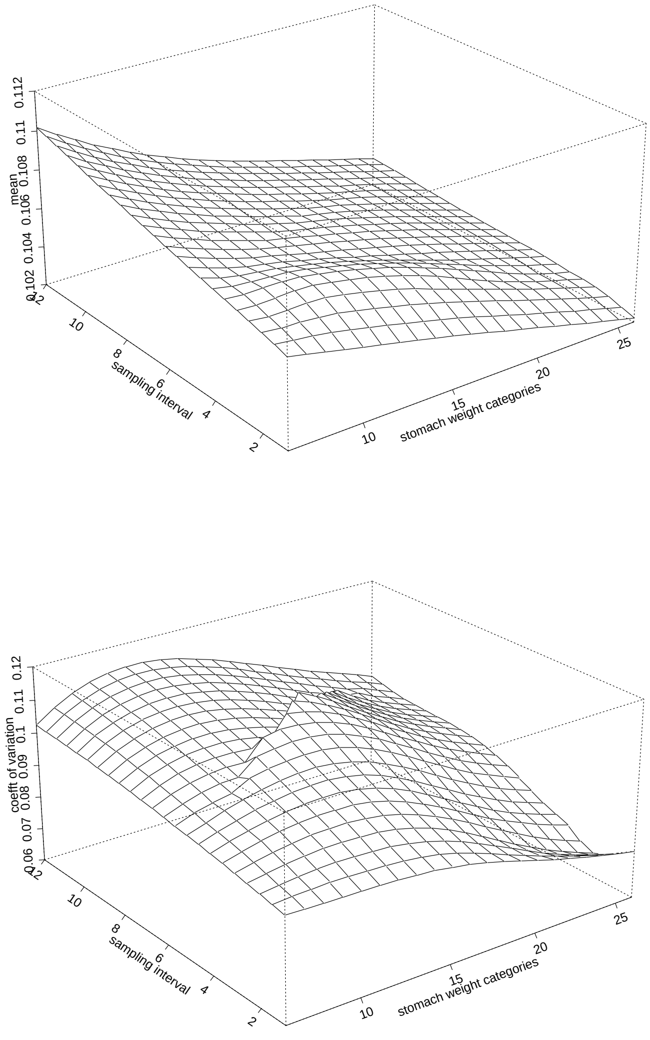


Figure 5.8. Variation in a) the average and b) the coefficient of variation of the amplitude of the feeding rate oscillations with sampling interval and number of stomach weight categories for 100 samples of 500 individuals. The population value is 0.1.

In my next set of illustrations, I shall illustrate the results of the same experiments, but with samples of 100 individuals instead of 500. I can then analyse the consequences of changing the sample size as well as the sampling interval and number of stomach weight categories in this time dependent problem.

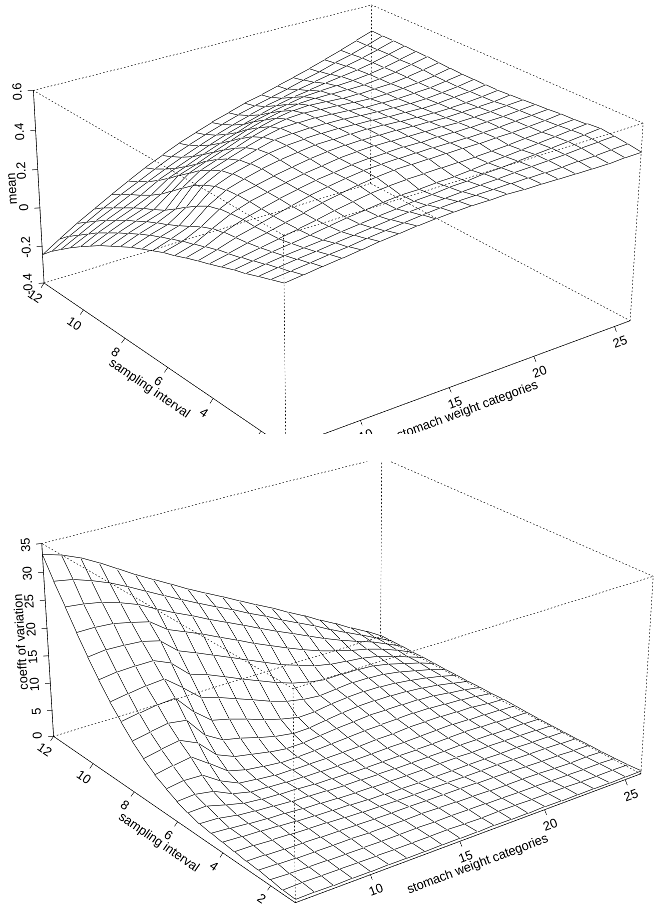


Figure 5.9. Variation in a) the average and b) the coefficient of variation of the mean of the meal size distribution with sampling interval and stomach weight categories for samples of 100 individuals. The population value is 0.5 grams.

The average of the mean meal size, illustrated in figure 5.9a, most closely matches the population value for large numbers of stomach weight categories and this accuracy remains for all sampling intervals. However, as the number of stomach weight categories begins to decrease, at large sampling intervals, the average value begins to fall quite rapidly. For more frequent sampling, there is only a slight decrease in the average of the mean meal size.

For all very frequent sampling the coefficient of variation is very low and only increases slightly for less frequent sampling at high numbers of stomach weight categories. However, for small numbers of stomach weight categories, infrequent sampling produces a very high coefficient of variation indicating very great variability in the mean of the meal size distribution predicted by the sample.

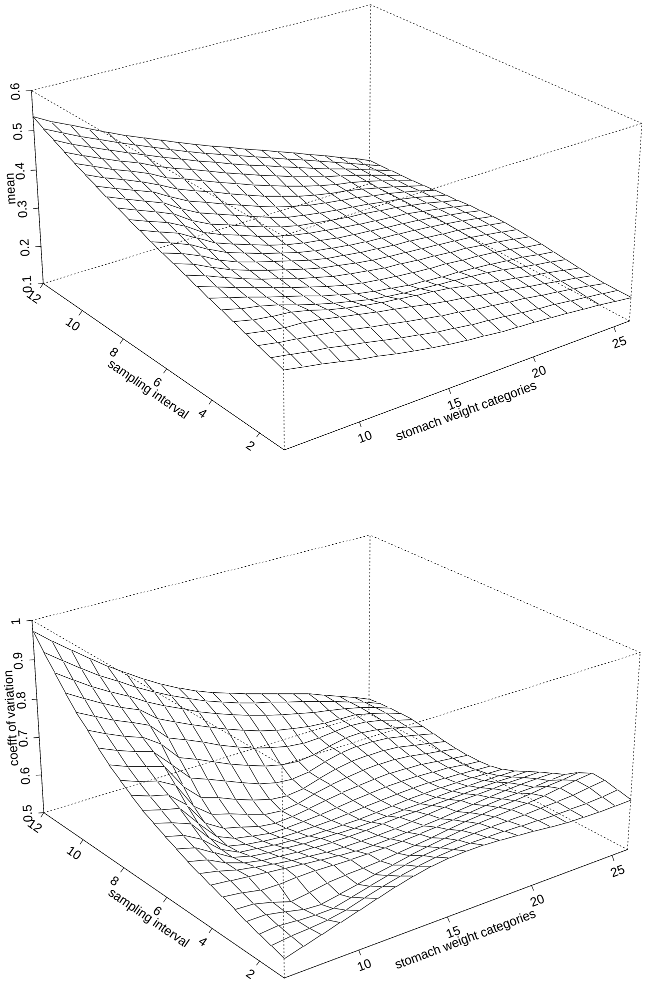


Figure 5.10. Variation in a) the mean and b) the coefficient of variation of the fitted standard deviation of the meal size distribution for samples of size 100. The population value is 0.05.

Once again, the mean of the fitted standard deviations is closest to the known population value for large numbers of stomach weight categories and very frequent sampling and increases to approximately ten times the population value for data which is infrequently sampled and categorised into a small number of intervals. Likewise the coefficient of variation shows a large increase for a small number of stomach weight categories at large sample intervals.

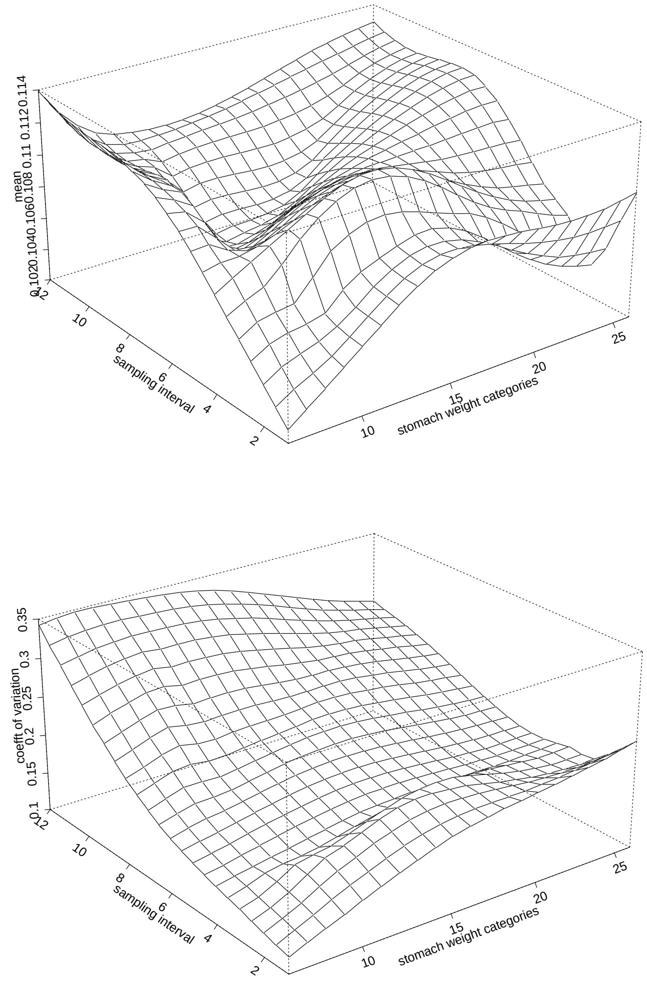


Figure 5.11. Variation in a) the mean and b) the coefficient of variation of the underlying feeding rate with sampling frequency and number of stomach weight categories for samples of 100 individuals. The population value is 0.1.

The two illustrations of the variation in the average value of the feeding rate parameters show quite a lot of peculiar peaks and troughs. However, the magnitude of these variations is extremely small compared to those of previous examples and the overall trend appears to show that the mean value is closest to the population value for frequent samples with larger deviations for infrequent samples and low numbers of stomach weight categories.

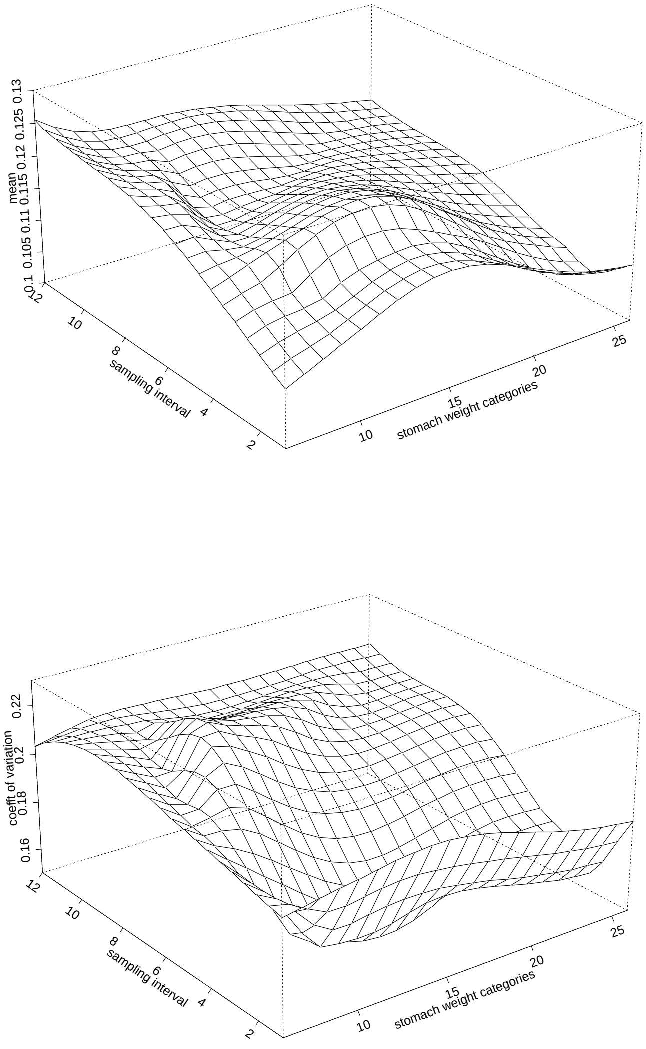


Figure 5.12. Variation in a) the average and b) the coefficient of variation of the amplitude of the feeding rate oscillations for samples of size 100. The known population parameter value is 0.1.

The coefficient of variation of the underlying feeding rate (figure 5.11b) increases considerably as the sampling interval increases, particularly for small numbers of stomach weight categories. Although the surface of the coefficient of variation of the amplitude of the feeding rate (figure 5.12b) appears to be a much more complicated shape, the overall variation is much less and the general trend is still to a higher coefficient of variation for infrequent sampling.

A brief initial comparison between the results of the experiments with large and small sample sizes shows similar trends in the overall shapes of the summary statistic surfaces. However, the deviations away from the population values and the value of the coefficient of variation for the smaller sample size tend to be larger and over a wider range of sampling frequency and number of stomach contents categories, which is as we would expect from the results of chapter four.

For both sets of sample sizes, we can see that the most outstanding feature of the illustrations is that the average of the fitted mean decrease and that of the standard deviation increases by quite large amounts as the number of stomach weight categories decreases, particularly at low sampling frequencies.

When the samples are categorised into a small number of categories, each category is much broader. In this case the population is feeding at a relatively low rate compared to its digestion rate and on a small meal source and therefore for much of the day the population is concentrated in the low stomach weight categories. So, by looking at the data, we can tell that the meal size distribution must have a relatively low mean and low feeding rate. However, we do not know the exact details of the stomach contents distribution, only the proportion in some very broad categories. So, it is possible that the data could be fitted as adequately using a normal distribution, (truncated and renormalised at zero) with a larger standard deviation and a peak at a much lower point than the population meal size distribution. It is not possible that the fitted meal size distribution could be centred much higher than the population distribution, as even with a small standard deviation, this feeding behaviour would predict too many individuals with high stomach weights as the digestion rate remains the same. Therefore, the average fitted mean decreases and the average fitted standard deviation increases as the number of stomach contents categories decreases.

This effect really only becomes important when we are dealing with less frequently taken samples. Obviously the temporal variations of the proportions of fish in each category which are accurately described when sampling is very frequent, indirectly give information on the stomach contents distribution at the previous time step. For example, the number of fish which are in a particular category at time t+1 depends on a combination of feeding behaviour during that time interval and also the distribution of stomach contents at time t. For infrequent sampling, for example twice a day, a number of different routes (combinations of feeding behaviour and stomach contents distributions) could be taken from one stomach sample to the other, while for more frequent sampling there will be less room for variation. Therefore, it seems that very infrequent data sampling and small numbers of stomach weight categories are a bad idea for attempting to infer population feeding behaviour.

Although the surfaces which describe the variations in the fitted underlying feeding rate and feeding rate amplitude both appear to be fairly noisy, there is in fact very little overall variation for either large or small sample sizes, compared to that of the other two parameters. The position and shape of the stomach contents distribution although dependent on the mean and standard deviation of the meal size distribution, the two feeding rate parameters are even more important. Quite small changes in their values will produce noticeable changes in the stomach contents distribution, even for small numbers of stomach weight categories with either increases or decreases in the proportion of the sample with high stomach weight categories. The only possible trend which appears in the illustrations is that predictions, once again, become less accurate and reliable for infrequent sampling and few stomach weight categories.

The aim of the experiments carried out in this section is to be able to conclude on a combination of sample size, number of stomach contents categories and sampling interval which is practical for use in actual data collection and will give reliable information about the feeding behaviour of the population from which the samples are drawn. This means we wish to find the combination which best predicts the population parameters, but also has a low coefficient of variation implying that we can be quite confident that if one such sample is taken from the population then its fitted parameters will quite accurately describe the feeding behaviour of the population.

Since the predictions of the underlying feeding rate and feeding rate amplitude appear to be relatively accurate for all sample sizes and combinations of sampling frequency and number of stomach weight categories, I shall concentrate on the results of the meal size parameters. From the previous discussion of the parameters describing the meal size distribution we can see that for large samples of size five hundred, predictions remain quite accurate and the coefficient of variation remains quite low for all stomach weight categories provided that sampling is at least every four hours. On the other hand if we wish to use smaller samples (size one hundred), samples must be taken quite frequently (hourly) or categorise into a large number of stomach weight categories. So, I shall conclude that provided the digestion rate and upper stomach limit are known and that the feeding timing and frequency can be assumed, then the feeding behaviour a population is adequately predicted by the behaviour inferred from either relatively small but frequent samples or larger less frequent samples.

5.5 Conclusion

In this chapter I have devised an alternative way of modelling the feeding and digestion process which involves the solution of finite difference equations. Quite broad discretisation speeds up the solution of the problem immensely and still gives solutions which adequately reproduce those of the partial differential equation approach. It is therefore possible to use this process in the solution of the time dependent inverse problem.

I have shown that the time varying feeding behaviour of a population can be inferred from the hourly outputs of its time dependent stomach contents distribution, provided that the number of meal sources is known and that the initial parameters are not too far from the optimum. In fact we can even infer the frequency and timing of the oscillations in the feeding rate.

As in chapter four though, we have to use very strict convergence criteria to prevent any confusion which may arise when attempting to fit the wrong number of meal sources or wrong feeding rate functions. However, when dealing with noisy data, this very low value of the least mean squared error required for convergence must be dropped as no predicted stomach contents distribution will give a perfect fit to the data. So, in this case convergence to the wrong feeding function may possibly occur, although this predicted behaviour is likely to be quite similar to that which the data was generated with. For example, a step function feeding rate function may be confused with a sinusoidal function oscillating in phase with the same frequency and amplitude. However, in all of the parameter fitting experiments involving noisy and categorised data I have assumed that the actual number, type of prey source and feeding rate function are known and therefore this problem does not arise.

I have tried to show in the experiments with simulated noisy and categorised data, how accurately feeding behaviour inferred from regularly sampled data describes that of the parent population from which it was drawn. The results indicate that if we want to sample a relatively small number of individuals (approximately 100), then they must be sampled very frequently (hourly) and categorised into no less than between five and ten stomach weight categories, to predict feeding behaviour which adequately describes that of the population from which it came. However, we have also shown that an alternative to such time intensive sampling is to take larger samples (500 individuals), as infrequently as every six hours and categorise their stomachs into at least about fifteen intervals.

All these experiments with simulated and noisy data have been conducted with a very simple example and as few parameters as possible. Earlier sections, however, have shown that the automatic fitting procedure can be used to solve the inverse problem in higher dimensions, so there appears to be no reason why these results should not be applicable to such multiple prey source, alternative feeding rate function problems. I shall therefore conclude that given an adequate set of data and that the optimisation routine is not started too far from the optimum, then we can infer the feeding behaviour of the population from which the data was drawn.

Chapter 6

Data collection and analysis

6.0 Introduction

So far, this thesis has concentrated on the construction of a continuous feeding and digestion model. The model has been tested for uniqueness and a semi-automatic method has been found for inferring the feeding behaviour from the variation in the gut contents distribution. Further experiments were carried out to check how well the feeding behaviour inferred from randomly chosen samples described that of the population from which they were taken. The results showed that the reliability of sample predictions does not deteriorate too much provided the samples are of at least 100 individuals, taken very frequently and categorised into a reasonable number of stomach weight categories (not many fewer than ten). All these experiments, however were carried out with samples taken from a population with known feeding behaviour, simulated by the model which has been formulated in this thesis. So, in the next section of this thesis, I shall attempt to infer the feeding behaviour of some real fish populations, with unknown feeding behaviour, from diel stomach contents samples.

This chapter serves as an introduction to this next section. It describes the details of the data collection and then goes on to discuss what analysis is carried out to justify using this data in comparison to the output of the previously constructed feeding and digestion model.

6.1 Data Collection

The data which has been used in this study was collected by Hall et al. (1995). The location at which the sampling was carried out in July and August 1989, was the north coast of Loch Gairloch, a sea loch on the north west coast of Scotland.

Fishing was carried out using a standard light trawl (cod end mesh 80 mm), fitted with 250 mm bobbin ground gear. Each trawl consisted of towing the net for approximately 15 minutes at 2.5 knots, in order to cover an average distance of 1 km. By combining measurements of the net size with the length of the tow, the mean area and volume covered by each tow were calculated to be $6820\ \mathrm{m}^2 \pm 46\ \mathrm{m}^2$ (standard error) and $27033\ \mathrm{m}^3 \pm 228\ \mathrm{m}^3$ respectively.

These short, but frequent samples provided large enough numbers of fish, but also kept seabed disturbance at a minimum. However, even taking such short samples repeatedly over a long period of time may affect the resident communities. For example, seabed disturbance may cause an increase in the availability of food. In which case stomach contents samples would not reflect those of the natural conditions and the whole structure of the local community may be altered by the influx of more predators. To combat this problem, three separate but similar sites were used for sampling, being trawled in rotation. Each area was therefore trawled only once in every three hours. It was shown in an earlier paper by Hall, Rafaelli and Thrush (1994) that disturbance only lasts for about an hour, after which fish populations return to their normal size. Disturbance of the sites was also minimised by fishing for only eight consecutive hours per day.

The sampling was carried out over a period of eight days between 27th July 1989 and 7th August 1989. The pattern of sampling used guaranteed that each hour was sampled at least twice so that stomach contents distributions and average size could be compared between days and sites.

After each catch the total number of fish was recorded and a maximum of fifty individuals from each of the predominant fish species were kept to use in the stomach contents analysis. The four main species caught during the trawls were the dab [*Limanda limanda* (L.)], plaice [*Pleuronectes platessa* (L.)}], haddock

[*Melanogrammus aeglefinus* (L.)] and whiting [*Merlangius merlangus* (L.)]. Immediately following capture, the body lengths of all fish were recorded. The stomachs of the whiting and haddock were removed and placed in formaldehyde solution, while the dab and plaice had formaldehyde solution injected into their stomachs for removal later in the laboratory.

Once in the laboratory, the stomach contents of each fish were removed and weighed before being freeze dried and re weighed to find the dry weight. Although it was not the intention of this study to go into a detailed analysis of diet composition by species, a brief examination of the stomach contents revealed that the diets appeared to be no different to those found in previous studies. The dab and plaice, along with the smaller haddock showed a preference for mainly benthic crustacea and polychaetes, while whiting and the larger haddock had mainly piscivorous diets which largely consisted of sandeels. These results are supported by Hall et al. (1990), Gibson and Ezzi (1986) and Gordon (1977) who have all conducted detailed diet analyses of the fish species populating the inshore waters of the west coast of Scotland.

Before the collected data could be used in any meaningful stomach contents analysis, in comparison with the model constructed in chapters two and three, some further checks were required to establish whether the data had been sampled from a closed population of similarly sized fish.

6.2 Data Analysis

Since the sampling was done over a period of days using different sites, several tests were carried out by Hall et al. to establish whether there are any significant trends in fish sizes with sample which may affect the patterns seen in the data.

Trends in the average body size of the species over the day, the sampling period and sampling areas were also investigated with non-parametric analysis of variance showing significant differences in body length between samples. For example, the average length of dabs sampled appears to be low at the start of the day (for all dates combined), then rises to a peak in mid afternoon, but then falls again later in the evening. In contrast the average length of sampled haddock shows no particular trend over the day, but appears to reach a minimum in the middle of the sampling period with highs at the beginning and end. These variations in mean size, however, occur over a very small range, 8-13% above or below the mean length of the species in question.

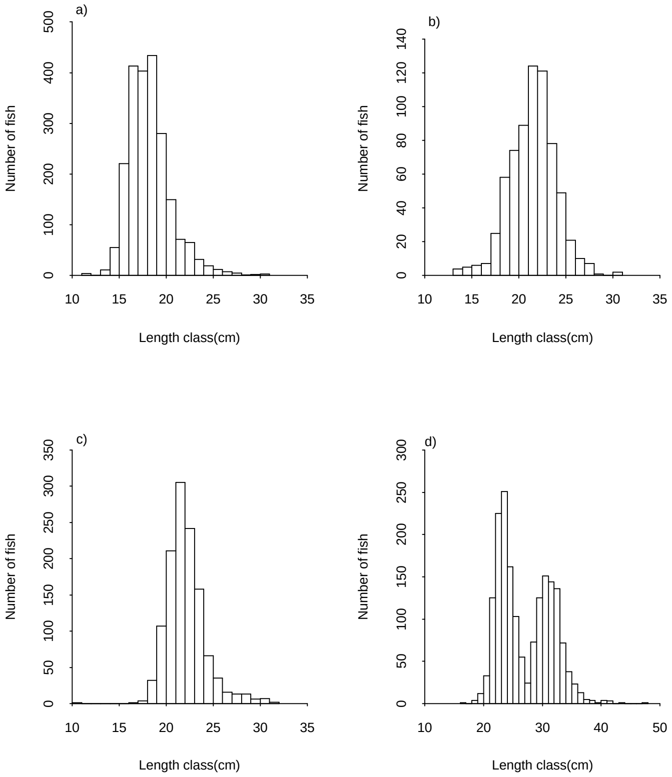


Figure 6.1. Length frequency distributions for all samples pooled for a) dab, b) plaice, c) whiting and d) haddock.

Due to the presence of only very small variations in the mean length coupled with the relatively narrow length distribution, shown in figure 6.1, it was argued that such samples could be used in a stomach contents analysis dealing with single populations of similarly sized fish. The bi-modal appearance of the frequency distribution of haddock suggest that two populations are present, which are likely to have different feeding behaviour, so in this case separate analyses was carried out for fish above and below 29 cm in length.

This, however, does not rule out the possibility that the population undergoes substantial immigration or emigration to and from the area of study as fish become sated or hungry. For example, it is quite possible that fish come to an inshore area to feed and them return offshore when sated. This would lead to a very unbalanced distribution of stomach contents in our area of study (inshore) and consequently very biased feeding behaviour. Unfortunately though there appears to be no practical way of monitoring this behaviour and since there are no significant changes in fish size, I shall assume that we are dealing with closed populations of fish.

Category	Lower bound	Upper bound
F_o	0	0
F_1	0	0.25
F_2	0.25	0.50
F_3	0.50	2.50
F_4	2.50	5
F_5	5	10
F_6	10	20

Table 6.1. Gut fullness boundaries for all of the species.

Once this has been concluded, the wet weight of the gut contents of each individual is standardised to its body weight using the gut fullness index, defined by

$$\mathrm{GFI} = \frac{\text{wet weight of gut content (g)}}{\text{total wet body weight (g)}} \times 100 \qquad (6.1).$$

For each species the GFIs were categorised into six gut fullness intervals, $\mathrm{F_o} - \mathrm{F_5}$, (seven in the case of whiting), shown in table 6.1.

Initially the categorisation was done separately for each combination of time, date and tow, so that gut fullness index comparisons could be made between different samples. None of the species exhibited any differences in gut fullness between days, so it is concluded that combining samples taken at the same time but on different days is justifiable. So, we now have a diel picture of the variation in proportion of fish in particular gut fullness index categories.

6.3 Gut contents variations

Most studies of fish feeding behaviour conducted using stomach contents data have been carried out using a very wide range of fish sizes. So, by using the GFI and standardising all measurements to percentage body weight it is then possible to make a sensible comparison between stomach measurements taken from fish of very different sizes.

However, the analysis of fish lengths described in the previous section concludes that the variation in fish length over each of the species is relatively small when compared to the actual size of the fish (approximately ±10% of the mean length). I shall therefore assume that the stomach contents samples have been drawn from a population of identically sized fish. The data can therefore be transformed back to actual stomach weights using the average weight of each separate population. The data is now in the more straightforward form of daily variation in proportions of the population contained in particular stomach contents categories, the width of which are also scaled from the gut fullness index values. These variations in stomach contents categories are illustrated in figure 6.2 and the actual stomach weight category boundaries are given in table 6.2. and attempt to fit the feeding and digestion model to the actual raw gut weight data.

	Dab	Plaice	Whiting	Small haddock	Large haddock
P_0	0	0	0	0	0
P_1	0.175	0.325	0.250	0.375	0.825
P_2	0.350	0.650	0.500	0.750	1.650
P_3	1.750	3.250	2.500	3.750	8.250
P_4	3.500	6.500	5.000	7.500	16.50
P_5	7.000	13.00	10.00	15.00	33.00
P_6	NA	NA	20.00	NA	NA

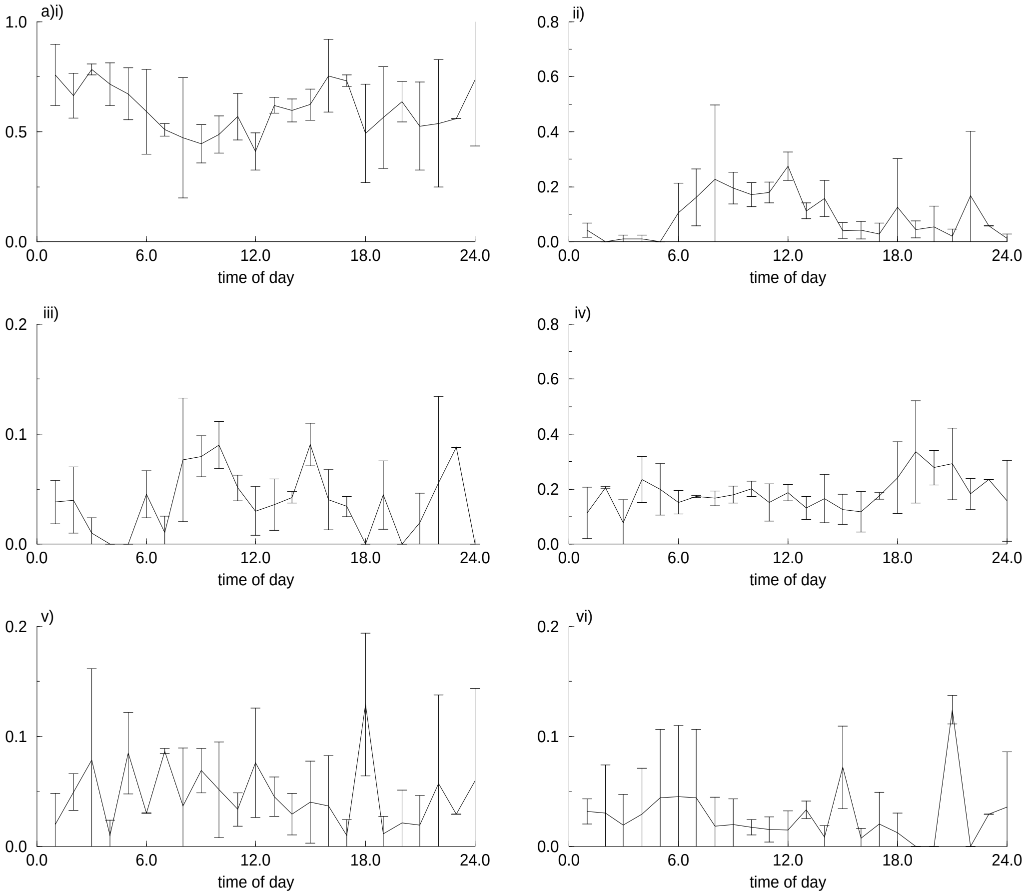
Table 6.2. Upper boundaries for the seven (where applicable) stomach contents categories for each of the five fish cohorts.

Although the error bars give an indication of the great variability between fish stomach contents samples at the same time, some patterns in the data are still visible. For example, the dab and plaice both show decreases in the proportion of empties in the early morning, which corresponds to increases in the contents of P_1, suggesting an increase in feeding at this point. In the case of the dab, however, this fluctuation does not extend to fullness category three which has relatively high stomach contents throughout the day with a small increase in the evening.

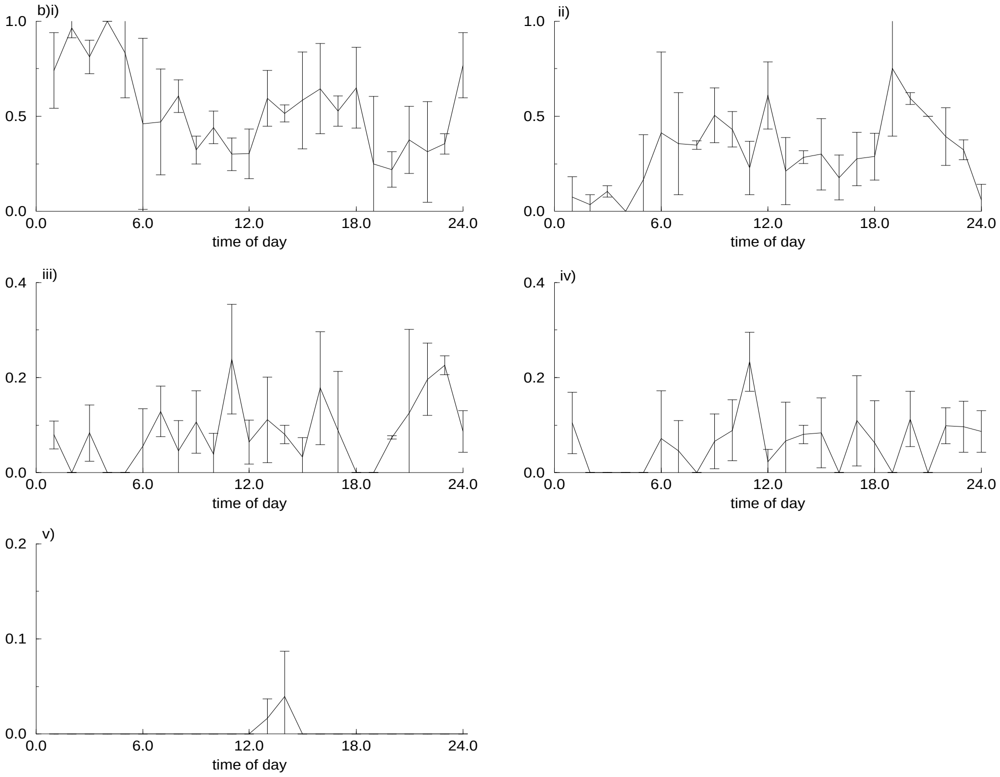
Other variations which are difficult to explain are observed for the whiting samples (fig. 6.2c) which show a decreasing number of empty stomach early in the morning which corresponds to increases in the upper stomach weight categories only.

We can also see at first glance that the stomach weight category variations for the small and large haddock show very similar patterns, which is quite reassuring. Although the haddock has been split into two groups, we would not expect particularly different feeding patterns to occur as a result of changes in size as the physiology of the two groups will be the same.

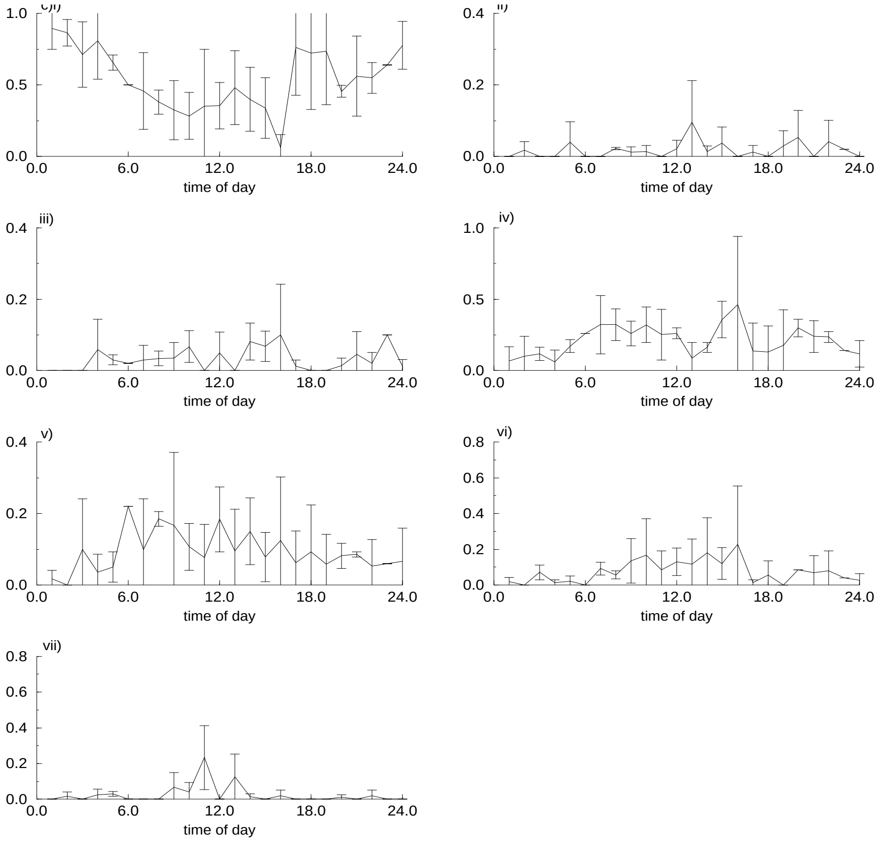
a) dab



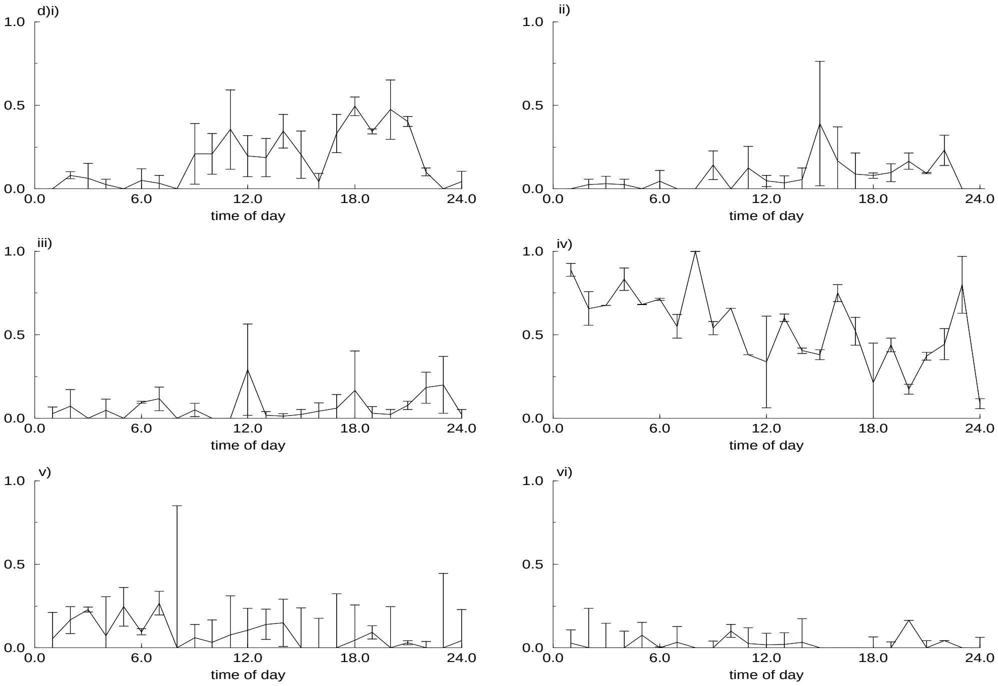
b) plaice



c) whiting



d) small haddock



e) large haddock

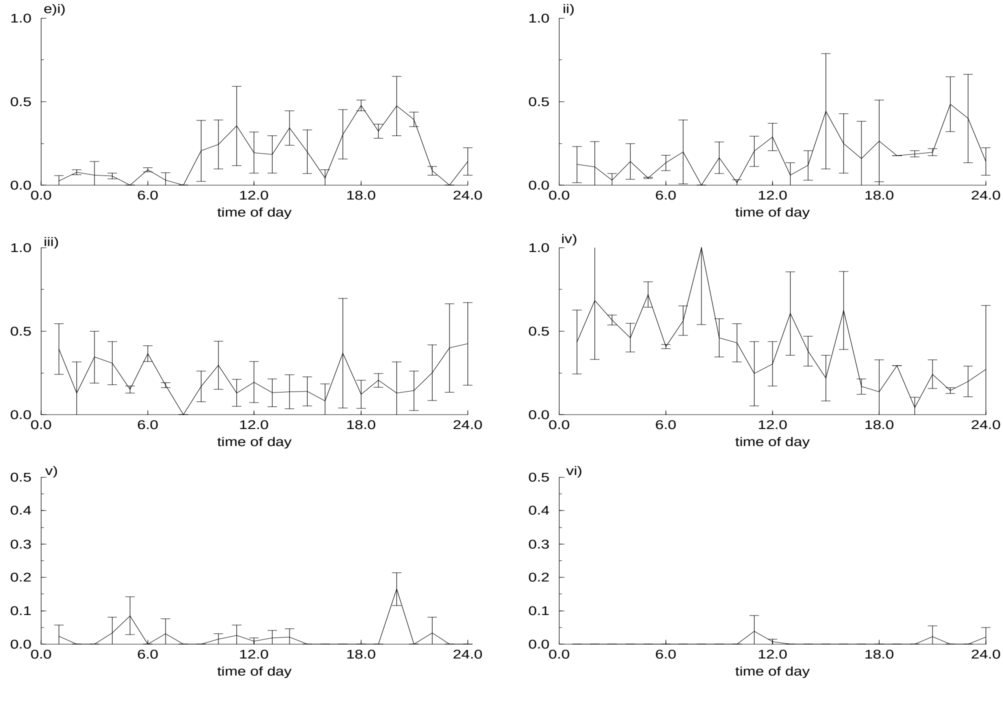


Figure 6.2. Daily variations in the proportion of the population in each stomach weight category for a) dab, b) plaice, c) whiting, d) small haddock and e) large haddock.

It is impossible to explain the dynamics of these stomach weight categories simply by considering the data alone. So, correctly categorised output from the feeding and digestion model can be compared to these stomach weight category variations in order to gain a more accurate insight into the feeding behaviour of these fish.

Chapter 7

Inferring feeding patterns

7.0 Introduction

In this section of the thesis I shall explain how the stomach contents data is used to establish the feeding behaviour of the population from which it was sampled. Chapters four and five explained a method for inferring the exact feeding behaviour, but the fitting procedures used, were required to start relatively near the optimum in order for convergence to occur. This is fine when we know the actual feeding behaviour of the population and are only trying to deduce the feeding behaviour of a simulated random sub-sample of individuals. However, when we are dealing with samples of real data, we have no previous knowledge of where the approximate optimum is. We have no way of knowing how many prey sources the population is feeding on or how the digestion rate is varying. Blindly attempting to use the semi-automatic optimisation method devised in chapters four and five, with a particular number of food sources and a fixed feeding rate function is therefore likely to lead to problems. So, in this chapter I shall use the simple alternative approach of varying the feeding parameters and comparing the output from the model to the stomach contents data until an optimum is reached. Although we cannot check that this optimum is global, it can be verified that a local optimum has been reached.

However, as well as the set of parameters defining the feeding behaviour of the population, the model requires a digestion rate and upper stomach contents limit. In previous chapters we have assumed that the values of these parameters are already known for the population in question.

It is possible to choose a sensible value for the maximum stomach contents of each species by considering the sampled stomach contents data. The upper limit of stomach fullness should be a value that is not exceeded by any of the stomach contents data, so I shall take this value to be equal to the upper limit of the upper stomach content category defined in table 6.2. So, for example the maximum possible stomach contents for the dab is assumed to be seven grams. Although we have no way of knowing the precise maximum stomach contents, it seems unlikely that it will make much difference to the model as most of the population in all five fish cohorts, have relatively low stomach contents and there are few fish in any of the upper stomach weight categories (refer to figure 6.2) close to this upper limit.

A value for the digestion rate constant, however, cannot be found by simple observations of the raw data. One option of dealing with the unknown digestion rate is to leave it as a free parameter in the feeding and digestion model, to be fitted along with the feeding parameters. This, however, could lead to grave errors in feeding behaviour inferences as even slight differences in the value of the digestion rate can produce massively different stomach contents distributions, as illustrated in figure 3.2. So, it is more sensible, in order to obtain meaningful results about the feeding behaviour of each species, to acquire values of the digestion rates from an independent source which I shall proceed to do in the next section.

7.1 Estimation of the digestion rate

Before it is possible to attempt inferring the feeding behaviour of the fish population from which the samples have been drawn, we need to know the digestion rate of the population. Figure 3.2 illustrated how even quite small changes in the digestion rate can affect the state of the stationary stomach contents distribution. So, an accurate value of the digestion rate is required in order to obtain any reliable results about the feeding habits of the population.

As we have a model representing the change in stomach contents distribution for a non-feeding population of fish, the members of which all follow a linear digestion model with digestion rate K, it would appear to be a straightforward task of fitting our model to evacuation data for the appropriate species. Most digestion studies however do not present their digestion data and just give a relationship defining the reduction in stomach contents with time which has been fitted to data derived from a number of digestion experiments. Instead data must be produced from these relationships by assuming an initial mean stomach contents and then calculating the mean stomach contents at hourly intervals. Our model can then be fitted to such a data set using the same method as chapter two and the digestion rate which gives the best fit can then be used in all future work on fitting the feeding and digestion model to the stomach contents data.

It seems unlikely that all fish species will have identical rates of gut evacuation, partly due to differences in size, as well as differences in species physiology, so here I shall explain these variations in gut contents depletion relationships. Many digestion experiments carried out by Jobling and Spencer Davies (1979), Jobling, Gwyther and Grove (1977) and Jones (1974) support these views, although they do not all agree that digestion is a linear process. In all fish species it was found that the evacuation rate increased with fish weight or length, obeying the power law relationship (Fletcher et al. 1984, Basimi and Grove 1985 and Jones 1974)

$$K \propto M^a \tag{7.1}$$

or

$$\mathrm{K} \propto \mathrm{L}^{\mathrm{b}} \tag{7.2}$$

where K is the digestion rate constant, M is the fish weight in grams, L is the length of the fish in centimetres and a and b are constants, which appear to be species dependent.

It has been known for many years that the digestion rate is also highly dependent on external conditions such as water temperature (Bajkov 1935). Elliott (1972) during his studies of brown trout found that the relationship was an exponential one

$$K \propto \exp(cT) \tag{7.3}$$

where T is the water temperature in °C and c is a species dependent constant. This theory was supported by Fletcher et al. (1984), Basimi and Grove (1985) and Grove et al. (1985).

I now need to find specific digestion rate-temperature-weight relationships for each of the four species from which the stomach contents data was sampled. A series of similar experiments conducted on the gastric evacuation of plaice (Basimi and Grove 1985) and dab (Fletcher et al. 1984), have found the average stomach contents of the population to obey

$$W(t)^{\theta} = W(0)^{\theta} - \tau(T,M)t \tag{7.4}$$

where S(t) are the average stomach contents at time t, τ(T,M) is a function which include the temperature (T) and weight (M) dependence and θ is a constant. The function τ(T,M) has been shown to take the form

$$\tau(T,M) = BM^{a}e^{cT} \tag{7.5}$$

where B,a and c are constants dependent on the species and are shown in table 7.1.

Species	θ	B	a	c
Dab	0.75	0.0068	0.43	0.041
Plaice	0.49	0.025	0.068	0.086

Table 7.1. Values of the average stomach contents depletion curve constants for the dab (Fletcher et al. 1984) and plaice (Basimi and Grove 1986).

A similar, but more complicated relationship is given for haddock by Jones(1974)

$$W(t)^{0.54} = W(0)^{0.54} - \frac{0.54Q10^{0.035(T_c - T_0)}}{175L^{-1.4}}t \qquad (7.6)$$

where T_c is the water temperature of the study, T_0 is $12^{o}\mathrm{C}$, L is the fish length (cm) and Q is the rate of elimination of 1 gram of food from a fish 40 centimetres in length.

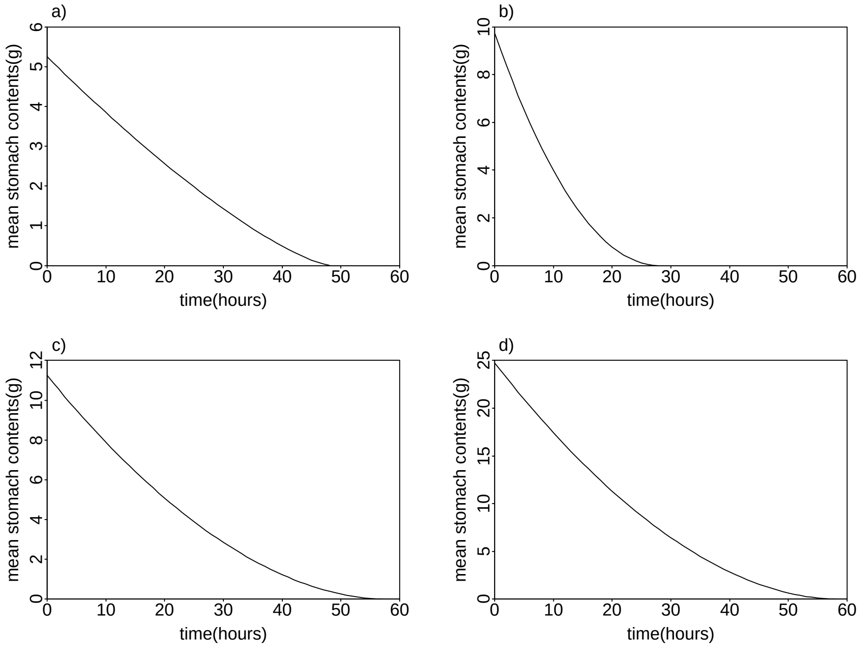


Figure 7.1. Mean stomach contents depletion curves generated by relations 7.4 and 7.5 for a) dabs (5.25g), b) plaice (9.75g), c) small haddock (11.25g) and d) large haddock (24.75g). The bracketed figures are the mean satiated stomach contents.

For each of these three species, I can now construct average stomach contents depletion curves. The average lengths and weights are calculated (see table 7.2) and a temperature of $13.2^{o}\mathrm{C}$ which is typical of the summer water temperature of Scottish west coast sea lochs, is used in equations 7.4 and 7.6 to generate the mean stomach contents depletion curves. The value of Q is taken to be 0.223, which is the value suggested by Hall (1987) as the mean of all known values. The depletion curves with initially satiated fish populations are illustrated in figure 7.1. I assumed that at satiation, the population stomach contents are distributed normally about the mid-point of the highest stomach contents category as defined in table 6.2.

Comparing figures 7.1a and 7.1b, we notice immediately that plaice must have a much higher digestion rate than dab, as they manage to completely evacuate their stomachs of a much larger meal in almost half the time. Also comparing the two haddock stomach contents depletion curves, we see that the time for complete evacuation is almost the same, even though the large haddock have an initial mean stomach contents of twice the size, implying that their digestion rate is approximately twice that of the small haddock.

I can now fit the linear digestion model to points taken at hourly intervals from the curves illustrated in figure 7.1. I shall assume that the initial mean stomach contents of the population is known and equal to that of the data to which we are attempting to fit the linear digestion model. I showed in chapter two that the shape of the population average stomach contents depletion curve is dependent to a certain extent on the initial distribution of stomach contents, so in the fitting procedure I shall allow both the digestion rate and initial standard deviation to vary. The best fit parameters are given in table 7.2 and the best fit curves are illustrated in figure 7.2.

	Weight(g)	Length(cm)	St. dev.	Dig. rate(g/h)
Dab	70	18.72	1.34	0.13
Plaice	130	21.96	3.36	0.55
Small Haddock	150	23.90	2.44	0.29
Large Haddock	330	32.11	3.87	0.62
Whiting	100	22.59	NA	0.15

Table 7.2. Mean weight and length and fitted digestion model parameters of the fish species used in the stomach contents analysis.

Although the standard deviation of the initial stomach contents distribution is unknown, its value does not actually affect the digestion rate by too much, which can be illustrated by fitting the digestion model with fixed initial standard deviation. In fact the digestion rate is relatively robust to changes in the standard deviation, with changes of 50 percent in the initial standard deviation producing deviations of less than five percent in the best fit digestion rate for all four fish cohorts.

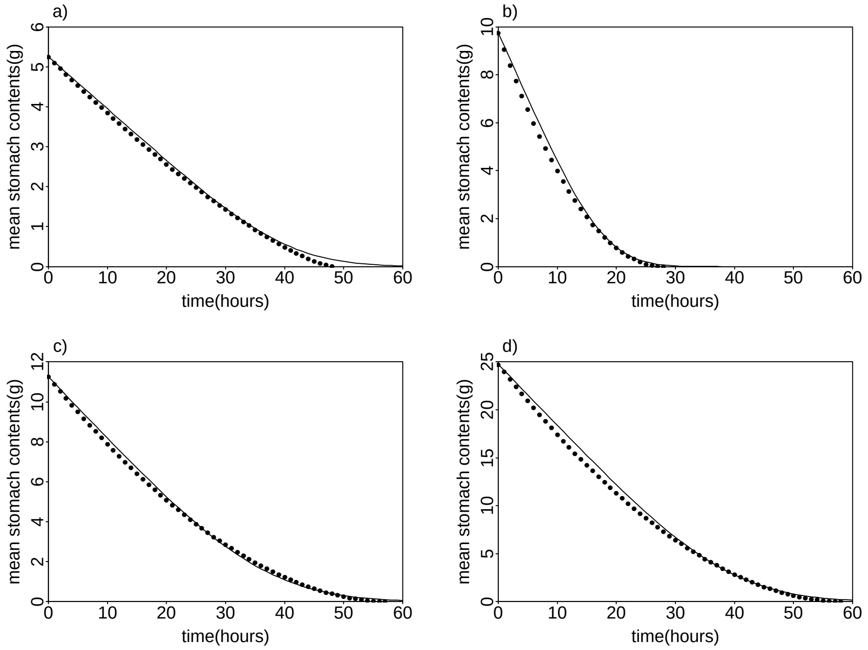


Figure 7.2. Mean stomach contents depletion data (points), together with the best fitting linear digestion curves for a) dabs, b) plaice, c) small haddock and d) large haddock.

No such expression for the depletion of the average stomach contents of whiting is available and therefore another method of calculating the linear digestion rate must be found. The studies of Bromley (1988) were based on experiments conducted on whiting and give a value for the linear digestion rate which can be corrected for body size and water temperature. This adjusted value of 0.15g/h agrees with an instantaneous digestion rate measured by Robb (1990).

Now that values for the linear digestion rate have been established, I can begin to consider how to attempt to fit the feeding and digestion model to these stomach contents data sets.

7.2 Methodology

Chapters four and five showed a semi-automatic way of inferring the feeding habits of a population from samples which had been taken at particular time intervals. It could not be completely automated however, as we had to know the basic structure of the meal size distribution i.e. how many prey sources there were and what type of distribution they followed. Also, when the data were very noisy, the fitting procedures had to be started with initial parameters quite close to the optimum fit, otherwise the computations required to reach the minimum took an inordinate length of time.

In this case we have no prior knowledge of the feeding behaviour of the fish populations under consideration and the only way to decide how many meal sources there are and how the feeding rate varies is by contemplating the variations in the stomach contents categories. This will give us an idea of when the feeding rate increases and decreases, but will not help decide on the number of prey sources.

I decided that the most practical approach would be to assume a maximum number of meal sources (three) and that the feeding rate of each meal source could switch between fixed values at particular times (maximum of four times) during the day and then attempt to find the optimum parameters by comparing by hand the model predictions and observed data. Considering the variation in the proportion of the population in each stomach contents category in chapter five (figure 5.4), gave us a good idea of how the feeding rate was varying i.e. at what times the rate was increasing or decreasing. However, the real data sets which we are considering here are much noisier than those simulated data sets which were used as examples in chapter five and so it is quiet difficult to decide whether an increase in the proportion of empty stomachs is due to a reduction in feeding rate or whether it is just noise. This problem can be alleviated slightly by taking a three-point running average of the data which smoothes the stomach contents data and the observed variations can now more confidently be attributed to changes in feeding behaviour rather than sampling error. These variations in smoothed data are shown in the next section in figures 7.3-7.7.

Initial attempts at fitting the model to the data were made by comparing the model predictions to the data by illustrations of the two data sets superimposed. This method probably being the most effective way of finding an approximate optimum. As the fit of the model becomes closer, however, small parameter changes which improve the fit of one of the stomach contents categories may reduce the fit of others. Eye-ball techniques are unlikely to be able to decide which parameter set gives a better overall fit and therefore an error measure must be used. Instead of using the usual mean squared error measure, used in previous sections, I decided that a more appropriate goodness of fit statistic was the normalised mean absolute error (Thiel 1966) defined by

$$E_{abs} = \frac{\sum_{i=1}^{N} \left| P_i(x) - O_i(x) \right|}{\sum_{i=1}^{N} O_i(x)} \tag{7.7}$$

where $P_i(x)$ is the ith predicted value of the quantity x, and $O_i(x)$ is the equivalent observed value.

The data sets which we are attempting to fit in this section appears to be quite noisy even after smoothing and even a few extreme outlying observed data points will give a small number of very large errors, causing a massive increase in the error measure. In such conditions, it is possible that the fitting procedure will be biased towards these outliers, with a reduction in fit of the many more representative observed data points. Using the mean squared error measure is likely to exacerbate this bias due to the squaring of the individual deviations between observed and predicted points. So I have chosen to use the normalised mean absolute deviation in this section, rather than the mean squared error, because of its decreased sensitivity to small numbers of outliers present in the observed data. The mean squared error was adequate for use in previous sections as the data, although noisy did not contain any extreme outliers.

The normalised mean absolute deviation is calculated for each stomach-weight category and then an overall score for the model is calculated. Since the measurements which are made for stomach-weight categories containing low average proportions of the population are relatively more affected by the noise than those containing high proportions, the overall model score is compiled by weighting each category score in proportion to the time averaged population of that category.

7.3 Results

The best predictions of the model superimposed on the observed three-point running averaged data together with an illustration explaining the inferred feeding regime for each of the five fish cohorts, are shown in figures 7.3-7.7. The fit of the model for the dab and plaice is very good, predicting most of the details of the variations in the stomach weight categories. The predicted stomach contents variations for the gadoids are less accurate than those for the flatfish (i.e. they give higher average values of E_{abs}) and do not predict some of the finer details. However, the basic features and average proportions over time are adequately predicted and the model continues to be quite visually and statistically convincing with relatively low error measure values.

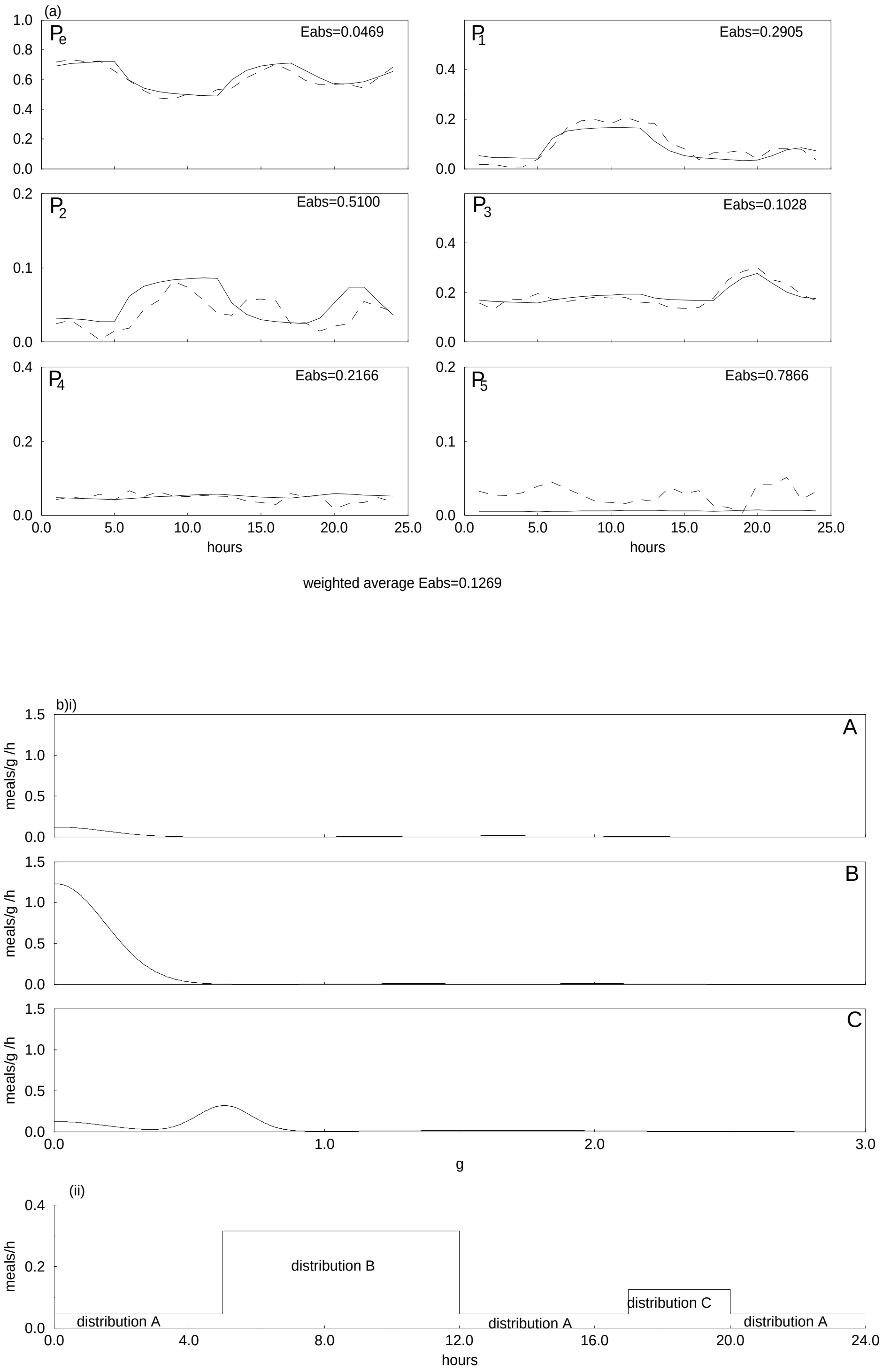


Figure 7.3. a) Model predictions (solid) for the proportion of guts in a series of weight categories compared with the observed data (dotted) for dabs, with the corresponding diel variation in meal size distribution (b). The illustration shows i) the meal size distribution in each period and ii) the variation in total feeding rate.

The model requires the maximum number of three meal sources to obtain a good fit to the dab data and has quite a complex feeding pattern. The population has one very large (mean 1.7g) meal source which is permanently available, but feeding occurs only at an extremely low rate - so low that it is almost impossible to see on the illustration of meal size distributions. An intermediate sized prey is fed on for a short period in the evening only, between the hours of 17.00 and 20.00 and finally there is a third quite small prey source which is available all the time but is consumed at a higher rate during the morning. These results imply the dab feeds throughout the day, with many meals being taken during the morning and a lower peak in the evening, but with a very low overnight feeding rate.

I shall now consider the feeding behaviour inferred from the stomach contents samples taken from a population of plaice. The predicted and observed variations in stomach contents categories are illustrated in figure 7.4. The observed patterns in the variations of the stomach contents categories of plaice are quite similar to those of the dab which seems sensible since we are dealing with similar types of fish. However, the feeding behaviour is much simpler as shown in figure 7.4b.

Plaice appear to feed on a very small meal source, but at quite a high rate in comparison to the feeding rate of dabs. Overnight the feeding rate is very low, but increases to almost three times during the morning and then in the evening between the hours of 18.00 and 21.00. So, although the feeding behaviour of the dab is more complicated the change in feeding intensity predicted by the model follows the same basic pattern for both species of flatfish, with high points during the morning and evening, which is quite reassuring.

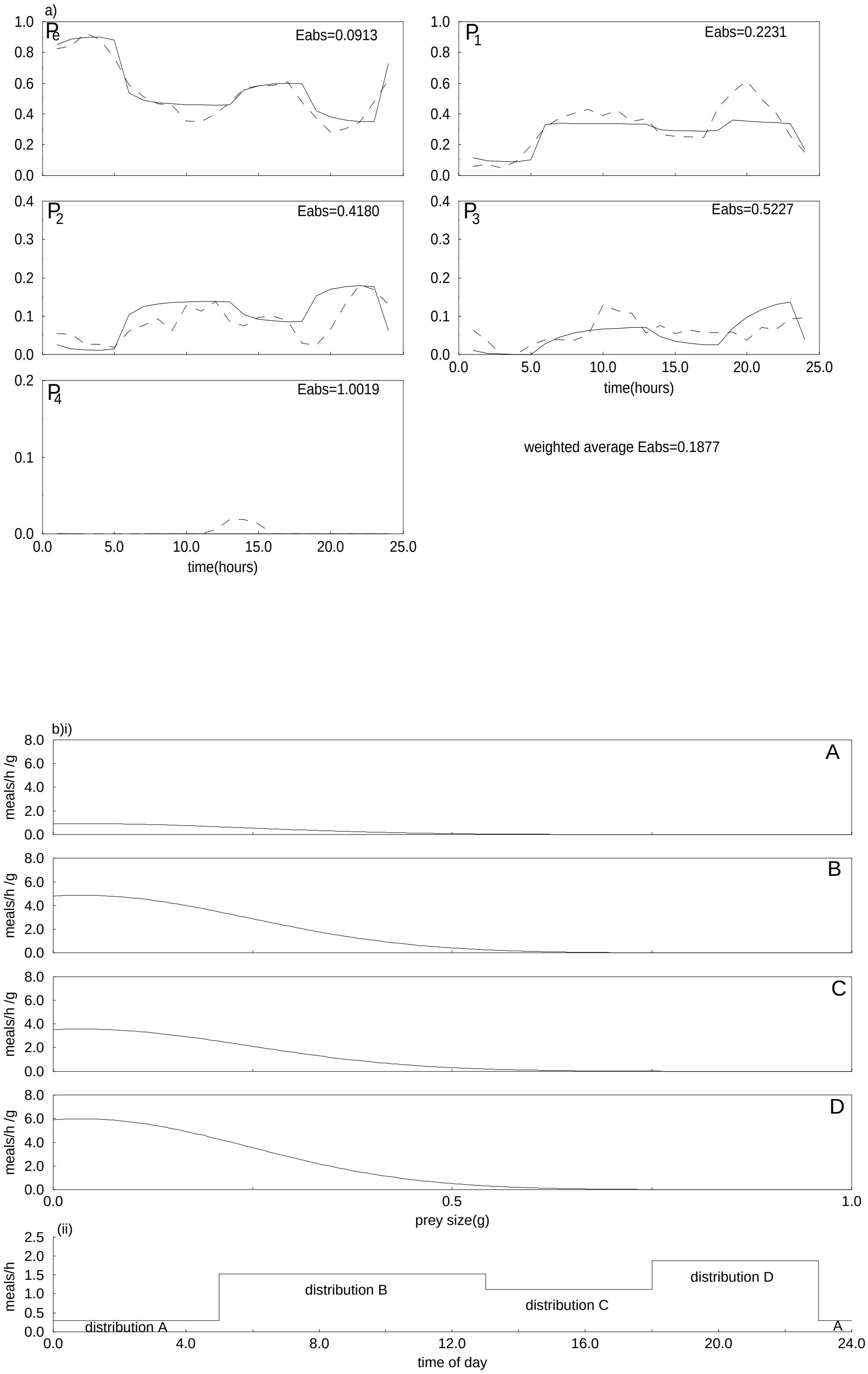


Figure 7.4. a) Observed (dotted) and predicted (solid) variation in the proportion of the population of plaice in each of a series of gut weight categories, with b)i) the meal size distribution during the four periods and ii) the variation in total feeding rate.

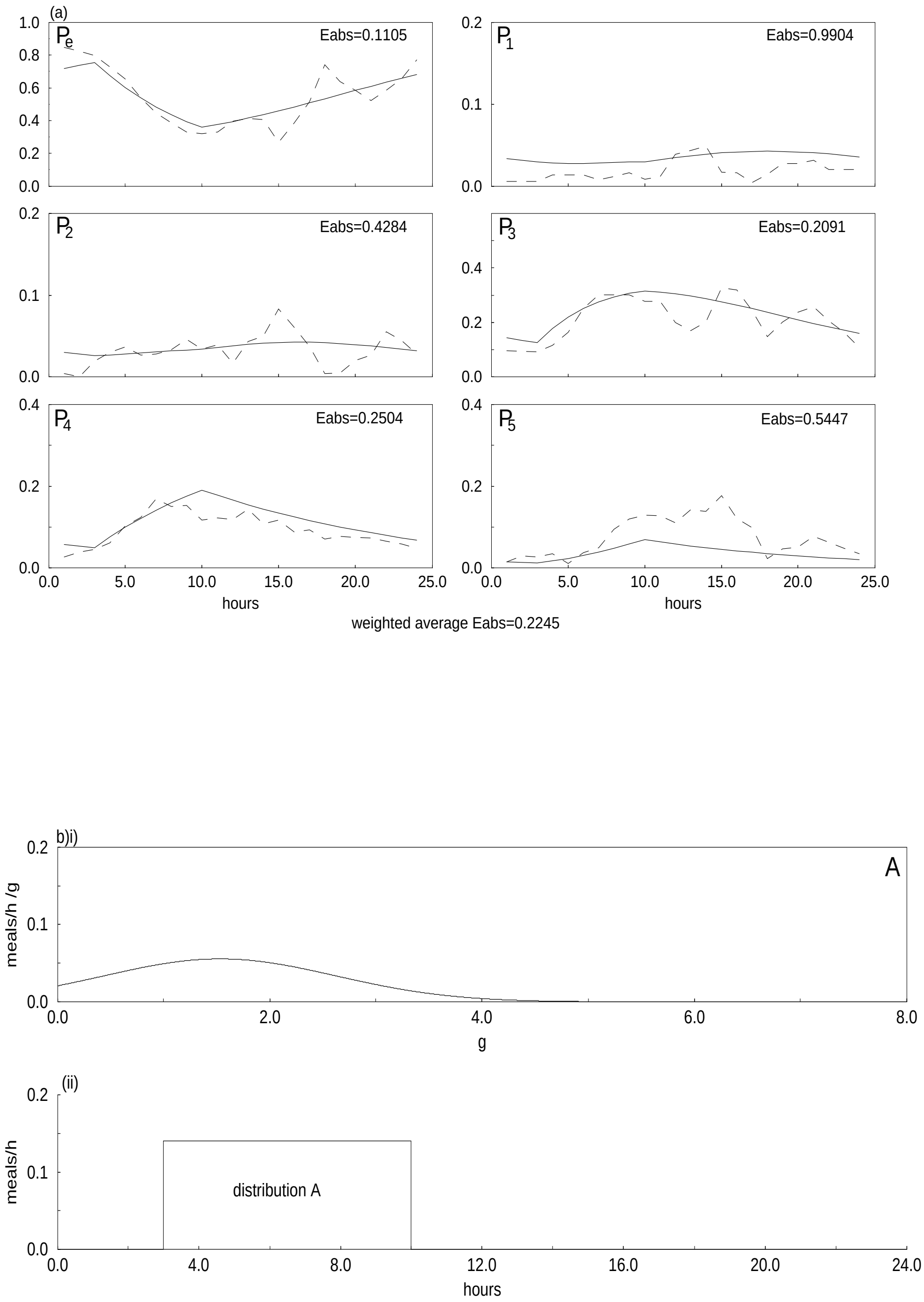


Figure 7.5. Observed (dotted) and predicted (solid) variation in the proportion to the population of whiting in each of a series of gut weight categories with b)i) the meal size distribution and ii) the variation in total feeding rate.

All three gadoid fish cohorts required a single meal source meal size distribution to reach the optimum fit, with the two sizes of haddock having very similar feeding behaviour. There are however, clearly discernible differences between the feeding behaviour of the whiting and haddock. This could be assumed just by comparing the observed stomach contents data sets, without even attempting to fit the model to the data. The proportion of the whiting population with empty stomachs is quite high overnight, but falls during the day, corresponding with an increase in the proportion of fish in categories P_3, P_4 and P_5 (the high stomach weight categories). The variations in the stomach contents of the haddock appear to be roughly the opposite of those of the whiting and therefore we can surmise that the feeding behaviour is quite contrary.

The predicted and observed variations in the whiting stomach contents data are illustrated in figure 7.5a. The optimum feeding behaviour is shown in figure 7.5b and amounts to feeding solely during the early morning on a relatively large, broadly distributed prey source.

In contrast, figures 7.6 and 7.7 show that the haddock feed at a low rate throughout the day except for a short period around midnight when their feeding rate becomes very high.

The validity of the model is increased as we see that the optimum set of parameters of the small and large haddock describe relatively similar feeding behaviour and that the large haddock feed on slightly larger meals than the smaller ones.

The credibility and accuracy of the model can be checked further by comparing the inferred feeding patterns to the results of other studies which have been carried out.

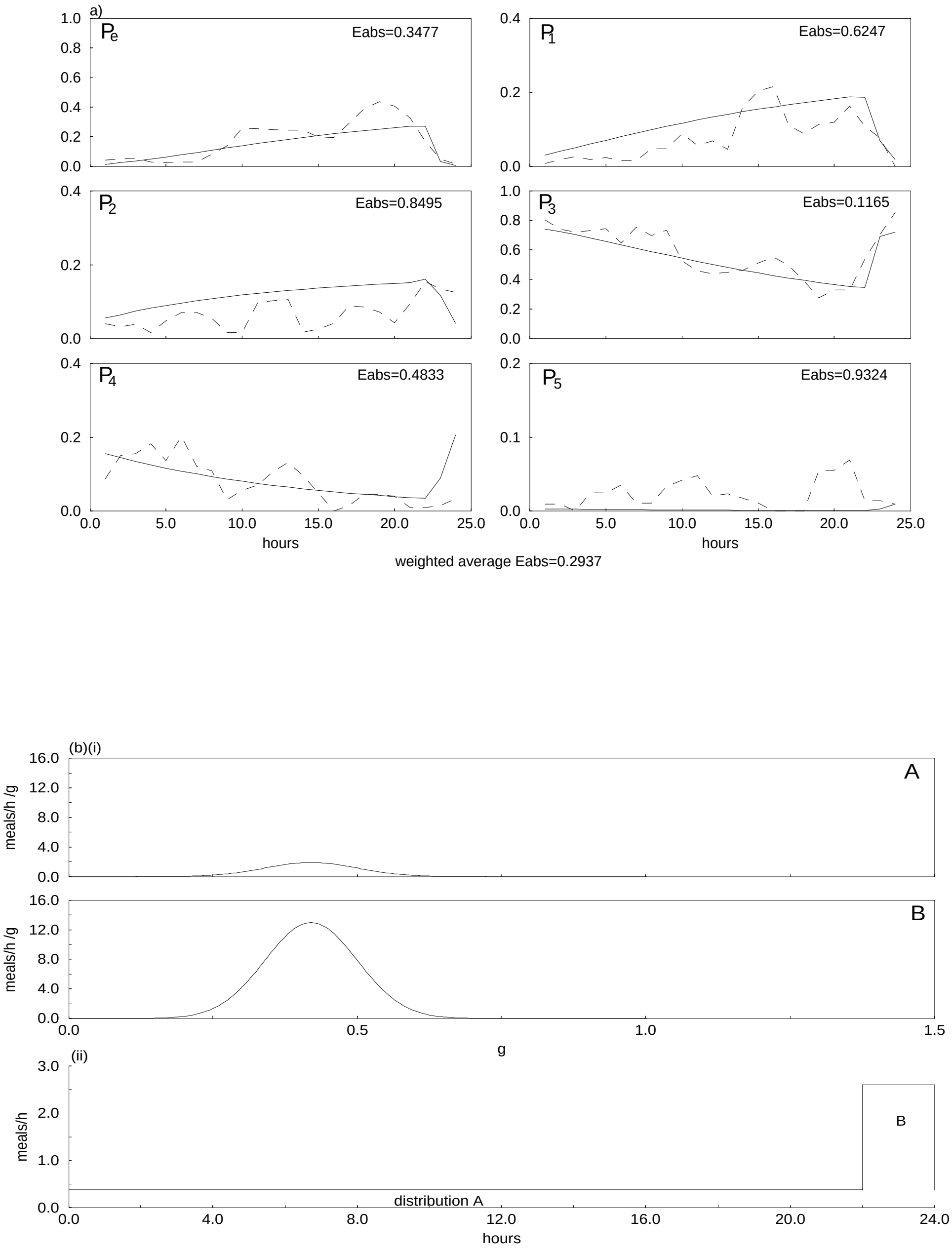


Figure 7.6. a) Model predictions (solid) for the proportion of guts in a series of weight categories compared with the observed data (dotted) for small haddock, with the corresponding diel variation in feeding (b). The meal size distribution in each period is shown in i), while ii) illustrates the variation in total feeding rate.

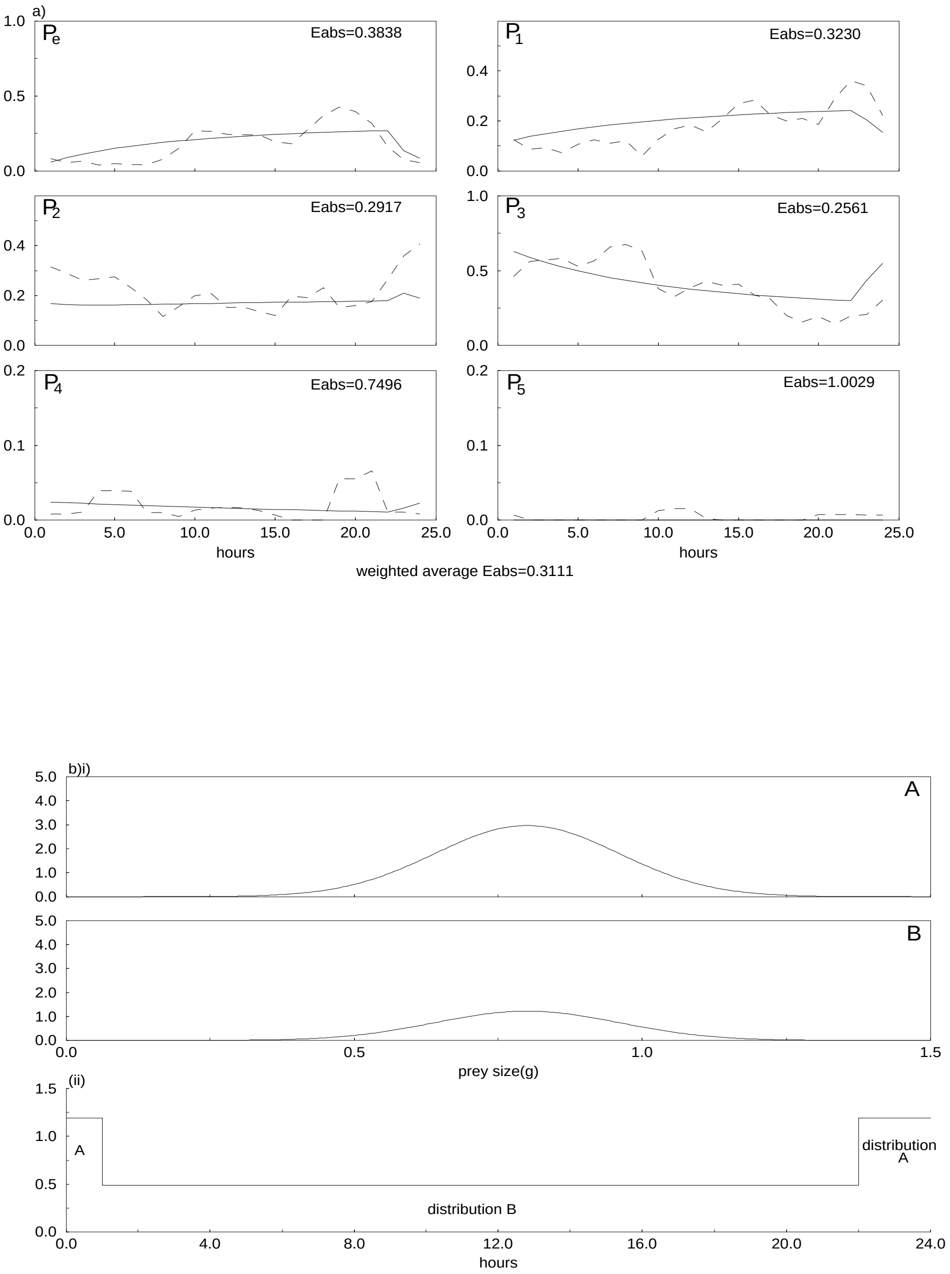


Figure 7.7. Observed (dotted) and predicted (solid) variation in the proportion of the population of large haddock in each of a series of gut weight categories, with b)i) showing the changing meal size distribution and ii) the variation in total feeding rate.

7.4 Checking the optimum

Since the model has been fitted to each of the data sets using a hand optimisation technique rather than an automated method, it is particularly important that we make certain that the feeding behaviour which has been inferred is actually an optimum. There is no way of checking that this optimum is global, but we can at least check that a local minimum has been obtained, by perturbing each of the parameters in turn and checking that the normalised absolute deviation is at a minimum. From such sensitivity analysis we can conclude that the values of the feeding parameters describing the meal source distributions and feeding rates do in fact give an optimum. However, we must further check the biological set-up of the model i.e. whether the number and type of meal source distributions has been chosen correctly and whether the changes in feeding are occurring at the most appropriate times. Rather than tediously varying the positions of the feeding switches and the numbers of meal source distributions in turn a more sensible approach is to consider some more biologically significant tests.

I shall first consider the number of meal sources on which each species feeds. Our results conclude that the dab feeds on three meal sources while all the other fish cohorts appear to feed on only one prey size distribution. As the rate of consumption of the very large meals by the dab is so low, it seems surprising that this meal source is necessary to obtain a good fit to the data. It is in fact very important to the accuracy of the fit, with the average E_{abs} increasing from 0.13 (minimum) to 0.49 when the large prey are not included. The consumption of extremely large meals, even at a very low rate means that some individuals will have quite large stomach contents and so omitting this meal source produces a quite marked worsening of the fit of the high stomach content categories. The medium sized prey source which appears during the evening is required to produce the observed reduction in empties which begins around

17.00h and also the corresponding increases in the proportion of the population in categories P_2 and P_3.

Looking at the variations in the stomach weight categories of the plaice, it seems likely that the same sort of feeding behaviour should be observed with the appearance of a medium sized prey in the evening. This however, produces too large a peak in categories P_2 and P_3 during the evening and too low a peak in stomach weight category P_1. So, the addition of an extra meal source fails to provide a better fit to the data.

Both the dab, plaice and whiting feed on some very small prey whose size distribution functions are very skewed to the left due to the truncation at zero. The effect of substituting a gamma distribution for a truncated normal was investigated in chapter four and we concluded that for noisy data, the fit of the two was indistinguishable. In this case, the gamma distribution provides a slightly worse fit to the data for the flatfish and a slightly better fit for whiting. However, in all cases the change in the total normalised mean absolute deviation is less than five percent and we once again can conclude that the type of distribution makes very little difference to the overall fit.

The final sensitivity test which I shall carry out is based on the timing of the feeding switches. By preserving the shape of the variation in feeding rate, but displacing its actual position throughout the day, I can show that we have found an optimum. Figure 7.8 illustrates the variation in the weighted mean absolute error with the timing of the first feeding switch compared to the assumed optimum timing.

The position of the minimum at zero hours, for all fish cohorts indicates that our method of hand fitting the model to the data has found an optimum. The minima observed for the gadoids are all very broad indicating a little uncertainty in the timing of the feeding switches. However in all cases this will be less than two hours. The more complicated feeding regimes of the flatfish, which have more than one high intensity feeding period, show another minimum in this sensitivity analysis, approximately twelve hours displaced from our model fit. For both species though the global minimum is at zero hours displacement and therefore we can safely conclude that our method has found the optimum timing.

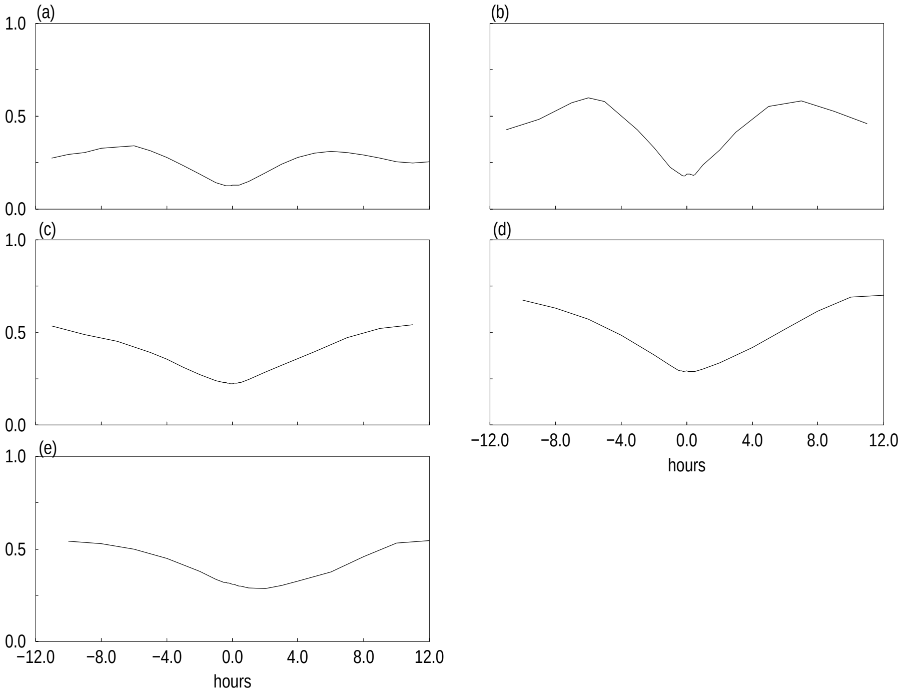


Figure 7.8. Variation in weighted mean absolute errors with time at which the feeding rate first switches compared to the optimum time for a) dabs, b) plaice, c) whiting, d) small haddock and e) large haddock.

Although our method of finding the optimum feeding behaviour was not particularly sophisticated, the combination of these simple sensitivity tests has proved that the parameters sets found do indeed describe an optimum feeding behaviour for the fish cohorts in question.

7.5 Discussion

Once we have established that our fitting procedure has produced an optimum fit to the stomach contents data, we must discuss how accurately this inferred feeding behaviour describes that of the population from which it was drawn. The results from chapter four indicated that samples taken from a population needed to contain approximately 100 individuals and should be categorised into no less than about five stomach weight categories in order to infer a reliable description of the stationary feeding behaviour of the complete population. Chapter five, though, which introduced time dependence into the parameter fitting problem, implied that even with samples of size 100, large errors in the estimates of population parameters could arise unless samples were taken very frequently. The real samples to which our model has been fitted in this section, although relatively small (maximum size of fifty individuals), are taken at hourly intervals and so quite a detailed description of the diel cycle is observed. I shall therefore assume that the feeding behaviour inferred from these samples adequately describes that of the populations from which they were drawn.

As well as possible difficulties due to the size of the samples, another worry must be that our samples are not being taken from a closed population. It is possible that the population undergoes regular immigration or emigration of individuals from other populations with different stomach contents distributions. For example, fish may come inshore to feed and then move offshore when full. Such a scenario would severely bias our conclusions about the feeding behaviour of the population as we are sampling only from an inshore area. In the construction of our model, we have also assumed that identical meal sources are available to the whole population which could be false if samples are taken over a wide area. In this case however, samples are taken over quite a small region and it seems unlikely that prey availability is likely to vary much over this area.

Further checks that the model has been formulated in a sensible way and can be used to give a satisfactory description of the variation in the stomach contents of a simultaneously feeding and digesting population of fish can be made by comparing the results of this section to those of other stomach contents studies.

I shall first consider the inferred feeding behaviour of the two flatfish species. Many studies have been carried out on the feeding patterns of flatfish, some of which support our results, while others do not. Gwyther and Grove (1981) carried out experiments in which dabs were fed using a demand system and concluded that the fish usually fed during the daytime, which is supported by De Groot (1971). More specific conclusions about the feeding behaviour of the dab were drawn by Knust (1986) who analysed fish stomach contents samples. He claimed that feeding occurred largely during the morning, though a lower second peak in the feeding rate was observed for samples taken in certain places, giving further support to our results.

The conclusion that plaice are mainly daytime feeders is supported by the studies of De Groot (1964) and Edwards and Steele (1968) who observed that the average gut contents generally rise during the day and fall during the night indicating an increased feeding rate during the day. Although Basimi and Grove (1985) found some evidence of feeding during the night (which does not in fact contradict our results as we do infer low overnight feeding), their sampled average gut contents are in general higher during daylight hours, which seems to imply that more feeding occurs during the day. The studies of Bregnballe (1961) give support to our variations in the feeding rate throughout the day, by suggesting peaks of feeding intensity at dawn and dusk.

The predictions made by the model that flatfish feed mainly during the day with peaks of feeding during the morning and evening are well supported by a large amount of the previous literature on the feeding patterns of flatfish. Some evidence, however, was found in laboratory experiments conducted by Hall (1987), that dabs feed mainly during the hours of darkness. These experiments, though, also indicated a great variation in the feeding behaviour of the dab with some of the individuals consuming most of their food during the daytime. So, I shall conclude, that since there is not a large amount of substantial evidence to contradict the results of our model, the flatfish are primarily daytime feeders relying on sight to catch their prey, with only low sporadic feeding during darkness.

The complicated composition of the meal size distribution of the dab predicted by our model is supported again to a certain extent by Knust (1986) who found that different organisms were consumed at different times of the day, with a larger prey source in the late evening. This agrees with our prediction of the appearance of the medium sized meal source between the hours of 17.00 and 20.00. Evidence for a similar variation in the prey composition of the diet of the plaice was found by Ansell and Gibson (1990) who claim that the diet changes with the tidal cycle. This contradicts our conclusion that plaice feed on a single meal source which is available at all times of the day.

Fewer studies have been carried out on the feeding behaviour of gadoids and therefore there is relatively little literature with which to compare our results. Our feeding pattern for whiting is supported by Gordon (1977) who concluded that whiting preying on other fish fed mainly during the early part of the morning. His stomach contents samples also agreed with our own, showing a peak in the proportion of empty stomach contents during the middle of the night. Experimental observations made by Hall (1987) suggested that there may be a high peak in feeding intensity during the very early morning, but that the same results could be observed from lower overnight feeding which is concordant with the predictions of our model.

Overall, the model performs quite well in the prediction of the observed stomach contents data. Most of the feeding behaviour which is forecast shows good agreement with studies conducted by other scientists and therefore provided we are able to make an independent calculation of the all important digestion rate, I can conclude that this model can be used to make some useful inferences about the feeding behaviour of a population of fish from frequently taken stomach contents samples.

Chapter 8

Daily consumption rate calculations

8.0 Introduction

The value of the results of chapter seven only become fully recognised when they are coupled with total food consumption rate calculations, which are useful to many ecological studies. Growth and reproduction in individuals is influenced by their energy intake which in turn is dependent on the type and amount of food consumed. Such energy calculations are necessary for studies of enery flows in marine food webs. A knowledge of total population food uptake rates is required when considering the dynamics of complex animal communities, in order to determine the effect of a particular species on its prey and also on other competing populations.

Food consumption rates are intrinsically linked to digestion rates and therefore are dependent on a large number of external factors. Here, however, I shall not go into the entailing complex arguements and the discussion will concentrate on the methods of calculation of food consumption.

The most obvious way of finding out how much fish eat is by watching. Field observations, however, are impossible, so all studies are carried out in the laboratory. Elliott(1975) attempted to reproduce the natural environment of the trout in the laboratory and calculated the daily consumption rate by counting the number of prey items of a particular size which are consumed within a twenty four hour period. An alternative method which is used by Jones (1978), Majkowski and Waiwood (1981) and Majkowski and Hearn (1984) is the energy requirement technique. By making estimates of the growth rate in the wild and the amount of energy required for reproduction, the amount of energy and therefore the daily food ration required for survival can be calculated. The final technique is the analysis of stomach contents samples (Eggers1977, Elliott and Persson 1978, Pennington 1985). Once the digestion rate is known, calculations of the daily ration are usually made by comparing successive stomach contents samples, making an hourly calculation and then summing this over the whole day.

All three of these methods have their particular advantages and disadvantages. From laboratory experiments quite accurate measurements and observations can be made. However, laboratory conditions can never fully reproduce those of the natural environment, where the fish can move freely and have a wide range of prey items to choose from. Estimations made using energy methods, although useful in food web studies, have a prerequisite of many energy requirement calculations which could all lead to errors in the final calculation. One of the advantages of the stomach contents analysis technique is that the samples may be taken of fish feeding in their natural habitat, though an independent method of calculating the digestion rate parameter is still required.

In this case we have managed to infer the daily feeding pattern of the populations in question by fitting a feeding and digestion model to the stomach contents data. So, a more elegant way of calculating the daily consumption rate would be to utilise the feeding rate definitions made in the construction of the model and compare the results with those of some of the more established daily ration calculation methods.

8.1 A daily ration calculation

Before making any calculations of daily food ration from the results of chapter seven, some further definitions are required. The feeding function $R(t)M(m)dm$ was defined as the rate in meals per hour at which an individual ingests meals between sizes m and $m+dm$ provided the meal does not overfill its gut. From this definition we can express the consumption rate of an individual in grams per hour as

$$\Psi(w,t) = R(t)\int_0^{w_F - w} mM(m)dm \qquad (8.1)$$

and the instantaneous population average food uptake rate at time t as

$$C(t) = \int_0^{w_F} f(w,t)\Psi(w,t)dw. \qquad (8.2)$$

The parameters defining the feeding function which were inferred from the stomach contents in chapter seven can now be used in the calculation of C(t). The variation in the population food uptake rate for each of the five fish cohorts is illustrated in figure 8.1.

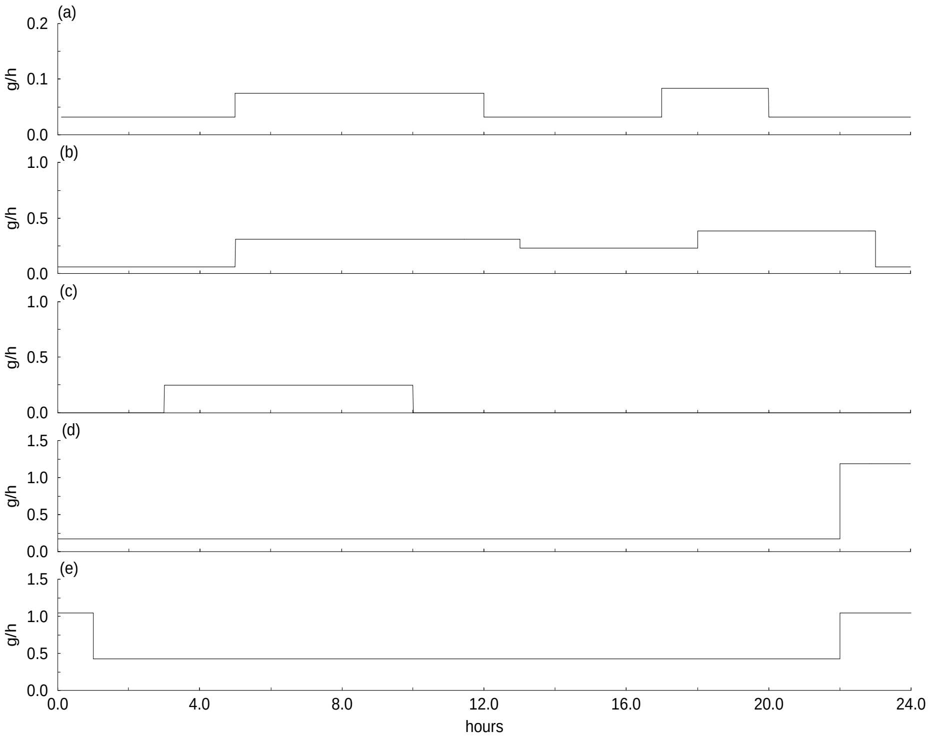


Figure 8.1. Variation in the food consumption rates of a) dabs, b) plaice, c) whiting, d) small haddock and e) large haddock inferred from the stomach contents data.

The total daily rations can then be calculated by integrating over the period of twenty four hours and are shown in table 8.1.

	Daily Uptake	
Species	grams	% body wt
Dab	1.2	1.7
Plaice	5.9	4.5
Whiting	1.7	1.7
Small haddock	6.2	4.1
Large haddock	12.2	3.7

Table 8.1. Daily uptake rates calculated using the optimum parameter sets.

8.2 A review of other daily ration estimation methods

Further checks on the validity of this feeding and digestion model can be made by comparing the results of the daily uptake calculations to the findings of other stomach contents based studies.

The first important suggestions about the calculation of daily ration from stomach contents measurements were made by Bajkov (1935), who proposed that the total amount of food eaten over a twenty four hour period C_{24}, could be expressed as

$$C_{24} = \overline{A}\left(\frac{24}{n}\right) \tag{8.3}$$

where $\overline{A}$ is the average stomach contents and n is the number of hours required for complete gut evacuation. Recent calculations have been more sophisticated and generally based on the individual feeding and digestion model

$$\frac{dW(t)}{dt} = R(t) - KW(t)^c. \tag{8.4}$$

Eggers (1977) assumed an exponential gut evacuation rate (c=1) and that the feeding rate R(t) is a constant or linearly increasing over certain periods of the day. From such a model he calculated the diel trajectories and daily ration of fish feeding under particular feeding regimes, but the work was purely theoretical and no comparisons with real daily variations in stomach contents data were made.

Consumption rate studies which incorporate comparisons with stomach contents data tend either to be based on the solution of the above equation when possible or on the concept that the amount of food consumed over a period of time by an individual must be equal to the change in its stomach contents plus the amount of food which has been evacuated (equation 2.1). Elliott and Persson (1978) assumed an exponential digestion rate and a constant feeding rate over a short period of time. Solving equation 8.4 under such conditions gives

$$W_t = W_o e^{-Kt} + \frac{R}{K}\left(1 - e^{-Kt}\right) \tag{8.5}$$

where W_o is the initial amount of food in the stomach. This formula can then be rearrange to give an expression for the hourly food consumption rate

$$R = \frac{\left(W_t - W_o e^{-Kt}\right)K}{1 - e^{-Kt}} \tag{8.6}$$

from which the actual food consumption over a particular time period can be calculated. Elliott and Persson (1978) found a reasonable amount of accuracy when comparing this method to actual individual measures of food consumption. However, this method is only applicable to cases of exponential digestion which we rejected in chapter two.

Since it is impossible, in general to monitor the stomach contents of individual fish at intervals over the period of a day, sequential stomach contents samples will incorporate many fish with a range of stomach contents. Therefore, it is usual to calculate the population average uptake rate over a particular time period, $\overline{\mathrm{U}_{\mathrm{t}}}$, using the expression

$$\overline{U_t} = \overline{W_{t+1}} - \overline{W_t} + \overline{D} \tag{8.7}$$

where $\overline{W_t}$ and $\overline{\mathrm{W}_{\mathrm{t+1}}}$ are the average stomach contents of the population at the beginning and end of the period and $\overline{\mathrm{D}}$ is the average amount of food evacuated over the period.

As I described in chapter two, though there is much disagreement about the type of curve which gastric evacuation follows. The evacuation rate, D(t), of an individual is usually described by

$$D(t) = KW(t)^c, \tag{8.8}$$

which implies that the stomach contents of a non-feeding individual obey

$$\mathrm{W}(t)^{1-c} = \begin{cases} \mathrm{W}_0^{1-c} - K(1-c)t & \mathrm{c} \neq 1,\ \mathrm{W(t)} > 0 \\ 0 & \mathrm{W(t)} = 0 \end{cases} \tag{8.9}$$

and

$$\mathrm{W}(t) = \mathrm{W}_0 e^{-Kt} \qquad \mathrm{c} = 1. \tag{8.10}$$

However, as I showed in chapter two, the shape of the population digestion curves can vary enormously due to the variations in the stomach contents across the population. The most important question which therefore must be answered before population average consumption rates can be calculated is how to determine the population average digestion rate over the period in question. Some studies claim that a form of equation 8.9 describes the depletion of average stomach contents of a population, sometimes the same as that assumed for the individual stomach contents depletion, while others calculate individual digestion rates and then average them over the population. Clearly these methods will have a significant affect on the calculations of the average consumption rate.

Two methods described by Basimi and Grove (1985) just treat the average digestion rate like the individual digestion rate by applying equation 8.8 to the average stomach contents of the population. Their first method assumes that none of the prey ingested during the time interval in question can be digested and therefore the digestion rate is based on the stomach contents at the start of the interval, giving the expression

$$\overline{U_t} = \overline{\mathrm{W}_t} - \left[\overline{\mathrm{W}_0}^{1-c} - K(1-c)t\right]^{1-c} \tag{8.11}$$

for the food intake of the population during the time period zero to t. Their second method supposes that all the food ingested is taken halfway through the period and then digestion of this newly ingested food can also occur, implying

$$\overline{U_t} = \left[\overline{\mathrm{W}_t}^{1-c} + \frac{K(1-c)t}{2}\right]^{\frac{1}{1-c}} - \left[\overline{\mathrm{W}_0}^{1-c} - \frac{K(1-c)t}{2}\right]^{\frac{1}{1-c}} \tag{8.12}$$

Pennington (1985) illustrates a method of individual food consumption, similar to that of Elliott and Persson, but more general in that it can be used with digestion models other than the exponential relationship. Starting from equation 8.4 he produced an expression for the average amount of food consumed per hour over a particular time interval, $\mathrm{U_T}$. By definition,

$$\mathrm{U_T} = \frac{1}{\mathrm{T}}\int_0^{\mathrm{T}} \mathrm{R(t)dt}, \tag{8.13}$$

which on substitution from equation 8.4 becomes

$$
\begin{aligned}
U_T &= \frac{K}{T}\int_0^T \mathrm{W}(t)^c\,dt + \frac{1}{T}\int_0^T d\mathrm{W}(t) \\
&= \mathrm{Kavg}\left[\mathrm{W(t)^c}\right] + \left[\mathrm{W}(T) - \mathrm{W}(0)\right]/T
\end{aligned}
\tag{8.14}
$$

where avg signifies the average value over the time interval. This measure can be converted to average population uptake by substituting population average stomach contents for individual stomach contents. Pennington also suggests that a more accurate estimate of $\overline{\mathrm{D}}$ can be made by calculating the digestion rate of each of the N individuals at the start of the feeding period and then averaging these across the population. His expression for average consumption per fish per hour, $\overline{\mathrm{U_T}}$, is then

$$
\begin{aligned}
\overline{U_T} &= K\sum_{i=1}^{N} avg\left[\mathrm{W}_i(t)^c\right]/N + \left\{\sum_{i=1}^{N}\mathrm{W}_i(T)/N - \sum_{i=1}^{N}\mathrm{W}_i(0)/N\right\}/T \\
&= \mathrm{Kavg}\left[\mathrm{W_c}(t)\right] + \left[\overline{\mathrm{W}(T)} - \overline{\mathrm{W}(0)}\right]/T
\end{aligned}
\tag{8.15}
$$

where $\mathrm{W}_i(t)$ is the stomach contents of fish i at time t and

$$
\mathrm{W}_c(t) = \sum_{i=1}^{N}\mathrm{W}_i(t)^c / N. \tag{8.16}
$$

All of the methods described here, when used with actual stomach contents data, make use of regular samples taken at relatively short time intervals. An alternative approach however, is carried out by Sainsbury (1986), who uses a similar idea to the work done in this thesis. He suggests fitting a model incorporating parameters which describe the feeding rate and length and time of feeding period to data for the full twenty four hour cycle. A non-linear least squares fit to the data would then provide estimates of the feeding parameters including the hourly food uptake rate. Results found using this model appeared to agree quite well with those of Elliott and Persson except when some feeding occurs throughout the day which violates the assumption made here that there is a distinct feeding period. The assumption made by Sainsbury, that digestion is an exponential process, implies that an analytic expression for the variation of the stomach contents during one feeding cycle can be found with relative ease, and that the model can be used with individual and average population stomach contents. So, although Sainsbury has made consumption rate estimates using the same basic method as this thesis, his particular model appears to be too specialised and not applicable to all types of feeding behaviour.

Of all the methods described here, the second of Penningtons methods would appear to be the most convincing for dealing with populations of fish. However, in the next section, I shall use several of the above methods to calculate the average population daily uptake from the stomach contents data which was analysed in chapter seven. The results can then be compared to those of the previous section.

8.3 Uptake estimation using alternative methods

In this section I shall compare the daily consumption rates calculated using the Basimi and Grove methods with those from Penningtons method and that derived in this thesis. Before calculations can begin, we require values for the parameters c and K, for each fish cohort. In chapter seven it was shown that the population digestion curve produced from the linear digestion model (Bromley 1988) with a particular linear digestion rate was almost identical to the evacuation curve produced by equation 8.8 with certain predefined species dependent values of c and K. The appropriate values are given in table 8.2.

As I explained in chapter seven, no such evacuation curve for whiting could be found and therefore a linear digestion model was assumed due to work by Bromley (1988) and Robb (1990).

Species	c	K	Origin
Dab	0.25	0.096	Fletcher et al. 1984
Plaice	0.51	0.221	Basimi & Grove 1985
Whiting	0	0.15	Robb 1990
Small haddock	0.46	0.119	Jones 1974
Large haddock	0.46	0.191	Jones 1974

Table 8.2. The evacuation curve parameters for each cohort of fish.

Since our data consists of hourly measurements of the proportion of each population in a particular gut weight category, I decided to evaluate hourly consumption rates and then sum these over the 24 hours in order to obtain the daily uptake rate. So, for all four methods we require the average stomach contents of the population at each sample point and the value of $\mathrm{W}_c(t)$. Since these values have to be calculated from our available data, which consists of varying proportions of fish in a number of stomach contents categories, I shall assume that the average stomach contents of the population at time t can be calculated by

$$\overline{\mathrm{W}(t)} = \sum_{i=1}^{M} p_i m_i \tag{8.17}$$

where $\mathrm{p_i}$ is the proportion of the population in category i, $\mathrm{m_i}$ is the mid point of category i and M is the number of categories.

Similarly I shall suppose that $\mathrm{W}_c(t)$ (used in 8.15 and 8.16) can be determined by

$$\mathrm{W}_c(t) = \sum_{i=1}^{M} p_i m_i^c \,. \tag{8.18}$$

The total daily uptake rates calculated by these three methods are given in table 8.3.

All three methods of calculation give some very peculiar negative values of the hourly uptake rate. These occcur when the average stomach contents at consecutive sample times fall by an amount which is larger than the hourly digestion rate and were also apparent in calculations made by Sainsbury (1986), who ignores them and appears to set them to zero.

Species	Thesis	Basimi & Grove	Pennington 1	Pennington 2
Dab	1.2	1.6 (3.7)	1.9 (3.8)	0.8 (3.2)
Plaice	5.9	1.4 (1.8)	2.0 (2.4)	1.9 (2.3)
Whiting	1.7	3.6 (14.5)	3.6 (14.5)	3.6 (14.5)
Small haddock	6.2	3.3 (6.9)	4.5 (7.7)	3.6 (7.1)
Large haddock	12.2	3.3 (11.4)	5.8 (12.0)	2.0 (9.7)

Table 8.3. Daily uptake rate (grams) estimated from the hourly gut contents data by three established methods compared to the method derived in this thesis. The brackets denote estimates in which negative hourly uptake values were set to zero.

Two sets of calculations are made of the total daily uptake, the first including the actual negative values and the second with the negatives set at zero. A comparison between the two values (the second is given in parenthesis in table 8.3) shows what a significant effect the inclusion of these 'negative consumption rates' has on the results. The estimates made using the second of the Basimi and Grove methods are not shown as they are almost identical to those of Penningtons first method. By considering equation 8.12, we can see that it reduces to Penningtons first method (8.14), for small sampling intervals.

Since the fish showed no evidence of regurgitation during sampling, these negative values must be due to either weaknesses in the methods of calculation or the noisieness of the data. The main stumbling block in all the calculations was how to determine the population average digestion rate over a particular time interval. The methods employed by Basimi and Grove and Penningtons first method both simply substitute population average stomach contents values into digestion equations which were formulated to describe the gut evacuation rate of an individual fish. Chapter two showed that the depletion of the population average stomach contents is unlikely to be identical to that of an individual who initially had stomach contents equal to the population average, due to the censoring of the digestion curve as some individuals become empty. These methods are therefore likely to give errors due to miscalculations of the average digestion rate. However, the many negative hourly consumption rate values cannot be attributed to these inaccurate calculations as these appear in all three methods of food intake calculation, including Penningtons second method which adopts a more legitimate method of average digestion rate calculation.

Another possibility as to the source of these negative values is the formulation of the digestion models. However, this seems unlikely as the values appear for all species So, it seem then that the problems must be attributed to the noisy data.

Our method calculated the daily uptake rate by fitting a feeding model to the data over the total twenty four hour period and found a small set of parameters which could be used to define the complete feeding behaviour over the day. The other three methods rely on calculations using successive hourly stomach contents samples which are very noisy due to totally random samples being taken from the complete population. Our method is therefore much less sensitive to the noise in the data and no negative consumption rates are apparent.

8.4 Discussion

A comparison of our calculated daily uptake values to those calculated by the other methods show some quite large differences for some of the species. The values calculate here for dab and haddock give reasonable agreement to those calculated by the other methods, lying approximately between the highest and lowest alternatives. However, the value calculated here for plaice is significantly higher than all other estimates, while this daily food uptake of whiting is noticeably lower.

Possible reasons for these infelicities can be seen by considering the shape of the population digestion curves assumed in all methods of calculation (reconsider figure 7.1). The population digestion curve assumed for plaice is much more curved than that of either the dab or haddock, while I have assumed a linear population evacuation curve for the evacuation of whiting. In the formulation of the feeding and digestion model explained in this thesis, I have assumed that the individuals in a population follow a linear digestion model, which is supported by Bromley (1988) and Robb (1990). The appearance of a curved population evacuation relationship is due to the increasing proportion of empty fish which can undergo no further reduction in stomach contents. The analysis used in the other methods assumes that the population digestion curve and individual digestion curve are the same. So, to match our population digestion model to those of plaice and whiting (the most extreme) will respectively require particularly high and low individual digestion rates. Our calculated daily consumption rates are consequently much higher for the plaice and much lower for the whiting. The use of the linear individual digestion model used in this calculation, though is strongly supported by the work of Bromley (1988) and Robb (1990).

In the hope of validating either view of the individual digestion process, further analysis of the results of the feeding and digestion model daily uptake calculations can be made by considering the growth rates inferred from the determined food consumption rates and making a comparison of these with the results of other studies. Jones (1978) derived an expression, from a series of laboratory experiments carried out by Jones and Hislop (1972) relating food consumption and growth in non-spawning haddock and whiting. He found that

$$F = 0.008M^{0.8}\exp(0.081T) + 1.27GM^{0.15} \quad (8.19)$$

where F is the rate of food consumption in kilocalories per day, M is the body weight in grams, G is the growth rate in grams per day and T is the temperature in ^{o}C. From this equation we can therefore calculate the appropriate value of the growth rate for three of the fish cohorts in question, provided that we can convert our measures of daily uptake in grams to energy uptake in kilocalories per day. Jones (1978) states that the mean calorific value of the food of haddock is 0.6kcal/g of wet weight food ingested, while it appears from Bromley (1988) that the food of whiting provides about 2.4kJ of energy per gram of wet food which is equal to approximately 0.57 kilocalories.

The results of uptake rate calculations made from the model described in this thesis give a daily rate of approximately 4% of the body weight which leads to a growth rate of about 0.6% body weight per day. The same calculations made using the results from the other food consumption rate estimates appear to be rather lower, -0.12 to 0.12% body weight for large haddock and 0.16 to 0.34% for small haddock. The calculation was then repeated for whiting and showed that the growth rate implied by the work of this thesis is almost zero, while the other estimates gives 0.44%.

All the growth estimates for haddock appear to lie within the range of values given by Jones (1978). The value calculated using the continuous digestion models seems to be towards the higher end of observed rates while the values determined from the other methods are much lower. Both estimates of the growth rate of whiting also seem quite sensible. Hence it is not possible to use this method of comparison to validate either opinions of the digestion process.

As there is strong support for the view that the digestion of an individual is linear and the differences in the results of calculations made from our model and those of others can be explained by the alternative opinions of digestion, and not a serious error in the formulation of the model, I shall conclude that the model gives a fairly reliable method of calculation of the daily food consumption rate of the species in question. Should we however, believe that individual digestion does not follow a linear model, then the calculations made in this thesis can easily be repeated by substituting the required individual digestion model into the original formulation of the model and recalculating the feeding parameters. Aswell as incorporating versatility, this model is also a great improvement to previously accepted consumption rate calculation techniques as it is affected much less by the noisieness of the consecutive stomach contents samples and calculates food intake by considering the variation in stomach contents over the whole day.

Chapter 9

Conclusions

9.1 Summary

The aim of this thesis was to gain an understanding of the mechanisms behind the observed dynamics of fish stomach contents samples. The strategy was to construct a model which incorporated a description of between fish stomach contents variability at a particular time and some simple assumptions about the feeding and digestion processes. The resulting model adequately predicts the main dynamic features observed in the data which was introduced in chapter six.

Using simple step functions at switches between feeding rates and continuous prey size distributions I have established the feeding patterns of four main fish species (dab, plaice, whiting and haddock) found in Loch Gairloch on the west coast of Scotland. The conclusions that the two flatfish species feed largely during the day with peaks of feeding at dawn and dusk agree with the results of many other studies of the feeding patterns of flatfish. In contrast I conclude that the whiting feed heavily during the early morning while haddock consume most of their food during the night. Reassuringly there is little difference between the feeding behaviour inferred for the two size groups of haddock although there are few other studies with which these results can be compared. In chapter eight I concluded that the total daily ration calculations made from these results were also quite convincing and any infelicities which occurred were due to the choice of digestion model rather than any serious faults in the model. This method of calculation also appeared to be less sensitive to noisy sampled data than others.

As the most feasible way of learning anything about the feeding behaviour of fish is by studying stomach contents samples, chapters four and five concentrate on the question of the reliability of results inferred from relatively small samples. The most interesting results come from chapter five which considers the time dependent feeding rate case. I conclude here that if the number of stomachs sampled at each time interval is to be small (less than 100), then the samples must be taken very frequently (hourly) in order that the feeding behaviour inferred from such samples adequately predicts that of the population. However, if larger samples of fish are taken (greater than 500 individuals), then it is feasible to sample as infrequently as every six hours provided that the stomachs are categorised into at least fifteen stomach weight categories. These results show that we can quite accurately infer the feeding behaviour of a population of fish from samples collected at intervals throughout the day provided that the above sampling requirements are met.

9.2 Discussion

The first section of this study deals with the construction and dynamics of the feeding and digestion model. Chapter three clearly illustrates the mechanisms for changes in the structure of the stomach contents distribution of a population of fish which would not be evident if only the mean stomach contents of a population was considered.

The construction of the model, however, does involve a number of assumptions which may be questionable when the output of the model is compared with any real data. Chapter two initially constructs a model to describe the variation of the stomach contents distribution of non-feeding population of fish. I have assumed that the digestion behaviour of all individuals is the same which implies that the population is one of identical individuals. The length analysis of the fish in the sample with which this model is compared later in the thesis shows only a very small variation in fish size and therefore it appears that in this case this supposition should not give misleading results.

At this stage in the developement of the model I was also required to assume that we are dealing with a closed population of fish which is not subject to any significant immigration or emigration from another population with a different stomach contents distribution. The data which are considered in the latter part of the thesis were sampled from inshore waters off the west coast of Scotland. It is possible that there is movement of fish into and out of this area of study which may be connected to their feeding habits. For example, fish may move inshore to feed and then when satiated may return to offshore waters. In such a case, our samples would be of fish from different populations which have moved inshore to feed and therefore cannot be compared to the output from the model which describes the daily fluctuations in the stomach contents of a closed population of fish. Although analysis of the lengths of fish in the samples indicates no significant change in the size of the fish during the day, it does not prove that fish are not moving between two or more sites.

Obviously even if the population is a single well-mixed entity not subject to outside interference it is possible that all individuals may not be subject to the same prey distribution. If this was the case our model would again be inaccurate as it makes the assumption that all individuals are exposed to an identical prey distribution and so have equal likelihood of consuming a particular prey.

However, despite these possible flaws in the construction of the model, the conclusions drawn about the feeding habits of the fish species sampled from Loch Gairloch largely agree with those of other authors which suggests that we are justified in making these simplifying assumptions or at least that they are not too significant to the results obtained.

The whole of this thesis was initiated by the Loch Gairloch data provided by the Marine Laboratory, Aberdeen and described in chapter six. Consequently the attempts at inferring the feeding patterns and processes made in chapter seven were carried out before the work described in chapters four and five. Therefore the fitting of the model to the stomach contents data was carried out using eye-balling methods combined with a measure of goodness of fit rather than the semi-automatic method of finding the optimum fit described in the middle section of this thesis. Such manual methods require further numerical experiments to verify that the method has at least found a local minimum.

The numerical experiments of chapters four and five also give requirements as to the size and frequency of sampling in order that the feeding behaviour inferred from such samples adequately predicts that of the population from which it was sampled. Ideally we would have liked the sampled data considered in chapters six to eight to consist of samples of at least 100 individuals sampled relatively frequently (every hour or two). However, since the sampling was carried out several years before the work of this thesis I could make no demands on the specifications of the samples. The sampling consisted of retaining a maximum of fifty individuals of each species for stomach contents analysis, which is slightly smaller than ideal. However, samples were taken hourly and therefore the accuracy of the results of chapters seven and eight can be relied on with a fair degree of certainty.

9.3 Further work

It appears that there are several obvious directions in which the work begun in this thesis could proceed. There appears to be no reason why this model should not be applicable to freshwater fish as well as marine animals and therefore if appropriate data sets are available the model could be used to infer the feeding behaviour of a wide range of other fish species. However, stomach contents data alone are not sufficient as we require an independent method of calculation of the digestion rate of the individuals of the population. Obviously if the independent digestion data suggested an alternative digestion model (for example exponential in the case of Elliotts trout data), then the appropriate alterations can be made to the complete feeding and digestion model. One further requirement would also be a repeat of the length analysis of chapter six to verify that the population under consideration consists of identical fish which therefore have the same digestion rate.

Following the work of chapter five it seems reasonable to assume that the modelling of any further stomach contents samples should be conducted using the discrete map approach which gives a much quicker solution than the differential equation method. The condition 5.1 was chosen only for convenience, but other maps could be constructed in which fish can digest across two boxes in the space of one time interval. This would lead to further discrete map options, possibly with increased speed and accuracy.

At present the assumptions made by the model about the feeding process are very straightforward and perhaps questionable. For example, is it reasonable to assume that fish will eat provided that the prey will fit into their stomach? So, following this reasoning, an extremely full fish will go on consuming very tiny prey. Obviously at the same time its stomach contents will be decreasing due to digestion and therefore it will soon be able to consume larger prey again. However, a more realistic assumption may be that as an individuals stomach contents get higher the feeding rate decreases. The feeding rate of a population may also decrease due to a decrease in the availability of prey due to predation. Further refinements could therefore be made to the model by including a reduction in the feeding rate during an intense feeding period.

The most obvious direction which any continuation of this work would take would be on the optimisation methods and the quesion of automatic fitting. I did not attempt to use the semi-automatic fitting method on the Gairloch data in chapter seven, partly because this work was done previous to that of chapters four and five and also because the data is very noisy and the fitting method failed when started far from the optimum. Using the discrete method of solution of the partial differential equation established in chapter five, it may be possible to completely automate the fitting procedure. The solutions are obtained much faster using this method and therefore it may not be unreasonable to consider including a relatively fine search over a particular parameter space in order to locate an initial minimum. The position of this minimum could then be used to provide the initial parameter vector required to start the previously used optimisation procedure. Given a fairly fine search grid and an error surface which does not include any extremely narrow, steep minima which may be missed by an initial search, it seems possible that such an extension could provide a fully automated optimisation technique.

Appendix A. Numerical solution of the feeding and digestion equation

The partial differential equation model of feeding and digestion is discretised in the weight dimension and then the derivatives are approximated using central differences everywhere except at the edges where on sided differences are used. The result is the system of ordinary differential equations shown below which is then solved using the fourth order Runge-Kutta method.

$$\frac{dP_e}{dt} = K\frac{(3f_1 - f_2)}{2} - R(t)P_e \tag{A.1}$$

$$\frac{df_1}{dt} = K\frac{(f_2 - f_1)}{\Delta w} - U(0,t)f_1 + R(t)M(\Delta w)P_e \tag{A.2}$$

$$\frac{df_2}{dt} = K\frac{(f_3 - f_1)}{2\Delta w} - U(\Delta w,t)f_2 + R(t)M(2\Delta w)P_e + F(2\Delta w,t) \tag{A.3}$$

$$\vdots$$

$$\begin{aligned}\frac{df_{N-1}}{dt} = K\frac{(f_N - f_{N-2})}{2\Delta w} &- U([N-1]\Delta w,t)f_{N-1} + R(t)M([N-1]\Delta w)P_e \\ &+ F([N-1]\Delta w,t)\end{aligned} \tag{A.4}$$

$$\frac{df_N}{dt} = -K\frac{(f_N + f_{N-1})}{2\Delta w} + R(t)M(N\Delta w)P_e + F(N\Delta w,t) \tag{A.5}$$

If the weight dimension is discretised into N intervals each of width Δw, the variables f_1 to f_N represent the proportion of the population in each of these N intervals and $\Delta w = \frac{w_F}{N}$ where w_F is the maximum stomach contents of an individual.

Appendix B. Optimisation Routines

A number of optimisation routines are used extensively throughout this thesis, so here I shall include a more formal explanation of the mechanism by which each method proceeds.

1. The simplex method

Suppose $\mathbf{P_0}, \mathbf{P_1}, .., \mathbf{P_n}$ are the n+1 vertices of the initial simplex and that Q is the function we are attempting to minimise. I shall further define Q_i as the value of the function Q at $\mathbf{P_i}$ and let

$$Q(\mathbf{P_H}) = Q_H = \max_i(Q_i) \tag{B.1.1}$$

and

$$Q(\mathbf{P_L}) = Q_L = \min_i(Q_i). \tag{B.1.2}$$

At each stage of the procedure the parameter vector which gives the highest value of the function Q, $\mathbf{P_H}$, is replaced by a new point which is defined using three operations - reflection, contraction and expansion about the centroid of the simplex which is defined as $\mathbf{P_C}$.

The first step is to reflect $\mathbf{P_H}$ about the centroid using

$$\mathbf{P_R} = (1+\alpha)\mathbf{P_C} - \alpha\mathbf{P_H} \tag{B.1.3}$$

where α is a positive constant, the reflection coefficient.

If $Q(\mathbf{P_R}) < Q_L$ then expand the parameter vector $\mathbf{P_R}$ using

$$\mathbf{P_E} = \gamma\mathbf{P_R} + (1-\gamma)\mathbf{P_C} \tag{B.1.4}$$

where γ is the expansion coefficient, greater than unity. If $Q(\mathbf{P_E}) < Q_L$ then $\mathbf{P_H}$ is replaced by $\mathbf{P_E}$ and the process is restarted, while if $Q(\mathbf{P_E}) > Q_L$ then the expansion step has failed and $\mathbf{P_H}$ is replaced by $\mathbf{P_R}$ before restarting.

If $Q(\mathbf{P_R})$ lies between Q_L and Q_H then $\mathbf{P_H}$ is replaced by $\mathbf{P_R}$ and the routine is restarted with a new simplex, unless $Q(\mathbf{P_R})$ is a new maximum, in which case we define the new $\mathbf{P_H}$ to be either the old $\mathbf{P_H}$ or $\mathbf{P_R}$, whichever has the lowest Q value, and then make a contraction using

$$\mathbf{P_S} = \beta\mathbf{P_H} + (1-\beta)\mathbf{P_C} \qquad \text{(B.1.5)}$$

where β is the contraction coefficient, lying between 0 and 1. $\mathbf{P_S}$ is then accepted as the new parameters vector and the routine is restarted with the new simplex, unless $Q(\mathbf{P_S}) > \min(Q_H, Q(\mathbf{P_R}))$, in which case all the $\mathbf{P_i}$'s are replace by $(\mathbf{P_i} + \mathbf{P_L})/2$.

This process is repeated until the required convergence criteria have been met. The constants α, β and γ give the factor by which the volume of the simplex is changed by the operations of reflection, contraction and expansion respectively.

2. DUD

Suppose that $\mathbf{P_0^{(k)}}, \mathbf{P_1^{(k)}}, .., \mathbf{P_n^{(k)}}$ are the n+1 parameter vectors used in the kth iteration of the DUD optimisation routine. The parameter vectors are re-ordered so that $Q(\mathbf{P_0}) \geq Q(\mathbf{P_1}) \geq \cdots \geq Q(\mathbf{P_n})$, where Q is the error function between the data points **y** and the fitting function **f**, which we are attempting to minimise. (The superscripts have been dropped for convenience). The routine approximates **f(P)** by a linear function **l(P)** which is equal to **f(P)** at these n+1 points. The worst previous parameter, $\mathbf{P_0}$, is then replaced with the parameter vector $\mathbf{P_{NEW}}$ (or a point on the line between $\mathbf{P_{NEW}}$ and $\mathbf{P_n}$) which minimises the distance between **l(P)** and **y**, to give the new set of parameter vectors to be used in the next iteration.

The linear approximation is written as a function of the vector α where

$$\mathbf{P} = \mathbf{P_n} + \Delta\mathbf{P}\alpha \tag{B.2.1}$$

where the ith column of the matrix **ΔP** is given by

$$\Delta\mathbf{P_i} = \mathbf{P_i} - \mathbf{P_n} \qquad \mathrm{i} = 0,1,..\mathrm{n}-1. \tag{B.2.2}$$

The linear approximation of the fitting function is given by

$$\mathbf{l(P)} = \mathbf{f(P_n)} + \Delta\mathbf{F}\alpha \tag{B.2.3}$$

where the ith column of **ΔF** is given by

$$\Delta\mathbf{F_i} = \mathbf{f(P_i)} - \mathbf{f(P_n)} \qquad \mathrm{i} = 0,1,..\mathrm{n}-1. \tag{B.2.4}$$

If the error measure which is being used is the sum of squared errors, then one iteration of this procedure consists of minimising

$$\mathrm{Q}(\alpha) = (\mathbf{y} - \mathbf{l}(\alpha))^{\mathrm{T}}(\mathbf{y} - \mathbf{l}(\alpha)). \tag{B.2.5}$$

Substituting equation (A.2.3) into (A.2.5) and differentiating and rearranging this expression gives

$$\alpha = (\Delta\mathbf{F}^{\mathbf{T}}\Delta\mathbf{F})^{-1}\Delta\mathbf{F}^{\mathbf{T}}(\mathbf{y} - \mathbf{f(P_n)}) \tag{B.2.6}$$

which can be used in equation (A.2.1) to calculate a new value of **P**, $\mathbf{P_{NEW}}$, and the next iteration begins.

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