ASSESSMENT OF ALLOMETRY AND LENGTH-AT-AGE IN THE GROWTH OF FISHES

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ABSTRACT

Changes in biomass are monitored as variations of body condition, which is usually a quantitative index based on empirical equations without a proper theoretical background. A review of the length-weight relationship and the commonly used condition factors from a morphometric point of view show that the analysis of the length-weight relationship as a consequence of an ellipsoid body shape gives insights on the real meaning of condition and the length-weight relationship itself, providing also elements to clarify serious misconceptions about its parameters and its general meaning. A generalised equation for the length-weight relationship is derived from an ellipsoid body shape. This equation explains other models for the length-weight relationship and condition indexes previously developed as especial cases of the generalised equation. An analysis of the different definitions of condition reveals that condition can be interpreted as heaviness and as an element for describing body fitness, but it do not have to be interpreted as well-being or goodness. For growth in size at age, in this study I propose an alternative method for selection of the best model between the most widely used ones for fish stock assessment (Logistic, von Bertalanffy, and Richards, including their exponential expressions, and Gompertz). The method is based on two general models, one for single exponential and other for double exponential curves. The selection is done by exploring the stability and accuracy of each parameter during the fitting of the General Models, by the evaluation of the goodness of fit, interpretation of the statistical error distribution and the residuals' distribution shape. The model worked well on data sets with known distributions and also on a real previously published data set. In some fish populations, the length-at-age equation can be a better fit if a power constant is introduced as a new parameter. This is the equivalent of considering that the power constant in the generalized von Bertalanffy length-at-age equation could be different from 1.0. There are no antecedents of the effect of a power constant different from 1.0 on the correct assessment of weight-at-age from length-at-age data, but in this study I show that a value different from 1.0 in the power constant may be the result of the body morphometric growth. The omission of the power constant may affect the estimation of parameters of the length-at-age equation by introducing a systematic deviation from the true value that increases as age decreases The propagation of the error introduced by such omission is particularly important when the equation growth parameters are used in further models. A corrected equation for evaluation of length-at-age based on the Bertalanffy model is derived by the inclusion of a power constant, and the method for the correct estimation of the parameters of the equation is given.

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TO MY LOVED ONES

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Johnny
Ernesto

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CHAPTER 1

GENERAL INTRODUCTION

1.1 IMPORTANCE OF THE DATA ANALYSIS

Fish stock assessment relies on strong mathematical background and mathematical models are the mainstay for the quantitative analysis of biological phenomena that determine the species population dynamics and potential exploitable biomass (Cushing 1981). "Accurate stock assessment is a key requirement for successfully implementing fisheries management policies" (Chen 2001, p. 2139). Reliable data must be gathered in order to undertake a scientific evaluation of fisheries as renewable resources. Often the data are evaluated against model predictions, but in some cases there is a disagreement between data and models, which leads to undependable predictions (Rothschild 2000). The disagreement between data and models is especially important when these models are the basis for further calculations.

Data are some times forced to fit into proven and heavily supported models even when those models seem not to describe properly the data's distribution pattern they should explain. The clearest example of this is the stock and recruitment relationship that despite been derived from robust assumptions and seeming to work well in some cases, is far from reality in others (Rothschild 2000). An example is the Cod of the Central Baltic Sea (Figure 1) where spawning-stock and recruitment data appear to be randomly distributed without a definite pattern.

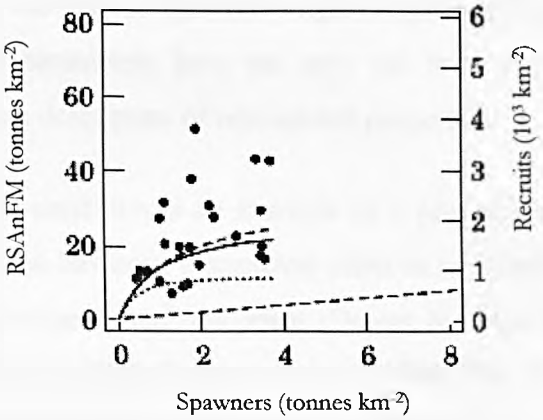

Figure 1: **The relationship between recruitment and spawning-stock biomass per km² for Central Baltic Sea Cod.** RSAnFM: resulting spawners assuming no fish mortality; Solid line: empirical Bayes estimate for the individual stock; dashed line: single stock maximum likelihood fit; dotted line: mixed model estimate of species mean; and straight dashed line: 1:1 replacement line (Myers 2001).

Some models are derived from pure empirical observations, for instance the length-weight relationship (Hecht 1916). In the power type length-weight relationship the exponent has been considered as having an ideal value of 3.0. This is a cubic law attributed to Fulton (1904), who clearly only stated the observation that if the linear body dimensions are doubled, the weight increases eight times, and above a certain point it increases at a greater rate than the cube of the length. In that work Fulton analysed data for different species and found that this relationship is not exact in many cases, but there is not a clear mention of the famous cubic law attributed to him (see also ponderal index in chapter 2), and even less a reference to a possible connection with the body's volume as some authors cite (e.g. Hostings & Dickie 1972; King 1995). The frequently cited work 'The sovereignty of the sea' (Fulton 1911) is "An historical account of the claims of England to the dominion of the British Seas and the evolution of the territorial waters: with special reference to the rights of fishing and the naval salute" (Fulton 1911), and has nothing to do with fish biology, cubic law, or condition. According to Hecht (1916), a notion of a cubic factor between length and weight has been applied since 1899. Recent publications (e. g Morato *et al.* 2001) show that for many species and sometimes also for subpopulations the cubic law does not apply, even worse, the power constant may change at different times during the life span and during the reproductive cycle (Le Cren 1951; Bolger & Connolly 1989). Regardless of who published the cubic law or if the power parameter is related to the cube and to volume, the fact is that the length-weight relationship is an empirical model for which it's parameters have not only not been properly understood, but frequently interpreted as descriptors of non-related properties.

The concept of condition is an example of a property of a fish that has no a clear meaning. Condition has been interpreted either as energetic contents, well-being, fitness, heaviness, robustness, and roundness (Bolger & Connolly 1989; Busacker *et al.* 1990; Ferron & Leggett 1994; Shulman & Love 1999; Rätz & Lloret 2002), and has been linked to the length-weight relationship (Le Cren 1951). At least four properties can be associated with such concepts: health, biomass, form, and volume, which lead to ambiguity because none of them is a proper indicator of all the others.

Ricker (1979) questioned the apparent lack of biological background in important models such as the size-at-age growth models of von Bertalanffy and

Gompertz, and the lack of satisfactory evidence of the models been close to 'developmental realities'. When referring to the asymptotic growth curves, he argues, "neither theory nor data are available to indicate that any one of the asymptotic curves should be preferred to any other, except on pure empirical grounds". Ricker also analyses and questions the experiments offered as evidence by von Bertalanffy (Bertalanffy 1957), finding them non-conclusive. Additionally, more uncertainty is added because von Bertalanffy derived the growth model mathematically using the cubic law as a basis, which as mentioned before, is not applicable to all fish species.

In practice, the previously mentioned models appear to be appropriate in many cases regardless of their drawbacks (Ricker 1979), so their application has been recommended on the condition of a proper assessment of their assumptions, properties, and limitations and the confirmation that uncontrollable factors have a minor impact on the end results. In practice, the models are oftenly applied routinely and interpreted without a proper knowledge of their underlying restrictions (Ratkowsky 1986). Often the influence of the assumptions on the interpretation of the result is ignored and often differs between analyses. As an example, few authors explore and support analytically why they chose a particular model in their papers; rather a short description of the models is usually presented. In most cases the selection of a model is based merely on its popularity (because it has been used in many cited papers), simplicity, and for producing better data fit.

Different paths can be explored in order to contribute to the solution of the problem just described, but they can be summarized into two basic options: development of new conceptual and mathematical models, or the optimisation of the existing ones. The fact that the existing models work in some cases reveal that at least the basic assumptions are correct and that the misfit observed in other situations does not necessarily reflect the failure of the models or the fundamental assumptions, but that some thing else is influencing. For instance, it is possible that the influence of other variables or parameters not considered in the model or in the methodology (Ratkowsky 1986) is causing problems (as will be shown in chapter four). It is also possible that some current models are particular cases of more general ones (Schnute 1981; Laslett *et al.* 2002), not necessarily any more complex, but more universal. It may occur that some methodological and computational sampling methods and calculation algorithms are not adequate (Vaughan & Kanciruk 1982; Castro & Lawing 1995), that some assumptions are not conceptual, but mathematically wrong (*i.e.* multiplicative instead of additive error), or that data may be unknowingly biased due to deterministic or random noise (Schaalje *et al.* 2002). Finally, the natural variability of the phenomena may be so high that more predictive precision becomes impossible (Rothschild 2000). These situations are easy to miss when models and methods are routinely applied and when the nature of the research is purely descriptive or more technical rather than scientific. It is also easy to discard a model because of its apparent incongruence with our data. However it is difficult to explain if its inapplicability is due to limitations in our data or to a disagreement between the model assumptions and the properties of the variables directly and indirectly involved, and the individual data. Other factors that could be involved include, the influence of other variables not considered (continuous and discrete), complexity, or the lack of a proper understanding of the problem. In fact, some models and even the relationship between variables have been rejected because people were unable to observe significant relationship, which does not mean that the relationship *per se* does no exist (Haddon 2001). This is often the case of the stock and recruitment relationship mentioned above.

Personally I am attracted to the optimisation of existing models as a first step. The reason is that there is proof that the apparent inapplicability of some models is due to some of the errors previously mentioned, for example, in the stock and recruitment case Walters & Ludwig (1981) found that the error introduced by the measurement of the stock size makes the data pattern more scattered as the spawning stock size increases. This gives the impression of no relationship between both variables, something similar to the example given in Figure 1. Additionally, Walters (1990) proposed a partial bias correction factor for auto correlated environmental effects on the estimation of parameters of the stock and recruitment relationship, which reduces the error due to the measurement of stock size.

In order to properly support the selection or discarding of a particular model it is necessary to consider not only the information about its underlying assumptions but also the knowledge of its theoretical background. In addition one must apply the proper numeric and graphical tools for data processing. Surprisingly, even when stock assessment is very reliant on mathematical procedures not many individual researchers develop their own data processing tools, but look for existing computer programmes and generic commercial software. Despite the existence of a variety of computational tools for the estimation of fish population parameters, most of them are merely a collection of programmes designed to routinely repeat a series of calculations and to present results as numeric tables and plots. The majority do not have the analytical tools that explore the 'what ifs' of models. In many cases researchers do not know how the programs they use work nor what algorithms are implemented. The lack of knowledge of the functioning of a method or algorithm may result in errors due to misconception rather than a failure of a model (Ratkowsky 1986).

The first attempts to automate calculations for fish population research were initiated in the seventies with programmable calculators (Kato 1978; Pauly 1984). With the rapid increase in availability of personal computers in the late eighties, quantitative analytical tools were written in Fortran and BASIC software languages (Dahlberg 1978; Gaschuetz *et al.* 1980; Pauly & David 1980; Stauffer *et al.* 1980; Rivard 1982; Korver 1983; Akamine 1984b, a). Whilst most of these programs were developed to solve particular problems, Hesse (1977), Hall (1981) and Sims (1985), were the first to publish works that consisted of collections of computer routines. The first comprehensive packages of analytical routines appeared in the eighties (Sparre 1987; Gayanilo & Pauly 1989). The work by Sparre (1987) was oriented to Apple computers and the others to the PC platform. A combined version of the two later programs appeared a few years ago (Gayanilo *et al.* 1996). Different authors and Institutions have been working with electronic data sheets, particularly Lotus (International Business machines, 2003) and Excel (Microsoft Corporation, 2003) (Garrod & Whitmarsh 1991; Holmes & Whitfield 1991; Sanders 1995). Several fully executable (independent of compiler software) institutional and commercial programs exist nowadays in this and related fields (Mesnil 1989; Sluczanowski *et al.* 1990; Coppola *et al.* 1992; Jarre 1992; Laval & Planes 1992; Stroemme 1992; Marschall 1993; Coppola *et al.* 1994; Seijo *et al.* 1994; Punt & Hilborn 1996). Considering the difficulty in finding software that covers most of the processing needs, the use of statistical packages as SPSS (SPSS Inc. 2003), SAS (SAS Institute Inc. 2003), Systat (Systat software Inc. 2003), Statistica (StatSoft Inc. 2003), Minitab (Minitab Inc. 2003) and Stata (Stata Corporation, 2003), with built in programming capacity, has permitted the implementation of *ad hoc* algorithms for particular needs. Stata also distributes a bulletin where such user generated programmes and algorithms can be published.

The more recent specialised programs are designed to process information and obtain results quickly. Some of the well-known packages (e.g. FISAT: FAO-ICLARM) were early built to work within the old DOS environment, now Windows implementations are available. In certain cases data capture (file formats etc.) is specific for each program. In addition, because of the internal data formats, information exchange with other software can often be hard if not impossible. Different programs show distinct attributes and are designed for distinct purposes such as research, teaching, and data storage.

As new methods are developed and different approaches applied, controversy about validity and adequacy of methods and software requirements frequently arise (*i.e.* Mejer 1983; Pauly 1985, 1986a, b; Nagai & Miyabe 1987; Sparre & Garcia 1987; Millar 1989; McManus 1990; Campbell 1991; Hammers & Miranda 1991; Kell 1991; Landry & Melancon 1991; Pauly & Sparre 1991; Restrepo & Powers 1991; Terceiro *et al.* 1992; Stickney 1994; Endo & Zhang 1995). As opposed to spreadsheets and statistical software programming, the main disadvantage of stand-alone executable applications is that the user cannot modify them. However, the major advantages are that the user does not need to be skilled in programming, that commercially expensive spreadsheets are not necessary, and that the user does not have to verify particular parameters of the program for every case and for every run. Software updates and corrections are relatively simple in non-executable files and programs such as spreadsheets, however, misuse by end users can frequently occur by over customisation.

Software for the analysis of fish populations and fisheries data involves the fusion of Biology, Mathematics (general Math and Statistic) and Computing. Because of the complexity of biological systems, models are simplified in different ways, particularly by considering them as black box systems (Sych 1974) and by minimising the number of variables via setting specific assumptions. Due to ecological and environmental variability can occur significantly over time, models need to be adapted to different situations by reviewing the relevant assumptions.

Recent advances in statistics have resulted in a growing emphasis on exploratory data analyses, Bayesian and iterative and intensive calculation methods such as Bootstrap, Jack Knife and Monte Carlo, which have been developed alongside developments in computer hardware and software (Halfon 1989; Chen & Paloheimo 1995; Endo & Zhang 1995; Restrepo & Powers 1995; Kinas 1996). These techniques have proved to be powerful tools for identifying departures from the models under consideration (i.e. model misfit) and violation of model assumptions. Some of these techniques have even been implemented as alternatives to traditional linear methods for estimation of statistical variability (Quinn & Deriso 1999; McCallum 2000), for instance Hinrichsen (2002) applied bootstrapping to estimate accuracy of alternative stochastic growth rate estimates for salmon populations.

1.2 AIMS OF THIS WORK

This work follows the premise that a review of the theoretical and empirical assumptions of basic models is necessary for analytically finding the sources of incongruence in data fitting, for the improvement of its predictive power, and for the choice of explanatory models over descriptive models. This review must be based on alternative approaches, on the use of improved tools: (technological, mathematical, and for data processing), and on the development of my tools, particularly in regard to mathematical and computing.

In this thesis I provide insights in to the misconceptions of three basic and widely known topics, whose implementation are in general routine: the length-weight relationship and the condition factor; the fitting of size-at-age growth models; and the effects of an allometric factor on the von Bertalanffy length-at-age growth model. Misconceptions or error in model fits can be critical to the correct estimation of biomass in fish populations when assessing the size of a population. The analyses undertaken are supported by the implementation of the underlying assumptions in *ad hoc* software developed by myself for calculations and graphical representation of data. This software is the main tool used for the quantitative and visual description undertaken in this study.

1.3 ORGANISATION OF THIS THESIS

Chapter two is dedicated to the length-weight relationship as special case of morphometric growth. It includes a brief reference to the fundamentals of the length-weight relationship and condition factor, and a review of the meaning of condition. There is also a review of the theoretical length-weight relationship from a morphometric approach, its relationship with the body's volume, the influence of the body density as a constant and as a variable, and an interpretation of the real meaning of its parameters based on the morphometric approach. An example of the application of the main statements is also included.

Chapter three contains a review of the size-at-age growth, a description of the Logistic, von Bertalanffy, Richards, and Gompertz size-at-age growth models plus the exponential expression of first three. An equation of a generalised expression that includes the previous models as special cases is developed, and a method for the selection of the best size-at-age individual growth model among the previously mentioned is formulated. The method is based on the assessment of the stability and accuracy of the parameters in the generalised equation through non-linear fitting, using an *ad hoc* implementation of the Levenberg-Marquardt method.

In Chapter four the presence of a morphometric factor due to allometric growth is identified, the influence of the morphometric factor on the von Bertalanffy length-at-age growth is evaluated, and its repercussions on the estimation of weight-at-age from length-at-age data is demonstrated. Guidelines for detecting existence of the morphometric factor are specified, and a method for the assessment of growth-at-age from length-at-age data is given.

Each chapter includes a summary of the general trends in the research on each topic.

CHAPTER 2

MORPHOMETRY, LENGTH - WEIGHT RELATIONSHIP, AND CONDITION FACTOR

2.1 ABSTRACT

Evaluation of growth-at-age is important for the assessment of biomass. Changes in biomass are monitored as variations of body condition, which is usually a quantitative index based on empirical equations without a proper theoretical background. A review from a morphometric point of view of the length-weight relationship and the commonly used condition factors show that the analysis of the length-weight relationship as a consequence of an ellipsoid body shape gives insights on the real meaning of condition and the length-weight relationship itself, providing also elements to clarify serious misconceptions about its parameters and its general meaning. A generalised equation for the length-weight relationship is derived from an ellipsoid body shape. This equation explains other models for the length-weight relationship and condition indexes previously developed as special cases of the generalised equation. An analysis of the different definitions of condition reveals that condition estimated from the length-weight relationship can be interpreted only as heaviness and as an element for describing body fitness.

2.2 JUSTIFICATION

"The role of growth in population dynamics is subtle and complex, more than the mere increment in weight. Any animal eats and grows to avoid death, and the bigger fish are the survivors … Hence, growth processes may be at the centre of the population regulatory mechanisms." (Cushing 1981). Biomass is a function of the population growth (number of individuals), body growth (growth-at-age), and morphometric growth (change in shape). Population growth depends on fecundity and survival. Growth at age and morphometric growth depend principally on the availability of energy and natural physiological processes (Russell 1931; Liao *et al.* 1995). Many other spatial and temporal factors affect the production of biomass in fish populations, for instance pollution, behavioural, genetic and evolutionary changes, environmental variables, interactions with other species, human impact, and changes in the structure and dynamics of the ecosystem's equilibrium. Some of them are temporal, others unpredictable, and others are not quantifiable (Nykolsky 1963; Nikolskii 1969; Everhart & Youngs 1981; Liao *et al.* 1995).

An holistic approach may be preferred in order to predict or at least assess the existing biomass, but the system's complexity makes it impossible to monitor all related variables therefore relatively simplistic models must be developed. Simplistic models are based on the variables with the most predictive power. They are also based on variables that are generally related, even when there might not be a true dependency. A mathematical dependency does not necessarily mean a biological relationship and caution has to be taken when explaining or attributing biological properties based on mathematical relationships. The independent variables might also be a by-product of other complex biological and ecological processes.

The assessment of biomass gain due to body growth in a population is fundamental for the evaluation of yield and as a reference parameter to evaluate the population's condition. Hence the correctness and evaluation power of models used for the assessment of morphometric growth and growth-at-age has to be assured (Blackwell *et al.* 2000).

Morphometric growth assessed from the relationship between weight, length, height, and width (breadth) has been used as an estimator of condition (Hecht 1916). Condition is usually quantified from indices that compare the present weight against a reference value in order to measure how different is the actual weight. Unfortunately there are different interpretations of the term condition and different ways to evaluate it, which makes its evaluation, interpretation and utilisation confusing (Blackwell *et al.* 2000). Therefore the correct meaning of condition from these different mathematical approaches has to be determined as a first step and a method of measurement with a sound theoretical basis also needs to be developed (Ferron & Leggett 1994; Shulman & Love 1999; Blackwell *et al.* 2000).

The meaning, quantification and mathematical background of the influence of the morphometric growth on the estimation of biomass is a result of empirical work that has been disregarded due to its apparent mathematical simplicity, and because serious misconceptions about its background are taken as true without a theoretical evaluation.

In this chapter the concept of condition will be analysed from a morphometric point of view and the most appropriate definition will be derived. The main equations for evaluation of the length-weight relationship and the condition factor will be critically compared, and a generalised equation based on body shape will be proposed for both. An example of misconception of the meaning of condition and the length-weight relationship will be included.

2.3 ANTECEDENTS

2.3.1 MORPHOMETRY, SHAPE AND FORM

According to the Oxford Dictionary (TLC 1998), Morphometry is defined as "The process of measuring the external shape and dimensions of landforms, living organisms, or other objects", and the term shape is intended as "The geometrical aspect of the body". These are very general definitions of both terms, but are very close to the way they are used when related to condition and condition factor. There are diverse definitions of morphometry depending on the biology field they are used (mainly in genetics and evolution), and more elaborated definitions of shape primarily based on geometrical and mathematical properties of the living organisms. A good review of these concepts can be found in Bookstein 1989, Sumers 1989, and Sundberg 1989.

When the body shape and size change in specific patterns during the life span, the shape can be inferred from a basic morphometric growth model, based on the rate of change of the main growth axes (see Relationship between volume, biomass on page 24). For some authors, the shape inferred from a basic morphometric growth model based on the rate of change of the main growth axis can be more properly called form. While shape is an instantaneous characteristic that is affected by many factors in time, form is a stable attribute applicable to whole populations.

Temporal changes in shape are mainly caused by changes in soft body structures. The accumulation and lost of fat, and muscle size are product of complex biochemical changes in lipid and protein contents that produce temporal changes in body shape. Highly reversible changes in chemical composition of the fish body may be periodic and unsystematic (Shulman & Love 1999), and are mainly observed on soft structures, which are able to change quickly in relation with the lifespan. These changes are usually due to normal metabolic events such as the reproductive cycle, and can be seasonal as a product of food abundance and environmental conditions

(Shulman & Love 1999). Some changes occur randomly as a function of multiple factors, for instance food availability, illness, and parasitic infestation.

Permanent changes of shape are the result of differential growth rates of the hard structures that integrate the different parts of the body. The effect of periodical and random factors on hard structures such as bones, otoliths, and scales is observed as periodic changes in their growth rate. The differential growth rates on average will help to define the morphometric and size-at-age growth patterns along the life span (Merret & Haedrich 1997: chapter 5). When the effects of periodical and random factors are continuously positive or negative respect to the average, the magnitude of the growth parameters is changed (Law 2000). The most extreme effects are due to severe ecological conditions, especially during the early stages of development, and are observed as abnormal overall morphometric proportions in the body size. More subtle changes in shape occur in fish populations as a result of the continuous influence of ecological factors over time. These effects are noticeable when comparing populations from different generations or different geographical zones and usually may be associated with evolutionary factors (Law 2000).

According to Law 2000, periodical monitoring of morphometric parameters may be important for monitoring the condition of fish populations, and to understand the adaptations of populations to the environment.

2.3.2 ANTECEDENTS OF MORPHOMETRY

The existence of quantitative relationships between different dimensions of the body has been known for several centuries, and according to Thompson (1942), probably Spencer published the first discussion on this topic in 1871, with the title “Recent Discussions on Science, ...”. Thompson (1942) published an extensive treatise of growth and form in animals based on morphometric analysis. Gould (1966) analysed morphological, physiological, and chemical factors as variates of size. Gould (1966) suggests also that size differences are related to ontogeny and phylogeny. Morphometry has been employed as a tool for systematic studies with different levels of mathematical complexity (e.g. Kerby 1979; Chernoff & Miller 1982; Barbour & Chernoff 1984; Chernoff 1986; Creech 1992; Behnke 1995). It is also a tool in fisheries to discriminate between different populations and subpopulations (e.g.

McGlade & Boulding 1986; Treer 1993; Colman 1995; Szlachciak 1996; Velasco *et al.* 1996; Hood & Heins 2000). It has been used for remote measurement of body dimensions (e. g. Winans & Nishioka 1987; Loy *et al.* 2000), to detect in the body as a whole or in particular structures the influence of different factors such as ecological interactions and fishing activity (e.g. Cohen & Fishman 1980; Webb 1986; Chauvelon & Bach 1993; Bublitz 1996; McEdward & Herrera 1999; Simoneau *et al.* 2000), and to estimate the body condition (e.g. Portia 2000; Carscadden & Frank 2002; Kurkilahti *et al.* 2002; Rätz & Lloret 2002).

2.3.3 CONDITION FACTOR (CF)

2.3.3.1 The concept of condition

There is not a unique definition of condition, but the term is used to identify different characteristics in fish biology. For instance, body condition has been intended as an index of energy reserves (Rätz & Lloret 2002), nutritional status (Ferron & Leggett 1994), goodness and fitness (Bolger & Connolly 1989), well-being (Anderson & Gutreuter 1983; Bolger & Connolly 1989; Busacker *et al.* 1990), and heaviness or plumpness of fishes.

Intended as an index of energy reserves and nutritional status, condition is mainly assessed by measuring the lipid and protein contents in the body tissue (e. g. Parker & Vanstone 1966; Adams & McLean 1985), by proximate analysis (Love 1980), Calorimetric analysis of energy content (Warren & Davies 1967), and the RNA-DNA ratios (Bulow 1987).

Intended as fitness, goodness, well-being, and heaviness, condition is measured by the indices of well-being (Fitzgerald *et al.* 2002), which for the whole fish may be the Fulton-type condition factor, relative condition factor, and relative weight condition factor (Anderson & Gutreuter 1983). These three condition factors are mathematical functions of the body weight and length (Weatherley 1972; Anderson & Neumann 1996), with the assumption that the well-being of a fish is greater when it is heavier, rather than lighter, at a given length ((Weatherley 1972; Bolger & Connolly 1989; Anderson & Neumann 1996).

Fitness is a fundamental concept frequently used to mean condition, but also has not been properly defined, particularly in fisheries and fish biology fields. From the genetic point of view, fitness can be interpreted as "the representation of an individual's genes – or descendants – far in the future" (Brommer *et al.* 2002), and it can be measured by quantifying the lifetime reproductive success (Brommer *et al.* 2002). Lifetime reproductive success can be a better measure of fitness than any single component of fitness such as survival in a particular life-history stage (Endler 1986). From an evolutionary approach, natural selection can be defined as "the differential reproduction or survival arising from heritable variation in phenotypes" (Endler 1986), therefore fitness can also be measured by the heritability of morphological and behavioural traits (Sinervo & Zamudio 2001). Ecologically, "Fitness is the capacity of an individual or population to maximize reproductive success by the production of viable offspring" (Price 1975). And according to the Oxford Dictionary (TLC 1998), fitness is "(A numerical measure of) ability to survive and reproduce in a particular environment", and also "The quality of having exactly the right measurements".

Goodness (as "excellence in respect of some quality", TLC 1998), well-being (as "in a satisfactory state", TLC 1998), and good health are informal terms to designate an state of good or satisfactory appearance, quality, size, and shape of the fish body.

Heaviness intended as body plumpness is the concept that more directly points to something that can be directly and unambiguously measured: the amount of biomass. Because weight and length are estimators of size (biomass size, and geometric size), the assessment of condition by the condition indices that calculate biomass relative to a given geometric size can be more appropriate (see Blackstone 1987; Sundberg 1989). In this context, condition may be more properly defined as heaviness (as it will be discussed in 2.4.2.2).

Due to condition is mainly assessed in fisheries, and fish biology by the indices of well-being, I will concentrate in this document on the interpretation of condition as measured by the indices of well-being, omitting any reference to the index of energy reserves and nutritional status. Because several concepts of condition are still involved behind the indices of well-being, a discussion of the right meaning of condition as a consequence of the mathematical analysis usually involved in the assessment of condition by the indices of well-being will be discussed later (see 2.4.2, p. 34).

Basically, the condition factor as an index of well-being is conceived as an index of biomass to detect departures either from a reference weight, from an ideal weight, or from the natural weight at a particular length. The concept of ideal can be related to the organisms and species best fitted, while the concept of normal (normal weight, length, condition, etc.) can be associated to representative average values for populations and subpopulations with good or satisfactory body appearance, body quality, body size, and body shape.

Bolger & Connolly (1989), identified eight forms of the index and 17 different procedures to estimate body condition from the length – weight relationship that were used in different studies published in two main journals from 1969 to 1986. They also mention other indices that consider other parts of the fish's body.

The different indices reported by Bolger & Connolly (1989), are all variations of the length – weight relationship. They mainly differ in the particular considerations taken to select individuals with common characteristics, for instance, sexual maturity, age group, season, and sex. Some indices measure the condition of individuals while others the condition of subpopulations.

2.3.4 MATHEMATICAL DESCRIPTION OF THE LENGTH - WEIGHT RELATIONSHIP

The dimensions of different parts of an animal's body have been described by simple mathematical equations. A simple relationship could be linear if their relationship is isometric during the life span, otherwise, polynomial, logarithmic and trigonometric functions may be more appropriate.

As a first approach, it is noticeable that there is a power relationship between the length and weight of fishes (Hecht 1916). Equation (1) is the basic function that relates body length with weight.

$$W = aL^b \tag{1}$$

W: Weight

L: Length

a, *b*: Constants

b: Constant (allometric factor)

For many species the value of b is near 3.0, and a about 2x10^{-2}. In the centimetre-gram-second system (cgs), weight is measured in grams and length in centimetres, b is dimensionless and a has a unit of WL^{-b} (Xiao 1998), which is equivalent to g*cm^{-b} . Only when $b = 3.0$, a has units of density (g*cm^{-3}).

2.3.4.1 Ponderal index

Thompson (1942) suggested that if $b = 3.0$, a might be considered as an index to monitor the fish condition by finding the body heaviness with respect to a particular length. He called this the Ponderal Index (equation (2)).

$$k_i = a = \frac{W}{L^3} \tag{2}$$

k_i : Ponderal index

Sparre & Venema (1995), employ "*q*" to identify $k_i = a$, calling it just condition factor.

Livi, 1987 (cited by Thompson 1942) possibly was the first to employed a linear index derived from the length-weight relationship as a cubic root transformation of a, and assuming isometry. That index was also called the ponderal index (equation (3)), and the cubic root transformation was used as a parameter to obtain an index with a linear distribution.

$$P_i = a^{1/3} = \frac{W^{1/3}}{L} \tag{3}$$

P_i: Ponderal index

P_l is used here to represent the ponderal index, but probably some authors might prefer to call it *K*, as Livi, R (1897) in "L'indice ponderale, o ropporto tra la statura e il peso. Atti Soc. Romana Antropologica, V" (cited by Thompson 1942). There has been some discussion about terminology and the mathematical expression of equations (2) and (3) in the past, but in this document, I prefer to use P_l for the linear index and emphasize the biological and quantitative meaning rather than conventionally accepted terminology.

The weight increases in relation to the volume and relates to the length through a mathematical power function (King 1995). If the equation's exponent is statistically equal to 3.0 the body growth is considered isometric, otherwise growth is considered allometric. There is negative allometry when the equation's exponent is lower than 3.0, and positive allometry when higher than 3.0. There is not a unique definition for allometry (See Blackstone 1987 for a review of the concept and definition of allometry), but it is basically interpreted as meaning unequal morphometric growth; Isometry is the opposite to allometry (equal morphometric growth).

There was a common perception, primarily stemming from Fulton (1904), that a value of 3.0 for *b*, should be the ideal for all fishes, and departures from that value could reflect special events or even abnormalities. As a consequence, this perception strengthened the value of the length-weight relationship as a monitor of fish condition assuming the power constant to be equal to 3.0 in equation (2). Actually Fulton never suggested a value of 3.0 for *b* in his 1904 publication; nor proposed equation (2) in that publication, however equation (2) is erroneously known today as the Fulton condition factor and referenced to Fulton 1904. He expressed under the title "A Law of Growth" that "*fishes approximately double their size and increase their weight about eight times after they have reached sexual maturity*; or that *fishes attain sexual maturity when they reach about half their maximum length and about one-eight of their maximum weight*", which has nothing to do with the cubic law attributed to him.

These two expressions of the condition factor rely on the following two assumptions: the ideal value of exponent *b* should be 3.0 (isometric growth), and such value should be applicable to all species.

2.3.4.2 Relative condition factor

The main problem with calculating a proper condition factor is the definition of the ideal weight. Empirically the next two options have been followed to find a suitable definition of the ideal weight:

1) To use reference values and constant expressions, *i.e.*: theoretical values, parameters and data values historically recorded, experimental results, and theoretical expressions such as the Fulton condition factor.

2) To consider, not reference values and constant expressions but the magnitude of the equation's parameters derived from the length – weight relationship.

If the only purpose of the CF is to monitor variations in the total weight for individual fishes or subpopulations, regardless of the other variables, the first option is good enough. Actually, reference values have been used in the past: particularly the ratio of weights, and the Fulton theoretical expression.

To detect changes in condition in individual fishes, the ratio between the measured weight (Observed), and either the reference or the ideal weight can be used (equation (4)). In this case, the expected weight is derived from the Length –Weight relationship for a specific length (equation (1)). The expected weight is also called theoretical weight and it is considered an estimator of the ideal weight at a particular length.

$$RCF = \frac{W_o}{W_e}; \qquad W_e = aL_o^b \tag{4}$$

RCF: Relative Condition Factor

W_0: Observed weight (measured)

W_e: Expected weight (estimated, theoretical or ideal)

L_0: Observed length

The advantages of the relative condition factor are:

a) The expected weight is a result of the influence of all individual data.

b) Unless the presence of serious outliers in the data set, or data misrepresentation, the expected weight will be closer to the geometric mean of the weight at the particular length if more than one fish with the same size exists.

c) According to the central limit theorem (Sokal & Rohlf 1969), the expected weight will be closer to the average (in this case the geometric mean because of the power relationship between length and weight), which is most likely to be the ideal as the number of data increase, and if the data are truly representative of the individual weights in the population. If survivors are the most fit and the ones with the optimum shape, then the estimated length-weight relationship will be representative of the most fit.

d) Statistical data variability in terms of standard deviation can be calculated.

The most important limitations to the advantages are the presence of serious outliers and data misrepresentation. Their occurrence is a result of incorrect or difficult measurement, defective measurement techniques, inadequate sampling, and improper data processing tools. They could all be improved with experience, technology and advances in the mathematical field over time.

The main problems with the relative condition factor are:

1) The choosing of appropriate data sets to estimate the ideal parameters of the length-weight relationship.

2) Different subgroups may have different average morphometric proportions, which may be temporal (random and seasonal), so advantage a) can become a disadvantage.

3) To know when to change the data set in order to adjust for changes in the populations' average morphometric proportions over time.

Problem 1) is difficult to solve. One approach is to use large data sets from different populations covering long periods of time. However, there are no antecedents on how to assess changes introduced by exploitation and natural evolutionary changes of condition.

Problems 2) and 3) have been confronted by the use of categorical variables, restricting comparisons to groups and individuals with common characteristics (same sex, maturity index, age, etc.).

2.4 PROPOSED APPROACH FOR THE LENGTH – WEIGHT RELATIONSHIP AND CONDITION FACTOR

As can be inferred from the introduction, there are two main approaches to evaluate condition regardless of its conceptual meaning: comparisons with respect to standard values or expressions, and taking the value of the constant a of the length-weight relationship as a reference. Both are empirically based on the length-weight relationship.

The ponderal index k_i is a special index widely used even when is based on assumptions difficult to find in most species, particularly because many species do not have isometric growth. The importance of considering at least the two parameters of the empirical length-weight relationship (as in equation (4)) can be based on the fact that both parameters a and b of the equation for the length-weight relationship (equation (1)) are highly variable (Cone 1989). The following study highlights this observation.

In research on fish populations in the Azores archipelago, Morato *et al.* (2001) found that from 15 species, two showed significant differences for b between female and male and of 21 species, one had significant differences between populations from different islands. From Table 1, only 3 species were non significant from 3.0 ($P > 0.05$) for fishes with non-differentiated sex, females and males. For the other species juveniles, females, or males as particular *groups* were not significantly different from 3.0. For some species the high statistical variability (standard deviation > 0.01) makes the results non-conclusive while for other species there is not enough evidence.

Because the parameters a, and b of the length – weight relationship (equation (1)) can be statistically different by sexes, geographic location, and morphometric growth pattern for different species, for populations and subpopulations of the same species, and even for a same group of individuals at different times, neither the Fulton condition factor nor the ponderal index can be standard reliable estimators of the actual condition factor.

Table 1: **Significance levels for 19 coastal fish species of the Azores.** H_0: $b = 3.0$; ND= no differentiated sex; F= female; M= Male; All data= ND + F + M; ↔ = not reliable but possible, y = yes, n = no. Missing values (no registered sex) were not considered.

SPP	ND	F	M	All data	Significance
Abudefduf luridus	0.1507	**0.0177**	**<0.001**	**<0.001**	n, y, y
Bothus podas	0.4300	0.2883	0.4472	**<0.001**	n, n, n
Choris julis	**0.0031**	0.7038	**<0.001**	**<0.001**	y, n, y
Chromis limbata	0.0606	0.6508	**<0.001**	**0.0041**	n, n, y
Diplodus sargus	**0.0132**	**0.0353**	0.4344	**<0.001**	y, y, n
Gaidropsarus guttatus	0.6666	**0.0164**	0.4912	**0.0279**	n, y, n
Labrus bergylta	0.2988	**<0.001**	0.2511	**0.0249**	n, y, n
Mullus surmuletus	**<0.001**	**<0.001**	0.9835	**<0.001**	y, y, n
Phycis phycis	1 Datum	0.8349	No data	**0.0037**	?, n, ?
Pomatomus saltator	1 Datum	**0.0033**	0.1793	0.5330	?, y, n
Sarda sarda	No data	0.7002	0.1289	0.1520	?, n, n
Scorpaena maderensis	**0.0012**	**0.0114**	0.8217	**0.0069**	y, y, n
Scorpaena notata	0.6011	0.9368	0.5293	0.0646	↔, n, n, n
Serranus atricauda	0.0388	**<0.001**	**0.0199**	**<0.001**	?, ?, ?
Seriola rivoliana	1 Datum	0.1905	0.5384	0.1457	¿, n, n
Sparisoma cretense	0.2936	**<0.001**	**<0.001**	**<0.001**	n, y, y
Sphyraena viridensis	0.1470	0.6709	0.1506	0.7133	↔, n, n, n
Thalassoma pavo	**<0.001**	0.3516	**0.0085**	**<0.001**	y, n, y
Trachinotus ovatus	No data	1 Datum	No data	**<0.001**	?, ?, ?

In order to assess the real meaning, usefulness of and the best way to evaluate the condition factor it is necessary to know how each parameter is interrelated, both mathematically and biologically and not just empirically. Before attempting any definition of condition based on the variables measured to estimate the condition indices (length and weight), I will develop next a mathematical expression for the condition factor not based on the empirical length-weight relationship, but on a basic morphometric fish-like shape (ellipsoid shape: see 2.4.1.1 bellow), which as we will see, includes the length-weight relationship and practically all indices of condition previously mentioned. I also will show that the mathematical expression based on the morphometric fish-like shape agrees more with the concept of condition as an estimator of heaviness and fitness (see 2.4.2.1). This approach will also explain a model reported as new for the length-weight relationship (Jones *et al.* 1999) and a condition factor (Richter *et al.* 2000) recently reported as new (see 2.4.2.3 and 5.1.1). Actually, equations for the relationship between different parts of the fish body as the proposed by Jones *et al.* and Richter *et al.* were used since the beginning of the previous century by Heinke, 1907, and Crozier and Hetch, 1915 (both cited in Hecht 1916).

Once a quantitative expression for condition based on sound principles is constructed, a description of the meaning of the parameters will be undertaken to reveal how condition can be properly interpreted (see 2.4.2.1).

2.4.1 LENGTH – WEIGHT RELATIONSHIP, DENSITY, AND A GENERALIZED RELATIVE CONDITION FACTOR

2.4.1.1 Relationship between volume, biomass and length for a fish-like shape

The relationship between weight as an estimator of the biomass, and length (length from head to tail) as an estimator of the size can be better explained from a theoretical approach, assuming a tri-dimensional, pisciform body shape. This assumption implies that fish volume must be basically a function of one point of growth based in three longitudinal axes: length, width and height.

The term length (L) refers to the distance on the line from snout to tail that can be explained within the pisciform shape. Because fishes are not totally elliptical, in practice this length is closer to the standard length (length of the body of a fish from the tip of the snout with the mouth closed to the end of the vertebral column; the base of caudal fin to be precise). Fork length (length of the fish from tip of snout with the mouth closed to tip of the shortest ray of the caudal fin, or to the centre of the fin if the tail is not forked), and total length (the overall length of a fish, measured from the tip of the jaw with the mouth closed and extending to the tip of caudal fin) should give proportional results if their mathematical relationship with respect to the standard length is linear.

The volume of a pisciform shape can be calculated from equation (5), which corresponds to an ellipsoid (Hockaday *et al.* 2000).

$$V = \frac{4\pi}{3} LHD \tag{5}$$

V: Fish Volume

L: Length

H: Height

D: Width

Accordingly to the definition of density (specific gravity) = ρ, Volume and Weight as an estimator of Mass are related as follows:

$\rho = W / V$; therefore, $W = \rho V$, and $V = W / \rho$

By substituting volume in equation (5), the factor density is added, obtaining the equation for the length weight relationship of an ellipsoid like shape as a function of its orthogonal dimensions:

$$W = \rho \frac{4\pi}{3} LHD \qquad (6)$$

The three orthogonal axes are mathematically related in a proportional scale; such relationship may be linear or non-linear. If shape is not constant with time, the relationship between dimensions of the axes of growth in respect to L will tend toward a power relationship as follows,

$$H = a_H L^{b_H} \; ; \; D = a_D L^{b_D}$$

When substituting H and D in equation (5), the equation of weight as a function of a particular longitudinal dimension is obtained (equation (7)). This is the length – weight relationship for an ellipsoid like shape in terms of a single longitudinal dimension (in this case L).

$$W = \rho \frac{4\pi}{3} L a_H L^{b_H} a_D L^{b_D} = \rho \frac{4\pi}{3} a_H a_D L L^{b_H} L^{b_D}$$

$$W = \frac{4\pi}{3} \rho \; a_H a_D L^{1+b_H+b_D} \qquad (7)$$

The length-weight relationship as a product of the body shape (equation (7)) is comprised of three components: a morphometric, a geometric, and a structural component. The power of L in equation (7) is the sum of the morphometric constants (SAC); this is equal to $1+b_H+b_D$. Notice that the morphometric constants are complementary to the one of the reference dimension L, in this case b_L. SAC is properly a morphometric factor, which is not related to the volume, contrary to the suggestion by a number of authors (e.g. Hostings & Dickie 1972; King 1995), but to the body's morphometry. Actually, SAC, volume, and weight depend on the body morphometry.

The product of all coefficients (PC) in equation (7) has three components built into it: density (ρ), a geometric constant $4\pi/3$, and the length-weight proportion constants ($a_H a_D$). However, as stated previously, there are really two components, a geometric one that is associated with the ellipsoid geometry ($a_H*a_D*4*\pi/3$), and a structural one (ρ), determined basically by its chemical composition; the morphometric coefficients in *PC* are also complementary to the one of the reference length L (a_L).

When morphometric body growth is isometric, the mathematical relationship between the axes of growth is linear (shape does not change with size), $b_H=b_D=1.0$, then the *SAC* =3.0. It is important to note that a *SAC* = 3.0 does not necessarily mean isometry: $1+b_H+b_D$ can still be equal to 3.0 for $b_H \neq b_D$.

All parameters of equation (7) are expected to be unique for a single individual, while different subgroups in a cohort can statistically have particular values. For populations the SAC tends to become asymptotic to a specific value and for the species is expected to be statistically distinctive. If the morphometric factor (SAC) tends to be asymptotic for a species, the only source of temporal variability of weight accordingly to equation (7) is the variable part of PC.

Both the volume and weight are dependent on the morphometric component, which should be unique to the population (with small variability between individuals) and its magnitude and variability should be species specific. The *PC* is expected to be highly variable, random and vary seasonally. Density and the length-weight coefficients are not actually constants, but can be highly dynamic due to temporal and continuous changes in chemical composition in the proportion of lipids, protein, etc. (e.

g. Kora *et al.* 2000), and shape. In fact their variability is the main source of variability in weight with respect to length.

2.4.1.2 Agreement with the length-weight relationship

Actual data for density, height, and width, for a particular species are generally hard to find because they are not routinely measured for practical reasons. In order to show the agreement at least in data distribution between the classical empiric length-weight relationship (equation (1)) and equation (7) that is derived assuming that fish shape can be represented by an ellipsoid, a data set with the following attributes was created (Table 2): values for height (H) and width (D) are given up to one decimal place to resemble the normal precision at which those dimensions are measured; $H = L/3$, $D = L/5$, density (ρ) = 0.07, volume (V) is estimated from equation (5), and weight (W) from equation (6). Table 2 also contains results of regressions of L, H, D, and W respect to each other.

Table 2: **Parameters of the length-weight relationships between length (*L*), height (*H*), width (*D*), weight (*W*) and volume (*V*) for data generated from equations (5) and (6).** *L-W*: length-weight relationship, *H-W*: height-weight relationship, *D-W*: width-weight relationship, *a* and *b*: parameters of each relationship.

L	*H*	*D*	*V*	*W*
1	0.3	0.2	0.251327	0.017593
2	0.6	0.4	2.010619	0.140743
3	0.9	0.6	6.78584	0.475009
4	1.2	0.8	16.08495	1.125947
5	1.5	1.0	31.41593	2.199115
6	1.8	1.2	54.28672	3.80007
7	2.1	1.4	86.2053	6.034371
8	2.4	1.6	128.6796	9.007574
9	2.7	1.8	183.2177	12.82524
10	3.0	2.0	251.3274	17.59292

	a	*b*
L-W	0.0175929	3.0
H-W	0.65158968	3.0
D-W	2.19911484	3.0
L-H	0.30000003	1.0
L-D	0.20000004	1.0

If the length-weight relationship can be explained assuming an ellipsoid shape, the following is expected: power relationships between length and weight, height and weight, width and weight, and length and volume; isometric growth because shape does not change with respect to length (power constant in the length-weight relationship should be equal to 3.0); and, the calculation of density by equation (7) after evaluating the parameters of the relationships *L-H* and *L-D* should equal the *a priori* value given to density. The results are as follows.

As predicted, data for H-D, D-W, L-W, and L-V distribute accordingly to a power distribution (Figure 2) and W-V is linear with slope 1/ρ (Figure 3). Notice that a linear relationship between weight and volume is possible only for an isometric morphometric factor, otherwise a power relationship is expected; this lends weight to the hypothesis that weight does not depend linearly on volume, but on the morphometric factor.

It can be observed in Table 2 that the morphometric constant (*b*) is equal to 3.0, confirming isometric growth for weight against each length and between lengths. Parameter *a* for each regression is close to the initial values assumed: *a* for *L-H*= 0.30000003 agrees with the value expected (0.3) after rounding 0.33 up to one decimal place; *a* for *L-D* = 0.20000002 agrees with the value assumed (0.2). Finally, from equation (7), density reaches the following value:

$$a_{L-W} = \frac{4\pi}{3}\rho\, a_H a_D;\ \rho = \frac{a_{L-W}}{\frac{4\pi}{3} a_H a_D} = 0.069999$$

Which is the value assumed for ρ (0.07). These results confirm the agreement between the empirical length-weight relationship and the generalised length-weight relationship derived assuming an ellipsoid shape.

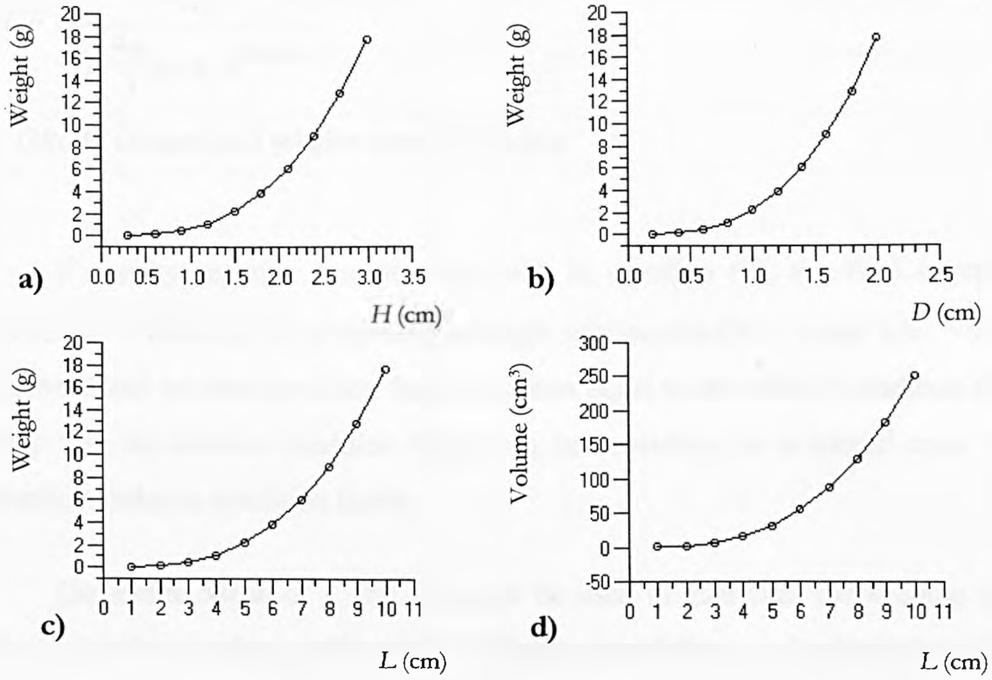

Figure 2: **Distribution of *H-W*, *D-W*, *L-W*, *L-V*, and *W-V*.** *H-W*: height-weight relationship (a), *D-W*: width-weight relationship (b), *L-W*: length-weight relationship (c), and *L-V*: length-volume relationship (d).

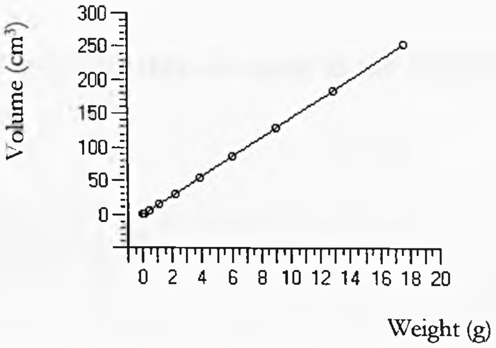

Figure 3: **Distribution of Volume with respect to Weight.**

2.4.1.3 A generalized relative condition factor

When length (L), height (H), and width (D) are the main axes of growth, W from equation (7) can be used as expected weight (We) in equation (4) to calculate a generalized relative condition factor (equation (8)).

$$GRCF = \frac{W_o}{\rho \frac{4\pi}{3} a_H a_D L^{1+b_H+b_D}} \tag{8}$$

$GRCF$: Generalised relative condition factor

If density remains constant with size in equation (7), the final expression $W = SC\ L^{SAC}$ turns out to be the length-weight relationship ($SC = a$ and $SAC = b$), and the generalized relative condition factor becomes equal to the relative condition factor. In this way the relative condition factor can be considered as a special case of the generalized relative condition factor.

Geometric Mean of L and W_O must be used to guarantee the keeping of the same scale when working with groups of fishes (populations and subpopulations) for the following reason: only in the linearised equation of the Length-Weight relationship, the average (arithmetic mean) of the logarithms of weight corresponds to the average (arithmetic mean) of the logarithms of length, this is,

$$\overline{Log(W_e)} = Log(a) + b(\overline{Log(L_0)})$$

The average of the logarithms is equal to the logarithm of the nth root of the individual products:

$$\frac{1}{n}\sum Log(x_i) = Log\left[(\prod_{i=1}^{n} x_i)^{\frac{1}{n}}\right] = Log(GM(x))$$

Therefore, the antilogarithm of the arithmetic mean of the logarithms (antilogarithm of left term in the previous equation) is equal to the geometric mean (antilogarithm of the right term).

For the Length-Weight relationship:

$$GM(W_e) = a\ (GM(L_o))^b$$

This is why $GM(W_o)$ should be used in order to keep the same scale. Working with the logarithmic expressions is an option that produces the same result.

The generalized relative condition factor has basically the same advantages and same problems as the relative condition factor, in fact, the generalized relative condition factor is harder to estimate and impractical to implement because a lot of extra effort is required. The advantage of this expression is in the meaning of the relative condition factor and the possibility to understand its changes in magnitude by tracking the changes of its components, particularly in the morphometrics and geometrics. An understanding of the meaning also helps to better understanding different author's findings with respect to the association of condition with other biological factors such as size-at-age, fat composition, energy storage, and prey density (Brown & Murphy 1991; Childress 1991; Neumann & Murphy 1992; Liao *et al.* 1995).

2.4.1.4 Influence of density on the generalized relative condition factor

As seen mathematically in 2.4.1.1 (p. 24), density is expected not to keep constant but to be a highly variable parameter (not including spontaneous changes in shape such as those related to buoyancy or defence, but mainly physiological, biochemical, and ecological changes such as gonad growth, energy storage, and food availability). An idea of the magnitude of the effect of physiological, biochemical, and ecological changes on body weight can be obtained from the following example (Shulman & Love 1999):

Cod is not considered a fatty fish, and from 60 to 80 % of the cod fresh body muscle is normally water (70% in average). In laboratory experiments with juvenile cod during starvation periods (protein depletion) the water content increased up to 86%, after that level the fish died. In adult fishes that had spawned several times the water content in the muscle reached up to 95%, and at the end of the experiments survivors looked thinner, but due to part of the protein was substituted by water (from 70 to 95%). Even when Shulman & Love (1999) do not report any figures for density, it can be inferred that an important change not only in weight, but also in density occurred.

To date there has been no systematic investigation in to how much the assumption of constant density can affect the length-weight relationship, even though more than 50 years ago Kesteven (1947) warned about its relationship with respect to weight and volume, suggesting that a failure in the understanding of the phenomenon can arise in the development of formulae that do not properly represent the intended assumptions.

There is no information on the mathematical nature of the influence of density on the length-weight relationship, but some insights can be attained by the quantitative evaluation of linear (e. g. Kora *et al.* 2000) and multiplicative effects on weight. A linear effect is expected if there is a change in density in proportion to length: for instance, a variation of 10% of lipids in the total weight (this is equivalent to: 0.1 * density). A multiplicative change is expected when the change is size-dependent and non-linear, for instance when sexually mature females increase their gonad maturity index with their age or length (for example $\rho = \rho + 0.001 * L$).

A linear effect is expected when all individuals in a population appear to achieve a comparative change in condition (heavier or lighter than the average). This is shown by a change in the product of constants (*PC*) without affecting sum of morphometric constants (*SAC*) in equation (7). A multiplicative consequence will be seen when just part of the population changes its condition affecting *SAC*; actually this change may follow a cyclical trend.

Table 3: **Hypothetical data set.** Data generated from an ellipsoid fish-like shape (Figure 4). *L*: length; *H*: height = *L*/3, *D*: width = *L*/5, and ρ: density = 0.07; *V* (volume) is estimated from equation (5), and $W = \rho V$; *W1%* and *W2%*: weights obtained after a linear increase of 1% and 2% in density; and *WAllom* : weight after a non-linear increase on density ($\rho = \rho + 0.001 * L$).

L	*H*	*D*	*V*	*W*	*W1%*	*W2%*	*WAllom*
1	0.3	0.2	0.2513274	0.0175929	0.017769	0.0179448	0.0178442
2	0.6	0.4	2.0106193	0.1407434	0.142151	0.1435582	0.1447646
3	0.9	0.6	6.7858401	0.4750088	0.479759	0.484509	0.4953663
4	1.2	0.8	16.084954	1.1259468	1.137206	1.1484657	1.1902866
5	1.5	1	31.415927	2.1991149	2.221106	2.2430972	2.3561945
6	1.8	1.2	54.286721	3.8000705	3.838071	3.8760719	4.1257908
7	2.1	1.4	86.205302	6.0343712	6.094715	6.1550586	6.6378083
8	2.4	1.6	128.67964	9.0075745	9.09765	9.1877259	10.037012
9	2.7	1.8	183.2177	12.82524	12.95349	13.081743	14.474197
10	3	2	251.3274	17.59292	17.76885	17.944777	20.106193

Table 3 contains the data for the exploration of the effects of density on weight. The data are based on the assumption of an ellipsoidal shape and isometric morphometric growth. A linear change on density of 1% and 2% is tested (*W1%* and *W2%*), also a non-linear factor (*WAllom*) on all data instead of just part of the population to simplify the analysis ($\rho = \rho + 0.001 * L$).

The main assumption in this example is that there is a linear relationship between the axes of growth, therefore isometric growth. From equation (6) a is expected to be close to 0.0175. The corresponding shape is shown in Figure 4.

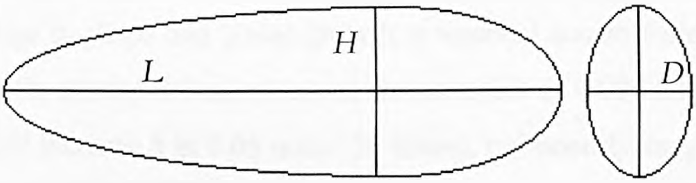

Figure 4: **Hypothetical fish-like shape.** Hypothetical fish-like shape used to generate the simulated data on Table 3. *L*: length; H: height = *L*/3; *D*: width = *L*/5.

Parameters obtained by least square fits by each weight as function of *L* are summarised in Table 4. The morphometric factor shows this to be isometric as expected (*P*>0.9999), and for all cases a and b obtained are also as expected, but not for the non-linear factor (*WAllom*).

Table 4: **Parameters of length-weight relationship for the hypothetical data set in** Table 3. a : coefficient, and b : power of the length-weight relationship; ρ density; H_0: b= 3.0 (test for isometry); *W* : weight; *W1%* and *W2%*: weight obtained after a linear increase of 1% and 2% in density; and *WAllom* : weight after a non-linear increase on density ($\rho = \rho + 0.001 * L$).

	a	b	H_0: b=3.0	ρ
W	0.017593	3.0000	*P*>0.9999	0.07
W1%	0.017769	3.0000	*P*>0.9999	0.07 * 1.01
W2%	0.017945	3.0000	*P*>0.9999	0.07 * 1.02
WAllom	0.017519	3.0523	*P*= 6.7919E-6	ρ + 0.001* L

Notice that a linear change in density (*W1%* and *W2%*) appears as a change in a only, and a non-linear change results in a modification of b. In this case the difference between expected and observed parameter a for the non-linear factor (*Wallow*) ought to be caused by calculation rounding error, but with actual organisms a change on a may be also observed. It can be concluded from this theoretical analysis that a non-linear change in density can cause a modification of the parameters of the length-weight relationship, which can be wrongly assessed as a morphometric change.

Some fish species suffer drastic seasonal changes in their body's biochemical composition, for example Whiting (Jacobsen *et al.* 2002). Strauss & Bond (1990) provide a warning about the influence of water and lipid content, development of gonads and fullness of the stomach on the density of a fish. Lipid content, for example, can reach more than 10% of the total weight in capelin (Yaragina & Marshall 2000). Added to a change in shape and gonad growth, a seasonal accumulation of lipids also implies a change in density. In our example, an increment of 0.001 units in density per unit of length will increase *b* in 0.05 units (50 times), erroneously suggesting a change in morphometry rather than density.

2.4.2 THE MEANING OF CONDITION AND CONDITION FACTOR

As mentioned before (see 2.3.3.1), condition has been interpreted mainly as well-being, good health, goodness, fitness, and heaviness. This section is dedicated to explore each of the previous definitions and try to clarify the meaning of condition and condition factor by taking as the main reference the equations used in the field to quantitatively evaluate both parameters. In this section the following questions will be analysed: What is condition and how can it be measured? Is the weight a reliable estimator of condition? Are the length-weight relationship and the length-weight relationship of ellipsoid-like shape reliable estimators of the optimal weight? Is it better to include as many variables as possible in the estimation of weight to make it more reliable?

2.4.2.1 The concept of condition and its measurement

Bolger & Connolly 1989 pointed out that the study of condition in fisheries ecology "is usually based on the analysis of length-weight data and assumes that the heavier fish of a given length are, the better their condition. It is believed to be a good indicator of the general 'well-being or fitness' of the population under consideration". Because condition as index of energy reserves and nutritional status is not commonly used in the field, it can be inferred that the most appropriate meaning of condition should be associated to the indices of well-being (Fitzgerald *et al.* 2002). Condition is usually associated to the indices of well-being as goodness, well-being, good health, heaviness, and fitness (see The concept of condition: 2.3.3.1, page 15).

As we saw in 2.3.3.1, goodness (intended as excellence in respect of some quality, TLC 1998), well-being (as in a satisfactory state, TLC 1998), are informal terms related to a reference quality or satisfactory state. Both quality and satisfactory state are not tangible entities; therefore these concepts should not be taken as valid.

Condition and condition factor as an index of condition, can not be interpreted as good health due to a degree of condition different from the average (relative condition factor $\neq 1$), can either reflect abnormalities like tumours, tissue swelling, infestation by parasites, etc., or just normal variable factors, for instance a well exercised body (Yogata & Oku 2000), maturity or hepato-somatic index. Similarly, different groups or individuals may show statistically the same relative condition factor to normal ones, which means that total weight, and even less, the condition factor that depends on weight, cannot be the only factor to define good health.

Good quality cannot be measured in terms of weight for biological phenomena. A continuous tendency to increase weight may be good for some organisms but not for others, and even for the same organisms this quality may not always be beneficial. Goodness as intended here is more a utilitarian than a biological concept. It is desirable that the biological concept of condition is not based on an abstract notion, but on a measurable parameter useful to track more or less magnitude rather than good or bad quality, the term goodness is not considered adequate to identify the condition.

The term fitness when the quality of having exactly the right measurements (TLC 1998) seems to agree with the genetic and evolutionary concept of fitness if we consider that the living organisms (the survivors) are the most fit and the ones with the right measurements. From this point of view the term fitness appears more objective than well-being and good health, but it is still abstract because a better morphometric reference point than the indices of well-being is needed to define the right measurements.

Due to the response variable in the indices of well-being is weight (as an estimator of biomass) relative to length (as an estimator of geometric size), The concept of condition can be approached in measurable terms from two different points of view, one is associated with heaviness and it is related to the total biomass, meanwhile the other is linked to fitness as having the right measurements. Weight is biologically the right parameter to quantify heaviness, but is not enough for fitness because as seen in equations (7) and (8), morphometry and density have to be also considered.

2.4.2.2 Weight as a reliable estimator of condition

Heaviness is more important from a fisheries approach in order to assess yield, and fitness is a property especially important from the fish biology's point of view. Heaviness is intrinsically the amount of biomass, and total weight is undoubtedly its best and reliable estimator.

Nowadays the assessment of fitness is been mainly approached in two ways: by increasing the number of parameters, and by focusing comparisons on particular cases with as many factors in common as possible to minimize unwanted influences. A third way much used in the past is by considering *a priori* known magnitudes and mathematical expressions as reference parameters (for example historical and published data, plain averages, and the Fulton equation). For practical purposes the monitoring of individual body structures such as liver, muscle, and gonad size, as indicators of energetic contents have been more important than finding the optimal dimensions. Eviscerated weight and other measures such as the gonadosomatic and hepatosomatic indices have been monitored for such purposes.

In order to quantify fitness it is not only necessary to identify the adequate response and descriptor variables, but also their optimal magnitudes for individuals, populations, and species. Total weight is the proper response variable and length from head to tail the best descriptor (standard length shows less variability than other dimensions). Because size and biomass are both visible manifestations of metabolism, which is not a one-way process, but a reversible function of anabolism and catabolism, biomass as weight is a highly variable parameter over time, and can show negative and positive changes. Even when not noticeable reversible, size as length, particularly head to tail, is also highly variable between individuals. Because of this variability, individuals and sub-populations with the same body size are not necessarily equal, for instance, a poorly nourished adult may present the same size and weight as a healthy juvenile. Because of biological complexity, metabolic changes during the life cycle, and evolutionary processes, the analysis of particular cases and situations by categorical variables such as age, sex, and maturity index will give simpler and more direct results than general and complex models.

2.4.2.3 The number of variables involved

The number of parameters to measure is an important factor, particularly for fieldwork where a large number of measurements per individual can compromise the complete sampling campaign. While no new more efficient methodologies are developed, practical needs have to be considered against accuracy and precision of results. If weight can be reliably estimated from morphometric parameters, it is possible to reduce the number of linear dimensions as possible at a low loss of accuracy and precision, depending on the reversibility and variability of the longitudinal predictor variables as described below.

Jones *et al.* (1999) found more accuracy (based on the coefficient of determination of linear regressions) in the estimation of biomass for chinook salmon (*Oncorhynchus tshawytscha*) and Atlantic salmon (*Salmo salar*) by using the following equation,

$$M = BL^2 H$$

M: biomass
L: fork length (Length of the fish from tip of snout with the mouth closed to tip of the shortest ray of the caudal fin, or to the centre of the fin if the tail is not forked).
H: Height
B: Constant

This is a particular case of equation (6) for $SAC = 3.0$ due to constant density and isometry ($b_D = 1.0$ and $b_H = 1.0$). It is not expected that this equation will work with shapes with allometric width because $L*D$ approximates to L^2 only if the relationship between length and width is isometric, nor when density is variable as seen in 2.4.1.4.

In practical work the previous equation may lead to higher accuracy than the length-weight relationship only if H has low variability, and there is isometry and constant density because it includes the actual values of H instead of relying on only one variable (L); Even better accuracy might be expected when considering also the width as in the length-weight relationship of an ellipsoid-like shape. In both cases, the gain in accuracy must be evaluated against the effort needed to take extra measurements over and above weight and length, and against the variability introduced by including redundant variables with a loss of precision. Also, the implementation of the length-weight relationship of an ellipsoid-like shape and the generalized relative condition factor may be impractical due to the difficulty in the estimation of fish density.

For species whose shape deviates from the basic 3-axes of growth (shapes different from ellipsoid or with more than one 3-D coordinated system), equation (7) will produce inexact results, detectable as deterministic error. In those cases one of the most recent approaches for biomass estimation, based on the analysis of body truss (geometric framework of the body) must be considered (McGlade & Boulding 1986; Creech 1992; Beddow & Ross 1996; Beddow *et al.* 1996; Hockaday *et al.* 2000).

It can be demonstrated that equation (7) keeps the same form regardless of the position of the orthogonal axis of growth. The same applies for changes in the geometric constants (allometric length-length growth), and for cylindrical and rectangular prism shapes.

2.4.3 A PARTICULAR EXAMPLE

Equations (2) and (3) are not reliable estimators as condition factors for all species because they are based on very particular assumptions. However, they are special cases of the length-weight relationship, and the length-weight relationship is a special case of length-weight relationship derived from the ellipsoid form (in the same way, the relative condition factor is a particular case of the generalised condition factor).

If there are not important departures from the ellipsoid shape, the body dimensions are accurately measured, and appropriate statistical tests are applied, the length-weight relationship of an ellipsoid-like shape fulfils with the three criteria suggested by Hurlbert (1978) for the selection of reliable indices: appropriateness, simplicity, and statistical correctness. Therefore, the equation for the length-weight relationship of an ellipsoid-like shape and the generalized relative condition factor can be considered as adequate descriptors of the relationship between weight and length, and the condition factor intended as heaviness.

Once the adequate equations to describe the length-weight relationship and the relative condition factor are identified, the challenge is finding the optimal weight if the condition factor is intended to evaluate heaviness, and also the right morphometric dimensions if intended to measure fitness (fitness in shape). For heaviness the first option is the weight with respect to length of a particular group. Additionally other categorical variables must be considered for fitness because there is not an absolute set of right measurements for the full life span and all temporal, geographical, ecological and environmental conditions. By common sense the spatial and temporal dimensions, sex, age, and maturity index are expected to be part of the main categorical variables.

The analysis of the length-weight relationship of a sub-sample of North Sea plaice, *Pleuronectes platessa* L. (458 females from 10 to 15 years of age from several samples taken in 1985 in the North Sea) will help to highlight some misconceptions about the length-weight relationship, the importance of categorical variables and the importance of an objective theoretical approach over empirical assumptions.

The objective is to evaluate the influence of gonad maturity on condition by the analysis of the length-weight relationship in female plaice, combining ages 10 to 15 years. In order to do so parameters of the length-weight relationship were obtained by least squares for three groups of female plaice: with maturity index 2, maturity indices 4 and 5, and maturity index 7. Maturity index (GI) was categorised as: juvenile (1), ripening (2), spawning (3,4,5), and spent (6,7) (Wimpenny 1953).

Age group 10-15 was considered because they present dramatic changes in gonad size, and to exclude fishes that were too young and too old (to decrease the influence of outliers). It is expected that total weight of organisms with maturity indices lower than 3 will not be influenced by gonad growth. Maturity index 7 will contain fishes post gonad growth i.e. spents, and maturity indices 3 to 5 will fully show the effect of the gonad factor. Maturity indices 3 and 6 were excluded in order to avoid the influence of boundaries.

In this case, the categorical variables are age and maturity index. Maturity index is the main grouping variable associated to gonad size. And age is a narrowing factor to avoid unwanted noise introduced when including too young or too old individuals. A selection of 1-year classes may be preferred for a finer study, but for this example the interval of ages selected is reasonable due to the apparent high variability of growth at the selected ages.

According to Anderson & Gutreuter (1983) "$b < 3$, represents fish that become less rotund as length increases, whereas when $b > 3$ fish become more rotund as length increases". Common sense also suggests that for a same length and a same *a*, a $b < 3$ will produce a lower weight than a $b > 3$ in the length-weight relationship. Based on the these premises, an increase on *b* for organisms with maturity indices 4 and 5 respect to organisms with maturity index 2 and maturity index 7 (Table 5) might be interpreted as a potential higher condition attributable to bigger gonad size (organisms with maturity indices 3 to 5 might be 'more rotund' than organisms with maturity indices lower than 3 and organisms with maturity index 7).

Table 5: **Parameters of the length-weight relationship for three categories of maturity index in females of *Pleuronectes platessa*.** GI: gonad index; *a*: coefficient, and *b*: power of the length-weight relationship; SD: standard deviation; p(=0): significance level of the null hypothesis H_0: $b = 0$ (test for relationship between length and weight); and p(=3.0): significance level of the null hypothesis H_0: $b = 3.0$ (test for isometry).

GI		Parameter	SD	p(= 0)	p(= 3.0)
All	La	-2.41814	0.12870973	2.2503E-58	4.229E-157
	b	**3.2453407**	7.68027E-2	1.100E-157	1.50089E-3
2	La	-2.01516	0.18685353	9.1939E-20	7.2572E-55
	b	**3.03557946**	0.11098899	9.0433E-56	0.74905291
4 & 5	La	-2.25838	0.28654131	5.2148E-11	3.4586E-27
	b	**3.14654473**	0.17194837	4.0286E-27	0.39724785
7	La	-2.17383	0.14784577	2.4784E-32	1.1509E-80
	b	**3.07327912**	8.84154E-2	3.2161E-80	0.40835048

The regression for all females generates the biggest *b*, suggesting that on average all individuals are 'more rotund' than for particular levels of maturity index; this is a contradiction of the previous reasoning that can lead to different speculations about the equality of *a*, presence of outliers and influential cases, insufficient data, etc.

Scatter plots for all data and for each of the three groups show no apparent anomalies such as presence of outliers, or lack of data (Figure 5). Even the group with less data shows a linearly congruent distribution.

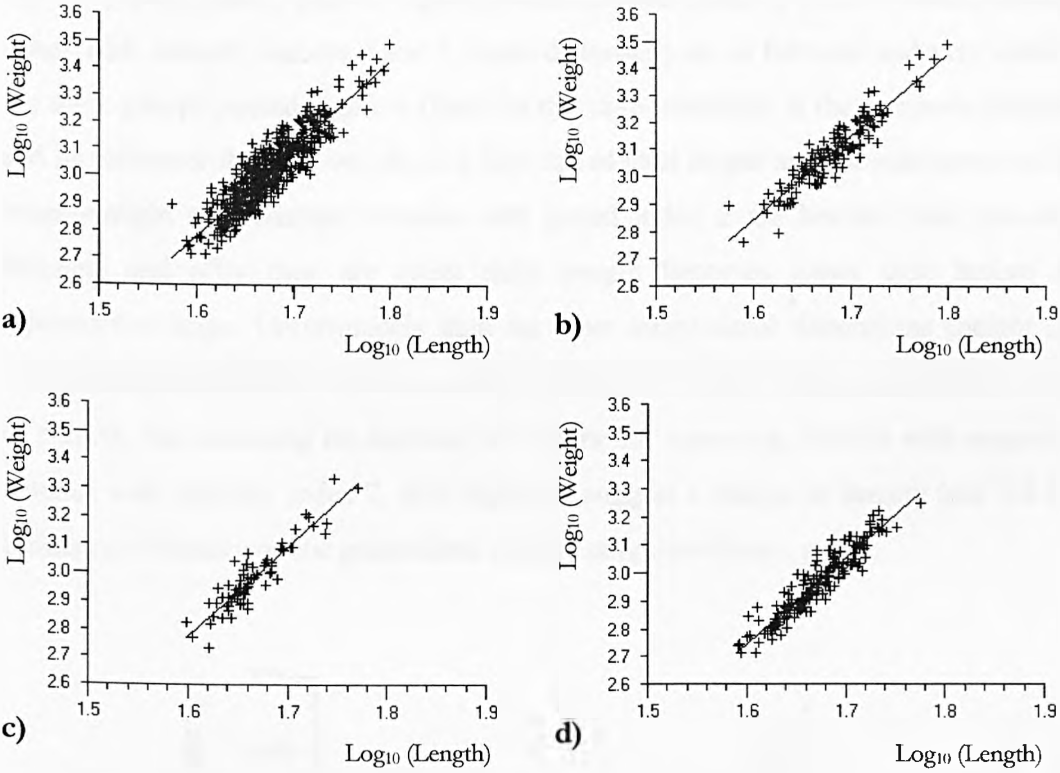

Figure 5: **Length-weight least square fits for North Sea Plaice females from 10 to 15 years of age, all of them and at three levels of gonad maturity.** All individuals (a), with maturity index 2 (b), with maturity indices 4 and 5 (c), and maturity index 7 (d).

If females with maturity indices 4 and 5 are 'more rotund' and less heavy than the rest, then in this case either weight is not an exclusive function of the volume, or the volume has nothing to do with b, or b is inversely proportional to volume. From 2.4.1.4 (Influence of density on the generalized relative condition factor), we know that b is an exclusive result of the morphometric growth, and an apparent variation of b can mask the effect of density when density behaves as a variable and not as a constant. In this case the difference in b for each group is not a result of changes in morphometric growth, but of changes in density in the product of coefficients. In living organisms the geometric proportion between total length and height of female plaice does not change, and the width does not vary appreciably, in fact, the gonads are visible as a sausagelike longitudinal protuberance in the lower side of the body, which produces an slight increment in volume.

In the plot of fitted curves (Figure 6), the heavier group is the one with maturity index 2 (open circles), and the lighter is the one with maturity index 7 (filled circles); fishes with maturity indices 4 and 5 (open diamonds) are in between and very close to the three groups pooled together (line). In this case heaviness is the reference property and its estimator the total weight as a function of total length and the parameters of the length-weight relationship. Females with gonad index 2 are heavier than spawning females, and after they are spent their weight becomes lower than before the reproductive stage. Unfortunately data for other longitudinal dimensions (height and width) are not available in order to check variations in volume and assess the influence of density, but assuming no decrease of volume for spawning females with respect to females with maturity index 2, their lightness suggest a change in density (see 2.4.1.4: Influence of density on the generalized relative condition factor, p. 31).

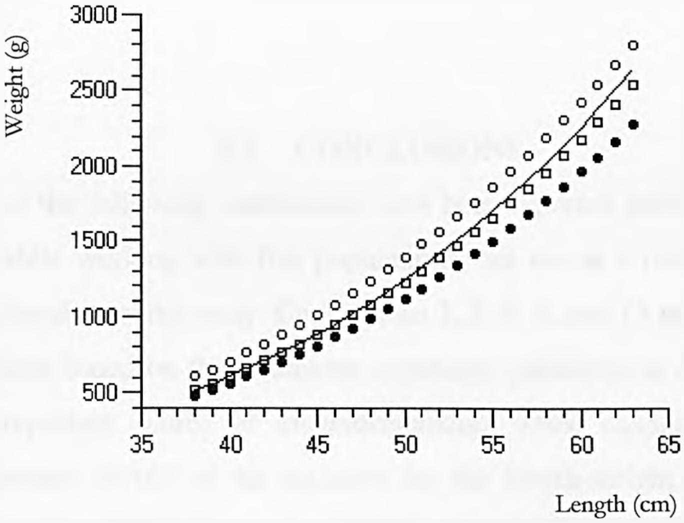

Figure 6: **Fitted Length-weight curves for North Sea Plaice females from 10 to 15 years of age and three levels of gonad maturity.** Line: all females pooled together, open circles: maturity index 2, open diamonds: maturity indices 4 and 5, and filled circles: maturity index 7.

Once spent (maturity index 7), a further decrease in weight is observed and also a possibly reduction in volume may happen. Shulman & Love 1999 point to a heavy increase of protein in fishes before the spawning season and during the juvenile stage with an increase in weight, a change in the body chemical composition (protein and lipids) during the spawning season, and a depletion of protein after spawning. These authors also say that protein is removed from the musculature and substituted by liquid in the post-spawning period, and "the length/weight ratio therefore underestimates the loss of nutritional 'condition'". Those changes described by Shulman & Love 1999 are clearly evidence of body density change.

By taking the length-weight relationship for all females from 10 to 15 years of age as reference regardless of their maturity index and their average length, the generalised relative condition factor can be estimated as an indicator of condition intended as heaviness.

Consequently with the length-weight relationship of an ellipsoid-like shape (equation (7)), density and the orthogonal dimensions must be measured in order to assess condition in terms of fitness. An alternative option is to construct categorical tables and plots, or plots of percentile curves (Murphy *et al.* 1990; Childress 1991) and carry out comparative evaluations.

2.5 CONCLUSIONS

Some of the following conclusions have been reported previously by others as observations while working with fish populations, but not as a result of a theoretical analysis as undertaken in this study. Conclusions 3, 5, 8, 9, and 13 refute the validity of many conclusions based on the allometric constants, published to date. Conclusion 7 clarifies an important source of misunderstanding when changes in the sum of allometric constants (SAC) of the equation for the length-weight relationship of an ellipsoid-like shape (equation (7)) are attributed exclusively to morphometric changes, particularly to 'rotundness' without considering the density factor.

1) The employment of reference values (*i.e.* theoretical values, historically recorded parameters and data values, and experimental results) and constant expressions (*i.e.* the Fulton condition factor) will induce deterministic error if the analysed data do not follow the original assumptions on which the reference values and expressions were based.

2) Total weight does not depend exclusively on volume, but also on the morphometric growth factor and specific Gravity (density).

3) SAC is always a constant parameter in the length-weight relationship and its magnitude is exclusively a product of the morphometric growth.

4) A SAC = 3.0 does not mean that weight is exclusively related to the body volume.

5) A SAC $\neq$ 3.0 will always mean allometry, if no other variables than L, H, and D (for instance ρ) are involved.

6) The influence of density should be evaluated before considering the estimation of the expected weight.

7) In the length-weight relationship of an ellipsoid-like shape, and length-weight relationship, a linear variation of ρ will only affect the sum of coefficients (*SC*), and if non-linear will alter mainly the sum of allometric constants (*SAC*).

8) The concept of isometry that is based on the magnitude of b in the length-weight relationship of an ellipsoid-like shape (equation (7)), and length-weight relationship (equation (1)), must be reconsidered in the fact that $SAC = 1+b_H+b_D$ can still be equal to 3.0 for $b_H \neq b_D$, and may be the product of a non-constant density.

9) Condition has been erroneously viewed as only one property. It has to be separated at least into two different concepts: heaviness and fitness.

10) For the determination of condition as heaviness, total weight is the best response variable and length from head to tail the best predictor.

11) For determination of condition as fitness, total weight must be evaluated by considering different categorical variables.

12) There is no ideal or optimal biomass and size, therefore, the weight estimated from the length-weight relationship and the length-weight relationship of an ellipsoid-like shape does not have to be considered as that, but as the one that is the product of the average population distribution.

13) Departures from 1.0 in the condition factor may reflect departures from an average condition, but also the presence of other variables that have not been considered as predictors, for instance density.

2.6 ADDITIONAL COMMENTARIES ON CONDITION ASSESSMENT FROM THE MORPHOMETRIC APPROACH

As mentioned previously, the length-weight relationship is the result of the empirical description of the distribution of weight with respect to length. Effort has been expended to find an empirical association between biological properties (such as nutritional status, feeding success, fitness, energy storage, maturity etc.) and morphometry (particularly the length-weight relationship). Most of the results were only useful for the particular cases for which they were developed because many of the biological properties are difficult to score (Ferron & Leggett 1994), and because clear empirical relationships are usually not based on theory, particularly when they seem too obvious (such is the case of the length-weight relationship).

Sometimes results depend on the approach used to assess the biological properties, for example, muscular fitness (as protein production) can be better monitored by the DNA/RNA ratio rather than the relative condition factor (Shulman & Love 1999). This emphasises the importance of the knowledge of the theoretical background for even the simpler models, and the correct meaning of the parameters involved, as it was done in this study for the length-weight relationship and the condition factor.

Regarding the morphometric approach, there are two main avenues for relating shape and condition: the 3-D modelling of shape, and the construction of a geometric framework of the body known as body truss. Here the 3-D modelling of a pisciform shape was approximated to a tri-dimensional ellipsoid (Figure 7).

More complex shapes with more than one three-dimensional Cartesian axis of growth in the same longitudinal axis can be built from a combination of simpler geometric solids as truncated ellipsoids, cylinders and truncated cones. For most fish species the simple ellipsoid form with one tri-dimensional point of growth (three orthogonal linear dimensions: length, height and width) is enough to describe the relationship between biomass (weight) and size. This is why the length-weight relationship is so simple.

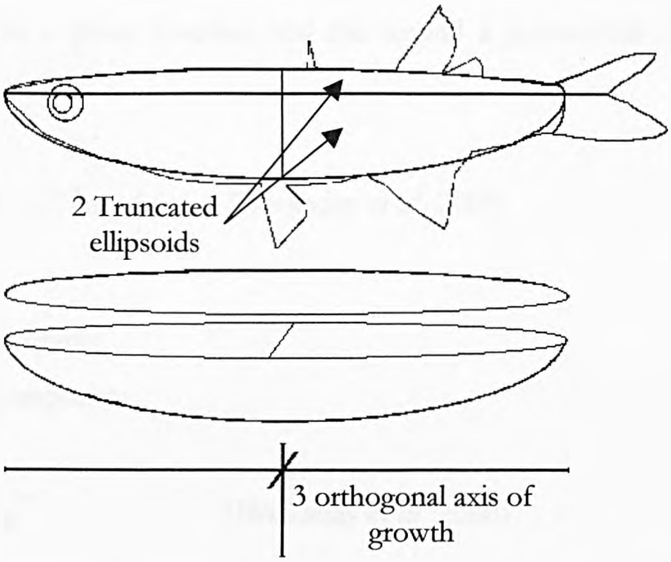

Figure 7: **Example of 3-D modelling.** Fish like shape with 1 set of 3 orthogonal axis of growth approximated by 2 truncated ellipsoids.

The truss approach is oriented to finding the most influential body dimensions (principal shape components) that can describe the body form regardless of size (the morphometric growth is considered), and their association to the body biomass. In the following example of body truss (Figure 8) the shape components are shown as linear dimensions taken from several control points (landmarks) in a 2-D view of the body (Busacker *et al.* 1990).

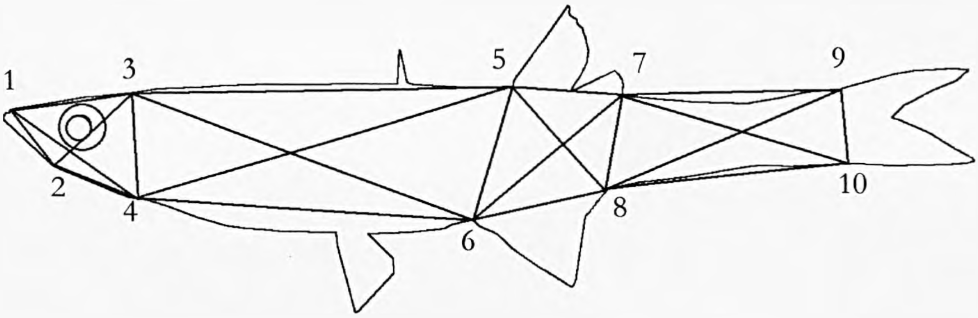

Figure 8: **Example of body truss**. 10 control points and 21 shape components (1-2, 1-3, 2-4, … 9-10).

The number of landmarks, linear dimensions and mathematical relationships are different for each shape. Equations (9) and (10) are examples of models for estimation of biomass based on the truss approach for x_i shape components. The first equation describes a linear function and the second a polynomial function between components.

$$Log_e M = \sum_{i=1}^{n} \{C_0 + C_i Log_e(x_i)\} \quad \text{(Hockaday } et\ al. \text{ 2000)} \tag{9}$$

M: Weight.

C_0 to C_i: Constants

x_i: i Shape component

$$M = C_0 + \sum_{i=1}^{n} C_i\, x_i^{pi} \qquad \text{(Hockaday } et\ al. \text{ 2000)} \tag{10}$$

pi: Positive integer

CHAPTER 3

AGE AND GROWTH: SIZE AT AGE

3.1 ABSTRACT

Growth, defined as increases in size at age, is basically the result of the organisms' metabolic activity. Morphological, physiological, ethological and ecological factors determine the growth process. A common problem found when estimating growth in size at age for populations is to decide which model to choose. The choice of the best model mainly depends on the trend in complexity of the response variable (size), growth characteristics, objective pursued, and the availability of data. Other recommendations concentrate mainly on statistical population attributes, particularly shape and distribution of residuals, structure of the statistical error, and power of fit. For growth in size at age, in this study I consider the earlier recommendations and propose an alternative method for selection of the best model between the most widely used ones for fish stock assessment (Logistic, von Bertalanffy, and Richards, including their exponential expressions, and Gompertz). The method is based on two general models, one for single exponential and other for double exponential curves. The selection is done by exploring the stability and accuracy of each parameter during the fitting of the general models, by the evaluation of the goodness of fit, interpretation of the statistical error distribution and the residuals' distribution shape. The model worked well on data sets with known distributions and also on a real previously published data set.

3.2 JUSTIFICATION

Length and weight are the most common dimensions measured to indicate fish size. Weight is the most direct indicator of biomass, but because it is highly variable with respect to age, a more uniform longitudinal dimension is preferred when a good length – weight relationship exists. The increase in size with respect to age is the result of the organisms' metabolic activity; this phenomenon is known as somatic growth. Morphological, physiological, ethological and ecological factors not only determine the growth process, but when extreme they also affect the survival success.

Despite the multitude of factors that influence growth, the relationships between size and age follow distinctive patterns in most fishes that can be acceptably described by simple mathematical expressions. For the adult stanza (Le Cren 1951; Ricker 1979) of the life cycle, the most widely used equations to describe somatic growth are derivations of a rate of increase in size. The basic equation template (Ricker 1979) from which most of the growth models are derived is:

$$\frac{dy}{dt} = ay - f(y) \qquad \text{when } f(y) < ay\text{, and} \tag{11}$$

$$\frac{dy}{dt} = f(y) - ay \qquad \text{when } f(y) > ay \tag{12}$$

y: size (length or weight)

a: constant

$f(y)$: function of size

The Logistic equation is a single exponential derivation in linear scale[1] of equation (11), The Gompertz equation is derived from a multiplicative scale version of equation (11), the von Bertalanffy equation is the best known derivation of equation (12), and the Richards equation is a derivation of equation (11) that includes an allometric factor. All these equations are frequently used in fish biology and stock assessment, and for some authors (West *et al.* 2001) most of their parameters have a biological meaning, but at least for Ricker (1979), these are practically useful, even without a proven biological basis.

A common problem found when estimating growth is to decide which growth model to choose. There are different approaches to find an acceptable answer, depending principally on the following four factors:

1) The trend in complexity of the response variable (shaped by the number of variables involved, data variability, cohorts' diversity).

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[1] The term Linear scale refers to mathematical linear scales, while Multiplicative scale denotes non-linear trend, but can be linearized by logarithmic transformation. The central tendency estimator for Linear scales is the average, and the statistical error is variance related (additive error); The central tendency estimator for multiplicative or logarithmic scales is the arithmetic average of the logarithmic data, whose antilogarithm equals the geometric mean, and the error is related to the variance of the logarithmic data (non-additive error).

2) The growth characteristics (longevity, seasonal changes in metabolism, morphometry, differential growth due to precocity, dwarfism or polymorphism).
3) The objective pursued (estimation of key parameters such as growth rate and asymptotic size, data estimation, hypothesis testing, pattern recognition, identification of important events as periods of rapid growth, inflection points, strength of seasonal trends).
4) The availability of data (gear efficiency, sample representativeness, distribution and aggregation patterns, missing values).

In most cases the selection of specific models has been primarily for practical reasons, such as compatibility of the output with previous results, reduction of effort, time and costs, and methodological resemblance to similar studies; secondarily from the objective pursued; thirdly from the data availability, and lastly from the need to emphasize the fundamental attributes of the population.

In general, modern recommendations for the selection of the best model concentrate mostly on the population attributes due to the development of powerful tools for sampling and data processing, particularly mathematical and statistical methods, and hardware and computing algorithms. Quinn & Deriso (1999) recommend taking the shape of the data distribution and the structure of the statistical error distribution as the main criteria. For Hilborn & Mangel (1997), the choice of the best model is the result of the confrontation of the results against the original data (power of fit) from different approaches; they mention the following three approaches: Classical hypothesis testing, likelihood approach (McCallum 2000), and bayesian approach (Quinn & Deriso 1999; McCallum 2000).

Specifically for growth (size at age), in this study I consider these recommendations and propose a method for the selection of the best model between Logistic, von Bertalanffy, Richards, and Gompertz. The proposed method is based on two general models, one for single exponential (general model 1) and other for double exponential patterns (general model 2). The problem is tackled by exploring the stability and accuracy of each parameter during the fitting of either of the General Models (see Properties to analyse, p. 62), by the evaluation of the goodness of fit (Sokal & Rohlf 1969), the interpretation of the distribution of the statistical error and the shape of the distribution of residuals, the value of the sum of squared residuals (RSS: Hoaglin *et al.* 1983; Quinn & Deriso 1999; McCallum 2000), the value of the maximum log likelihood (MLL: Cerrato 1990; Quinn & Deriso 1999; McCallum 2000), and the Schnute's F statistic (Schnute 1981; Quinn & Deriso 1999). The General Models also include the potential to explore the exponential expression of Logistic, Bertalanffy, and Richards curves, different parameterisations of Gompertz, and simple exponential functions.

For fitting purposes I developed a computer programme based on the Levenberg– Marquardt method (Marquardt 1963), which is an iterative routine (Press *et al.* 1989), and followed a likelihood approach for confrontation between observed and predicted values by using goodness of fit. I support the numerical analysis with graphical representation of the outputs, including scatter plots of observed data, fitted results, and distribution of residuals.

3.3 OBJECTIVE

The objective is to develop a method for selection of the best size-at-age growth model from the most commonly used methods in fish stock assessment: Logistic, von Bertalanffy, Richards, and Gompertz, and exponential variants of the Logistic, von Bertalanffy, and Richards.

The main size-at-age growth models can be pooled in two general models: single and double exponential. The capacity of each individual model as part of any generalised model to fit a particular data set will depend on the following properties: trend compatibility of the data distribution respect to the curve shape of the model, power of fit, fit convergence and stability (tendency to reach a single solution), and compared accuracy between models (capacity to output sound values) of each parameter and each particular model in a generalised model.

3.4 ANTECEDENTS

3.4.1 IMPORTANCE OF AGE AND GROWTH IN FISHERY SCIENCE

For Hilborn & Walters (1992) p. 21, “The essential biological feature of any fishery is the dynamics of the fish population; the analysis of population dynamics involves trying to make predictions about the birth, death, growth, and movement processes of the fish". In practical terms, the biological background of fishery science relies on three parameters: recruitment, mortality, and growth (Brander 1994). In ecological terms, recruitment is the main input and mortality the main output of individual units to the fishery, while individual growth is the main source of biomass gain, and size-at-age is considered as the main factor of body size growth (Cushing 1981).

3.4.2 ANTECEDENTS OF SIZE AT AGE GROWTH

Growth is a highly complex process in fish and is influenced by numerous biotic and abiotic factors (Brett 1979). Abiotic factors such as salinity and dietary carbohydrate levels (Rosas *et al.* 2001), oxygen consumption and metabolism (Pichavant *et al.* 2000), light, survival, metabolism and behaviour (Appelbaum & Kamler 2000), and temperature and metabolism (Burel *et al.* 1996), are examples of environmental variables affecting growth. Biotic factors may be physiologic, for example the metamorphic process from larval to juvenile stages and its effect on protein production (Christensen & Korsgaard 1999); ethologic, for instance the strategy of early seaward migration and the minimisation rate of protein turnover (Morgan *et al.* 2000); or purely metabolic as feeding time and ration with relation to nitrogen metabolism (Verbeeten *et al.* 1999).

Growth is an extensively studied phenomenon and has been investigated in deep from different approaches. There are many publications concerning growth in fish biology, fish stock assessment, and fisheries, but perhaps the most complete and widely known are those by Bagenal & Tesh 1978, Summerfelt & Hall 1978, Ursin 1979, Weatherley & Gill 1987, and Busacker *et al.* 1990.

The first attempts to quantitatively model body growth for populations of fish were oriented to separately describe different stanza[2] (Le Cren 1951; Ricker 1979) of the life cycle by using exponential, power, and logarithmically linearised power functions. According to Ricker (1979), the Gompertz equation is perhaps the oldest

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[2] Stanza is a term that means stage and refers to the different anatomic-morphologic-physiologic phases of the body development. According to Ricker 1979, the term stanza was introduced by Vastenov 1953 (I doubt it because Le Cren, 1951 already utilized it in the same way) and it is used in the late history life stages of fishes in order to differentiate from the early developmental stages.

growth curve for older stanza originally developed in 1825 for the distribution of age in human populations. Verhulst (in Ricker 1979) proposed the logistic curve in 1838, and Pütter (in Ricker 1979) introduced an equation for growth in length at age in 1920 that according to Ricker (1979) was reparameterizated by von Bertalanffy in 1934 (see 3.4.3.1, p. 55). Different researchers have developed versions of these equations either independently or by reparameterizing them. Most applications of these models in fish biology, stock assessment, and fisheries are reparameterizations of the original differential forms.

The word ‘time’ is taken in this thesis as a synonym of age because age is a measurement of time relative to an initial event in life history.

3.4.3 MATHEMATICAL DESCRIPTION OF GROWTH

The absolute rate of growth is defined as $\frac{dw}{dt}=\frac{w_2-w_1}{t_2-t_1}$, with w_1 as the weight at time t_1 and w_2 as weight at time t_2, while the relative rate of growth (also known as the specific or intrinsic growth rate) is: $\frac{dw}{wdt}=g=\frac{w_2-w_1}{w_1(t_2-t_1)}$

By setting $f(y)=by^2$, $y=w$, $a/b = W_\infty$, and $b=g$ in equation (11), the absolute rate of growth in the logistic equation for weight (equation (13)) is obtained (Ricker 1979)

$$\frac{dw}{dt}=gw-\frac{g}{W_\infty}w^2=\frac{gw(W_\infty-w)}{W_\infty} \qquad (13)$$

w: Weight at time $= t$

W_∞: Asymptotic weight

g: Instantaneous rate of growth when w approaches to 0

The absolute rate of growth for the Gompertz equation (equation (14)) is derived also from equation (11) by defining $f(y)=by(\ln(y))$, $y=w$, $e^{a/b} = W_\infty$, and $b=g$ (Gregg *et al.* 1964; Ricker 1979)

$$\frac{dw}{dt} = aw - bw(\ln(w)) = gw(\ln(W_\infty) - \ln(w)) \tag{14}$$

The absolute rate of growth for Pütter and von Bertalanffy equations (equation (15)) is obtained by setting $a = k$ and $b/a = L_\infty$ for length in equation (12):

$$\frac{dl}{dt} = k(L_\infty - l) \tag{15}$$

k: Pütter growth coefficient or Brody coefficient

L_∞ : asymptotic length

The absolute rate of growth for Richards equation is (Ricker 1979; McCallum 2000):

$$\frac{dw}{dt} = c_1 w + c_2 w^n \tag{16}$$

c_1, c_2, n : constant

3.4.3.1 Models

There are two general attributes shared by these growth models: a similar trend, and an asymptotic tendency. The trend, typically positive for fishes, can be evaluated according to its rate of change, and the asymptotic tendency in relation to an asymptotic value (asymptotic size). These two parameters, rate of change and asymptotic size, appear in the integrated forms of the absolute growth rates of equations (13) to (15). The integrated equations used for this work are parameterised versions of the original integrations.

Mathematically, parameterisation means any transformation from a substitution, addition, or elimination of parameters of the basic integrated form by considering special or general situations. For example, for the Pütter equation, the integrated form

$$l = L_\infty - ce^{-kt}$$

Can be parameterisated to the von Bertalanffy model by considering the special case when $l = 0$. At $l = 0$ the value of t will be equal to t_0, and c will be:

$$0 = L_\infty - ce^{-kt_0};\ ce^{-kt_0} = L_\infty;\ c = L_\infty e^{kt_0}.$$

Assuming the increment of length from $l_0 = 0$ to l_t (the length at age = t):

$$l_t - l_0 = l_t - 0 = l_t = L_\infty - ce^{-kt} - (L_\infty - ce^{-kt_0}) = c(e^{-kt_0} - e^{-kt}),$$

and substituting c by $L_\infty e^{kt_0}$ (when $l = 0$):

$$l_t = L_\infty e^{kt_0}(e^{-kt_0} - e^{-kt}) = L_\infty(1 - e^{kt_0}e^{-kt}) = L_\infty(1 - e^{k(t_0-t)}) = L_\infty(1 - e^{k(t-t_0)}).$$

Which is the length-at-age von Bertalanffy model.

Analogous procedures are followed for this and other growth models, thus creating different variants of the original models. In this study the term versions is also used to refer to those different variants of the original model.

The Logistic model for growth (Equation (17)), has three parameters (Meyer *et al.* 1999).

$$s = s_\infty\left(1 + e^{-k(t-t_i)}\right)^{-1} \tag{17}$$

s_∞: Asymptotic Size

k: Growth Rate constant[3] (steepness of the sigmoidal curve)

t_i: Time at the inflection point (k/2)

The generalised von Bertalanffy model, equation (18), includes four parameters (McCallum 2000).

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[3] As reaffirmed in 3.4.3.2, p. 59, k is not the actual growth rate, but a constant contained in the root differential equation from where these equations are derived (actual growth rate function). k is mainly known as the "Intrinsic rate of growth").

$$s = s_\infty\left(1 - e^{-k(t-t_0)}\right)^b \tag{18}$$

s_∞: Asymptotic Size

k: Growth rate constant (steepness of the curve)

b: Allometric constant ($b \approx 1$ when s = length; $b \approx 3$ when s = weight)

t_0: Time at which $s = 0$

The Richards model, equation (19), includes also four parameters (Sit & Poulin 1994; Gille 1998).

$$s = s_\infty\left(1 - c\,e^{-k\,t}\right)^b \tag{19}$$

s_∞: Asymptotic Size

k: Growth rate constant (steepness of the curve)

c: Constant

b: Allometric constant

There are at least three different equations derived from the Gompertz model as a result of different parameterisation strategies. Gompertz 1 (equation (20)) has four parameters and is hard to fit considering the four parameters, because k appears twice in it. By considering λ/k as a single constant the fitting is easier. Gompertz 2 has three different parameters and is also difficult to fit because one of the k's is associated with $1/k$. Gompertz 3 is the basic integration of equation (14) with three parameters.

(Quinn & Deriso 1999)

$$Y_t = Y_0\, e^{\left(\frac{\lambda}{k}\left(1-e^{-kt}\right)\right)} \tag{20}$$

Y_0: Theoretical Initial Size

λ, k: Constants

(Quinn & Deriso 1999)

$$Y_t = Y_\infty\, e^{-\left(\frac{1}{k}\,e^{-k\,(t-t_0)}\right)} \tag{21}$$

Y_∞: Asymptotic Size

λ, k: Constants

t_0: Time at which the $Y_t = 0$

$$Y_t = Y_\infty e^{-e^{-k\,(t-t_i)}}$$

Transformed from (Sit & Poulin 1994) (22)

f, k, and t_i: Constants

Gompertz 1, 2 and 3 are the most commonly used parameterised versions of the Gompertz model. In the following description the symbol Y_t is used instead of s in order to differentiate them from the previous single exponential models.

A version of the Gompertz model (Gompertz 4) developed by Jørgensen in 1994 (in Gamito 1998) has three parameters only (equation (23)). This is a variant of equation (20) for weight, with $\mu_0 = \lambda/k$. Fewer parameters speed up the fitting process and introduce less quantitative noise to the model, but too few parameters make the fitting by non-linear methods unstable.

$$w_t = w_0 \ e^{\mu_0 \left(1-e^{-kt}\right)} \tag{23}$$

w_t: Size (weight) at time = t

w_0: Theoretical Initial Size (initial weight)

μ_0: λ/k

t: time (age)

Equations (24) to (26) are exponential versions of equations (17) to (19) where a multiplicative scale of size is assumed. These are the equivalent of the natural logarithm transformation of size (F(t) = Ln(s)), and keep the same relationship between its parameters as the originals in equations (17) to (19), but their actual magnitudes are different (for example, s_∞ in equation (18) equals e^{s_∞} in equation (24)). Equation (24) is the exponential form of the generalised von Bertalanffy curve, equation (25) is the Generalised Richards exponential, and equation (26) the Generalised Logistic exponential.

$$Y = e^{s_\infty \left(1 - e^{-k\,(t - t_0)}\right)^b} \tag{24}$$

$$Y = e^{s_\infty \left(1 - c\,e^{-k\,(t - t_0)}\right)^b} \tag{25}$$

$$Y = e^{s_\infty \left(1 + e^{-k\,(t - t_0)}\right)^{-1}} \tag{26}$$

3.4.3.2 Characteristics of the growth models: asymptotic behaviour, *k*, t_0, and error distribution scale

All the equations previously presented include an upper asymptotic trend with L_∞ and W_∞ as the factors defining the asymptotic size in all cases, with exception of equations (20) and (23).

The constant *k* denotes the rate of change of the actual growth rate, which is the original differential expression from where the different equations where derived. This is not the actual growth rate, but the growth rates for each model are their first derivatives with respect to time (t) of the parameterised expressions: *Growth rate* = ds/dt. t_0 is a product of the parameterisation in different equations and stands for the theoretical initial time where $s = 0$.

Equations (17) to (19) work well when sizes are distributed normally for each age class. When this is not the case, handling of non-normality can be managed by changing the scale of the response variable in three ways: by using the Gompertz model (which is based on the assumption of a logarithmic growth rate in their differential expressions), by using the exponential expressions of equations (17) to (19), and by transforming the response and predictor variables (usually by log-transformation).

3.4.3.3 Comparison of parameters

Asymptotic parameters for different equations are statistically comparable as long as their error distribution is the same (normal or normally transformed). For models fitted by non-linear methods as the Levenberg-Marquardt, direct comparison of individual parameters is not recommended (Quinn & Deriso 1999; McCallum 2000). Cerrato 1990 found that the maximum log likelihood statistics is the best parameter for comparisons between models considering their full set of parameters at once. The Schnute's F statistics (Schnute 1981) is recommended when a particular model with fewer parameters is confronted against a general one. Growth rate for a particular age-class can be estimated by solving the first derivative (see 3.4.3.2, above).

3.5 METHOD

The method developed in this thesis consists of iteratively checking several properties described below during and after the sequential fit of each individual model contained in two general models. The fit of each model begins with the setting of all parameters but one as constant. If the fit successfully converges, the parameter is considered stable, a new parameter will be set as variable and the process is repeated until all parameters in the model become estimated or until no fit is possible. From the successfully fitted models, other properties also described bellow will be further considered to select the best model among them. The Levenberg-Marquardt method (Marquardt 1963) was chosen for data fitting and an *ad hoc* computer programme for its application was constructed.

Sample pre-processing is recommended before the implementation of the method. The general models, the criteria for selection of parameters and models, and the procedure of pre-processing are described as I follow.

3.5.1 GENERAL MODELS

I propose two general models that will contain the growth models to explore: a single exponential model (equation (27)), and a double exponential model (equation (28)).

The single exponential model (general model 1) is the generalised model for the Logistic, von Bertalanffy, and Richards models. All these growth models share the same parameters and can be considered as special cases of the Richards model. General model 1 incorporates two more parameters *a*, and *c*, which make it possible to convert between models.

$$s = s_{\infty}\left(a - c\ e^{k(t_0 - t)}\right)^{b} \tag{27}$$

s: Size

t: Time (age)

s_{∞}: Asymptotic Size

a: Constant (utility constant)

c: Constant (switch for the logistic model)

k: Constant (steepness of the curve)

t_0: Constant (parameterised age at $s = 0$)

b: Allometric constant

The double exponential model (general model 2) is the generalised model for the Gompertz model and related parameterised equations, and for the exponential Logistic, von Bertalanffy, and Richards models (see exponentials below). Some parameters in the general model 2 have a different meaning, depending on the model analysed, for instance, $c_{\infty} = w_0$ in general model 2 (G2) when exploring equations (20) and (23), and $c_{\infty} = Y_{\infty}$ (asymptotic size) for equations (21) and (22) for Gompertz 1 $c_{\infty} = 1$.

$$s = c_{\infty} e^{c_{s\infty}\left(c_a - c_c e^{-k(t - c_{to})}\right)^{c_b}} \tag{28}$$

S: Size

t: Time (age)

k, c_{∞}, $c_{s\infty}$, c_a, c_b, c_c, and c_{to}: Constants

Parameters a and c_a have a value of 1.0 in all models included in the general models 1 and 2. a and c_a are not substituted by the unit constant value and are maintained as parameters in order to provide further compatibility with single exponential equations, for example the following equation can be derived from equation (27) after setting $a = 0$, $c = -1$, and $m = s_{\infty}$.

$$s = m\ e^{k(t_0 - t)}$$

3.5.2 PROPERTIES TO ANALYSE: CRITERIA FOR SELECTING THE BEST MODEL

The trend compatibility of the data distribution with respect to the model shape will be evaluated in two ways: assessing the visual concordance between data and fitted curve (analysis of scatter plots of residuals), and assessing the visual and quantitative concordance between data and the fitted curve by using averages, medians, or geometric means (statistics of location: Sokal & Rohlf 1969) as central tendency estimators of size at each age value. An alternative to the second method is the visual examination of the trend followed by box and whisker plots (Velleman & Hoaglin 1981; Hoaglin *et al.* 1983) of size per each age group.

The power of fit is measured by the value of the sum of squared residuals (RSS: Hoaglin *et al.* 1983), and the value of the maximum log likelihood (MLL: Schnute 1981, 1982; Cerrato 1990; Quinn & Deriso 1999; Haddon 2001). The significance of individual models with respect to the general models is assessed with the Schnute's F test (SF: Schnute 1981; Quinn & Deriso 1999). Individual models with the lowest RSS and highest MLL are preferred; and stable individual models with non-significant Schnute F statistics are regarded as highly stable.

When referring to models or parameters, the term stability will be used in this thesis to indicate if a fit trial converges to a single solution when estimating parameters. An individual growth model will be stable as part of a general model (general models 1 or 2) if the magnitude of its parameters does not change after the remaining constant parameters in the general model are set as variables. When data are fitted equally well by more than one model, the most stable parameters will be the ones that show similar magnitudes in all models.

The term accuracy will be related to the capacity to output exact values (those closer to the actual ones). The best model will therefore be the more accurate among the stable models. Because the actual values for each parameter are unknown and assuming that data are non-skewed and representative of the population, a particular model will be considered accurate when its sum of squared residuals becomes minimum (the lowest RSS), its residuals distribute normally along the predictor and response variables without characteristic patterns, and when the particular model results non-significant with respect to the general model it belongs. When data are fitted equally well by more than two models, the most accurate parameters will be the ones with higher maximum log likelihood (MLL), lowest Schnute's F statistics (FS), and lowest RSS.

Stability and accuracy depend on the model equation (trend shape, presence and number of parameters, maximums, minimums, discontinuities, singularities), fitting method (initial guess for each parameter, fit direction, stability, parameters and acceptance threshold, number of iterations), rounding error, and data sampling properties (sample size, sample representativeness, outliers, precision, distribution of residuals, error scale –arithmetic or geometric).

When no fit, no stability or poor accuracy is found in a general or particular model, it indicates that the model is not appropriate to describe the data.

All the analyses will be undertaken using individual data for size and age. Statistics of location (Sokal & Rohlf 1969) will only be used in the pre-processing stage because they are helpful for visualising the central tendency of size at each age by considering their means, medians, or geometrical means instead individual values. Statistics of location will not be used in the main part of the methodological process because their application would ignore the standard error product of individual measurements, which is one of the criteria used to assess the power of fit.

3.5.3 SAMPLE PRE-PROCESSING

In order to evaluate the criteria in practice it must be remembered that the distribution of the statistical error, the non-additivity of the error, and the presence of outliers are three factors that strongly affect the fitting efficiency and predictability, influencing the selection of the best model, particularly for small samples[4]. A prior exploration of the size distribution at each age class by box and whisker plots (Velleman & Hoaglin 1981; Hoaglin *et al.* 1983) is recommended to provide visual

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[4] With respect to this issue, there is no real consensus as to how small a sample must be to be considered small (n<10?<10,000?). Based on statistical distributions (basically gaussian distribution), statisticians have set 30 as the limit for small data samples normally distributed (Sokal & Rohlf 1969); nevertheless, the point here is that the effect of outliers increases as the sample size decreases independently of its distribution, a non-additive error will skew the parameters if considered as additive, and a non-normal distribution of error goes against the parametrical assumptions. As an example, the fit from a sample of 10 individuals with a uniform residual error of 0.1 and no outliers can be more reliable than a sample of 2000 with residual error of 1.0 and one outlier 10 times bigger than the residual variance, if both are representative samples.

elements to identify the distribution of the statistical error, the non-additivity of the error, and the presence of outliers; the table of their non-parametrical boundaries can be numerically helpful. *A posterior* tracking of the source and meaning of the inconsistencies will help in deciding the significance of each alternative model and how to cope with the outliers. Stem and leaf plots (Velleman & Hoaglin 1981; Hoaglin *et al.* 1983) and normality tests are more powerful tools than box plots to visualise and quantify these factors, but unless enough data are available, these strict criteria are irrelevant. The use of statistics of location (Sokal & Rohlf 1969) is also recommended.

3.5.4 THE LEVENBERG - MARQUARDT METHOD (LMM)

The Levenberg – Marquardt method (Marquardt 1963) is a minimization method used for non-linear curve fitting. It switches between the inverse-Hessian method (Chapra & Canale 1999) when far from the minimum, and the steepest descent method when near the minimum (Marquardt 1963). It uses the first derivative to calculate new parameter values iteratively, and is considered as a good minimization method (Press *et al.* 1989). This method is widely used in science and engineering and is contained in most commercial computer mathematical packages.

A limitation found when using commercial computer packages is in that usually commercial computer packages do not give complete customisation, and in addition full control over calculations is not possible. This is because the makers of commercial computer packages usually do not publish the basic algorithms they implement, and their manuals describe the theory and mathematical backgrounds only, but not the actual code. In order to sort out this limitation, I made the implementation of the Levenberg-Marquardt Method (LMM) in a computer programme written in Pascal language (Delphi 5, INPRISE 1999). Part of the code was adapted from free code (Press *et al.* 1989; Burton *et al.* 1996; Mikulik 1998; Debord 2001, 2002; Pronin 2002). The building of the *ad hoc* programme was also necessary because the main purpose of the method proposed in this report is to explore and analyse rather than simply fit growth data.

Earlier computer implementations of the LMM were not stable or accurate enough (different output was obtained for different initial values and sometimes the fit was not achieved). The efficiency and accuracy depended on an appropriate initial guess of each parameter and the direction of the initial approximation. Finding more than one solution was common, and some programmes included a contour plot of the iterative output in order to help identify the potential solutions. Haddon (2001) suggests the Simplex Algorithm (Nelder & Mead 1965) as an accurate alternative.

The version of the LMM employed here was mainly adapted from the free code "Data Master 2000" (Pronin 2002). The compiled programme proved to be stable and accurate in all tests done. Even when some unstable behaviour was detected while fitting two of the equations in the general models, a reliable solution was found by selecting different combinations of variables, which is an indication of the power of the programme developed.

3.5.4.1 Partial derivatives

The partial derivatives to solve the inverse Hessian matrixes of the Levenberg-Marquardt method (Table 6 and Table 7) with the computer programme developed to fit the general models 1 and 2 were derived and verified against the commercial computer programme Mathematica (Wolfram Research, 2002. Web Mathematica: http://www.calc101.com/webMathematica/MSP/Calc101/WalkD).

Table 6 and Table 7 include the equations for the actual instantaneous rates of growth of the general models 1 and 2. Both growth rates are not constant, but a function of Age, which means that they are dependent on age.

Table 6: **Partial derivatives for General Model 1.** s : Size; t : Time (age); s_∞ : Asymptotic Size; a: Constant (utility constant); c : Constant (switch for the logistic model); k : Constant (steepness of the curve); t_0 : Constant (parameterised age at $s = 0$); b : Allometric constant.

General model 1	$s = s_\infty \left(a - c\ e^{k(t_0 - t)}\right)^b$
Instantaneous rate of growth	$\frac{\partial s}{\partial t} = \left(a - c\ e^{k(t_0 - t)}\right)^{b-1} e^{k(t_0 - t)}\ b\ s_\infty\ c\ k$
Derivatives	
$\frac{\partial s}{\partial k} = -\left(a - c\ e^{k(t_0 - t)}\right)^{b-1} e^{k(t_0 - t)}\ b\ s_\infty\ c\ \left(t_0 - t\right)$	
$\frac{\partial s}{\partial t_0} = -\left(a - c\ e^{k(t_0 - t)}\right)^{b-1} e^{k(t_0 - t)}\ b\ s_\infty\ c\ k$	
$\frac{\partial s}{\partial b} = \left(a - c\ e^{k(t_0 - t)}\right)^{b} Ln\left(a - c\ e^{k(t_0 - t)}\right) s_\infty$	
$\frac{\partial s}{\partial c} = -\left(a - c\ e^{k(t_0 - t)}\right)^{b-1} e^{k(t_0 - t)}\ b\ s_\infty$	
$\frac{\partial s}{\partial a} = \left(a - c\ e^{k(t_0 - t)}\right)^{b-1}\ b\ s_\infty$	

Table 7: **Partial derivatives for General Model 2.** s : Size; t : Time (age); k : Constant (steepness of the curve); c_∞, to c_b : Constants.

<table>
<tr><td>General model 2</td><td>$s = c_\infty e^{c_{s\infty}(c_a - c_c e^{-k(t-c_{to})})^{c_b}}$</td></tr>
<tr><td>Instantaneous rate of growth</td><td>$\frac{\partial S}{\partial t} = c_\infty c_{s\infty} c_b c_c k\, e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b} + k\,(c_{t_0}-t)} \left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b-1}$</td></tr>
<tr><td colspan="2">Derivatives</td></tr>
<tr><td colspan="2">$\frac{\partial S}{\partial c_\infty} = e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b}}$</td></tr>
<tr><td colspan="2">$\frac{\partial S}{\partial c_{s\infty}} = c_\infty e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b}} \left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b}$</td></tr>
<tr><td colspan="2">$\frac{\partial S}{\partial c_a} = c_\infty c_{s\infty} c_b e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b}} \left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b-1}$</td></tr>
<tr><td colspan="2">$\frac{\partial S}{\partial c_c} = -c_\infty c_{s\infty} c_b e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b} + k\,(c_{t_0}-t)} \left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b-1}$</td></tr>
<tr><td colspan="2">$\frac{\partial S}{\partial k} = c_\infty c_{s\infty} c_b c_c (t-1)\, e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b} + k\,(c_{t_0}-t)^{c_b-1}} \left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b-1}$</td></tr>
<tr><td colspan="2">$\frac{\partial S}{\partial c_{t_0}} = -c_\infty c_{s\infty} c_b c_c k\, e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b}} \left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b} \left(c_c - c_a e^{k\,(c_{t_0}-t)}\right)$</td></tr>
<tr><td colspan="2">$\frac{\partial S}{\partial c_b} = c_\infty c_{s\infty} e^{c_{s\infty}\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b}} \left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)^{c_b} \ln\left(c_a - c_c e^{k\,(c_{t_0}-t)}\right)$</td></tr>
</table>

3.5.4.2 Control of parameters

When a parameter is set as constant, its derivative becomes equal to zero and the programme uses the constant value given by the user instead the value of the derivative (0), which is a practical way to convert a parameter to a constant in order to differentiate between models. For example, in the Richards model c is set as variable and t_0 as a constant equal to zero, and for the von Bertalanffy model, t_0 is set as variable and c as a constant equal to one. This is equivalent to a conversion of the general model into a particular model by reducing the number of variables. Default values for each parameter are set automatically accordingly to the particular model chosen, but manual settings may be required depending on each data set when stability and accuracy of particular parameters or models is assessed. All parameters in both general models can be evaluated if the model results are stable for the data set in question, but a guess close to their actual value is necessary. To overcome this problem it is recommended to set all parameters as constant with average or expected values and make them a variable one at a time.

3.5.5 EVALUATION SEQUENCE

General model 1 was explored as the first option, followed by general model 2. When non-normal distribution of the residuals is detected, general model 1 may be discarded and a log transformation of the variables can be performed. The simpler equations in each proposed model have to be fitted first, followed by the complex ones in order to detect hard to fit and unstable variables. The following protocol for fitting the models was developed:

First: select the initial values for each parameter. Because the actual values for each parameter are unknown, I suggest the initial guesses displayed in Table 8 for the general model 1: this is because k oscillates between 0 and 3 for many species, the allometric constant b is usually close to 1.0 for length and 3.0 for weight, and in most cases t_0 is close to 0.0. Table 16 contains initial values suggested for parameters of the general model 2.

Table 8: **Initial settings for fitting von Bertalanffy (vBL for length and vBW for weight), Richards (R), and Logistic (L) for the fish species Smooth Oreo (*Pseudocyttus maculatus*).** S_∞ (Asymptotic size), k (Slope steepness), b (Allometric constant), and c and a (Constants) are the growth parameters contained in the General Model 1.

	vBL	vBW	R	L
s_x	1000	1000	1000	1000
k	0.5	0.5	0.5	0.5
t_0	0	0	0	0
b	1	3	1	-1
c	1	1	1	-1
a	1	1	1	1

Table 9: **Initial settings for fitting models in General Model 2 for Smooth Oreo (*Pseudocyttus maculatus*).** S_∞ (Asymptotic size), k (Slope steepness), b (Allometric constant), and c and a (Constants) are growth parameters for Gompertz 1 (G1), Gompertz 2 (G2), Gompertz 3 (G3), Gompertz 4 (G4), Exponential of von Bertalanffy (vBE), exponential of Richards (RE), and Exponential of Logistic (LE).

	G1	G2	G3	G4	vBE	RE	LE
k	1	1	1	1	1	1	1
c_x	0.5	0.5	0.5	0.5	0.5	0.5	0.5
c_{sx}	0	0	0	0	0	0	0
c_a	1	1	1	1	1	1	-1
c_c	1	1	1	1	1	1	-1
c_{t0}	1	0	0	1	1	1	1
c_b	1	100	1	1	1	1	1

Second: The first fit trial will consider all parameters as constant, except the asymptote (it is expected that the estimation of the asymptotic parameters becomes powerfully consistent because of the accuracy of the LMM).

Third: the processes of fitting will continue with the sequential change of the other parameters from constants to variables with the less stable parameters been converted last (t_0 for example).

3.5.6 CHOOSING THE BEST MODEL

The algorithm implemented in my computer programme forces calculations to run at least once. This is particularly useful to overcome intermediate solutions that may be unstable or rough approximations of the final value. By forcing calculations until the parameters do not change, a better fit can be achieved with more, reliable significant digits. There is also a tendency to keep new fits close to the previous one, as long as the new one becomes better than the previous. This behaviour is an advantage if the more stable and accurate parameters are introduced first, otherwise differences in the order of the selection of parameters may lead to different results.

Exploration of the simplest models should be the starting point. All parameters must be kept constant, except the more stable ones (usually the asymptotic parameter). Once an output is obtained, a new iteration has to be forced until the maximum number of iterations is reached, or until the output does not differ. If the output reaches a stable value, this output will be considered as a stable fit for that parameter.

After a stable parameter is fitted, a new parameter has to be converted to a variable, repeating the process until a stable fit occurs or stability is discarded. Complex models (with more parameters) should be explored at the end until the complete general model is ascertained.

From the mathematical point of view, the best individual model will be the most stable one. If more than one individual model is stable, accuracy has to be considered as a deciding criterion (see 3.5.2, p. 62).

With the purpose of considering if a fit is acceptable, the following must be accomplished.

a) Residuals have to be distributed without an identifiable pattern.
b) Residuals have to be distributed normally for each value of the predictor variable along the range of distribution of the response variable.
c) A low RSS and a high MLL will be preferred.

In order to have an independent estimation of the curve trend, it is also recommended to fit the same model by using the statistics of location average, geometric mean, and median size at each individual length. Regardless of the scale of the error distribution, the median should always be closer to the arithmetic and geometric means. This fit does not have any statistical value, but will help to visualise the general trend by reducing the effects of scale and outliers. When the distribution of the error is normal and outliers are absent, more accurate results will be achieved.

During the application of the method, empirical and biological explanations for the model parameters must be secondary to the mathematical reasoning.

3.6 RESULTS

3.6.1 PERFORMANCE ON A THEORETICAL DATA SET

3.6.1.1 The data

The ability to estimate the actual parameters of a model depends, among other factors, on the data precision. To assess the power of the proposed programme to find the actual values for each parameter, the programme output was tested with different data sets with known parameters and different precisions (different parameters were tested for each individual model). The following is the result of a test applied to the von Bertalanffy model.

A set of 50 data for theoretical ages 1 to 50 was created for the von Bertalanffy model with $L_\infty = 35$, $k = 0.085$, and $t_0 = 0.1666$.

Theoretical lengths were estimated by rounding to 1, 2, 3, and 4 decimal places in order to assess the influence of data precision on the fit. Table 10 contains the estimated lengths. vBL1 is the length estimated with precision of one digit, vBL2 is the length estimated with precision of two digits, and so on.

Theoretical weights were calculated assuming the following parameters for the length – weight relationship.

$$W = 0.0065L^{3.1}$$

Ten decimal places as is shown in Table 11 were maintained for the estimated weights to reduce extra noise due to its multiplicative scale. vBW1 is the weight calculated from vBL1, vBW2 the weight calculated from vBL2, and so on.

Table 10: **Hypothetical data sets with four levels of precision.** vBL1: length rounded to one decimal place, vBL2: length rounded to two decimal places, and so on.

Age	vBL1	vBL2	vBL3	vBL4
1	2.4	2.39	2.394	2.3936
2	5.1	5.05	5.051	5.0506
3	7.5	7.49	7.491	7.4911
4	9.7	9.73	9.733	9.7328
5	11.8	11.79	11.792	11.7917
6	13.7	13.68	13.683	13.6829
7	15.4	15.42	15.42	15.42
8	17	17.02	17.016	17.0155
9	18.5	18.48	18.481	18.481
10	19.8	19.83	19.827	19.8271
11	21.1	21.06	21.064	21.0635
12	22.2	22.2	22.199	22.1992
13	23.2	23.24	23.242	23.2423
14	24.2	24.2	24.2	24.2004
15	25.1	25.08	25.08	25.0804
16	25.9	25.89	25.889	25.8888
17	26.6	26.63	26.631	26.6312
18	27.3	27.31	27.313	27.3132
19	27.9	27.94	27.94	27.9395
20	28.5	28.51	28.515	28.5149
21	29	29.04	29.043	29.0433
22	29.5	29.53	29.529	29.5287
23	30	29.97	29.975	29.9746
24	30.4	30.38	30.384	30.3841
25	30.8	30.76	30.76	30.7602
26	31.1	31.11	31.106	31.1057
27	31.4	31.42	31.423	31.4231
28	31.7	31.71	31.715	31.7145
29	32	31.98	31.982	31.9823
30	32.2	32.23	32.228	32.2282
31	32.5	32.45	32.454	32.454
32	32.7	32.66	32.662	32.6615
33	32.9	32.85	32.852	32.8521
34	33	33.03	33.027	33.0271
35	33.2	33.19	33.188	33.1879
36	33.3	33.34	33.336	33.3355
37	33.5	33.47	33.471	33.4712
38	33.6	33.6	33.596	33.5957
39	33.7	33.71	33.71	33.7102
40	33.8	33.82	33.815	33.8153
41	33.9	33.91	33.912	33.9118
42	34	34	34	34.0005
43	34.1	34.08	34.082	34.0819
44	34.2	34.16	34.157	34.1567
45	34.2	34.23	34.225	34.2255
46	34.3	34.29	34.289	34.2886
47	34.3	34.35	34.347	34.3466
48	34.4	34.4	34.4	34.3998
49	34.4	34.45	34.449	34.4487
50	34.5	34.49	34.494	34.4936

Table 11: **Estimated weights up to 10 decimal places calculated from** Table 10. vBW1 corresponds to vBL1; vBW2 corresponds to vBL2, and so on.

Age	vBW1	vBW2	vBW3	vBW4
1	0.098077233	0.096815936	0.097319128	0.097268729
2	1.014801037	0.984275395	0.98487973	0.984637966
3	3.354310589	3.340465506	3.341848269	3.341986566
4	7.445703413	7.51732214	7.524509574	7.524030267
5	13.66934105	13.63346201	13.64063271	13.63955694
6	21.71436406	21.61624522	21.63094386	21.6304538
7	31.20524461	31.33104751	31.33104751	31.33104751
8	42.39406027	42.54886498	42.51787345	42.51400059
9	55.09925347	54.91480604	54.92401846	54.92401846
10	68.01041837	68.33036973	68.29832881	68.29939668
11	82.83024922	82.34444256	82.39293613	82.38687338
12	96.96334238	96.96334238	96.94980309	96.95251085
13	111.1542595	111.7494361	111.7792514	111.7837242
14	126.6896077	126.6896077	126.6896077	126.6960993
15	141.8736994	141.5235475	141.5235475	141.5305448
16	156.3661075	156.1790271	156.1603274	156.1565876
17	169.8425221	170.4370359	170.4568772	170.4608457
18	184.0846442	184.2937585	184.3565241	184.360709
19	196.9184401	197.7949513	197.7949513	197.7839787
20	210.3451112	210.5739919	210.6884955	210.6862051
21	221.9970228	222.9476269	223.0190331	223.0261746
22	234.0785433	234.8172741	234.7926244	234.7852298
23	246.5978275	245.8341767	245.9613404	245.9511657
24	256.9339336	256.4102855	256.5149572	256.5175744
25	267.5596245	266.4839046	266.4839046	266.4892759
26	275.7214556	275.9963833	275.88639	275.8781417
27	284.0503087	284.6115476	284.6957982	284.6986068
28	292.547957	292.8341396	292.9773021	292.9629837
29	301.2161751	300.6329516	300.6912395	300.6999834
30	307.0906254	307.9784321	307.919191	307.9251148
31	316.0470753	314.5422073	314.6624178	314.6624178
32	322.1153269	320.895418	320.956339	320.941108
33	328.262022	326.7179653	326.7796329	326.7827165
34	331.3649508	332.2996892	332.2061351	332.2092533
35	337.6303011	337.3151436	337.2521361	337.2489859
36	340.7928547	342.0634744	341.9362683	341.9203698
37	347.1780492	346.2151474	346.2472149	346.2536287
38	350.4008222	350.4008222	350.2715238	350.2618277
39	353.6438007	353.9692123	353.9692123	353.9757226
40	356.9070507	357.5621391	357.3982907	357.4081202
41	360.1906384	360.5201183	360.5860388	360.5794464
42	363.4946301	363.4946301	363.4946301	363.5112015
43	366.819092	366.1525588	366.2191752	366.2158442
44	370.1640903	368.8236224	368.72322	368.7131808
45	370.1640903	371.1716042	371.0035564	371.0203589
46	373.5296912	373.1922021	373.1584645	373.1449701
47	373.5296912	375.2202383	375.1186596	375.1051172
48	376.915961	376.915961	376.915961	376.9091678
49	376.915961	378.6168675	378.5827985	378.5725782
50	380.3229661	379.9813306	380.1179598	380.1042954

3.6.1.2 The application of the method

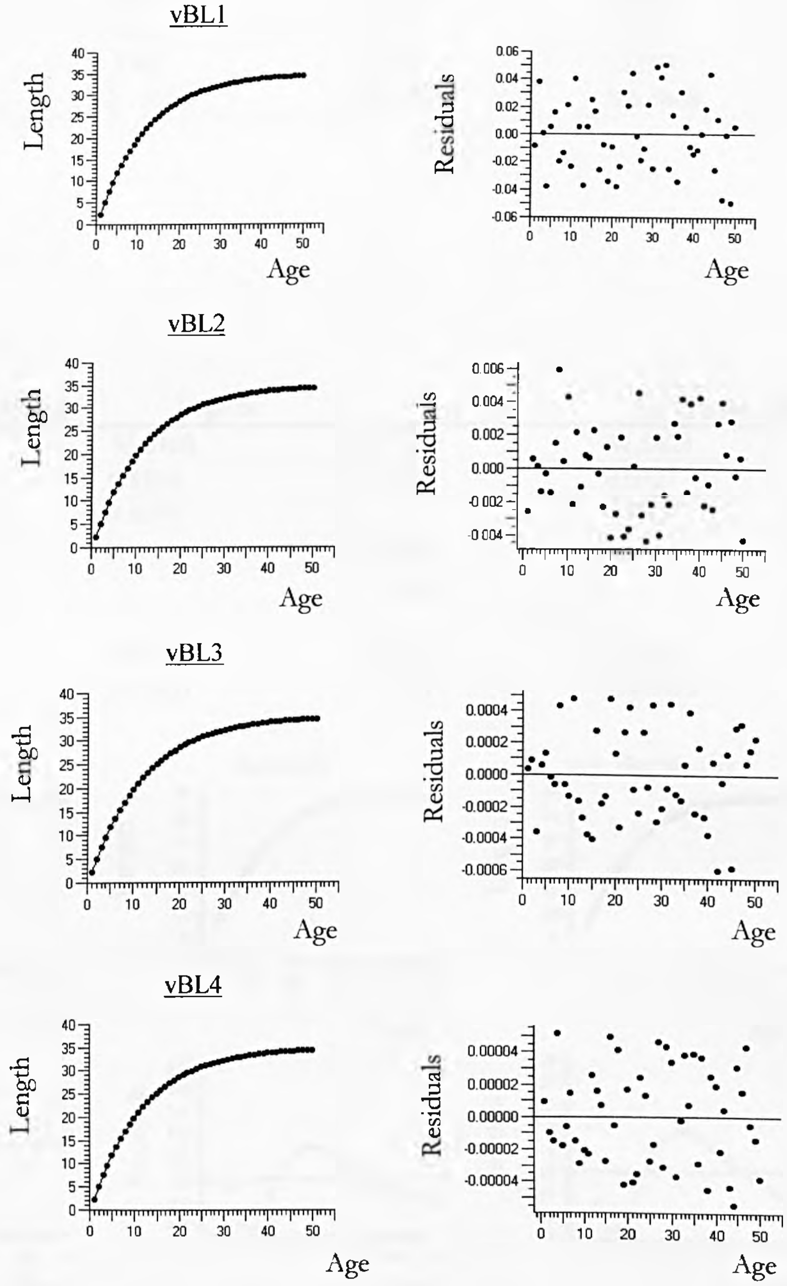
It can be seen from the magnitude of the fitted parameters in Figure 9 that the resemblance to the original parameters increases for length with the data precision level. The fit improves generating smaller residuals squares sum (RSS), bigger maximum log likelihood (MLL), and lower orders of magnitude for residuals (10^{-2}, 10^{-3}, and 10^{-4} cm).

Comparable results are obtained for weights (Table 12). In this case k is the more accurate parameter, followed by W_{inf} and b. t_0 is the less accurate parameter (more distant to the actual value, *i.e.* less exact).

The capacity to assess the best model depends on the power to get a good fit (goodness of fit) and the confirmation that the model appropriately describes the data pattern. The tools employed here to measure the goodness of fit are the square sum of residuals (RSS) and the maximum log likelihood (MLL). A high MLL and a low RSS for a particular model indicates that such model should be preferred over the other alternatives. Plots of residuals are the tools to visually reveal whether the model is an adequate descriptor of the data. The visual analysis reveals patterns in the distribution of residuals if any, and models with residuals showing no systematic patterns are preferred.

To assess the ability of the programme to find the actual model, the programme output was tested with different data sets belonging to different classical growth models. Lengths were calculated for 50 hypothetical ages from 1 to 50 ages units, using theoretical parameters chosen in order to make the lengths at each age as close as possible between different models (Table 10). All lengths were rounded up to one significant digit to keep the maximum noise produced by rounding to the nearest when taking real measurements. The measurement of the degree of tolerance to data variability is not a target in this test; therefore, in order to avoid the effect of other sources of error (e.g. Cerrato 1991; Pilling *et al.* 2002), perfect data sets were simulated for the testing of each model.

Both plots for residuals and fitted curve for the Logistical model are shown in Figure 10. As expected, the RSS and plot of residuals are powerful criteria for selection of the best model that describes the data when the model is stable. The best model has the lowest RSS, highest MLL, and its plot of residuals shows to the eye a more homogeneous distribution of residuals around 0.0 without particular distribution patterns.



n	50
L_{inf}	35.003129
k	0.084911
t_0	0.160416
RSS	0.035301
MLL	110.4495

n	50
L_{inf}	35.000980
k	0.084989
t_0	0.166878
RSS	0.000356
MLL	225.3395

n	50
L_{inf}	35.000181
k	0.084998
t_0	0.166447
RSS	3.9045×10^{-6}
MLL	338.1876

n	50
L_{inf}	35.000009
k	0.084999
t_0	0.166597
RSS	4.3955×10^{-8}
MLL	450.3559

Figure 9: **Fit of a same data set at different levels of precision achieved by rounding individual lengths to one, two, three, and four decimal places.** vBL1: length rounded to 1 significant digit, vBL2: length rounded to 2 decimal places, and so on; L_{inf}, k, and t_0: parameters of the von Bertalanffy model; RSS: square sum of residuals; MLL: maximum log likelihood.

Table 12: **Parameters estimated for weights fitted from** Table 11. vBW1 corresponds to vBL1; vBW2 corresponds to vBL2, and so on.

	vBW1	vBW2	vBW3	vBW4
W_{inf}	396.9271	397.7707	397.6775	397.6711
k	0.0858	0.0849	0.0849	0.0850
t_0	-0.0629	0.1664	0.1665	0.1665
b	3.2209	3.0982	3.0999	3.1000
RSS	23.5610	0.2382	0.0027	3.1759
MLL	0.2195	62.7108	174.2553	285.7868

	Original (Logistic)	Logistic	Richards	von Bertalanffy
Sinf	33.5	33.5105	34.2410	34.5829
k	0.18	0.1801	0.1062	0.0927
t_0	8.8	8.8079		0.7903
b	-1		1.3094	
c	-1		Unstable	
a	1			
RSS		0.044962	20.6379	27.6255
MLL		99.2461	-47.8514	-54.8499

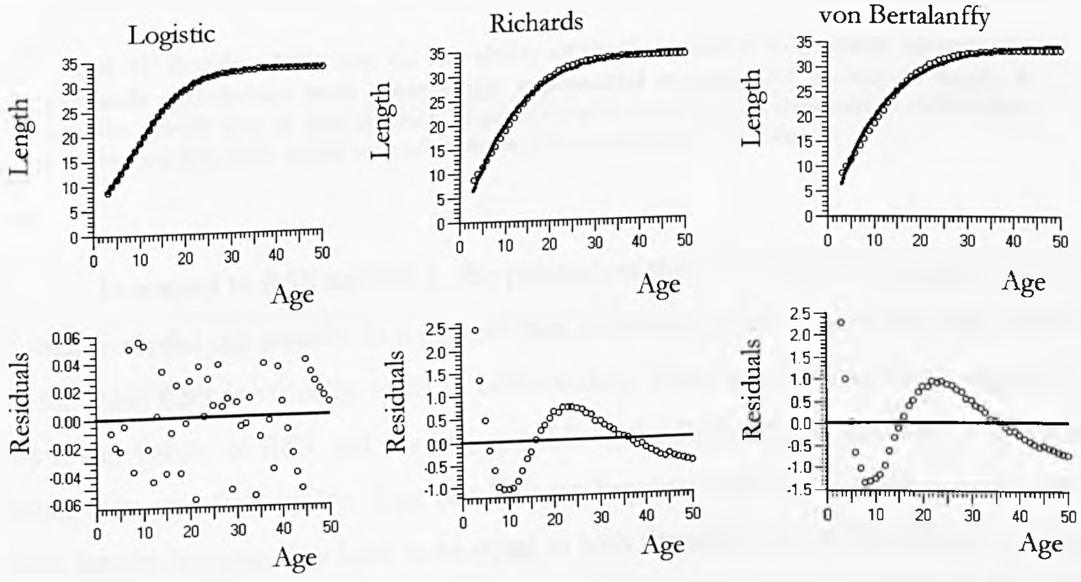


Figure 10: **Results of the test for the ability of the programme to properly identify the logistic distribution from other single exponential models.** *Sinf*: asymptotic length, *k*: intrinsic growth rate, t_0: time at which length is equal to zero, *c* and *a*: constants to differentiate between models, RSS: square sum of residuals, MLL: maximum log likelihood.

The data generated with the Richards model were a better fit with the Richards curve as shown in Figure 11 (lower RSS and higher MLL). Scatter plots and fitted curves no longer will be displayed for most of the remaining cases of this test because the residuals plots are more informative for revealing distribution patterns than the Age – length plots and their fitted curves.

	Original (Richards)	Logistic	Richards	von Bertalanffy
Sinf	35	34.3073	35.0015	35.3164
k	0.12	0.1986	0.1196	0.1026
t_0	0	8.8877		1.6166
b	1.55		1.5402	
c	1		1.0012	
a	1			
RSS		22.5768	0.0363	2.3544
MLL		-50.0064	104.3250	4.2486

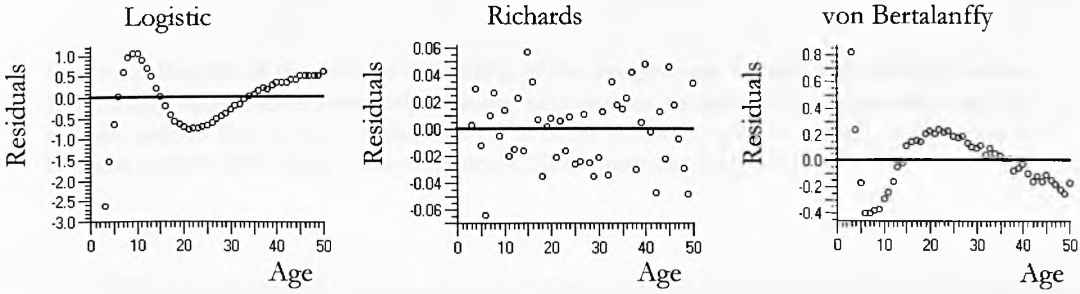


Figure 11: **Results of the test for the ability of the programme to properly identify the Richards distribution from other single exponential models.** Sinf: asymptotic length, *k*: intrinsic growth rate, t_0: time at which length is equal to zero, *c* and *a*: constants to differentiate between models, RSS: square sum of residuals, MLL: maximum log likelihood.

In respect to RSS and MLL, the parameters shown in Table 13 suggest that the Richards model can equally fit a data set that distributes as the von Bertalanffy model. In this case RSS is virtually equal in both models. From a non-conservative approach the lower values of RSS and the higher MLL in the Richards model make it slightly better than von Bertalanffy. This can become important when calculating *k* and *Sinf* from lengths because they have to be equal in both fits regardless of the value of t_0, any departure of *b* in Richards from 1.0 means an allometric misfit masked in the von Bertalanffy t_0 (as analysed more in deep in the next chapter).

	Original (von Bertalanffy)	Logistic	Richards	von Bertalanffy
Sinf	35	34.2194	34.9934	34.9966
k	0.12	0.2266	0.1201	0.11997
t_0	2	8.2964		1.9925
b	1		1.0039	
c	1		1.2689	
a	1			
RSS		40.5277	0.0423	0.0427
MLL		-64.0478	100.6704	100.4465

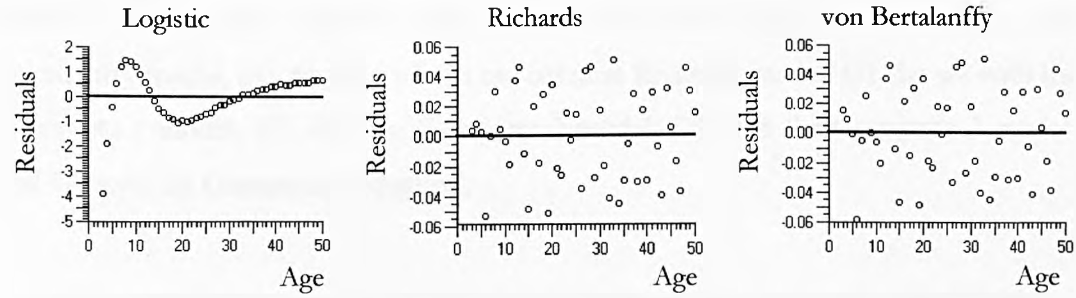


Figure 12: **Results of the test for the ability of the programme to properly identify the von Bertalanffy distribution from other single exponential models.** Sinf: asymptotic length, *k*: intrinsic growth rate, t_0: time at which length is equal to zero, *c* and *a*: constants to differentiate between models, RSS: square sum of residuals, MLL: maximum log likelihood.

With exception of the Gompertz 3 data, the models the data came from fitted the rest of the data sets better. Gompertz 3 data set was not fitted by the exponential of Richards, Gompertz 1 and 2 models at all. Gompertz 3 model was highly unstable even with its own data set.

Table 13: **Results of the test for the ability of the programme to properly identify double exponential distributions from other double exponential models.** *Csinf*: asymptotic length, *k*: intrinsic growth rate, *Ct0*: time at which length is equal to zero, *Ca*, *Cb*, and *Cc*: constants to differentiate between models, RSS: square sum of residuals, MLL: maximum log likelihood.

	Elo	EvB	Eri	G1	G2	G4
Sinf	-3.5501	3.5499	3.5470	2.2762	2.2845	2.2762
k	0.1199	0.1200	0.1201	0.1197	0.1201	0.1197
t_0	-0.7489	-4.7000	0	0	$-3.2\ \mathrm{x}10^{-19}$	0
b			0.5017	1	1	1
c			1.0016	1	1	1
a				1	1	1
c_{inf}				3.5644	3.5623	3.5644
RSS	0.0380	0.0396	0.0451	0.0365	0.0349	0.0365
MLL	103.2692	102.2492	99.1251	104.1953	105.2739	104.1953

Double exponential models resulted harder to fit than single exponential ones. The data sets used for testing the ability of the method to properly identify the double exponential distributions from other double exponential models where generated from the parameters listed in Table 14. Those parameters were selected in order to make individual lengths as similar as possible at each age in each model. Common parameters in all models were also kept as similar as possible; actually, *k* is the same for all models while *Sinf* is for most of them. Elo is the set of parameters according with the exponential logistic model, EvB is the set with the exponential von Bertalanffy model, Eri the set with the exponential Richards model, G1 the set with the Gompertz 1 model, G2 with the Gompertz 2 model, G3 with the Gompertz 3 model, and G4 with the Gompertz 4 equation.

Table 14: **Parameters used to simulate the data sets used for testing the ability of the method to properly identify the double exponential distributions from other double exponential models.** Elo is the set of parameters accordingly with the exponential logistic model, EvB with the exponential von Bertalanffy model, Eri for the exponential Richards model, G1 for the Gompertz 1 model, G2 for the Gompertz 2 model, G3 for the Gompertz 3 model, and G4 for the Gompertz 4 equation.

	Elo	EvB	Eri	G1	G2	G3	G4
Sinf	-3.55	3.55	3.55	2.28	2.28	1	2.28
k	0.12	0.12	0.12	0.12	0.12	0.12	0.12
t_0	-0.75	-4.7	0	0	0	6.5	0
b	-1	1	0.5	1	1	1	1
c	-1	1	1	1	1	1	1
a	1	1	1	1	0	0	1
c_{inf}	1	1	1	3.55	3.5	35	3.55

3.6.1.3 Analysis of results

Precision is not a problem for the calculation of asymptotic size (in this case asymptotic length). The calculated value is 0.0089% units of length apart from the actual value, and 3 $x10^{-2}$ units away from the precision level used to register size (1 $x10^{-1}$).

The calculated value is 0.1% units of length different from the actual value, but because the magnitude of *k* is in 1 $x10^{-3}$ unit, the magnitude of this parameter is more affected than the asymptotic length at the same precision level used to register size (1 $x10^{-1}$).

t_0 is the parameter calculated with the lowest precision (0.5% units). The estimation of t_0 will always be uncertain because size and age cannot be registered at higher precision levels. Fortunately, this parameter is usually not used for different purposes other than the growth equations.

A similar behaviour is observed for weight, but with a general level of precision 10 times lower than for length (asymptotic weight= 0.2%, $k = 1\%$, $t_0 = 38\%$). This difference is quite high when considering that the variability (statistical error respect to the true value) depends on the precision of the data (number of significant digits).

Stability was not important for excluding parameters and models in this theoretical case. Because the data sets for different models were designed to lay as close as possible to the others, the differences appear only when comparing the distribution of residuals.

The lack of stability for the Gompertz 3 model emphasises the need to set limits to the upper and lower values for models, by introducing both the asymptotic size (upper limit) and t_0 (lower limit) as parameters: Gompertz 3 model does not include t_0. This is why it is hard to get a good fit when young or old individuals are absent in data sets. Based on the patterns in the distribution of residuals, the method was efficient for discarding the inappropriate models in such a way that with the exception of Gompertz 3 model all departures from the model where easily detected.

It is expected that the Richards model can fit data distributed accordingly to the generalised von Bertalanffy model because the later can be considered as a special case of the first as seen in the equations below. In practice the Richards model occasionally produces similar values for the parameters of the von Bertalanffy distribution and sometimes constitutes a better fit (smaller RSS, and bigger MLL).

$$s = s_\infty\left(1 - e^{-k(t-t_0)}\right)^b = s_\infty\left(1 - ce^{-kt}\right)^b \text{ for } c = e^{kt_0}$$

As a general conclusion, the method is effective in identifying the right model if data are distributed according to any of the models the method is designed for. Other properties such as accuracy, and the ones suggested as part of pre-processing could not have been tested with this data set, but they will be applied in the following section.

3.6.2 APPLICATION ON A KNOWN CASE

The evaluation of the threshold data variability at which the method can find the best model is a task that goes beyond the original objectives of this thesis; therefore no further attempt will be made for testing the method and the programme implemented on data sets with different levels of data variability. The application of the method on the following case is intended only to show the performance of the method on real data sets.

3.6.2.1 Problem

Smooth Oreo (*Pseudocyttus maculatus* Gilchrist, 1906) is a species exploited commercially for Australian local markets, including the Sydney Fish Market. The species belongs to the family Oreostomidae (Oreos), Order Zeiformes, and Class Actinopterygii (ray-finned fishes), and is distributed in the Southwest Atlantic (Heemstra 1990). Smith & Stewart (1994) estimated the von Bertalanffy parameters for this species from samples of commercial catches off Tasmania (Table 22). They selected the von Bertalanffy model due to its wide usage in the field (it is useful for data comparisons) and made their estimations using a non-linear method of the SAS statistics computer package (SAS Institute Inc., Cary, NC).

The same data set used by Smith & Stewart (1994) is analysed in this review with the proposed method. The data set contains measurements of age and standard length for 131 individuals of mixed sexes. Age is expressed in years and length in centimetres. Age was read to the closest year and length to the closest millimetre.

The objective is to assess if the von Bertalanffy model is the best model to describe this data set. Also to verify that the results obtained by the method proposed and the computer programme developed agree with those generated by other means.

3.6.2.2 The application of the method

3.6.2.2.1 Pre-processing

Visual and semi-quantitative analysis of the data distribution with box and whisker plots (Hoaglin *et al.* 1983) and statistics of location (Sokal & Rohlf 1969) is considered as a purely qualitative tool. In the box & whisker plots for length at each age (Figure 13) most boxes look symmetrical around the median and the skewed ones are randomly positioned on the plot. The box H-Spread (distance between the upper and lower hinges) is shorter for younger ages. Although when not enough older fishes are available, this may suggest that a multiplicative error can be expected (non-additive error: multiplicative scale). A closer look to the scatter plots of the fit of the different models and their plots of residuals (Figure 14 to Figure 16) reveals that there is not a clear tendency for the residuals to increase with respect to length; therefore an additive error can be assumed and additive error based tests can be used for comparisons between models (maximum log likelihood: MLL and Schnute's F test: SF).

As estimators of central tendency, the average and median values for length at each age class with more than two individuals per class (n>2) were similar at each age class (Table 16), which suggests that any skewness was not important.

The location at the mid distance between the two hinges of a box plot (MD) is a resistant parameter that indicates symmetry when equal to the median (for example, if median M = 3.5 and for upper hinge = 5.0 and lower hinge = 2.0, MD = (5+2)/2= 3.5). For this sample (Table 16), both median and MD where similar in most age classes with n > 2; even so, they were very close to the average in most cases (a parametric non-resistant estimator of central tendency). The difference between median and MD was always smaller than the standard deviation in each age class, which implies that the variations fall within an acceptable level of statistical error. In 50% of the age groups MD was higher than the median, in 45% it was lower and in 5% the values were equal. The pattern of the difference between MD and median was not length or age dependant and therefore not asymmetrical (*i.e.* is randomly distributed).

Table 15: **von Bertalanffy growth parameters for Smooth Oreo (*Pseudocyttus maculatus*) from average, geometric mean, and median length at each age class (46 age classes).** Average (A), Geometric Mean (GM), Median (M), and the parameters estimated (S&S) by Smith & Stewart (1994); RSS: residuals square sum, MLL: maximum log likelihood.

	k	t_0	*Linf*	RSS	MLL	No. of Iterations
A	0.0336	-3.1818	57.2625	4.8215	-13.3933	4038
GM	0.0334	-3.1997	57.3130	4.8862	-13.6999	4179
M	0.0332	-3.2624	57.3794	5.2573	-15.3836	4147
S&S	0.051	1.05	50.94	--------	--------	--------

In order to examine the general trend without the influence of many points, the von Bertalanffy model was fitted as a first step using average lengths at each age (year classes), using geometric mean lengths at each age, and using median lengths at each age (Table 15). Differences between the parameters were small, all curve fittings were achieved at similar number of iterations, and RSS and MLL results were similar for the average and geometric mean. For medians this parameter was slightly higher.

A light s-shape trend can be noticed from the box & whisker plot (Figure 13). This s-shape trend is revealed clearer in the scatter plots of the statistics of location (average, median, and geometric mean) with respect to age (Figure 18, p. 101).

Figure 13: **Length at age distribution for Smooth Oreo (*Pseudocyttus maculatus*).**

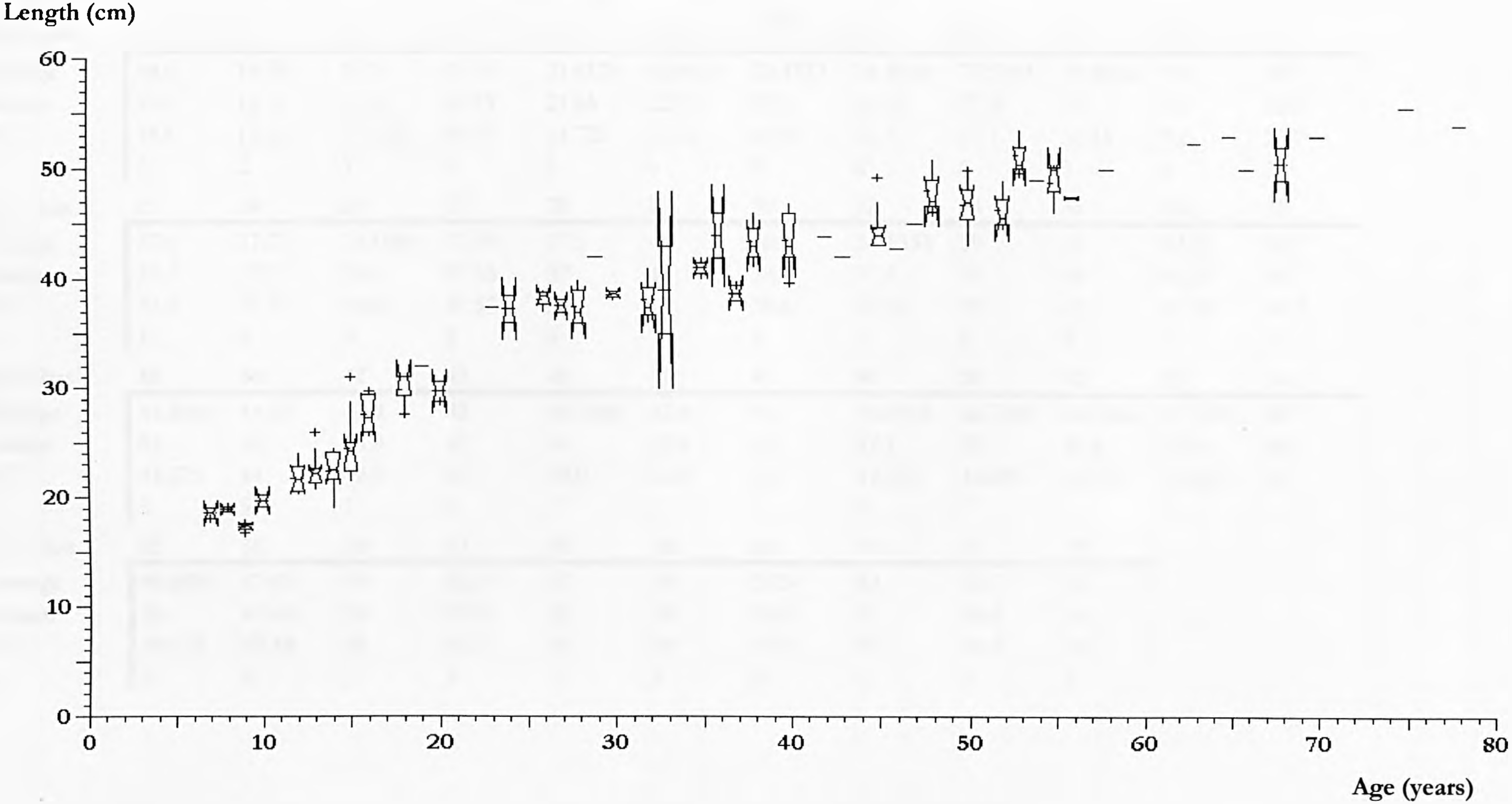


Table 16: **Central tendency of Length at each age class for Smooth Oreo (*Pseudocyttus maculatus*).** MD is the location at the mid distance between upper and lower box plot hinges (for example, for upper hinge = 5.0 and lower hinge = 2.0, MD = (5+2)/2= 3.5).

Age Class	7	8	9	10	12	13	14	15	16	18	19	20
Average	18.6	18.95	17.3	19.75	21.8125	22.4833	22.4333	24.4625	27.5333	29.8666	32	29.7
Median	18.6	18.95	17.4	19.75	21.65	22.15	22.5	24.25	27.3	31	32	29.7
MD	18.6	18.95	17.325	19.75	21.725	21.95	22.85	23.7	27.7	30.15	32	29.7
n	2	2	3	2	8	6	9	8	6	3	1	2

Age Class	23	24	26	27	28	29	30	32	33	35	36	37
Average	37.4	37.25	38.1666	37.55	37.5	42	38.6	38.1333	39	41	43.95	38.7
Median	37.4	37.25	38.5	37.55	37	42	38.7	37.4	39	41	43.95	38.7
MD	37.4	37.25	38.25	37.55	37.5	42	38.6	37.95	39	41	43.95	38.7
n	1	2	3	2	4	1	4	3	2	3	2	2

Age Class	38	40	42	43	45	46	47	48	50	52	53	54
Average	43.3666	43.52	43.8	42	44.5428	42.8	45	48.0666	46.7428	46.3666	51.2333	49
Median	43	43	43.8	42	44	42.8	45	47.1	47	45.6	50.4	49
MD	43.275	44	43.8	42	43.9	42.8	45	47.825	46.825	46.175	51.025	49
n	3	5	1	1	7	1	1	3	7	3	3	1

Age Class	55	56	58	63	65	66	68	70	75	78
Average	48.8333	47.45	50	52.3	53	50	50.5	53	55.6	54
Median	50	47.45	50	52.3	53	50	50.5	53	55.6	54
MD	49.125	47.45	50	52.3	53	50	50.5	53	55.6	54
n	3	2	1	1	1	1	2	1	1	1

3.6.2.2.2 Stability of single exponential models contained in general model 1

All models were tested using individual length and age data and not the central tendency estimators used previously in the pre-processing stage.

The logistic model fitted with no problems and resulted in stable parameters. The general model did not stabilise for all parameters set as variables. After $3x10^6$ iterations, *b* and *c* increased, t_0 decreased, and all of them varied without approaching to a particular value (Table 17). Because no clear tendency toward a constant result was detected, the process was stopped. The low maximum log likelihood for the fit of the logistic equation (just above of the one for the length-at-age von Bertalanffy which is the lowest: see Table 22), indicates that this is not the best fit. The unstable fit of the general model has a lower RSS and shows to be significant with respect of the logistic model according with the Schnute's F test (SF). A non-significant SF for a stable particular model with respect to a general model indicates a highly stable particular model.

Table 17: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*). Testing stability of the Logistic equation.** Final values for all parameters (general model 1) contrasted with those in the Logistic model. *a*, *c*, and *b* are kept constant in the logistic model (*a*= 1; *c*= -1; *b*= -1); SF: Schnute's F; Iter: number of iterations.

	Logistic (*a*= 1; *c*= -1; *b*= -1)	General model 1
Linf	51.2376	52.8665
k	0.0754	0.0556
t_o	15.6210	-25.5039
b		-282.4160
c		-0.0250
a		1
RSS	775.1771	725.6616
MLL	-302.3330	-298.0095
SF	SF= 4.2988 > ($F_{0.05(2, 126)}$= 3.07)	
Iter.	(2)	3,000,001

(1) Value of the constant parameter after set as variable.

(2) Not relevant.

The von Bertalanffy model fits the data well. Parameters *a* and *c* were very close to the *a priori* constant values (the difference was in the sixth significant digit, that is one less than the limit for the Pentium III processor that can be considered free from rounding error at its standard default settings), which according to the definition of stability previously given, means that parameters *a* and *c* were stable at their *a priori* constant values (Table 18, C and D), and *b* resulted an influencing parameter that modified the other parameters, particularly t_0 after setting it as variable (Table 18, A and B). All von Bertalanffy parameters were in agreement with all parameters in general model 1 after setting *b* as variable (Table 18, B and E). The general model is no significant with respect to the von Bertalanffy length-at-age model (Table 18-A) and the generalised von Bertalanffy equation (Table 18-B). The generalised von Bertalanffy equation shows a better fit than the von Bertalanffy length-at-age model.

Table 18: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*). Testing stability of the von Bertalanffy model.** Parameters of the Bertalanffy model (A) contrasted with those of the general model 1 after setting each constant one by one as variable (B, C, D), and final values for all parameters set as variables (E); SF: Schnute's F.

	A) $a = 1$; $c = 1$; $b = 1$	**B)** $a = 1$; $c = 1$	**C)** $a = 1$
Linf	56.2693	55.5782	55.5782
k	0.0355	0.0384	0.0384
t_o	-1.9935	-3.6572	-3.6572
b		1.1660	1.1660
c			1.0000000000046
a			
RSS	708.07270	707.4447	707.4447
MLL	-296.4023	-296.3442	-296.3442
SF	SF= 0.055< ($F_{0.05(2,126)}$= 3.07)	SF< $1*10^{-25}$ < ($F_{0.05(1, 126)}$= 3.92)	

	D) $c = 1$	**E)** General model 1
Linf	55.5782	55.5782
k	0.0384	0.0384
t_o	-3.6572	-3.6572
b	1.1660	1.1660 (1)
c		0.99999995128 (1)
a	1.000000000156	0.99999999893 (1)
RSS	707.4447	707.4447

(1) Value of the constant parameter after set as variable.

The Richards Model was successfully fitted to the data (Table 19). By keeping t_0= 0 as the Richards model states, the fitting variation concentrates on *c*. When *a* is set as variable there is redundancy in *c* and *Linf* that introduces unnecessary noise to the model (Table 19, B), due to *c/a* in Table 19-B equals *c* in Table 19-A. *k* and *b* stay as the most stable parameters in all situations (to the sixth and fifth significant decimal respectively), and *Linf* and *k* remain as the more accurate parameters after both t_0 and *a* are set as a constant (Table 19, A and C). Richards Model is no significant with respect to general model 1, and RSS is smaller than the one for the von Bertalanffy length-at-age equation (see Table 18-A and Table 19-A), but comparable with the generalised von Bertalanffy when added with the morphometric power constant *b* (Table 18-B and Table 19-A). MLL is bigger than the one for the von Bertalanffy length-at-age equation (see Table 18-A and Table 19-A), and similar to the generalised von Bertalanffy.

Table 19: **Growth parameters for Smooth Oreo (*Pseudocyttus □aculates*). Testing stability of the Richards model.** Parameters of the Richards model (A), *a* set as variable (B), and final values for all parameters set as variables (C); SF: Schnute's F; SF1: $F_{0.05(2,\ 126)}$; SF2: $F_{0.05(1,\ 126)}$.

	A) t_0= 0; a=1	B) t_0= 0	C) General model 1
Linf	55.5782	51.1488	55.5782
k	0.0384	0.0384	0.0384
t_o			-1.8122 x$10^{-6(1)}$
b	1.1660	1.1660	1.1660
c	0.8689	0.9330	0.8689
a		1.0738	707.4447$^{(1)}$
RSS	707.4447	707.4447	-296.3442
MLL	-296.3442	-296.3442	
SF	SF= $9.1*10^{-14}$ < ($F_{0.05}$= 3.07)	SF< $1.0*10^{-25}$ < ($F_{0.05}$= 3.92)	

(1) Value of the constant parameter after been set as variable.

3.6.2.2.3 Stability of double exponential versions of models contained in general model 2

The exponential version of the logistic model resulted unstable. The best fit showed strong residual heteroscedasticity and inaccurate values ($c_{s\infty}$=-3.8670, *k*= 0.1073, and t_0= 0.5474).

The exponential version of the Richards model showed a stable fit with lower RSS and higher MLL than those for the other double exponential models. All parameters were accurate and stable (Table 20). RSS for the exponential version of the von Bertalanffy length-at-age model is similar to the Gompertz 1, and Gompertz 2 models (Table 20 and Table 21). MLL is also comparable to the Gompertz 1, and Gompertz 2 models (Table 20 and Table 21). The exponential of the Richards model is the best double exponential model in general group 2 for describing this data set (lower RSS and higher MLL: Table 22).

Table 20: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*). Testing stability of the von Bertalanffy and Richards Exponential models (general model 2).** von Bertalanffy (A) with all parameters set as variables after setting $c_b = 1$, $c_c = 1$ and $c_a = 1$ as initial defaults; Richards (B) with all parameters beginning with $c_{t0} = 0$, $c_c = 1$, and $c_a = 1$ as default; RSS: Residuals square root; MLL: Maximum log likelihood; SF: Scnute's F statistics.

	A) vB $c_a=1$; $c_b= 1$; $c_c = 1$	B) Ri $c_a= 1$; $c_c = 1$
Linf$^{(0)}$	52.8738	55.3570
$c_{s\infty}$	3.9679	4.0138
c_a		
c_c		1.0000
c_{t0}	-15.1738	
c_b		0.2703
k	0.0555	0.0399
RSS	725.5268	710.6233
MLL	-297.9973	-296.6378
SF	$SF= 6.9 \times 10^{-4} < (F_{0.05(1, 125)}= 3.05)$	$SF=3.0 \times 10^{-6} < (F_{0.05(1, 125)}= 3.9)$

$^{(0)}$ Calculated from $c_{s\infty}$ (ln(*Linf*) = $c_{s\infty}$).

3.6.2.2.4 Stability of the Gompertz type models

Gompertz type functions (parameterisations of the Gompertz model) were fitted by setting parameters as variables in the following sequence: c_{∞}, k, $c_{s\infty}$, c_{t0}. Gompertz 1, Gompertz 2 and Gompertz 4 models were fitted successfully and all the parameters were accurate and stable, and comparable to general model 2 after converting all parameters to variables (Table 21). Gompertz 3 was unstable for all parameters but for *Linf* and *k*, which were lower than for the other double exponential models.

As was said before, all Gompertz variants are the same model with different parameterisations. Actually Gompertz 4 and Gompertz 2 are identical for fitting purposes; therefore both fits show exactly the same values for each parameter. The small differences in c_b, c_c, and c_{t0} between the three models are likely to be due to computing error. The difference between them is two significant digits smaller than the data precision (1 mm). RSS is the highest for Gompertz 1, Gompertz 2 and Gompertz 4 equations with respect to the other fitted models (Table 21 and Table 22). Gompertz models 1, 2, and 4 have virtually the same MLL. Their MLL is the lowest with respect to the other models (Table 21 and Table 22).

Table 21: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*). Testing stability of the Gompertz 1, 2, and 4 models (general model 2).** Gompertz 1 (A) after setting $c_b = 1$, $c_c = 1$, $c_a = 1$, and $c_{t0} = 0$ as defaults; Gompertz 2 (B) after setting $c_a = 1$, $c_b = 0$, and $c_c = 1$ as defaults; full General model 2 (C); RSS: Residuals square sum; MLL: maximum log likelihood; SF: Schnute's F statistics.

	A) Gompertz 1	B) Gompertz 2	C) All parameters but c_a
c_x	9.5900 (1)	52.8743	7.0865 (1)
c_{sx}	1.7071	1.7071	2.74522
k	0.0555	0.0555	0.0516
c_a			
c_c			1.0000
c_{t0}		-1.8742×10^{-8}	-8.2507
c_b			0.7884
RSS	725.5268	725.5268	719.7128
MLL	-297.9973	-297.9973	-297.4703
SF	SF= $0.5048 < F_{0.05(1, 125)} = 3.05$	SF= $0.3365 < F_{0.05(3, 125)} = 3.04$	

(1) c_x is equivalent to the length at age = 0.0.

Smith & Stewart (1994) did not present any plot of residuals, so I made one from their data and the parameters of the model reported by them (F-SS in Table 22). I also calculated the RSS within the same procedure in order to compare the goodness of fit against my results. The fit of the Smith & Stewart (1994) data was undertaken with their calculated k and t_0 to estimate the RSS. The resulting *Linf* was 0.1 cm higher than that reported, and comparing with a plot of their residuals (Figure 14) the plot was found acceptably similar to the one originally published. The RSS calculated directly from the data and the equation given by Smith & Stewart resulted similar to the estimated by the fit (834.1429> 832.9531). The difference lies in the level of precision used in reporting individual parameters.

Plots of the von Bertalanffy, Logistic, and Richards curves (Figure 15), exponential versions of these (Figure 16), and of the Gompertz type (Figure 17) were obtained except for Gompertz 3 and the exponential of the logistic model. Growth parameters for all equations except for Gompertz 3 and the exponential of the logistic were successfully calculated (Table 22). Gompertz 3 model was non-stable for c_{t0}. Only k and *Linf* were obtained for Gompertz 3.

The logistic model produced results different to the von Bertalanffy and Richards (Table 22): lower t_0 and *Linf* flattened the curve, despite the bigger value of k

(0.07 > 0.03). This resulted in a slightly bigger concavity of the curve to the left, under estimating length at younger ages and also under estimating length at older ages.

The plots of residuals in all cases looked similar. The number of iterations is not included because it depends on the threshold selected for the calculation of parameters and RSS, and on the initial guess of the parameters; those settings differ in different cases.

k was the most consistent parameter (stable and accurate), particularly for double exponential equations, and lower values were found for von Bertalanffy and Richards models. *Linf* was similar in Gompertz type curves, and smaller for general model 1 equations. t_0 and c_{t0} presented different values between general models (it was highly variable).

Table 22: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*)**. von Bertalanffy model (vBSS) estimated with SAS by Smith & Stewart (1994); von Bertalanffy model (F-SS) estimated with the authors data, *k* and t_0; Logistic (Lo), von Bertalanffy (vB), and Richards (Ri) for general model 1; Exponential versions of Logistic (E-Lo), von Bertalanffy (E-vB), and Richards (E-Ri) for group 2 in general model 2; Gompertz 1 and Gompertz 2 (Quinn & Deriso 1999), Gompertz 3 (Sit & Poulin 1994), and Gompertz 4 (Gamito 1998) as derivations of the Gompertz model (Go1, Go2, Go3, and Go4) in group 3 for general model 2.

			General Model 1		
			Group 1		
	vBSS	F-SS	Lo	vB	Ri
Linf	50.94	51.0697	51.2376	56.2693	55.5782
k	0.051	0.051	0.0754	0.0355	0.0384
t_0	1.05	1.05	15.6210	-1.9935	
b					1.1660
c					0.8689
RSS	-------	832.9531	775.1771	708.07270	707.4447
MLL		-307.0415	-302.3330	-296.4023	-296.3442
SF$_{0.025}$		> 3.07	> 3.07	< 3.07	< 3.07

	General Model 2						
	Group 2			Group 3			
	E-Lo	E-vB	E-Ri	Go1	Go2	Go3	Go4
Linf	Unstable	52.8738 [a]	55.3570 [a]		52.8743	52.4751	52.8743
k		0.0555	0.0399	0.0555	0.0555	0.0363	0.0555
c_{t0}		-15.1738			-1.87 10^{-8}	xxxx	-1.87 10^{-8}
c_b			0.2705				
c_x				9.5900 [b]	52.8743	-------	52.8743
c_{sx}		3.9679	4.0138	1.7071	1.7071		1.7071
RSS		725.5268	710.6233	725.5268	725.5268	-------	725.5268
MLL		-297.9973	-296.6378	-297.9973	-297.9973		-297.9973
SF$_{0.025}$		< 3.05	< 3.05	< 3.05	< 3.04		< 3.04

Linf: Asymptotic size = s_∞ in general model 1
k: Intrinsic rate of growth
t_0: Theoretical age (years) at length = 0
b: Allometric constant
c: Constant

RSS: Calculated Residual Sum of Squares
n: sample size = 131.
MLL: maximum log likelihood.

c_{t0}: Constant homologous t_0
c_b, c_x, and c_{sx}: constant
--------- Could not be calculated
xxxx: with no approximation to a particular value

[a] $c_{sx} = \ln(Linf)$
[b] "initial instantaneous size" (Quinn & Deriso 1999): Theoretical size (length) at age = 0

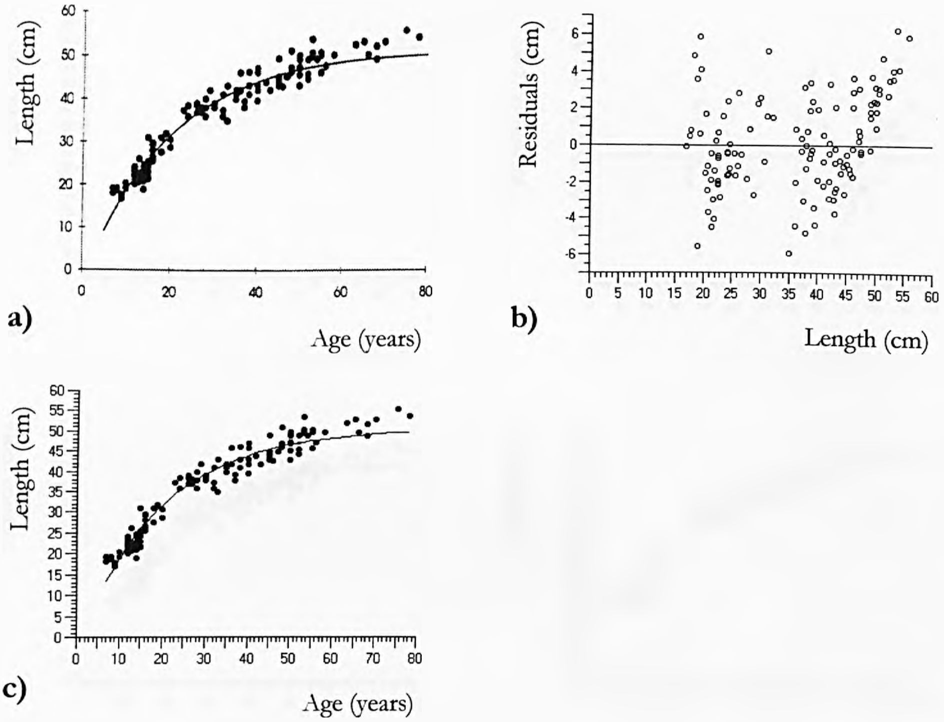


Figure 14: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*). Calculated by Smith & Stewart (1994).** a) Fitted von Bertalanffy curve and observed data; b) Residuals - fitted model; c) Fitted curve with the programme developed.

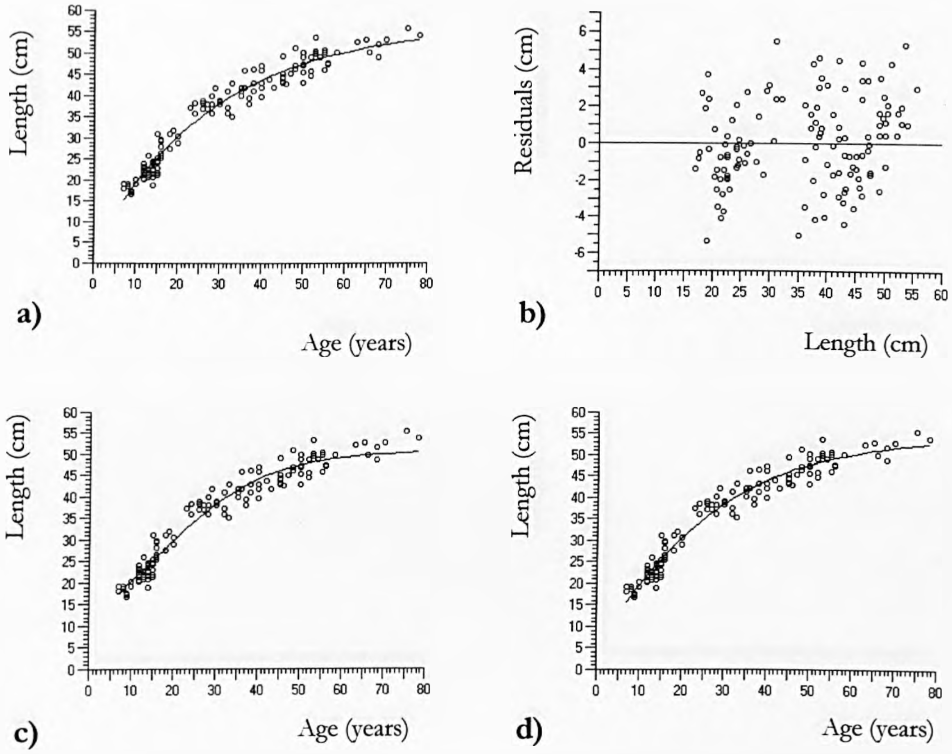


Figure 15: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*): general model 1.** a) Fitted von Bertalanffy curve, b) Residuals – fitted von Bertalanffy model, c) Fitted Logistic curve, d) Fitted Richards curve.

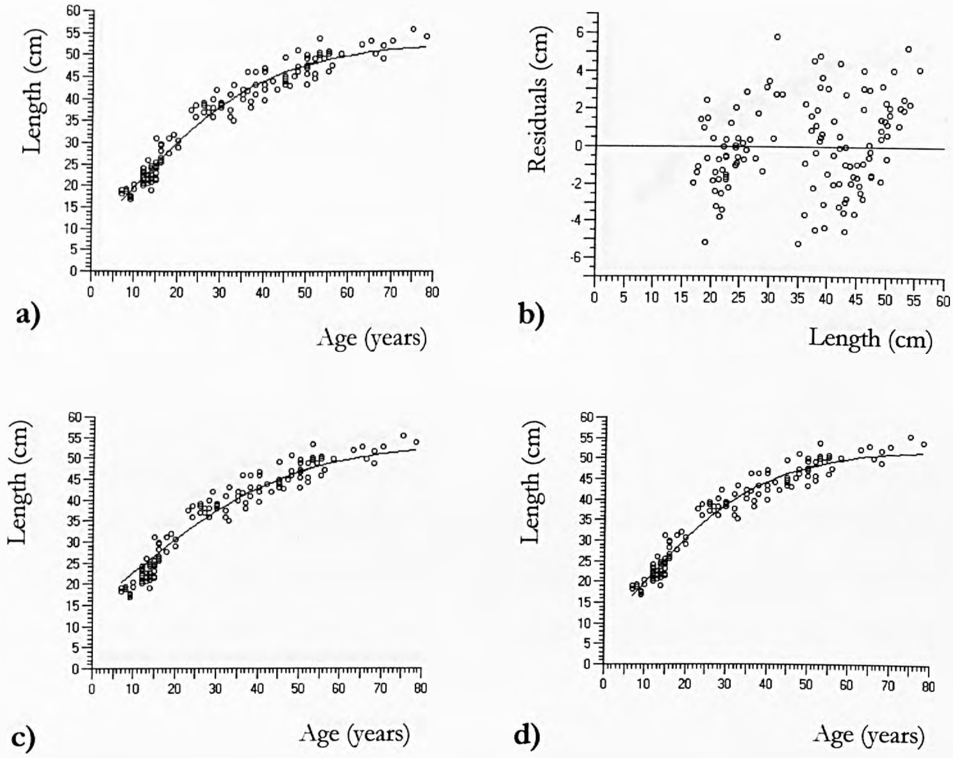


Figure 16: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*): general model 2 (exponential versions).** a) Fitted exponential von Bertalanffy curve; b) Residuals (exponential von Bertalanffy) - fitted model; c) Fitted exponential Logistic curve; c) Fitted exponential Richards curve.

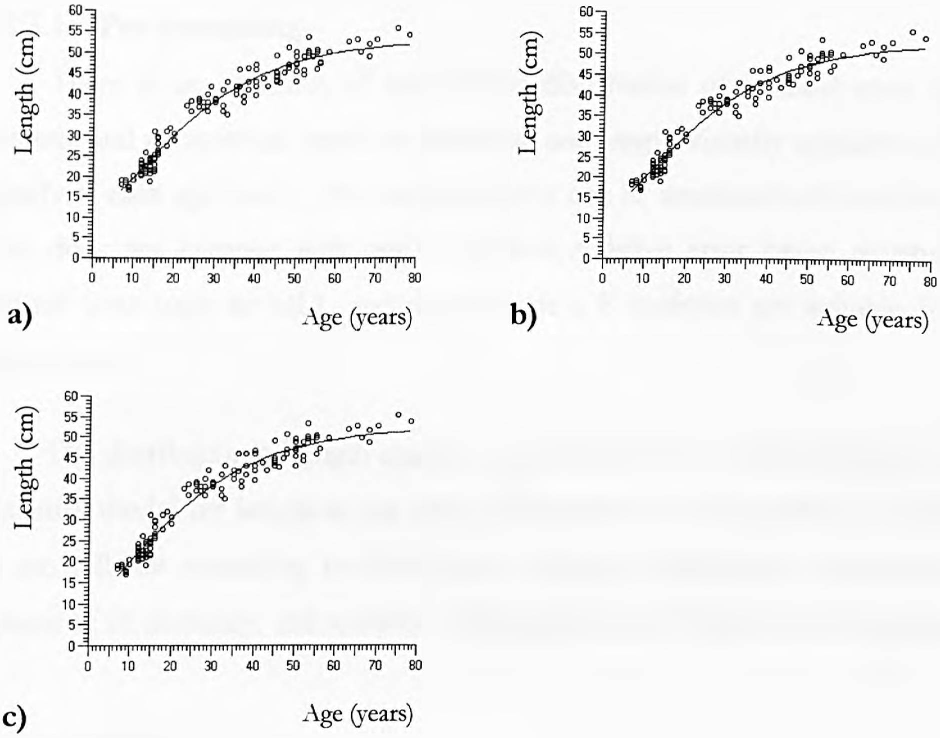


Figure 17: **Growth parameters for Smooth Oreo (*Pseudocyttus maculatus*): general model 2 (Gompertz type).** a) Fitted Gompertz 4; b) fitted Gompertz 1; c) Fitted Gompertz 2.

3.6.2.3 Analysis of results

3.6.2.3.1 Pre-processing

There is no evidence of non-normal distribution of residual error (fits with arithmetic and geometrical mean are identical, and length visually appears to distribute normally at each age class). The statistical error can be assumed to be additive (length spread does not increase with age); therefore additive error based parameters and statistical tests such as MLL and the Schnute's F statistics are suitable for model comparisons.

The distribution of length against age data follows an s-shape trend, so the von Bertalanffy model for length-at-age data is discarded as an appropriate model for this data set. All the remaining models match s-shape distributions; consequently their goodness of fit, accuracy, and stability will decide which of them is the most adequate.

3.6.2.3.2 Fitting

All models with the exception of Gompertz 3 and the exponential version of the logistic model fitted acceptably the data set. The good fit of the logistic curve suggests an s-shaped function.

a is redundant and useless as a meaningful variable in all models analysed (it resorts to a value of 1.0 when is set as variable), consequently it should to be kept constant as equal to 1.0 in all models.

Fits for von Bertalanffy and Richards equations resulted better than the original estimated by Smith & Stewart (S&S) using SAS because of their higher MLL and lower RSS. This results indicate that the implementation of the Levenberg-marquardt method for fitting done here gives better result than the one in SAS at the time the calculations by Smith & Stewart (1994) were done.

The Schnute's F test (SF) for S&S resulted significant when comparing the parameters obtained with SAS against general model 1, suggesting that such fit may not be considered as acceptable. Surely the model rejection is influenced by the low level of precision used by Smith & Stewart in reporting individual measurements, but the extent of the influence may not be enough to explain such high MLL.

Despite the good fit of the double exponential models, Richards and von Bertalanffy better fitted the data set (lower RSS and higher MLL). From all models the Richards equation seems to be the best model because it shows the lowest RSS and the highest MLL, and matches with the perception of an s-shape trend.

3.6.2.3.3 Stability

All single exponential models contained in general model 1 with exception of the logistic showed to be highly stable (with non-significant SF when compared with the general model they belong). The logistic model is therefore discarded as a potential option, nevertheless the logistic function may be considered as a reference to evaluate the magnitude of the estimated parameters and the general data trend just because it presented a good fit (based on RSS).

The most stable parameters were the asymptotic length (*Linf*) and *k* in all models; therefore, the model to choose should include at least one of these parameters.

The effect of *b* over t_0, *k* and *Linf* when introduced into the von Bertalanffy model (which makes *k* and *Linf* similar to those in the Richards equation) suggests that either an allometric factor could be masked in the original von Bertalanffy equation, producing apparent senseless values of t_0 (see next chapter), or that the von Bertalanffy model is not adequate to describe the data set. As mentioned at the end of 3.6.1.3, Richards and the length-at-age von Bertalanffy model are mathematically the same when *b* equals to 1.0. Different values for t_0, *k* and *Linf* between both models strength the possibility that an allometric factor may be influencing the von Bertalanffy model ($b \neq 1$). Such influence may also explain the higher von Bertalanffy SF (0.005> 9 10^{-14}), but it does not result big enough to become significant in comparison with general model 1. Regardless of the magnitude of the allometric factor, both Richards and von Bertalaffy result the most stable models. The stability of the Richards model and the exponential versions of the functions of group 1, Gompertz 1, Gompertz 2, and Gompertz 4 curves also imply the best model possibility should be s-shaped.

3.6.2.3.4 Accuracy

Accuracy cannot be properly assessed for the logistic model because *b* and *c* are not likely to change to positive values without a change of model. Even when the logistic model follows an s-shape trend and is well fitted, its parameters are less reliable because it has a higher RSS and it under estimates the length of fishes that are too young and too old.

The exponential of Richards is the most accurate of the double exponential models (SF= 3.0 10^{-6}), followed by the exponential of the von Bertalanffy (SF= 6.9 10^{-4}). Actually the magnitude of the parameters of the exponential of Richards is close to the von Bertalanffy and Richards models.

Gompertz 3 was hard to fit, reducing the possibility of a good assessment of the accuracy for each parameter in the double exponential curves. This behaviour was previously detected with the theoretical data set.

Parameters in general model 1 are more accurate than those in general model 2 (higher MLL and lower SF), and the differences in magnitude between the curves in general model 2 can be considered unacceptable even if we take into account that the differences fall within the level of precision used when recording individual measurements. This result does not contradict the idea that an s-shaped model is the most likely to best describe the data set.

Because the true value of each parameter is unknown, the most accurate models are expected to be the ones in which their parameters converge to the same value regardless if new constant parameters are converted into variables (those with the lowest SF when compared to their general models), so their parameters can be considered the most accurate and expected to be the closer to the real value. In this case the models with lowest SF were Richards and von Bertalanffy.

3.6.2.3.5 General evaluation

Based on stability and accuracy, the best model is expected to be s-shaped. Among the single exponential models available, the classic von Bertalanffy length-at age curve does not follow an s-shape trend (therefore is discarded).

Up to this point a double exponential curve do not match with the parameters and model fitted with SAS by Smith & Stewart (1994). Observing the following, sheds light on this discrepancy:

1) The fit obtained by SAS slightly under estimates length of older and younger fishes (see Figure 14-A compared with Figure 15-A and notice the upper corners of the plot in Figure 14-B compared with Figure 15-B). This can be also seen in the residuals plot (Figure 14-B), which followed a linear pattern for individuals older than 35 years (bottom left to top right), which is more obvious than the one for the fitted von Bertalanffy (Figure 15-B).

2) Residuals for the exponential von Bertalanffy (Figure 16-B) are more homogeneous to the eye (around 0.0) than the ones in the original fit (Figure 14-B). The under estimation for old and very small fishes is lower (notice the upper left and right corners of the plot in Figure 14-B compared with Figure 16-B). This lends more weight to the suggestion of an s-shape model.

3) Average, geometric mean and median size at each age class (Figure 18 and Figure 19) show that an s-shape is more likely, and that the growth pattern may be made up of several stanza (Le Cren 1951). As stated before, the work with location statistics (means, medians, and geometrical means) has no statistical importance because it neglects the individual spread error, but is valuable in identifying trends.

4) The parameters and model fitted with SAS show the biggest RSS, the lowest MLL and SF results significant, which means that such fit is not the best to describe the data set.

Applying the previous findings to the original data set, the Richards function is expected to be the best descriptor of the growth (length at age) of Smooth Oreo *Pseudocyttus maculatus* if there is no influence of a morphometric factor (see next chapter).

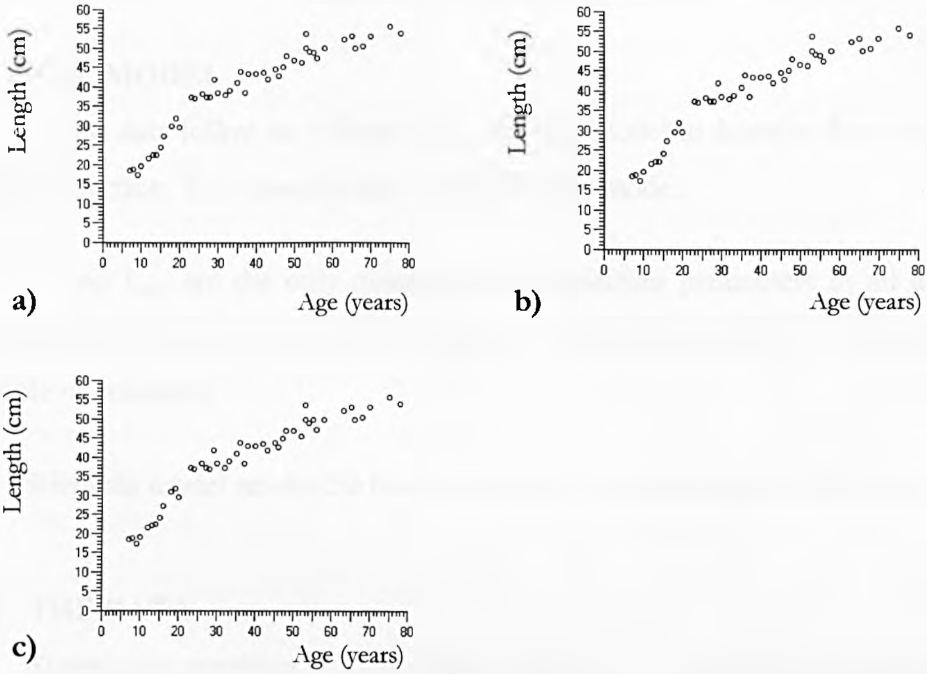
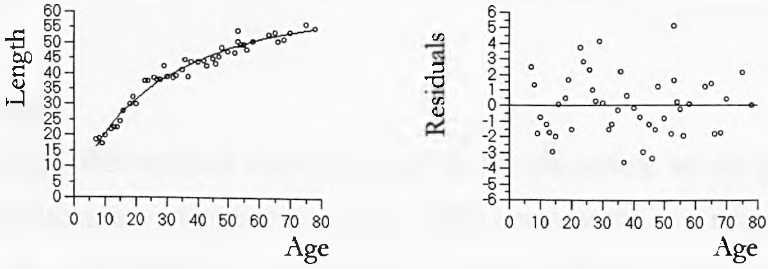


Figure 18: **Distribution of Location statistics (Length at each Age) for Smooth Oreo (*Pseudocyttus maculatus*).** A) Average length at age; B) Geometric mean at age; C) Median at age.

n	47
L_{inf}	59.6548
k	0.0259
b	0.6993
c	1.0149
RSS	177.5025
MLL	-97.9177

Richards



n	47
L_{inf}	59.6548
k	0.0259
t_0	0.5718
b	0.6993
RSS	177.5025
MLL	-97.9177

von Bertalanffy

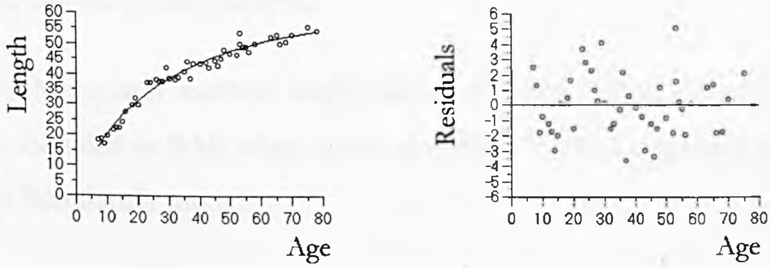


Figure 19: **Fit of Richards and generalised von Bertalanffy models with Average as location statistics (average length at each age class of one year) for Smooth Oreo (*Pseudocyttus maculatus*).** The generalised von Bertalanffy equation includes parameter *b* as a variable.

3.7 CONCLUSIONS

3.7.1 THE MODEL

As the data follow an s-shape trend; the best model to describe them must be an S-Shaped function. This discards the von Bertalanffy model.

k, and L_{inf}, are the only quantitatively significant parameters in all equations because they are the most stable and accurate. t_0 may have no place in the model (it is not stable or accurate).

Richards model results the best descriptor of the Oreo data distribution.

3.7.2 THE DATA

Statistically speaking, a high quality data set was explored: no influential and no aberrant residuals (Hoaglin *et al.* 1983), no influential data, and most ages represented. However, more younger and older fishes would improve the fit.

More analysis with complementary information sources is necessary in order to explore the apparent exponential stages, which may be indicative of stanza with a non-annual periodicity. Sex, cohort identification, allometry, reproductive cycle, and migratory behaviour are examples of such complementary information.

3.7.3 THE METHOD

Even when simple, this method showed its power for discarding severe cases of instability and lack of accuracy of parameters and models between the two proposed general models, and it was helpful in identifying the best model based on the distribution of the data, and the goodness of fit.

The Levenberg-Marquardt method implemented for data fitting generated a better fit than the one included in SAS when Smith & Stewart (1994) originally fitted their data with the von Bertalanffy model.

Some improvements are necessary, particularly developing rules to define the initial guess based on intrinsic properties of each data set with respect to each model.

3.8 COMMENTARIES

Different fitting methods and different commercially available computer programmes may produce different outputs as happened with the fit by Smith & Stewart (1994) using SAS compared with the computer programme developed during this study. For data interpolation purposes and gross pattern description, any of the well fitted models are equally as good as that estimated with SAS. However, more specialist tools are required for a greater assessment of key parameters such as growth rate and asymptotic size, pattern recognition, inflection points, and identification of important events such as periods of rapid growth, strength of seasonal trends, etc.

The efficiency of the method described, strongly relies on the computer programme developed, with the advantage that any part of the algorithm can be checked and optimised. This is not as easy with commercial packages were there may be no access to the basic algorithm. The main matter is not to discuss which programme is better, but to emphasise the importance of knowing what is inside the tool and how it works (not just the fundamentals) in order to totally understand and make the analysis of data interactive.

The analysis undertaken was based on a data set, which was assumed to be unbiased and to be representative of the population sampled. Whether the results reflect the true species biology, or whether there exists a biological meaning of parameters and models, or a biological reason for any particular trend, has to be proven by other means. The quantitative and qualitative approach suggested here (based on the exploratory analysis of data, power of fit, and the stability and accuracy of models and parameters) just reflects and emphasises data characteristics, and contrasts the data against the models intrinsic theory, but does not demonstrate any biological assumptions.

3.9 OTHER ALTERNATIVES

Other approaches have been suggested to improve the estimation of parameters in growth models, one is the further parameterisation of the well known growth models, particularly that of von Bertalanffy (Ross 1970; Gallucci & Quinn 1979; Schnute & Fournier 1980; Schnute 1985; Cerrato 1990).

Linear methods are now considered obsolete, but are valuable for testing data properties when can be implemented (Gregg *et al.* 1964; Sparre & Venema 1995). Nowadays, non-linear methods are preferred, particularly the Simplex method which was suggested earlier by Schnute (1982) and Newton related methods (used by SAS and other commercially available programmes). The availability of non-linear methods contained in prominent commercial packages is risky when blindly used just because they were applied in previous publications without a fair knowledge of the algorithms employed.

The generation of *ad hoc* models as simple polynomials (Roff 1980) and exponentials for specific stages of the life history, and the usage of generic methods for data fitting can be sufficient when interpolation is the main goal, but it will become useless when comparison of results is needed.

The von Bertalanffy growth curve is still the most widely used model to describe growth with previous studies for compatibility reasons and because its parameters are used as part of other models such as the Beverton – Holt yield-per-recruit for size-structured analysis (Haddon 2001).

3.10 NEWER APPROACHES IN MODELLING GROWTH

Research on growth at age follows three main lines: revisiting biological and ecological fundamentals with new knowledge and technological tools, optimising the classical methods with new mathematical and computational tools and methodologies, and incorporating newer models from other fields.

Newer approaches for the estimation of body growth are potential keys to finding parameters with real biological meaning in growth equations that become a step beyond the empirical and descriptive parameters in the growth models now used.

Some of the physiological factors recently analysed in search of the biological meaning of the growth parameters are the pattern of cell growth (Mombach *et al.* 2002), individual body and environmental energy dynamics (Lika & Nisbet 2000), physio-anatomical facts such as muscular hyperplasia and hypertrophy in post-juvenile stages (Mommsen 2001), the requirements for maintenance of body energy contents and maintenance of body weight (Watanabe *et al.* 2000), the effects of swimming exercise on the developing of body biomass (Yogata & Oku 2000), and the changes in the body tissue composition respect with time (Moltschaniwskyj & Jackson 2000).

Ecological factors such as temperature on larval and juvenile size-dependent growth (Otterlei *et al.* 1999), salinity on osmoregulation, food intake and growth regulation (Boeuf & Payan 2001), and growth rate on survival (Ottersen & Loeng 2000) among others, can also provide elements for more complex models that consider the environmental influence.

Optimisation of classical models and methodologies such as done in this study, evaluation of sampling strategies for estimation of growth parameters (Castro & Lawing 1995; Jones 2000), and evaluation of bias introduced by models assumptions (Bowker 1996; Wang & Somers 1996; Pilling *et al.* 2002) are a few examples of the tendency toward optimisation of classical methods by improving the data sampling and data analysis.

Development of variants of classical methods and models (Birch 1999; Porch 2002), and new and generalised fitting methods from other disciplines, particularly from the Economics field (Islam & Craven 2001; Le Van & Morhaim 2002) can be a good reference that may result on improvements of the current models and even in different approaches to the understanding and assessment of growth.

Special emphasis has to be given to the use of more complicated models such as those developed for human growth, which are based on polynomial chains and chains of exponentials that allow the description of different stanza along the life span (Sumiya 1999).

CHAPTER 4

MORPHOMETRIC GROWTH AND GROWTH AT AGE

4.1 ABSTRACT

Length-at-age growth models are preferred over weight-at-age growth models for the assessment of population size-at-age growth because of the ease of measuring length as opposed to weight and the problems associated with seasonal changes in weight due to condition and or spawning state. The generalised von Bertalanffy size-at-age growth model is the most widely used for fish populations. The length-weight power constant is part of the von Bertalanffy equation for weight-at-age growth but there is not an equivalent parameter in the Bertalanffy length-at-age equation.

In some fish populations, the length-at-age equation can be a better fit if a power constant is introduced as a new parameter. This is the equivalent of considering that the power constant in the generalized von Bertalanffy length-at-age equation could be different from 1.0. There are no antecedents of the effect of a power constant different from 1.0 on the correct assessment of weight-at-age from length-at-age data, but in this study I show that a value different from 1.0 in the power constant may be the result of the body morphometric growth. The omission of the power constant may affect the estimation of parameters of the length-at-age equation by introducing a systematic deviation from the true value that increases as age decreases The propagation of the error introduced by such omission is particularly important when the equation growth parameters are used in further models. A corrected equation for evaluation of length-at-age based on the Bertalanffy model is derived by the inclusion of a power constant, and the method for the correct estimation of the equation parameters is given.

4.2 JUSTIFICATION

The analysis of growth is usually directed to the examination of growth rates and the parameters of the length and weight at-age equations, particularly asymptotic length and weight. Standard length and total weight are the principal response variables, and time (age) the only predictor when dealing with growth at age equations. Historically, length-at-age models were preferred over weight-at-age models due to the ease of measuring length as opposed to weight, especially in the field. Also, there are seasonal positive and negative changes in weight due to changes in condition and/or spawning state. The inclusion of for example, stomachs in the weight introduces a source of variability in any model utilising weight due to variability in stomach contents.

The Generalised von Bertalanffy growth model (equation (29)) is the model most widely used in the field (Haddon 2001), and particularly in the case of weight probably is the best model for describing growth at age for many species. Regardless of the efficiency of this model to describe fish growth, it is also used in other models in fisheries, particularly for predictive models (Hilborn & Walters 1992; Castro & Lawing 1995; Sparre & Venema 1995).

$$S = S_\infty(1 - e^{-k(t-t_0)})^b \tag{29}$$

t: Age
S: Size at age t
S_∞: Asymptotic Size
k: Intrinsic growth rate
t_0: Time at which $S = 0.0$

The equation for length-at-age given by von Bertalanffy does not include the term b present in the generalised equation, and S_∞ is substituted by L_∞ (equation (30)). When size refers to biomass (weight), b takes the value of the power constant of the length-weight relationship (a value close to 3.0 for many species) and S_∞ is substituted by W_∞ (equation (31)).

$$L = L_\infty(1 - e^{-k(t-t_0)}) \tag{30}$$

L: Length at age t
L_∞: Asymptotic Length

$$W = W_\infty(1 - e^{-k(t-t_0)})^b \tag{31}$$

W: Weight at age t
W_∞: Asymptotic Weight

When a power constant analogous to b is introduced in equation (30), the value of the power constant is 1.0 for some cases as stated by the model, but for others (e.g.

Smooth Oreo (*Pseudocyttus maculatus*) and Blue-spotted rock cod (*Cephalopholis cyanostigma*), see 4.4.3, page 112), the power constant differs from 1.0. A value of the power constant $\neq 1.0$ implies that the parameters in the equation are insufficient to describe the growth in length of the fish over time. Therefore the equation needs modification.

There are no biological antecedents for why the power constant should differ from 1.0 when calculating the parameters of the von Bertalanffy length-at-age growth equation. A value of the power constant > 1.0 mathematically implies a curve s-shape, which can be consistent with some populations, but when an s-shape is detected a different growth model is assumed, usually the Gompertz model (Moreau 1987).

If the von Bertalanffy length-at-age growth model is forced on to the data (which is usually done), I found that this difference could bias the estimation of length in young individuals. The bias depended on how different the power constant is from 1.0, and if the difference is positive or negative. Therefore, I think it is important to determine the origin of the bias, construct a method to quantify it, and finally the way to correct it.

I deduce that the rate in which length approaches L_∞ as age increases does not follow the rate of the classical von Bertalanffy length-at-age relationship, but it does it in a power relationship with respect to the von Bertalanffy length-at-age model:

$L \neq L_\infty(1-e^{-k(t-t_0)})$ but $L = L_\infty(1-e^{-k(t-t_0)})^c$

This corrected rate of change produces an s-shape trend of the distribution of lengths respect to age, which has been observed previously for young individuals in some populations.

I also infer that this power constant may be the product of an allometric relationship between length and one of the other orthogonal dimensions (height or width), when the other orthogonal dimension distributes accordingly to the classical von Bertalanffy length-at-age growth equation.

4.3 OBJECTIVE

The main objectives are to identify the origin of the bias, to develop a method to quantify the bias, and correct the von Bertalanffy length-at-age growth equation if necessary.

4.4 ANTECEDENTS

4.4.1 BIOMASS, DENSITY, MORPHOMETRY, AND GROWTH

As mentioned in Chapter 1, morphometry and density are related to biomass by the length-weight relationship, and biomass is related to time by the size-at-age growth functions. The power constant *b* in the length-weight relationship and the von Bertalanffy weight-at-age model is the only mathematical parameter used in fish biology, fish stock assessment, and fisheries to link morphometry directly to size-at-age growth. Even when one might intuitively expect some relationship between both phenomena for length-at-age growth, nothing is included in the length-at-age von Bertalanffy model (equation (41)), in spite of the fact that theoretically, this model is derived from assumptions based on metabolism.

There are many publications concerning the length-weight relationship and the usage of its power constant in the von Bertalanffy weight-at-age equation, but in respect to the length-at-age equation there are no antecedents of a homologous power constant. An application of the power constant of the length-weight relationship for assessment of length-at-age growth was undertaken to overcome the high interdependency of parameters of the von Bertalanffy growth model (Jobling 2002), which affects the power of fit of traditional methods employed to estimate them. Bayley (1977) used the morphometric constant of the length-weight relationship in the von Bertalanffy model in order to develop a method that could avoid the dependency between parameters by independently estimating the instantaneous growth rate in terms of length, and the morphometric factor of the length-weight relationship. The influence of the allometric relationship between width or height, in respect to length on the von Bertalanffy length-at-age equation, was not explored by Bayley (1977) and Jobling 2002, neither was the possibility of a better fit in the relationship age-length implemented by considering the introduction of a power constant to the von Bertalanffy length-at-age equation.

4.4.2 TRADITIONAL FITTING OF MODELS TO SIZE-AT-AGE DATA

Linear methods are the traditional means for fitting growth-at-age models (von Bertalanffy, Logistic, and Gompertz), and were based on least square fits of linearized forms of such models. Because there are more parameters than predictor variables, some parameters were obtained using secondary methods, also based on least square fits of linearized equations, derived from the growth models.

The main secondary methods for estimating asymptotic length and intrinsic growth rate as the first step on the calculation of the other parameters in the von Bertalanffy length-at-age equation are the ones developed by Chapman (1961), Gulland-Holt (1959), and Ford–Walford (1933 and 1946). The parameter t_0 is obtained later by re-fitting the linearized von Bertalanffy equation as a function of age and including the values of the parameters previously calculated. Adding the power constant *b* from the length-weight relationship and substituting L_∞ by W_∞ calculated with the length-weight relationship, the weight-at-age equation is further obtained.

Algorithms for linear methods are widely known and abundantly documented in the literature. Jobling (2002) presents a brief and updated review, but perhaps the most in-depth presentation of such methods is given by Sparre & Venema (1995).

Non-linear methods (particularly Newton related iterative methods) produce in some cases better results than the classic methods when all age classes are well represented. However, they generate skewed results when just portions of the population are available, particularly for only young and only old individuals (Vaughan & Kanciruk 1982; Cerrato 1991; Haddon 2001).

Simplex and Levenberg-Marquardt methods are well known examples of non-linear methods. The extensive implementation of the Levenberg-Marquardt method is relatively recent (1963) and its application requires intensive calculations that can only be done by computers. Algorithms for these and other Newton related methods used to fit length-at-age growth are usually embedded into commercial statistical packages and are not fully documented. Regardless of the selection of the method for fitting the von Bertalanffy length-at-age growth model (linear or non-linear), by not including the power constant in the equation to fit (which is the equivalent to assume the power constant to be equal to 1) there is no chance of noticing any departure from 1.0, even when it exists.

4.4.3 THE VALUE OF THE POWER CONSTANT

The following species show a different level of divergence than 1.0 for the power constant. These species have a different longevity, their age was measured to different levels of precision (e.g. assigned to year class irrespective of time of capture, retained age to the nearest month relative to either spawning or assigned birth date etc), and the data sets were of different sizes. The natural variability of length with respect to age (standard deviation) also differs between species and sometimes also for different groups of age. Age-length data for smooth oreo (Smith & Stewart 1994), rock cod (Stewart 1998), and great scallops (*Pecten maximus* – Mollusca) were measured and provided by Dr B. D. Stewart. The data for an unexploited population of scallops belong to his current research program in the Port Erin Marine Laboratory, University of Liverpool, Port Erin, Isle of Man.

In order to assess the influence of the power constant in the von Bertalanffy length-at-age growth model for the three species, equation 8 was fitted with and without including the parameters b_{ab} by the Levenberg-Marquardt method. The same computer programme I developed for finding the best growth model in the previous chapter (section 3.5.4) was used here for the fitting process.

The smooth Oreo (*Pseudocyttus maculatus*) is a long-lived fish species with a low intrinsic growth rate (Figure 20), and fitted power constant greater than 1.16. The fit improves just a little for the power constant different from 1.0. Age is given at integer intervals of one year.

	pc =1.0	pc ≠ 1.0
L_{inf}	56.2693	55.5782
k	0.0355	0.0384
t_0	-1.9935	-3.6572
pc	1	1.1660
RSS	708.0727	707.4447
MLL	-296.4023	-296.3442
n	131	131

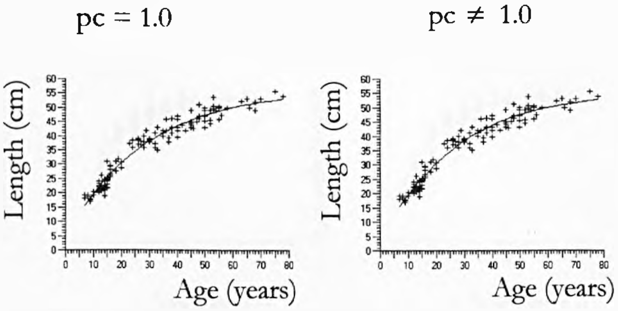


Figure 20: **von Bertalanffy Length-at-age equation for Smooth Oreo (*Pseudocyttus maculatus*) with and without the power constant (pc).** L_{inf}: asymptotic length, *k*: intrinsic growth rate, t_0: age when length = 0.0, *RSS:* residuals square sum, MLL: maximum log likelihood, *n*: sample size.

Blue-spotted rock cod (*Cephalopholis cyanostigma*) is a medium, lived fish species with average intrinsic growth rate (Figure 21) and a fitted power constant lower than 1.0. The fit slightly improves for the power constant different from 1.0. Age is given at fractional intervals of 0.25 of a year.

	pc = 1.0	pc ≠ 1.0
L_{inf}	288.8879	290.1829
k	0.1351	0.1272
t_0	-1.6653	-1.0342
pc	1	0.8389
RSS	31516.0975	31502.4175
MLL	-566.9162	-566.8865
n	137	137

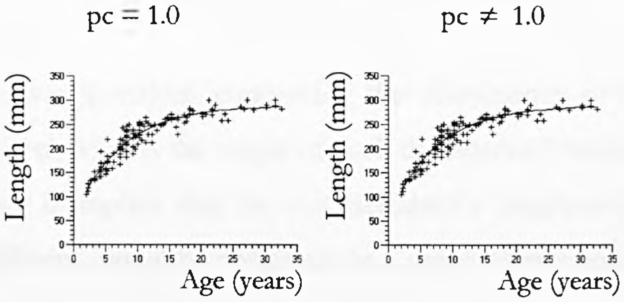


Figure 21: **von Bertalanffy Length-at-age equation for Blue-spotted rock cod (*Cephalopholis cyanostigma*) with and without the power constant (pc).** L_{inf}: asymptotic length, *k*: intrinsic growth rate, t_0: age when length = 0.0, *RSS:* residuals square sum, MLL: maximum log likelihood, *n*: sample size.

The scallop (*Pecten maximus*) is a comparatively short-lived shellfish species, with respect to the previous species (Figure 22), and has a higher intrinsic growth rate. The von Bertalanffy growth model can describe its growth-at-age relationship well, and the fitted power constant was slightly greater than 1.0 (power constant equal to 1.0567). This difference is so small that it can be considered null for practical purposes. The fit slightly improves for the power constant different from 1.0. Age is given at integer intervals of 1 year.

	pc = 1.0	pc ≠ 1.0
L_{inf}	154.7449	154.5781
k	0.4638	0.4722
t_0	0.2035	0.1491
pc	1	1.0567
RSS	8723.6976	8722.6053
MLL	-575.9495	-575.9389
n	170	170

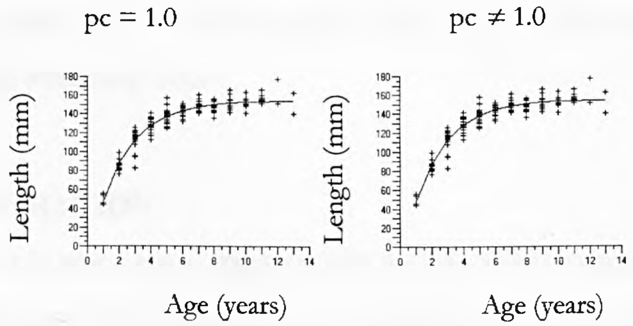


Figure 22: **von Bertalanffy Length-at-age equation for scallops (*Pecten maximus*) with and without the power constant (pc).** L_{inf}: asymptotic length, k: intrinsic growth rate, t_0: age when length = 0.0, *RSS:* residuals square sum, MLL: maximum log likelihood, *n*: sample size.

The degree of divergence of the power constant from 1.0 is different for each species. In all cases the inclusion of the power constant as an extra parameter contributed minimally to improve the fit, and because of a high variability of length at each age (as normally occur in natural fish and shellfish populations), it is not possible to estimate accurately the discrepancy between both fits (with and without the inclusion of the power constant).

Up to this point there are two questions concerning the discrepancy of the magnitude of the power constant. First, what is the origin of such divergence? Second, if a power constant different from 1.0 implies that the von Bertalanffy length-at-age model is not adequate, should a different model be preferred, or a proper correction be implemented?.

4.5 NEED OF A POWER CONSTANT ON THE VON BERTALANFFY GROWTH EQUATION

Multiple factors affect the fit of any model, but from a practical point of view the problem can be considered under four basic headings: the model is not the right one; the model is correct but one variable not considered might be affecting the phenomenon; the data are defective (systematic or random deviation); or the natural variability is so high that it is not possible to achieve better data precision.

Assuming that the choice of model is correct, I found that the second heading may be the most plausible, and that the origin of the divergence on the value of the power constant can be explained as a result of the morphometric relationship between length and the other basic three-dimensional morphometric dimensions (height and width). This finding is based on the reasoning below.

4.5.1 ALGEBRAIC DEMONSTRATION

The basic hypothesis is that in some cases length might not be related to age in a simple manner, but the relationship may be complex i.e. in conjunction with another morphometric variable (height or weight). The other morphometric variable may be related to age in a simpler manner. This relationship might change the scale in which length and age are related in the length-age equation. The morphometric relationship between length and the other dimension will be reflected in the value of the power constant (morphometric factor) of the power function that links them. I suggest that the influence of the morphometric factor can be demonstrated by the parameterisation of the von Bertalanffy weight-at-age equation (equation (31)) in terms of an allometric variable to length as follows.

In order to develop the equation of length-at-age growth with the morphometric factor it is necessary to initially obtain two equations: the first one is for the calculation of weight as a function of an allometric variable (length) from an isometric one (which is directly related to age accordingly to the von Bertalanffy equation), and the second for the asymptotic length as a function of the asymptotic weight. The procedure is as follow.

From the power relationship between length (L_B) and another linear dimension (L_A),

$$L_B = a_{ab}\ L_A^{\ b_{ab}}\ ;\ L_A = \left(\frac{1}{a_{ab}} L_E\right)^{\frac{1}{b_{ab}}}$$

And the length-weight relationship for L_A:

$$W_A = a_a\ L_A^{\ b_a} \tag{32}$$

The equation for the calculation of weight as a function of an allometric variable (Equation (33)) is obtained by introducing L_A in the previous equation,

$$W_A = a_a \left[\left(\frac{1}{a_{ab}} L_B \right)^{\frac{1}{b_{ab}}} \right]^{b_a} \tag{33}$$

Solving equation (33) for L_B:

$$L_B = a_{ab} \left(\frac{W_A}{a_a} \right)^{\frac{b_{ab}}{b_a}},$$

And substituting W_A with the asymptotic weight ($W_{\infty A}$), the equation for the calculation of asymptotic length $L_{\infty B}$ is obtained:

$$L_{\infty B} = a_{ab} \left(\frac{W_{\infty A}}{a_a} \right)^{\frac{b_{ab}}{b_a}} \tag{34}$$

Equation (35) is the von Bertalanffy expression for calculation of weight from age (t) for the isometric variable (height or width). The morphometric factor (b_a), product of the length-weight relationship between L_A and W_A is part of this equation. Notice that weight and asymptotic weight are not directly dependent from any length, but from t , t_0, k, and the morphometric constant b_a, which is the rate of morphometric growth of L_A respect to the body biomass W_A. W_A, $W_{\infty A}$, and b_a are associated with the isometric variable.

$$W_A = W_{\infty A}(1 - e^{-k(t-t_0)})^{b_a} \tag{35}$$

W_A: weight

$W_{\infty A}$: Asymptotic weight

k: Intrinsic growth rate

t: Age

t_0: Time at which $L_A = 0.0$

b_a: Morphometric factor in the L_A-W_A relationship

Replacing W_A in equation (35) with the right term in equation (33):

$$a_a\left[\left(\frac{1}{a_{ab}}L_B\right)^{\frac{1}{b_{ab}}}\right]^{b_a} = W_{\infty A}(1-e^{-k(t-t_0)})^{b_a}$$

And solving for L_B:

$$\left(\frac{1}{a_{ab}}L_B\right)^{\frac{b_a}{b_{ab}}} = \frac{W_{\infty A}}{a_a}(1-e^{-k(t-t_0)})^{b_a}$$

$$\frac{1}{a_{ab}}L_B = \left[\frac{W_{\infty A}}{a_a}(1-e^{-k(t-t_0)})^{b_a}\right]^{\frac{b_{ab}}{b_a}}$$

$$\frac{1}{a_{ab}}L_B = \left(\frac{W_{\infty A}}{a_a}\right)^{\frac{b_{ab}}{b_a}}(1-e^{-k(t-t_0)})^{\frac{b_a b_{ab}}{b_a}}$$

$$L_B = \left[a_{ab}\left(\frac{W_{\infty A}}{a_a}\right)^{\frac{b_{ab}}{b_a}}\right](1-e^{-k(t-t_0)})^{\frac{b_a b_{ab}}{b_a}}$$

The first right term is equal to $L_{\infty B}$ in equation (34) and b_a is eliminated in the last term of the right, producing equation (36), which shows that the morphometric factor (b_{ab}) must be part of the length-at-age equation of the von Bertalanffy model. Let us remember that b_{ab} is the power constant between two tri-dimensional longitudinal dimensions (one of them is length), and that b_{ab} equals 1.0 only when both are isometric. Only when this is true, the classic von Bertalanffy length-at-age is true.

$$L_B = L_{\infty B}(1-e^{-k(t-t_0)})^{b_{ab}} \tag{36}$$

For the position of b_{ab} as a power constant and not as a coefficient, b_{ab} influences directly the parameters k and t_0 inside the parenthesis in equation (36), but not $L_{\infty B}$. This is particularly important when b_{ab} is allometric and is not included in the model, making k and t_0 deviate from the true value. This effect explains why $L_{\infty B}$ is more accurate than k and t_0 in all models analysed in this thesis.

The divergence of $L_{\infty B}$ from the true value is lower for non-linear methods because the fit depends on a differential approach toward iteratively finding new solutions, contrary to linear methods based on average distances. This explains why the stability during the fit process can be a good estimator of the adequacy of individual parameters and also of whole models (one of the main assumptions in the previous chapter).

The algebraic reasoning may be sound, but what about data sets? How much can the morphometric factor affect the calculation of weight from length-at-age fits? And how similar is this phenomenon to the cases previously presented? The following example, utilising theoretical data sets, is intended to clarify these questions.

4.5.2 ASSESSMENT OF WEIGHT-AT-AGE FROM LENGTH-AT-AGE DATA

The equation for weight-at-age growth from length-at-age data, including the morphometric factor, is derived from equation (36) by the following procedure.

Similar to L_A in equation (32), the equation for calculation of weight from an isometric dimension is

$$W_b = a_b L_B^{\ b_b}$$

Solving for L_B,

$$L_B = \left[\frac{1}{a_b} W_B\right]^{\frac{1}{b_b}} \tag{37}$$

For asymptotic L_B,

$$W_{\infty B} = a_b L_{\infty B}^{\;b_b} \tag{38}$$

Substituting L_B from equation (37) in equation (36),

$$\left[\frac{1}{a_b} W_B\right]^{\frac{1}{b_b}} = L_{\infty B}(1 - e^{-k(t-t_0)})^{b_{ab}}$$

Solving for W_B,

$$\frac{1}{a_b} W_B = L_{\infty B}^{\;b_b}\,(1 - e^{-k(t-t_0)})^{b_b b_{ab}}$$

$$W_B = a_b L_{\infty B}^{\;b_b}\,(1 - e^{-k(t-t_0)})^{b_b b_{ab}}$$

The first right term corresponds to the right side of equation (42), so, by introducing $W_{\infty B}$ in the previous equation the following function for calculating weight-at-age from length-at-age is obtained:

$$W_B = W_{\infty B}(1 - e^{-k(t-t_0)})^{b_b b_{ab}} \tag{39}$$

For the direct weight-at-age estimation, the equation to fit is:

$$W_B = W_{\infty B}(1 - e^{-k(t-t_0)})^{b_{wb}} \tag{40}$$

where: $b_{wb} = b_b \, b_{ab}$

Notice that b_{wB} is equal to b_b only if b_{ab} is equal to 1.0, this is possible only if L_B distributes isometrically. The following example illustrate the application of these derivations.

In order to show numerically the influence of the morphometric factor (equations (39) and (40)) on the calculation of weight-at-age from length-at-age data, two simulated data sets for 10 age classes is used. A data variable equivalent to the fish body height (L_A) is calculated according to equation (41). L_A is a morphometric dimension that distributes in a simple manner to the classical von Bertalanffy length-at-age equation. The second data set equivalent to length (L_B) is the dimension taken as a reference to explain the influence of the morphometric factor between L_B and L_A on the von Bertalanffy length-at-age model (L_B is allometric to L_A).

$$L_A = L_{\infty A}(1-e^{-k(t-t_0)}) \tag{41}$$

$$L_A = 23.5(1-e^{-0.55(t-0.1666)})$$

t: Age

L_A: Length at age t

$L_{\infty A}$: Asymptotic length for L_A

k: Intrinsic growth rate

t_0: Time at which $L_A = 0.0$

W-L_B is the weight calculated from the length-weight relationship between L_B and W, by the following hypothetical equation, fitted by least squares:

$$W = 0.029554\ L_B^{2.60837}$$

Table 23 contains the results of the fitting of weight-at-age from length-at-age data without and with the morphometric factor.

WG_{3B} is the weight calculated from the standard von Bertalanffy weight-at-age equation with b_b as the morphometric factor from the length-weight relationship, and L_∞, k, and t_0 from the von Bertalanffy length-at-age equation fitted with the Levenberg-Marquardt method from *Age* and L_B data.

MWG_{3B} is the weight calculated from the von Bertalanffy weight-at-age equation, which includes the morphometric factor b_{wb} ($b_{wb} = b_{ab}\ b_b$). b_{ab} is obtained by fitting the von Bertalanffy length-at-age expression that includes the morphometric factor (equation (36)) with the Levenberg-Marquardt method from *Age* and L_B data. b_b comes from the length-weight relationship.

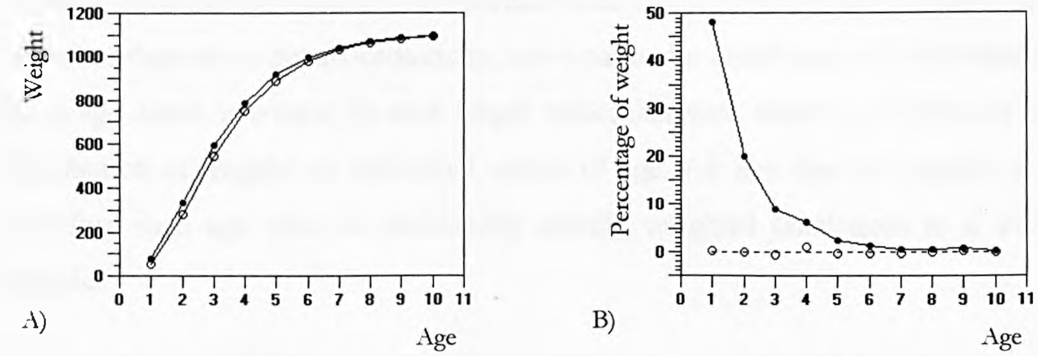
Table 23: **Estimation of weight-at-age growth from length-at-age data using the von Bertalanffy equations.** L_B: length of the positive allometric dimension; *W*: original weight; *W-*L_B: calculated weight from the length-weight relationship of weight and L_B; WG_{3B}: weight calculated from the L_B–at-age growth equation; *%Dif* = (WL_B / WG_{3B} * 100)-100: effect of the morphometric factor in WG_{3B} as percentage of WL_B. MWG_{3B} and *M%Dif* are the equivalent to *%Dif*, but considering the morphometric factor.

Age	L_B	*W*	WL_B	WG_{3B}	*%Dif*	MWG_{3B}	*M%Dif*
1	17.81	54.06	54.05	80	48.0111	54.1	0.092507
2	33.52	281.18	281.3	337.4	19.94312	281.5	0.071098
3	43.25	546.96	546.85	596.6	9.097559	543.8	-0.55774
4	48.65	743.05	743.27	788.9	6.139088	750.8	1.013091
5	52.19	892.79	892.71	915	2.496891	890.5	-0.24756
6	54.11	981.17	980.93	993	1.230465	977.8	-0.31908
7	55.22	1034.2	1034.29	1039.7	0.523064	1030.4	-0.3761
8	55.77	1061.41	1061.37	1067.2	0.54929	1061.3	-0.0066
9	56.05	1075.19	1075.33	1083.2	0.731868	1079.2	0.35989
10	56.32	1089.1	1088.89	1092.5	0.33153	1089.6	0.065204

Plots of data in Table 23 appear in Figure 23. From Figure 23-A the actual predictions apparently do not differ much from the real data after considering the morphometric factor, but the systematic deviation between them can be high for key ages (Figure 23-B). Such divergence is important not only by its magnitude, but particularly for its systematic pattern.

The estimated weights are closer to 0.0 percent of difference after including the morphometric factor (open circles in Figure 23-B). The estimated weights follow a random pattern: some differences are positive while other negative, meaning that such differences are not systematic and are due to the fit (open circles in Figure 23-B).

Both fits with and without morphometric factor result non-significant from the general model, meaning that both are good fits of the data set ($SF< F_{0.05}$). Because the fit including the morphometric factor shows lower RSS and higher MLL, the model that includes the morphometric factor as a power parameter has to be considered the best fit. Additionally, the Schnute's F test shows that the model without the morphometric factor is significant from the one that includes it ($SF= 8.3284 > F_{0.05(1,6)}= 5.99$).



	No morphometric factor	With morphometric factor
L_{inf}	56.7631956	56.609953
k	0.527518	0.558188
t_0	0.290331	0.142405
b		1.196417
RSS	0.1519	0.0636
MLL	6.7440	11.0964
n	10	10
SF	SF= 3.4701< F0.05(2, 5)= 5.79	SF= 4 x10^{-14}< F0.05(1, 5)= 6.61

Figure 23: **Weight-at-age growth from length-at-age data with and without introducing the morphometric factor in the von Bertalanffy growth-at-age models.** A) Estimated weight obtained with no morphometric factor (closed circles) and introducing the morphometric factor (open circles). B) Percentage of over estimation without morphometric factor (closed circles), and with morphometric factor (open circles); horizontal dashed line denotes perfect prediction; SF: Schnute's F statistics.

4.5.3 AN EXAMPLE OF THE INFLUENCE OF THE MORPHOMETRIC FACTOR ON THE ESTIMATION OF WEIGHT-AT-AGE GROWTH

Hypothetical data sets are chosen because the intrinsic variability in real age-length data is a factor that cannot be objectively controlled, and the use of real data would imply the setting of different assumptions that might make any conclusion uncertain.

The example is based on the data set generated in the previous section with a hypothetical length-at-age von Bertalanffy model between L_A (height) and age (t), and a hypothetical length-weight relationship (L_B-W_B). Notice that L_A (height) is directly related with t. Both hypothetical data sets are perfectly distributed accordingly to the classical length-at-age von Bertalanffy model and the length-weight relationship (the distance between each data and the perfect value is purely due to the rounding factor); therefore there is no heteroscedasticity, nor a particular distribution of individual error. Each age datum is unique for each length value; therefore, there is no influence of any distribution of lengths on individual values of age. All age data are equally spaced; therefore each age value is statistically equally weighted (analogous to a stratified sample).

A data set with an allometric relationship between L_A and L_B (L_B: length), and another set with an isometric relationship between L_A and L_C (L_C: width) were derived. L_C is intentionally set to be longer than L_B and L_A in order to show that the phenomenon does not depend on the actual data size (or shape), but on the allometric relationship.

Age is expressed in integer units. The main set of lengths (L_B) is rounded up to one decimal digit, and the rest up to two decimal places in order to resemble the precision used when collecting data.

4.5.3.1 A hypothetical distribution

Data for this example are contained in Table 24. All data are derived from L_A, which follows a von Bertalanffy age-length distribution (equation (41)). L_C is isometrically related to L_A, and L_B is allometrically related to L_A. In this case L_B is analogue to the standard length and L_A is just a dimension allometrically related to such standard length (let us say that it may be the height). The main point is that L_A directly follows the von Bertalanffy model and due to L_B is not isometric with L_A, so the von Bertalanffy length-at-age fit of L_B will produce incorrect estimates for its parameters if the morphometric factor is not considered. Consequently such behaviour will not occur with L_C that relates isometrically with respect to L_A. Theoretically the morphometric factor will not affect the weight-at-age fit of L_A, but it will influence the one for L_B (which is not directly related with t).

Table 24: **Hypothetical data generated from a length-at-age von Bertalanffy equation.** L_A: hypothetical length derived from equation (41), L_B: positive allometric length from equation (42), L_C: isometric length from equation (43), $w_{2.9}$: weight from equation (44) with $b_a = 2.9$, $w_{3.0}$: same as before, but with $b_a = 3.0$, and $w_{3.1}$: weight with $b_a = 3.1$.

Age	L_A	L_B	L_C	$w_{2.9}$	$w_{3.0}$	$w_{3.1}$
1	8.6	17.81	19.18	43.6	54.06	67.04
2	14.9	33.52	33.23	214.61	281.18	368.38
3	18.6	43.25	41.48	408.33	546.96	732.67
4	20.6	48.65	45.94	549.08	743.05	1005.56
5	21.9	52.19	48.84	655.7	892.79	1215.61
6	22.6	54.11	50.4	718.35	981.17	1340.16
7	23	55.22	51.29	755.84	1034.2	1415.06
8	23.2	55.77	51.74	775.06	1061.41	1453.56
9	23.3	56.05	51.96	784.79	1075.19	1473.07
10	23.4	56.32	52.18	794.59	1089.1	1492.75

Age and L_A are related accordingly to equation (41), which is the classic von Bertalanffy expression for length. Any departures from the model are due to rounding error and the size of the data set.

L_B is a positive allometric dimension related to L_A by equation (42).

$$L_B = a_{ab} L_A^{\,b_{ab}} \qquad (42)$$

$$L_B = 1.5\ L_A^{\,1.15}$$

The isometric dimension L_C is related to L_A by equation (43).

$$L_C = a_{ac} L_A^{\,b_{ac}} \qquad (43)$$

$$L_C = 2.3\ L_A^{\,1.0}$$

Data sets for weight $w_{2.9}$, $w_{3.0}$, and $w_{3.1}$ are calculated from equation (44) with $b_a = 2.9$, $b_a = 3.0$, and $b_a = 3.1$ respectively.

$$W_A = a_a L_a^{\,b_a} \qquad (44)$$

$$W_A = 0.085\ L_a^{\,b_a}$$

4.5.3.2 The fit of the weight-at-age relationship

Table 25 contains the results of the weight-at-age fit. Asymptotic weight is the best-fitted parameter with values different from the expected ones in less than two thousandths of the parameters value. *k* is different within two significant digits and t_0 is one significant digit adrift from the true value. In general, the fit is poor particularly for t_0 and *k*. *b* is over-estimated in all cases and the divergence is bigger as the length-weight morphometric factor increases. The introduction of the theoretical allometric constant (Table 25-B) improves the fit. The low data precision and the small number of data (n = 10) are other factors that negatively affect the fit (see 4.5.3.5, p. 128).

Table 25: **Fit of the weight-at-age von Bertalanffy equation for three different weight morphometric values.** W_∞, is the asymptotic weight, *k* the intrinsic rate of growth, t_0 the time at which length is equal to 0.0, and *b* the allometric constant. Capped symbols correspond to the theoretical (expected) values.

A) Direct fit

	$\hat{W}_\infty$	W_∞	k	t_0	b	$\hat{b}$
$W_{2.9}$	804.4808	804.3144	0.5624	0.1023	3.1375	2.9
$W_{3.0}$	1103.1193	1102.8148	0.5628	0.0966	3.2624	3.0
$W_{3.1}$	1512.6181	1512.0701	0.5634	0.0897	3.3920	3.1

B) Replacing *b* by its theoretical value

	$\hat{W}_\infty$	W_∞	k	t_0
$W_{2.9}$	804.4808	805.3458	0.5542	0.1851
$W_{3.0}$	1103.1193	1104.2893	0.5544	0.1861
$W_{3.1}$	1512.6181	1514.1903	0.5546	0.1871

$\hat{k} =$ 0.55 $\hat{t}_0 =$ 0.1666

4.5.3.3 The fit of the length-at-age relationship

In general, all parameters are better estimated from the length-at-age relationship (L_A in Table 26-A) than from the weight-at-age (Table 25-A); the asymptotic parameters fit well in both cases. This finding confirms that the fit of the age-length relationship is better over the age-weight relationship (even for perfect distributions as analysed here).

Intrinsic growth rate (k) and t_0 (Table 26-A) are the same up to three to four significant digits respectively for the isometrically related variables (L_A and L_C). The asymptotic lengths are also similar to their theoretical values.

Asymptotic length fits well for the allometrically related variable L_B, but not k nor t_0. The intrinsic rate of growth is 4% overestimated and t_0 is almost 75% higher than the real value. There is clearly more than a random error problem.

Table 26: **Fit of the length-at-age von Bertalanffy equation with and without morphometric factor.** L_∞ is the asymptotic length, k the intrinsic rate of growth, t_0 the time at which length is equal to 0.0, and b the allometric constant. Capped symbols correspond to the expected values.

A) Normal fit (with no morphometric factor $b_L = 1.0$)

	$\hat{L}_\infty$	L_∞	k	t_0	b_L	$\hat{b}_L$
L_A	23.5	23.51525	0.55161	0.17542	1	1.0
L_B	56.600374	56.76319	0.52751	0.29033	1	1.15
L_C	52.405	52.43955	0.55169	0.17546	1	1.0

B) Adding the morphometric factor to the model

	$\hat{L}_\infty$	L_∞	k	t_0	b_L	$\hat{b}_L$
L_A	23.5	23.50340	0.55833	0.14099	1.04179	1.0
L_B	56.600374	56.60995	0.55818	0.14240	1.19641	1.15
L_C	52.405	52.41273	0.55851	0.14047	1.04246	1.0

C) Introducing the theoretical value of the morphometric factor

	$\hat{L}_\infty$	L_∞	k	t_0	b_L	$\hat{b}_L$
L_B	56.600374	56.6403	0.5518	0.1760	1.15	1.15

The estimation of the asymptotic parameters improves by including the allometric factor as in the case of weight-at-age (Table 26-B): k and t_0 were similar up to three and two significant digits respectively for the three dimensions. The estimated allometric constants are close to the theoretical values.

The fact that the morphometric constant is close to 1.0 for the isometric variables reaffirms the power to detect the isometric relationship and indicates that a departure from 1.0 means allometry. This makes it possible to identify the influence of the morphometric factor on the length-at-age relationship.

The estimation of k and t_0 improves once the theoretical value of b is introduced in to the model as constant (Table 26-C).

4.5.3.4 Methods for fitting the growth curves

In order to show that the estimation of the parameters L_∞ and k does not depend on the non-linear method selected for fitting (Levenberg-Marquardt method), these parameters were estimated through three classical methods without including the morphometric factor: Gulland – Holt, Chapman and Ford – Walford (see 4.4.2, p. 111). These fits produce comparable results to those previously analysed for L_∞ and k, but not for t_0 (Table 27).

Table 27: **Fit of the length-at-age von Bertalanffy equation by classical methods (Gulland-Holt, Chapman, and Ford-Walford).** L_∞ is the asymptotic length, k the intrinsic rate of growth, and t_0 the time at which length is equal to 0.0.

		L_∞	k	t_0
L_A	Gulland-Holt	23.51733	0.537088	0.087306
	Chapman	23.51687	0.550676	0.089175
	Ford-Walford	23.51687	0.550676	0.089175
	Theoretical	23.5	0.55	0.1666

		L_∞	k	t_0
L_B	Gulland-Holt	56.80152	0.510819	0.083984
	Chapman	56.79931	0.522528	0.08638
	Ford-Walford	56.79931	0.522528	0.08638
	Theoretical	56.600374	0.55	0.1666

		L_∞	k	t_0
L_C	Gulland-Holt	52.44359	0.537177	0.085156
	Chapman	52.44255	0.550772	0.087015
	Ford-Walford	52.44255	0.550772	0.087015
	Theoretical	52.405	0.55	0.1666

As shown in the previous chapter asymptotic size (in this case L_∞) is the most accurate and most stable parameter, followed by k. This is why all methods including these are very reliable for the calculation of such parameters.

As for the non-linear fit, L_B is also influenced by the morphometric factor (L_B in Table 27). In this case L_∞ deviates to a greater extent from the theoretical value than in the non-linear method.

4.5.3.5 Number of age categories

The number of age categories is an important factor when fitting growth-at-age. In general, the fit for bigger numbers of age classes improves with and without the morphometric constant (Table 28 compared to Table 26).

Table 28: **Fit of the length-at-age von Bertalanffy equation with extended age categories.** L_∞ is the asymptotic length, k the intrinsic rate of growth, t_0 the time at which length is equal to 0.0, and b the allometric constant. Capped symbols correspond to the expected values.

A) Normal fit (with no morphometric factor $b_L = 1.0$)

	$\hat{L}_\infty$	L_∞	k	t_0	b_L	$\hat{b}_L$
L_A	23.5	23.5127	0.5481	0.1649		1.0
L_B	56.600374	56.9588	0.5058	0.2288		1.15
L_C	52.405	52.4330	0.5482	0.1649		1.0

B) Adding the morphometric factor to the model

	$\hat{L}_\infty$	L_∞	k	t_0	b_L	$\hat{b}_L$
L_A	23.5	23.5077	0.5500	0.1622	1.0061	1.0
L_B	56.600374	56.6238	0.5496	0.1632	1.1552	1.15
L_C	52.405	52.4226	0.5499	0.1623	1.0056	1.0

C) Introducing the theoretical value of the morphometric factor

	$\hat{L}_\infty$	L_∞	k	t_0	b_L	$\hat{b}_L$
L_B	56.600374	56.6323	0.5484	0.1656	1.15	1.15

It can be assumed from this example that a morphometric factor may affect both length-at-age and weight-at-age equations. It can also be inferred that any estimation of weight-at-age growth from length-at-age data may lead to wrong estimates. The formalisation of these assumptions is given below.

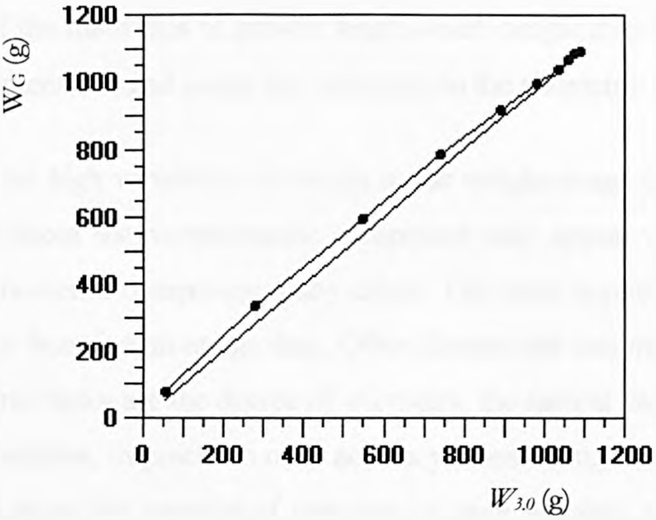
4.6 IMPORTANCE OF THE MORPHOMETRIC FACTOR ON THE ASSESSMENT OF LENGTH-AT-AGE GROWTH

Once the possible influence of the morphometric factor on the length-at-age fit of the von Bertalanffy model is accepted, there are three basic questions about its importance on the assessment of growth: How to determine if a certain linear parameter is morphometrically problematic?, How much can this omission influence the assessment?, and how many species have been influenced in their assessment by this omission?. The first question has been addressed previously, but a short answer is by checking the difference between the parameters k and L_∞ with and without the morphometric factor. There is not a single answer to question two, but I will highlight below some guidelines toward a solution; and finally, I do not have data to answer the last question, but will explore some starting points.

4.6.1 DETERMINING WHICH VARIABLES ARE AFFECTED BY THE MORPHOMETRIC FACTOR

A linear variable is not affected by its morphometric factor if it relates directly to age accordingly to the von Bertalanffy model, therefore the parameters obtained by fitting the length-at-age von Bertalanffy equation without the morphometric factor should give the same result as when it is included.

Plots of residuals of weight-at-age estimates with respect to observed weights against predictor, response, and fitted variables can show patterns on their distribution that may be product of the influence of the morphometric factor. Unfortunately such patterns can also be mistaken with pure departures from the model due to the morphometric effect been systematically bigger for young ages and reduced as the asymptotic length is approached.



$W_{3.0} = 0.029554 L_B^{2.60837}$	Estimated weight from Table 24
$W_{LB} = 1111.385(1-e^{-0.52751(t-0.29033)})^{2.60837}$	Estimated weight from Table 26-A (Asymptotic weight was obtained with the previous equation from asymptotic length = 56.76319):

Figure 24: **Effect of the morphometric factor on a longitudinal dimension.** $W_{3.0}$ is the weight estimated from the length-weight relationship, and W_G is the weight calculated from the fitted length-at-age von Bertalanffy model.

A more reliable visual approach is attained by comparing fitted weights from the von Bertalanffy model against the estimated weight from the length-weight relationship. Both distributions should fall over a straight line with slope = 1.0 if the morphometric factor does not affect the length-at-age growth (Figure 24).

4.6.2 INFLUENCE OF THE MORPHOMETRIC FACTOR ON THE ASSESSMENT OF WEIGHT-AT-LENGTH FROM LENGTH-AT-LENGTH FITS

The influence of a morphometric factor depends on whether the length-at-age distributes according to the von Bertalanffy model, otherwise a different model should be considered. If the length-at-age data set does not seem to conform to the von Bertalanffy model, the following factors ought to be considered.

There is strong possibility that departures will occur if the length-weight relationship is allometric, but temporal circumstances may mask a true morphometric factor, for instance reproductive seasons and starvation periods. The analysis of growth as a function of the main axis of growth length-width-height may be enough to reveal the isometric dimensions and assess the influence on the allometric variables.

Due to the high variability of weight in the weight-at-age data, comparisons of fits with and without the morphometric component may appear non-significant even when the morphometric component really exists. The same applies for the assessment of weight-at-age from length-at-age data. Other factors that can mask the existence of the morphometric factor are the degree of allometry, the natural variability of predictor and response variables, in precision or in accuracy when taking data, how well all ages are represented along the interval of variation of each variable, and the number and periodicity of the age classes (for example, five yearly divisions are too few for the hypothetical population used here, quarterly or even bi-monthly units could produce better results).

A positive-allometric factor of 1.15 in the relationship L_A-L_B (Table 24), produced a negative-allometric value of 2.60837 (Table 29) in the L_B-W relationship. This value is a bit bigger than the lowest found by Morato *et al.* 2001 for some fish species in the Azores. In both cases L_C remained isometric. Assuming a reference age of one third of the life span (in this case three years $\approx$ 10/3), an over-estimation on weight between 9 and 1 percent is predicted for ages between three and six years (Table 29). For a fishery that would depend mostly on age classes close to the reference age this would produce an under estimation of at least 10% in weight.

Table 29: **Effect of the morphometric factor on weight-at-age growth estimation from the length-at-age von Bertalanffy equation.** L_B is the allometric longitudinal variable; Ref*W* is the reference weight; L_B-*W* is the weight calculated from the fitted by least squares length-weight relationship of L_B and Ref*W* with $a = 0.029553577$, and $b = 2.60836952$; *W_vB* is the weight-at-age calculated from the length-at-age fit, and *%Dif* is the effect of the morphometric factor as percentage of weight over-estimation.

Age	L_B	Ref*W*	L_B-*W*	*W_vB*	*%Dif*
1	17.81	54.06	54.05	80	48.0111
2	33.52	281.18	281.3	337.4	19.94312
3	43.25	546.96	546.85	596.6	9.097559
4	48.65	743.05	743.27	788.9	6.139088
5	52.19	892.79	892.71	915	2.496891
6	54.11	981.17	980.93	993	1.230465
7	55.22	1034.2	1034.29	1039.7	0.523064
8	55.77	1061.41	1061.37	1067.2	0.54929
9	56.05	1075.19	1075.33	1083.2	0.731868
10	56.32	1089.1	1088.89	1092.5	0.33153

4.6.3 NUMBER OF SPECIES INFLUENCED BY THE OMISSION OF THE MORPHOMETRIC FACTOR IN THE VON BERTALANFFY GROWTH EQUATION

Because there is no antecedent of the inclusion of an allometric factor as a power constant in the von Bertalanffy length-at-age equation, there is no clue of how many species may be influenced by the omission of such a factor. Perhaps the most reliable indicator whether a species may be influenced by the omission of the morphometric factor is the presence of an s-shape pattern in the lower part of the plot of the length-at-age relationship. This pattern has been detected in “short-lived species” (Moreau 1987), and the over estimation of juvenile growth by using the von Bertalanffy model has been detected for different species of abalone in California (Rogers *et al.* 2002). Yamaguchi 1975 (in Moreau 1987) reports that “the von Bertalanffy growth function is unable to describe the sigmoid length-growth resulting from an inflection point early in the life of fishes”. Because the classical von Bertalanffy length-at-age equation does not predict an s-shape distribution for juveniles, any s-shape may be a case of a species influenced by the omission of the morphometric factor in the von Bertalanffy length-at-age equation. Moreau (1987) points out that the s-shape is characteristic of some anadromous and diadromous fishes, and short-lived species of tropical flood-plains, but it may not be exclusive to those species. The following are some guidelines to help identify this phenomenon.

As a first step, an in-depth analysis of the power of the von Bertalanffy model to describe fish growth is necessary for those species that are assessed from length-at-age data. The power of description should be based on the contrasting of pure mathematical assumptions against the properties of the distribution of size-at-age variables under different biological conditions. Empirical considerations as 'the biological meaning of t_0' or 'the incapability of explaining the age of fishes longer than L_∞' should be avoided.

Secondly, for those species for which their growth-at-age relationship can be described throughout the von Bertalanffy model, a review based on a morphometric analysis against weight for large data sets, and separated from other seasonal variables such as maturity indices will be necessary.

The length-weight morphometric constant is not a good initial reference. On the one hand a length-weight morphometric constant close to isometry is not a guarantee of the low influence of the morphometric factor, because two allometric longitudinal variables one positive allometric and other negative allometric can attenuate the final result by producing a sum of allometric constants equal to 3.0, which can be erroneously interpreted as isometry. On the other hand it is more likely for height and width to become allometric than for standard length to do so.

Richter *et al.* (2000) found for milkfish (*Chanos chanos*) that height and width are isometric, but width and length are allometric. This is a potential case of the effect of the allometric factor on weight-at-age determination from length-at-age data. The authors noticed those relationships when trying to assess the condition using the Fulton condition factor. In the end they opted for an alternative condition factor that included the width instead height, as proposed by Jones *et al.* (1999).

4.7 CONCLUSIONS

The von Bertalanffy equation for length-at-age growth must include a morphometric factor.

The absence of the morphometric factor can be misleading as to why the model may not fit the data well.

The morphometric factor is equal to 1.0 when the longitudinal variable that relates in a simple manner to the standard von Bertalanffy for length-at-age equation is isometric to length.

An allometric factor produces a change in the scale of the longitudinal variable.

A positive allometric factor will cause under estimation of length and a negative allometric factor causes over estimation of length.

The effect of the morphometric factor on length is systematic - bigger for young ages, it becomes less as the asymptotic length is approached.

The morphometric factor directly influences the intrinsic rate of growth and t_0, but not the asymptotic length.

Theoretically the morphometric factor can be very important for the accurate assessment of weight-at-age growth when calculated from length-at-age data.

All the classical methods of assessing fish growth need to be revisited and re-examined. The application of new mathematical methods, computer algorithms and methodologies for data analysis has the power to fully examine the available data. This may lead to new insights into the growth in fishes and possibly improved data for stock assessments, and possibly generate new and improved models and methods.

CHAPTER 5

SUMMARY AND CRITIQUE

5.1 THE LENGTH-WEIGHT RELATIONSHIP AND THE CONDITION FACTOR

5.1.1 THE MEANING OF THE LENGTH-WEIGHT RELATIONSHIP AND ITS PARAMETERS

The derivation of the generalised length-weight relationship from an ellipsoid shape and the inclusion of the density factor is an easy and obvious task that may have been done before, and if so, it surprisingly has not acquired enough popularity to be published and taken as a basic reference to show the meaning of the parameters of the length-weight relationship. The lack of knowledge of the meaning of the parameters of the length-weight relationship leads not only to misinterpretations, but unknowingly to the proposal of new models for the length-weight relationship and condition factor, which are simply special cases of the generalised model derived from the ellipsoid shape. For example, in recent publications (Jones *et al.* 1999; Richter *et al.* 2000) the authors propose new equations to obtain better fits for the estimation of the length-weight relationship and condition based on special assumptions as an isometric length-width relationship that may not apply to all species. Richter *et al.* (2000), who correctly mention the equation for the ellipsoid shape, misinterpret the meaning of density and the proportionality constants (geometric constants) in their equations five to seven, even when they are using the same equation published by Jones *et al.* (1999) as a reference for their new condition factor. The application of the models proposed by the authors without a proper evaluation of the intrinsic assumptions may result in the propagation of errors and wrong conclusions when applying the new empirical models, especially when the application is repetitive and without a proper review of the theoretical background.

5.1.2 CONDITION, HEAVINESS AND FITNESS

It is necessary to have a clear idea about the meaning of condition before estimating and comparing indices. The most widely used condition indices seem to refer to heaviness, which is an important parameter from a utilitarian point of view, but it is clear that weight is not an objective estimator of fitness and that any attempt to interpret fitness from weight alone is risky. The assessment of condition as heaviness is important because many ecological and physiological factors have a feedback effect on the body weight. Even when the sources of an atypical weight may be unknown, the magnitude of weight by itself is an indicator that something is abnormal and its evaluation can become useful in the assessment of its potential ecological and economic impact.

Condition has not been properly exploited as a valuable parameter in fish stock assessment, perhaps for the ambiguity of its concept or for the lack of stable and comparable estimators. Nevertheless it is an important parameter in aquaculture and fish biology. Condition, considered as fitness (as the result of the relationship between biomass, geometric size and shape) could be applied in fisheries to assess the impact of the fishing activity on exploited populations. It is widely known that heavily exploited stocks have higher proportions of younger and smaller individuals than lightly exploited and undisturbed stocks mainly due to size selectivity, therefore the systematic monitoring of fitness might be considered This is not the place to discuss the relationships between size-survival and size-fecundity, nor the occurrence of precocity and dwarfism as responses to size selectivity. However, if the fishing activity severely affects size, all those aspects need to be studied in order to evaluate the critical condition below of which the impact of fishing becomes unacceptable.

5.1.3 A CATEGORICAL ANALYSIS FOR EVALUATION OF CONDITION

By reviewing the effect of body density on the length-weight relationship, it became evident that a single equation for the full population describes just the average relationship and that portions of a same population may present different patterns at different times due to different causes, for example females during the reproductive season will show departures from the average trend, and possibly this departure may be size dependent. At that stage a departure from the average heaviness do not have to be considered as an abnormality and also its comparison against the value predicted from the equation alone may be senseless. In this case an equation or equations for average females at different maturity stage may be more valuable than the general single equation, which emphasize the need for categorical variables as a source of reference standards.

A more proper reference for comparison of condition may be a chart, a table or set of equations of percentile distribution of weight and size (Blackwell *et al.* 2000), similar to those used in humans, or plots of condition as a function of feed as used for fish larvae (Ferron & Leggett 1994). Those resources should be constructed by considering different categorical variables such as geographic location, sex, age, and maturity stage among others, and ideally should be updated whenever there are natural and/or anthropogenic changes in the populations.

5.1.4 OTHER INDICES FOR THE EVALUATION OF CONDITION

The coefficients of the length-weight relationship can be used as *ad hoc* condition indices similar to the ponderal index. Assuming that all coefficients are constant, the indices CF_{LHD} and CF_L (equations (45) and (46)) can be derived from the equations for the general length-weight relationship and general condition factor (chapter 2), and may be multiplied by a power of 10 to avoid working with decimal numbers (*i. e.* 100 or 1000). A normal condition factor ($CF_V = 1.0$) will be equivalent to the value of a of the length-weight relationship multiplied by the power of 10.

$$CF_V = \rho \frac{4\pi}{3} = \frac{W}{LHD} \qquad (45)$$

$$CF_L = \frac{4\pi}{3} \rho \; a_H a_D = \frac{W}{L^{1+b_H+b_D}} \qquad (46)$$

Other indices for size-independent density may be parameterised from equation (46) in special cases when two or three of the longitudinal body dimensions are isometric. For example, the derivation for height (H) isometric to length (L) is:

$$CF_{LD} = \frac{4\pi}{3} \rho \; a_H a_D = \frac{W}{L^{1+b_H} L^{b_D}}$$

Due to $D = a_D L^{b_D}$, $a_D = \frac{H}{L^{b_D}}$. By substituting a_D in the previous equation,

$$CF_{LD} = \frac{4\pi}{3} \rho \; a_H \frac{D}{L^{b_D}} = \frac{W}{L^{1+b_H} L^{b_D}}$$

$$CF_{VD} = \frac{4\pi}{3} \rho \; a_H = \frac{W}{L^{1+b_H} D}$$

Following the same procedure than for height and length, the rest of the possible indices are the following:

(47)

$$CF_{VH} = \frac{4\pi}{3}\rho\ a_D = \frac{W}{HL^{1+b_D}} \qquad \text{A}$$

$$CF_{VD} = \frac{4\pi}{3}\rho\ a_H = \frac{W}{DL^{1+b_H}} \qquad \text{B}$$

$$CF_{VHD} = \frac{4\pi}{3}\rho\ = \frac{W}{HDL} = CF_V \ \text{(Same as equation (45) for the ellipsoid shape)} \qquad \text{C}$$

For isometry between longitudinal dimensions (for b_H=1, or b_D= 1 or b_H= b_D= 1), and size-independent density, the following equations result as special cases of the previous ones in a similar process than for (47)-A, (47)-B, and (47)-C:

(48)

$$CF_{LH} = \frac{4\pi}{3}\rho\ a_H = \frac{W}{L^2 D} \ \text{(Isometric height: } b_H = 1\text{)} \qquad \text{A}$$

$$CF_{LD} = \frac{4\pi}{3}\rho\ a_D = \frac{W}{L^2 H} \ \text{(Isometric width: } b_D = 1\text{)} \qquad \text{B}$$

$$CF_{LHD} = \frac{4\pi}{3}\rho\ a_H a_D = \frac{W}{L^3} \ \text{(Isometric height and width: } b_H = b_D = 1\text{)} \qquad \text{C}$$

The last index is the Fulton condition factor, which is true only for full isometric growth of the orthogonal axes.

Further research is necessary to derive indices for when density is size-dependent because its mathematical distribution is unknown, but I suspect that it may either be a power or a transcendental function (exponential, trigonometric or the inverses of both).

5.2 THE REALISM OF GENERAL SIZE-AT-AGE MODELS

The two general models to assess the best size-at-age growth model in chapter 3 proved to be useful, but are they real? The general equations used as a reference to find the best fit among different models do not constitute a proper model, but just an abstract entity with absolutely no meaning either mathematically or biologically. There is no mathematical link between the logistic, the generalised von Bertalanffy and the double exponentials, such as Gompertz, because all of them are a consequence of different mathematical assumptions with respect to the specific growth rates from which they are derived. Changing from one model to another in the general equation by sign switching and reparameterisation does not mean that both models are equivalent or mathematically related due to their differential background is different, for example when shifting from von Bertalanffy to logistic model (equations (17) and (18)) the value of b and c in general model 1 (equation (27)) changes from 1 to –1, and t_0 (the time at which the size is equal to zero) becomes the time at the inflection point instead. If the new equation fits the data better, it just means that it is more likely that the data are better explained by the assumptions of the new model. It does not signify that both models are mathematically related. Furthermore, it does not denote that the general equation is a generalised model that includes both individual models.

More research is necessary, not to find new models, but to understand the biological principles underlying the phenomenon of growth, to identify its best descriptor variables, and to find their mathematical relationship. Something similar but far more complicated than that presented for the length-weight relationship.

During the presentation of the method to assess the best size-at-age growth model no attempt was made to consider the estimated variance for each fitted parameter as a tool for comparison. The main reason is that direct comparison of individual parameters is not recommended (Quinn & Deriso 1999; Haddon 2001). However, complete functions can be statistically compared by different methods, such as the analysis of residual sum of squares (Chen *et al.* 1992), and the likelihood ratio test (Kimura 1980; Kimura 1990; Haddon 2001). These methods depend on the residual error and not on the individual variables' error as in the linear methods.

5.3 THE MORPHOMETRIC FACTOR

The von Bertalanffy model works well for many species, but its mathematical origin is not fully known. I personally think that regardless of the biological assumptions, it is likely that the intrinsic growth rate of the von Bertalanffy growth mode and the one in the Richards model are the same. Actually, both the Richards equation and the generalised von Bertalanffy equation are the same, but because the von Bertalanffy equation has an analytical origin and its basic mathematical assumptions were not properly clear, both were perceived as different. For some authors (e. g. Schnute 1981; Laslett *et al.* 2002) the von Bertalanffy model became considered as a special case of the Richards model. The only difference is the absence of the morphometric factor in the von Bertalanffy age-length equation, which as was shown here, should be included (concordantly with the generalised von Bertalanffy equation).

The equality of both models can be seen through the parameterisation of the generalised von Bertalanffy model as follows,

$$Y = Y_\infty(1-e^{-k(t-t_0)})^b = Y_\infty(1-e^{-kt}e^{kt_0})^b$$

If $c = e^{kt_0}$ then,

$$Y_\infty(1-e^{-k(t-t_0)})^b = Y_\infty(1-ce^{-kt})^b$$

The right term is the Richards equation. In this case there is no change of assumptions but just a simplification of terms, which suggests that both models are the same.

5.4 GENERAL CONCLUSIONS

As a first step, more research on the bio-mathematical meaning and correct evaluation of growth must be undertaken, followed by a review of the methods and models that use its results. This will help to incorporate corrections and improvements to the models that depend on the evaluation of growth parameters. From the analysis undertaken here, it is clear that some figures for some species whose weight-at-age growth was calculated from length-at-age data may be over or under estimated and its repercussion must be evaluated, especially where these data are used for management purposes. It is also clear that some suppositions about morphometric growth should be reviewed.

Finally, this work could not have been done without the computer programming performed. The independence from commercial and existing computer packages helped to avoid mechanically following the same assumptions, and fitting models found in previous works. It also gave me the opportunity to question about some inconsistencies between my data and the fits. In the same way, the independent programming task permitted *ad hoc* exploration and evaluation of different perspectives. The algebraic demonstrations and quantitative exemplifications given here are the final result of a process initiated with the contrasting of individual programming algorithms against data sets with known properties as a product of specific assumptions from different models. The construction of algorithms was followed by the exploration of properties of real samples against the assumptions contemplated in the algorithms. In the end, the links between algorithms, mathematics, and models permitted the derivation of the algebraic explanations presented here. This approach also helped to keep away from the temptation of *a priori* attributing the inconsistencies found to 'possible' biological reasons without further analysis. Even when modest, I consider the programming effort highly valuable; despite it is not noticed in the final product. I categorically refuse to accept that programming is just for programmers, mathematics for mathematicians, and biology for biologist: I consider that the basic difference between a naturalist and a biologist as a scientist is the power to explain mathematically the biological phenomena, that mathematics is not just a tool, but the basic language of nature and building algorithms is one of the most powerful ways to develop explanations on how nature operates. If the work with fish populations can be considered as been done by an "ecological detective" (phrase attributed to Jon Schnute: in Hilborn & Mangel 1997), building mathematical and computer algorithms is equivalent to 'reconstructing the story'.

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