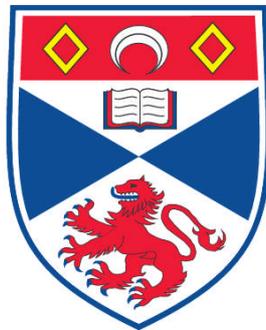


**PREDICTING FOOD CONSUMPTION AND PRODUCTION IN
FISH POPULATIONS: ALLOMETRIC SCALING AND
SIZE-STRUCTURED MODELS**

Rodrigo Wiff

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



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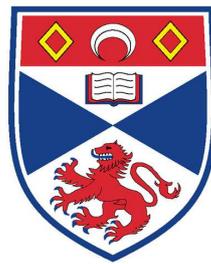
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PRODUCTION IN FISH POPULATIONS: ALLOMETRIC
SCALING AND SIZE-STRUCTURED MODELS

Rodrigo Wiff



Thesis submitted for the degree of
DOCTOR OF PHILOSOPHY
in the School of Biology
UNIVERSITY OF ST ANDREWS
ST ANDREWS
JANUARY 2010

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This thesis is dedicated to the memory of my mother, Erika Onetto (R.I.P).
For a life of love and inspiration to her family.

Esta tesis está dedicada a la memoria de mi madre, Erika Onetto (Q.E.P.D). Por
una vida de amor e inspiración para su familia.

Abstract

Life-history traits in fish populations are highly correlated. A subset of these correlations are called allometric scaling, they refer to biological processes which can be described using body size as independent variable. Particularly, allometric scaling related with food consumption (Q) and biomass production (P) has gained the attention of ecologists for several decades. This thesis proposes a quantitative framework for food consumption, which allows both the identification of the mechanisms underlying the allometric scaling for Q and the development of a predictive model for consumption to biomass ratio (Q/B) in fish populations. This thesis is based on the fact that food consumption can be inferred from first principles underlying the von Bertalanffy growth model. In addition, it has been noticed in the literature that biomass production and food consumption show similar allometric scaling dependence, therefore, both can be derived from these first principles. Thus, a similar quantitative framework was used to produce models for P/B in fish populations. Once functional forms for production and food consumption were identified, a third model was developed for the ratio between production and consumption (P/Q). This ratio is usually named ecological efficiency because it determines how efficiently a population can transform ingested food into biomass. Several authors have noticed that P/Q remains invariant (independent of body size) across species. From a theoretical point of view, the results presented here allow the first quantitative explanation for the existence of the allometric scaling for Q/B and the invariance of P/Q across fish species. These results, together with the explanation for allometry in P/B reported in the literature, suggest that the regular across-species pattern for the trio $\{P/B, Q/B, P/Q\}$ can be explained by basic principles that underpin life-history in fish populations. This quantitative framework for the trio $\{P/B, Q/B, P/Q\}$ is based on an explicit dependence with body size, which simplifies the estimation of these quantities. Model complexity depends, in part, on which data are available. Models were applied to real

data from commercially important species fished in Chile. Statistical properties of the new models were evaluated by an intensive resampling approach. The simplest possible model for the trio $\{P/B, Q/B, P/Q\}$ rests on the assumption of a stable age distribution. These quantities have a key importance in ecosystem modelling because they determine population energetics in terms of food intake by predation and the transformation of this energy into population biomass of predators. Application of the new models produces results which were comparable to those given by standard methods. This thesis is a result of multidisciplinary research which attempts to make a contribution to the understanding of the mechanisms underlying the allometric scaling of food consumption and production in fish populations. It proposes models for the trio $\{P/B, Q/B, P/Q\}$ and thus, has the potential to be widely applicable in fisheries science.

Declarations

I, Rodrigo Wiff, hereby certify that this thesis, which is approximately 25000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in October 2005 and as a candidate for the degree of Doctor of Philosophy in Biology and Statistics in August 2006; the higher study for which this is a record was carried out in the University of St Andrews between 2005 and 2009.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in Biology and Statistics in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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- A random day during the summer 2003 Luis (Lucho) Cubillos called me to his office at the Instituto de Investigación Pesquera (Talcahuano, Chile). He knew I was interested in quantitative ecology, and that day he noted a really important fact; production as well as consumption are defined by very similar equations and both processes show similar dependence with body size in an across-species comparison. He also pointed out the importance of these processes in ecosystem modelling. That day Lucho recommended I have a closer look at these processes and lent me various publications on the subject. A year later I gathered all these thoughts together and finally wrote a first draft of the proposal for this thesis. Many thanks Lucho who encouraged me to study this topic.
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Notation

The following notation is listed here for an easy reference, being used throughout this thesis.

Parameters and functions	Definition
-----------------------------	------------

Size and age

a	Age
a_0	Size at age 0 of the von Bertalanffy growth function
a_m	Age at maturity
a_1	Age-at-first capture
a_∞	Maximum age
\mathfrak{S}	Parameter of the trade-off between l_∞ and k
h	Scaling factor for the trade-off between l_∞ and k
k	Growth rate coefficient of the von Bertalanffy growth function
l	Body length
l_m	Length at maturity
l_∞	Asymptotic body length
l_{max}	Maximum length
l_h	Length at 50% of selectivity
l_0	Length at zero age
t	Time
w	Body mass
w_∞	Asymptotic body mass
y	Year
α	Parameter of the length-weight relationship
β	Parameter of the length-weight relationship
σ^2	Variance of the length-at-age
τ	Otolith radius

Metabolism

A	Assimilation rate parameter
b	Parameter of the gross conversion efficiency in Pauly's model
b_2	Parameter of the gross conversion efficiency in the empirical model
α_2	Parameter of the gross conversion efficiency in the empirical model
c	Catabolism parameter
d	Allometric scaling factor for anabolism
f	Faeces
H	Anabolism parameter
I	Assimilation
K	Gross conversion efficiency
p	Proportionality constant of surface
s	Effective physiological surface

Parameters and functions	Definition
Metabolism	
s_2	Specific dynamic action
T	Temperature factor
T^c	Mean annual temperature of the body water
u	Excretion
η	Allometric scaling factor for for catabolism
ι	Surface power exponent
Population	
B	Biomass
$f(l)$	Probability density function of lengths in the population
F	Fishing mortality
N	Cohort size
M	Natural mortality rate
$P_y(a)$	Probability mass function of the age a
Q	Instantaneous consumption rate of a group of individuals
R	Recruitment
S	Selectivity
Z	Total mortality rate
ϕ	Proportionality constant between CV and a_m
ω	Shape parameter of the selectivity
ψ	Proportionality parameter linking fishing and natural mortality
Consumption	
G	Annual ration
G_d	Daily ration
q	Instantaneous consumption rate of an individual
μ	Aspect ratio of the caudal fin
ϱ, ν	Binary variable indicating the type of food
Others	
n	Number of fish sampled
r	Correlation coefficient
ϵ	Failure probability
ϖ	Indicator function

Abbreviations Definition

Abbreviations

vB	von Bertalanffy
VBGF	von Bertalanffy growth function
C	Consumption-to-biomass ratio of a group of individuals
λ	Production-to-biomass ratio of a group of individuals
ρ	Production-to-consumption ratio of a group of individuals
Eqn	Equation
g	Grams
CV	Coefficient of variation
CI	Confidence interval
s.d	Standard deviation
<i>FR</i>	Freshwater environment
<i>MA</i>	Marine environment
MLE	Maximum likelihood estimator
pmf	Probability mass function
pdf	Probability density function
S-R	Stock-recruitment relationship
MFZ	Management fishing zones
TAC	Total allowed catch
TL	Total length
IFOP	Instituto de Fomento Pesquero

Glossary

- **Age at first capture:** is the minimum age at which fish could be targeted by the fishery.
- **Allometry:** growth of a part of an organism in relation to the growth of the whole organism or some part of it. The measurement or study of this growth.
- **Allometric scaling:** the study of biological processes where the independent variable is the body size.
- **Anabolism:** the phase of metabolism in which simple substances are synthesized into the complex materials of living tissue.
- **Apparent specific dynamic action:** is the increased metabolic rate a fish experiences following ingestion of a meal.
- **Assimilation:** the conversion of nutrients into living tissue; constructive metabolism.
- **Bias:** systemic inaccuracy in data due to the characteristics of the process employed in creation, collection, manipulation, and presentation of data, or due to faulty sample design of the estimating technique.
- **Biomass production:** total amount of somatic tissue accumulated in a population during a given time period.
- **Bootstrap:** randomization test which involves generating subsets of the data on the basis of random sampling with replacement.
- **Catabolism:** the metabolic breakdown of complex molecules into simpler ones, often resulting in a release of energy.

- **Cohort:** group of fish in a stock, which were generated during the same spawning season and are born at the same time.
- **Conditional probability:** the probability of one event, A, occurring given that another, B, is already known to have occurred.
- **Cross-sectional estimator:** a random variable or function used to estimate population parameters from cross-sectional data.
- **Cross-sectional data:** observations of many individuals (subjects, objects) at a given point in time.
- **Daily ration:** amount of food consumed per individual per day.
- **Ecological efficiency:** the ability of the organisms at one trophic level to convert to their own use the potential energy supplied by their foodstuff at the trophic level directly beneath them.
- **Excretion:** the act or process of discharging waste matter from the blood, tissues, or organs.
- **Expected value:** for continuous random variables with a density function it is the probability density-weighted integral of the possible values. For discrete random variables this is equivalent to the probably-weighted sum of the possible values.
- **Fitness:** the relative ability of an organism to survive and transmit its genes to the next generation.
- **Gross conversion efficiency:** is a measure of the ability of an organism to convert ingested food into new tissue.
- **Invariant:** is a mathematical concept meaning a quantity which remains unchanged under certain classes of transformations. In case of life history invariant, the transformation is the jump from one specie to another or, alternatively, the displacement along space described by life history parameters.
- **Knife-edge-selectivity:** assumption where fixed fishing mortality rate is inflicted on all age/length groups above a certain age/length.

- **Life history:** the sequence and timing of events that occur between birth and death.
- **Lifespan:** the average or maximum length of time an organism can be expected to survive.
- **Longitudinal estimator:** a random variable or a function used to estimate population parameters from longitudinal data.
- **Longitudinal data:** observations of a given unit made over time. Such data can usually be represented as a time-series.
- **Maximum Likelihood estimator:** is a popular statistical method for fitting a statistical model to data, and providing estimates for the model's parameters.
- **Pristine condition:** is the state of a stock in a pure condition before fishing exploitation.
- **Probability density function:** mathematical function which allocates probabilities of particular observations occurring. The probability density function may be used to construct a frequency distribution of certain events occurring either discretely or continuously.
- **Probability mass function:** a function which gives the relative frequency of each possible value of the random variable in an experiment involving a discrete set of outcomes.
- **Recruitment:** the residue of those larvae that have: (1) dispersed; (2) settled at the adult site; (3) made some final movements toward the adult habitat; (4) metamorphosed successfully, and (5) survived to be detected by the observer.
- **Scaling:** how the structure and behaviour of a system vary with its size.
- **Selectivity:** ability to target and capture fish by size and species during harvesting operations, allowing bycatch of juvenile fish and non-target species to escape unharmed. In stock assessment, it is conventionally expressed as a relationship between retention and size (or age) with no reference to survival after escapement.

- **Stable age distribution:** the proportions of the population in different age classes when the rate of increase has converged to a constant.
- **Steady-state condition:** where all the biomass renewal is compensated with total mortality.
- **Trade-off:** an exchange of one thing in return for another, especially relinquishment of one benefit or advantage for another regarded as more desirable.

The von Bertalanffy Growth Function

Throughout this thesis I use the concepts underlying the the von Bertalanffy growth function (VBGF) to derive models of production and consumption in fish populations. In this section I show the mathematical derivation and basic physiological principles underpinning the VBGF.

Several equations have been proposed to describe animal growth. However, most of them provide only a phenomenological description of growth. Of the mathematical functions applied to fish, the VBGF is used more widely by fisheries scientists (Chen et al, 1992). Perhaps, because it was derived from general principles underpinning biological mechanisms, it is simple to apply and it provides a good description for the growth of most fish species.

According to Bertalanffy (1938), growth in animals is conceived as a net result of two opposing processes, anabolism and catabolism. Anabolic processes involve synthesis of protein, while catabolic processes degrade it. One of the fundamental principles of the VBGF outlines that catabolism occurs in all living cells and results in the break down of body substances; it is therefore proportional to the mass of an individual. Anabolism is the processes of building up and thus, it is proportional to respiratory rate. Such general principles lead to the following differential equation for growth processes:

$$\frac{dw}{da} = Hw(a)^d - cw(a)^\eta \quad (1)$$

where $w(a)$ is the body mass at age a , and H and c are the proportionality constants for anabolism and catabolism, respectively. Terms d and η are referred to as the

allometric scaling factors for anabolism and energy cost, respectively. To make use of this equation, it is necessary to define the terms d and η . Eqn (1) indicates the net growth result of two processes with opposite tendencies, one increasing body mass, the other decreasing body mass. Note this definition of Eqn (1) implies that growth may be negative (when anabolism < catabolism) or it ceases when catabolism is equal to anabolism. von Bertalanffy explicitly stated that the surface area limits anabolism and thus it is proportional to a power function of length. Catabolism occurs in all living cells of an animal and is thus directly proportional to the mass of the individual's body. Thus, the above equation can be now written in the form:

$$\frac{dw}{da} = Hs - cw(a) \quad (2)$$

where s refers to the limiting physiological surface of the organism. In these terms, H can be seen as the rate of synthesis of mass per unit of "physiological surface" and c is the rate of destruction of mass per unit of mass. This equation can be solved if we can make an assumption of the relation between w and s . von Bertalanffy expresses both s and w in terms of the linear dimension, length (l) of the organism. If it is assumed that the organism is growing isometrically, then we can write:

$$\begin{aligned} s(l) &= pl^\iota \\ w(l) &= \alpha l^\beta \end{aligned} \quad (3)$$

where p and α are proportionality constants and ι and β are power factors of physiological surface and weight, respectively. In the original formulation of VBGF (Bertalanffy, 1938) it was considered that $\iota = 2$ and $\beta = 3$. Therefore, growth rate in a linear dimension is:

$$\begin{aligned} \frac{dw}{da} &= \frac{d(\alpha l^\beta)}{da} \\ &= 3\alpha l^2 \frac{dl}{da} \end{aligned} \quad (4)$$

substituting Eqn (4) and (3) on Eqn (2) gives:

$$\begin{aligned} \frac{dl}{da} &= \frac{Hpl^2}{3\alpha l^2} - \frac{c\alpha l^3}{3\alpha l^2} \\ &= \frac{Hp}{3\alpha} - \frac{cl}{3} \end{aligned} \quad (5)$$

and, setting $E = \frac{Hp}{3\alpha}$, $k = \frac{c}{3}$ we have:

$$\frac{dl}{da} = E - kl \quad (6)$$

the solution of which is:

$$l(a) = \frac{E}{k} - \left[\frac{E}{k} - l_0 \right] e^{-ka} \quad (7)$$

where l_0 is the length of an organism at zero age. Now, as $a \rightarrow \infty$, $l(a) \rightarrow \frac{E}{k}$; that is, as the organism increases in age its length increases to an asymptote which is the greatest possible length that the organism, under given conditions, can attain. von Bertalanffy denotes this maximum length by l_∞ , so that the previous equation becomes:

$$l(a) = l_\infty - (l_\infty - l_0)e^{-ka} \quad (8)$$

the corresponding equation for growth in weight is obtained by substituting w in terms of l in the above expression,

$$w(a) = w_\infty - [(w_\infty - w_0)e^{-ka}]^3 \quad (9)$$

where w_∞ and w_0 are the weights corresponding to lengths l_∞ and l_0 .

Note that parameter k is proportional to the catabolism parameter c and therefore it is proportional to the rate of destruction of body material per unit of weight and time. Taking into account that the greater part of catabolism involves protein breakdown (Beverton and Holt, 1957), von Bertalanffy took the rate of excretion of some starving animals (including fish) as a measurement of their catabolic rate. Thus, experimental estimates of k were obtained which match well with those obtained by fitting the VBGF to length at age data. This fact, as von Bertalanffy pointed out, is substantial evidence that parameter k has a physiological meaning. VBGF has parameters that are fully interpretable from basic principles and thus, it is possible to infer consumption rates from individual growth. Further analysis in this thesis will use these first principals to propose models of consumption and production in fish populations.

Eqns (8) and (9) are not often used in the fishery literature. A simplified model is usually applied by parameterizing w_0 in terms of time. In this context, parameters k and w_∞ can be used to specify an age a_0 at which an organism would have been of zero age. Thus setting $w(a) = 0$, and $a = a_0$ in Eqn (9) gives

$$w_0 = w_\infty (1 - e^{ka_0})^3 \quad (10)$$

and substituting Eqn (10) on Eqn (9) we have

$$w(a) = w_\infty [1 - e^{-k(a-a_0)}]^3 \quad (11)$$

similarly, Eqn (8) becomes

$$l(a) = l_\infty [1 - e^{-k(a-a_0)}] \quad (12)$$

Figure (1) shows a diagram of the “specialized VBGF” in length.

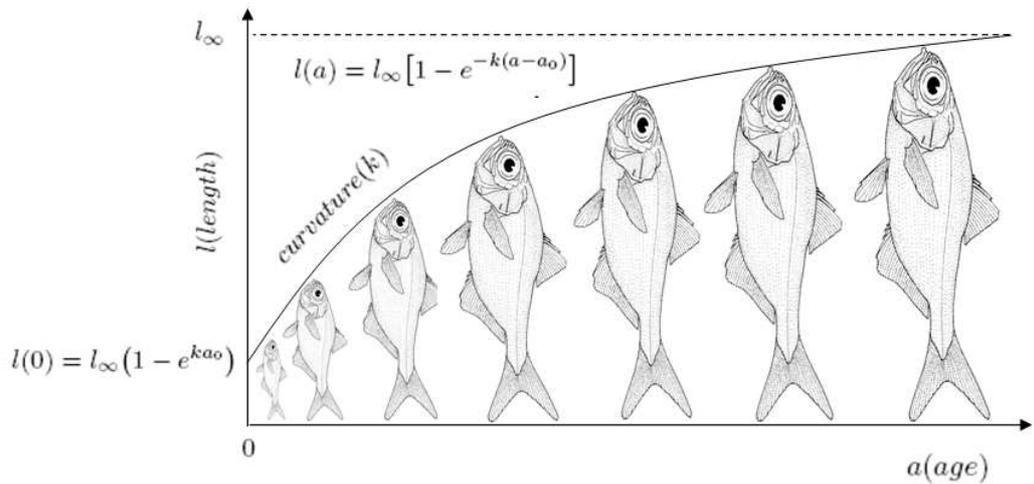


Figure 1: “specialized” von Bertalanffy growth function in length

Eqns (11) and (12) are the original models proposed by Bertalanffy (1938) and are known as “specialized VBFG” because ι and β are set at specific values. Pauly

(1981) demonstrated that Eqn (2) could also be solved for values other than $\iota = 2$ and $\beta = 3$. Eqn (2) can be solved if we can make an assumption of the relationship between ι and β . Temming and Herrmann (2009) demonstrated that $d = \iota/\beta$ in Eqn (1). Parameter d simply represents allometric scaling of anabolism. Parameter ι is usually restricted to $2 < \iota < 3$ whereas β is typically ≈ 3 in fish species. For the analytical solution, $\eta = 1$ and parameters H , c and ι are re-parameterized in terms of $D = \beta(1 - d)$, $H = \beta k w_\infty^{(1-d)}$ and $k = c/\beta$. For details see (Temming and Herrmann, 2009). Solving Eqn (1) for these new parameters yields:

$$w(a) = w_\infty [1 - e^{-Dk(a-a_0)}]^{1/(1-d)} \quad (13)$$

Similarly, VBGF in length is:

$$l(a) = l_\infty [1 - e^{-Dk(a-a_0)}]^{1/(\beta(1-d))} \quad (14)$$

Models in Eqns (13) and (14) are usually referred to as the "Generalized VBGF", because they can be reduced to their corresponding specialized form (Eqns 11 and 12) by setting up $d = 2/3$ and $\beta = 3$.

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Chapter 1

General Introduction

When we think of the branching process of speciation through evolutionary time, we realize that the process is not totally random. The set of species that we find in any section taken across this branching process, are result of certain rules established by natural selection, and the processes of mutation and genetic drift. Despite the enormous complexity of ecological systems, the existence of such rules implies that at least some ecological processes can be described by simple relationships. One subset of these rules is known as "allometric scaling", which refers to those regularities seen across-species that are function of individual body size. In a historical context, most research efforts have addressed allometric relationships in which the response variable is an individual level attribute such as metabolic rate (Kleiber, 1932), lifespan (Charnov and Berrigan, 1990), sexual maturity (Jensen, 1996) and growth (Charnov et al, 1993). However, allometric scaling is also common at higher levels of organization, such as the population, community and ecosystem (Marquet et al, 2005). This fact underscores the importance of body size at all levels of organization, and opens the way for synthesis and integration across these levels.

At the population level, allometric scaling of biomass production and food consumption have been widely used in estimating these quantities for empirical models.

Banase and Mosher (1980) compiled empirical estimates of annual production (P) and biomass (B) across a wide range of animal taxa, including fish, and Palomares and Pauly (1998) compiled similar information on food consumption (Q) and B , for fish populations. In both compilations these estimates were standardized and re-expressed as ratios of annual production to biomass (P/B) and annual food consumption to biomass (Q/B). Although derived from heterogeneous sources, these estimates of P/B and Q/B show surprisingly regular patterns with individual body size. For example, if P/B and Q/B are plotted against the individual body size on a log-log scale, the points fall along a straight line with negative slope.

Not only have the regularities of allometric scaling been intensely studied in ecology, Beverton and Holt (1959), pioneers in the study of meta-analysis in fish biology, collected life history parameters for a large number fish species belonging to different taxa. They pointed out three important quantities which remain constant across fish species: the ratio between the instantaneous mortality rate (M) and the parameter k of the von Bertalanffy growth function (VBGF), the product of M and the age at sexual maturity (a_m), and the ratio between the length at maturity (l_m) and the asymptotic length (l_∞). This trio was called “the Beverton-Holt life history invariants” by Charnov (1993). “Invariant” is a mathematical concept meaning a quantity which remains unchanged under certain classes of transformation, and which provides a way to identify the conditions under which two mathematical objects are equivalent (Olver, 1995). In the case of the life history invariants, the transformation is the jump from one species to another or, alternatively, the displacement along the space described by life history parameters. The existence of such invariants, as in the case of mathematics, is a reflection of a fundamental symmetry among the objects (Charnov, 1993). Other authors (Slobodkin, 1960; Welch, 1968; Turner, 1970) have

demonstrated that ecological efficiency, denoted by the ratio P/Q , is also, relatively constant across species that have similar trophic habits. Thus, P/B and Q/B seem to obey an allometric scaling pattern whereas P/Q is a life history invariant in fish populations.

These regularities have puzzled ecologists for many decades, but we are now beginning to understand the mechanisms that produce them (Brown and Gillooly, 2003). West et al (1997) were able to explain the allometry of metabolism at the individual level, by noting that the networks which transport material within living bodies have a fractal-like structure. Charnov (1993) and Jensen (1996) have shown that allometric scaling that involves lifespan, sexual maturity and growth can be explained as a trade-off between reproduction and survival. At the population level, the scaling of P/B across species can be explained by the fact that the ratio of body size at sexual maturity to asymptotic body size is constant (Roa and Quiñones, 1998) for individuals whose growth can be described in terms of the VBGF. However, the mechanisms underpinning the allometry for food consumption described in Palomares and Pauly (1998) and the constancy of ecological efficiency remain unknown. Here, I propose a mechanistic explanation for these constancies based on the VBGF. I focus principally on fish species, although the model can be easily extended to other taxa. Although, several equation have been proposed to describe growth in fish, only few of them are derived from fundamental principles (West et al, 2001). The VBFG is a mechanistic growth model is conceived as a net result of two opposing fundamental processes, anabolism and catabolism. Anabolic processes involve synthesis of protein, while catabolic processes degrade it. Thus, the VBGF is a convenient model for processes related to biomass production and food consumption because it generally provides a good description of fish growth and individual food consumption can be inferred

from its principles (Temming, 1994; Essington et al, 2001). This study, taken together with the work of Roa and Quiñones (1998), describes a connection between allometry in population energetics, (namely, in P/B , Q/B and P/Q) and the von Bertalanffy principles for individual growth.

The estimation of these population energetic ratios is not just of theoretical interest. P/B is important in population dynamics because it is the rate at which population biomass is replaced. The estimation of Q/B is of basic importance in multispecies models that incorporate trophic interactions (Ross, 1986). And P/Q is an important quantity in ecosystem models because it indicates the efficiency with which a population transforms ingested food into biomass. According to Koziowski and Weiner (1997) empirical patterns in allometry can be explained in two ways. Across-species allometries may reflect some functional relationship between body size and physiological attributes. However, they may also be by-product of some other underlying mechanism or mechanisms. Understanding these underpinning mechanisms may help us connect population energetic processes such as P/B , Q/B and P/Q with individual body size. Therefore, one way to develop predictive models for these quantities is to explicitly consider the way in which they depend on body size. This is particularly important because existing methods for P/B and Q/B generally rely on the empirical equations derived from allometric relationships that were described above (Banse and Mosher, 1980; Palomares and Pauly, 1998), or on ad-hoc models such as that developed by Mertz and Myers (1998) for P/B , and by Pauly (1986) for Q/B and P/Q . The empirical equations for P/B and Q/B are easy to apply, but they generally lack theoretical support and they cannot account for shifts in population structure. The ad-hoc models rely on assumption involving steady-state of the biomass (where all renewal is compensated with mortality) and/or stable age distribution (constant

recruitment and age-dependent mortality). They may also include several parameters which cannot be interpretable in biological terms. These limitations suggest that alternative approaches, estimating P/B , Q/B and P/Q based on size structure of populations, should be explored.

Modelling population processes by using their size structure can permit a smooth integration of single-species fishery models into ecosystem models. The ecosystem models that have been developed for aquatic systems generally rely on a size-based approach (see Jennings and Blanchard, 2004; Hall et al., 2006). This approach allows single and multispecies models to be unified and generalised by adding explicit dependence on size. This thesis has two main objectives. First, I use the physiological principles of anabolism of the VBGF to explore the mechanisms that underpin allometry in Q/B and the invariance of P/Q . Second, I propose predictive models for Q/B , P/B and P/Q based on population size structures. I also quantify the uncertainty associated with these new using computationally-intensive statistical techniques. Finally, I illustrate how these models can be applied to a number of commercially important fish that are exploited in Chilean waters.

This thesis proposes a quantitative framework for population energetics processes that helps to explain reported allometric scaling relationships and provides simplified methods for the estimation of P/B , Q/B and P/Q in wild populations. It is structured into six chapters plus an appendix. Chapter 1 is a general introduction and chapter 6 is a general discussion. Chapter 2 provides a mechanistic explanation for the Q/B allometry in fish by using physiology of growth. Chapter 3 proposes a model for Q/B in fish populations derived from the framework developed in chapter 2, which explicitly related Q/B and population size structure. In chapter 4, I develop a model for P/B that is derived from the allometric principles discussed in

Roa and Quiñones (1998), which connects P/B with population size structure. This quantitative framework for P/B also allows for across-species comparisons. Chapter 5 describes a simple model for P/Q in fish population based on body size and using equations for P and Q derived in previous chapters. This model provides a theoretical explanation for the constancy of P/Q across species. Finally, the appendix explains how the growth parameters used to illustrate the models in chapters three, four and five were estimated.

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Chapter 2

Allometric scaling of consumption rates

Chapter based on: Wiff, R and R. Roa-Ureta. 2008.– *“Predicting the slope of the allometric scaling of consumption rates in fish using the physiology of growth”* Marine and Freshwater Research. **58**, 912-921

2.1 abstract

Allometric scaling has been observed in many aspects of fish biology. Empirical studies have shown that individual and population rates of food consumption for single and multi-species datasets show positive allometry. However, the ratio of population consumption to biomass shows negative allometry when evaluated across species. In this paper, a theoretical explanation is proposed that predicts the magnitudes and signs of the allometric slopes for consumption and consumption/biomass within and among species. It is proposed that the ultimate cause of the allometries related to food consumption in fish lies in the physiology of growth. In the context of von Bertalanffy growth, the allometric slopes are caused by the constraints imposed on anabolism by the surfaces absorbing oxygen, by the volumetric relationship between linear body size and body mass, and by a dimensionless growth parameter.

2.2 Introduction

Life-history traits of fish correlate with body size. These relationships are commonly described as allometric scaling laws. Scaling laws might involve parameters of mortality and growth (Pauly, 1980; Charnov et al, 1993), sexual maturity and lifespan (Charnov and Berrigan, 1990; Jensen, 1996; Frisk et al, 2001), biomass production (Banse and Mosher, 1980; Downing and Plante, 1993) and food consumption (Palomares and Pauly, 1998). Charnov (1993) and Jensen (1996) have shown that allometric scaling that involves mortality, sexual maturity and growth can be explained as a trade-off between reproduction and survival. Scaling of the biomass-to-production ratio across species can be explained by the fact that the ratio of body size at sexual maturity to asymptotic size is constant and that growth can be described by the von Bertalanffy equation (Roa and Quiñones, 1998). In the case of food consumption rates, empirical studies have shown that individual consumption rates vary allometrically during ontogeny, with a slope close to 0.8 for some fish species (Cui, 1987; Elliott and Hurley, 1998). Palomares and Pauly (1998) compiled estimates of consumption standardised to biomass (Q/B ratio) for different populations and found that this ratio was related allometrically to body size. What is lacking, however, is a framework that allows these empirical relationships to be compared among individuals and populations, and that identifies the biological processes underlying these regularities in food consumption. In this paper, we propose a quantitative framework that predicts the slopes of the allometric scaling of food consumption for fish, both within and among species and at the individual and population levels. We show that, if growth is modelled according to the principle of von Bertalanffy, the underlying processes are a direct consequence of the physiology of growth.

2.3 The model

Von Bertalanffy's principle states that the rate of growth of an individual, whose size in linear dimensions is l , is determined by the difference between the build-up of body mass resulting from energy input, which is defined by a quadratic equation in l , and energy expenditure resulting from maintenance, which is described by a cubic equation in l :

$$\frac{dw}{da} \propto l(a)^2 - l(a)^3 = Hw(a)^d - cw(a)^\eta = Hw(a)^{2/3} - cw(a) \quad (2.1)$$

where a is age, $l(a)$ and $w(a)$ are length and body mass at age a , and the other terms are constants. Terms d and η are referred to as the allometric scaling factors for anabolism and energy cost respectively. In the original formulation of the von Bertalanffy growth function (VBGF) Bertalanffy (1938) $d = 2/3$ and $\eta = 1$. In a more general setting, d can take a value other than $2/3$, leading to a generalised VBGF, $w(a) = w_\infty [1 - \exp(-Dk(a - a_0))]^{\frac{1}{1-d}}$, where $D = \beta(1 - d)$ being β the power parameter of the length-weight relationship ($W(l) \propto l^\beta$), w_∞ is the asymptotic body mass, k is the growth rate coefficient defined by $k = c/\beta$ and a_0 is the age at $w_a = 0$.

The instantaneous consumption rate (q) of an individual at weight w is related to its assimilation rate (A) by $q(w) = (H/A)w^d$ (Temming, 1994; Essington et al, 2001). According to Temming (1994), H can be recast in terms of the generalised VBGF as $H = \beta kw_\infty^{(1-d)}$. Thus, an expression for the instantaneous consumption rate in which all parameters have a clear biological meaning is:

$$q(w) = \frac{\beta kw_\infty^{(1-d)}}{A} w^d \quad (2.2)$$

The instantaneous consumption (Q) of a cohort of size N is:

$$Q(w) = \frac{N\beta k w_{\infty}^{(1-d)}}{A} w^d \quad (2.3)$$

Note that $N(a) = R e^{-Za}$, where Z is the mortality rate and R is recruitment. Note here mortality is assumed constant through ages and thus, no density dependant variations are considered. The biomass (B) of a cohort of weight w is given by $B(w) = Nw$, so the Q/B ratio is:

$$\frac{Q}{B}(w) = \frac{\beta k w_{\infty}^{(1-d)}}{A} w^{d-1} \quad (2.4)$$

This equation represents the instantaneous Q/B ratio of a cohort of weight w . This ratio is a function of individual properties in the case when all individuals composing the cohort were born on exactly the same date and have identical growth parameters. In that case, a cohort's consumption (g^{-1}) is the same as the consumption of an individual (g^{-1}). Cohort abundance does count, even in an instantaneous formulation, if the individuals do not have the same birth date and/or identical growth parameters. We address this issue later by incorporating population size structure.

Eqn (2.4) can be recast in terms of body length using a suitable length-weight relationship, such as $w(l) = \alpha l^{\beta}$, where α and β are constants. Eqn (2.4) then becomes:

$$\frac{Q}{B}(l) = \frac{\beta k l_{\infty}^{\beta(1-d)}}{A} l^{\beta(d-1)} \quad (2.5)$$

At a particular point in time (t^*), a population is composed of multiple cohorts of

different ages, overlapping in space and time. Thus, Q/B for a population can be determined by summing the contributions of each cohort to Q/B at t^* :

$$\left. \frac{Q}{B}(w) \right|_{t^*} = \sum_a \frac{\beta_a k_a w_{\infty,a}^{(1-d_a)}}{A_a} w^{(d_a-1)} P(a) \quad (2.6)$$

where $P_y(a)$ is the proportional contribution of a cohort of age a to the population at time t^* , $P_y(a) = N(a)/\sum_a N(a)$, $\sum_a P_y(a) = 1$. The term $P_y(a)$ can be seen as the age structure and it is determined by the magnitude of recruitment and the mortality rate experienced by this cohort. Thus, $P_y(a)$ represents the discrete probability distribution of the population at time t^* . If all cohorts share the same VBGF and assimilation parameter (A), then we can accumulate the effect of age:

$$\begin{aligned} \left. \frac{Q}{B}(w) \right|_{t^*} &= \frac{\beta k w_{\infty}^{(1-d)}}{A} \sum_a w(a)^{(d-1)} P_y(a) \\ &= \frac{\beta k w_{\infty}^{(1-d)}}{A} E[w^{(d-1)}] \end{aligned} \quad (2.7)$$

where $E[w^{(d-1)}]$ is the expectation of $w^{(d-1)}$ in the population at time t^* . The equivalent population Q/B in terms of body length is:

$$\begin{aligned} \left. \frac{Q}{B}(l) \right|_{t^*} &= \frac{\beta k l_{\infty}^{\beta(1-d)}}{A} \sum_a l_a^{\beta(d-1)} P_y(a) \\ &= \frac{\beta k l_{\infty}^{\beta(1-d)}}{A} E[l^{\beta(d-1)}] \end{aligned} \quad (2.8)$$

It is apparent that the population Q/B depends on the expected value of body size across a population body size distribution. Note that Q/B can be estimated from Eqn (2.7) and (2.8) given a representative sample of weight or length from a

population. These models represent the population Q/B at a particular point in time. However, if suitable data are available, the dynamic behaviour of Q/B can be obtained by ordering the separate Q/B estimates in time. Point and integrated estimates of Q/B (obtained by integrating consumption, then biomass and dividing both; see Pauly (1986) for details) are comparable if the mortality rate remains constant across cohorts and between discrete recruitment events.

2.4 Theoretical predictions

Our objective was to see if we could predict the observed slopes of the empirical relationships between consumption and body mass using the equations derived in the previous section. The slopes are: (i) log individual consumption against log body size over a lifespan; (ii) log individual consumption against log body size among species; and (iii) log consumption to biomass ratio against log body size among populations. These relationships are usually used as empirical models to predict consumption in data-poor species and they modelling may help to understand the physiological basis for allometry scaling in consumption rates. For (i) the process is straightforward.

Isolating w in Eqn (2.2) and applying logarithms to both sides yields:

$$\log[q(w)] = \log\left[\frac{\beta k w_{\infty}^{(1-d)}}{A}\right] + d \log[w] \quad (2.9)$$

Generalisation to multi-species or multi-population cases is achieved by adopting different values of the growth (k, w_{∞}, d) and assimilation parameters (A) for each species/population; thus:

$$\log[q(w)]_j = \log\left[\frac{\beta_j k_j w_{\infty,j}^{(1-d_j)}}{A_j}\right] + d_j \log[w_j] \quad (2.10)$$

In the same manner, taking logarithms of both sides of Eqn (2.7) yields:

$$\log \left[\frac{Q(w)}{B(w)} \right]_j = \log \left[\frac{\beta_j k_j w_{\infty,j}^{(1-d_j)}}{A_j} \right] + \log \left[E \left(w^{(d-1)} \right) \right]_j \quad (2.11)$$

If length rather than body mass is used, the result is:

$$\log \left[\frac{Q(w)}{B(w)} \right]_j = \log \left[\frac{\beta_j k_j l_{\infty,j}^{\beta_j(1-d_j)}}{A_j} \right] + \log \left[E \left(l^{\beta(d-1)} \right) \right]_j \quad (2.12)$$

Note that the first term on the right-hand side of Eqns (2.9) to (2.12) is composed entirely of parameters that were assumed to be size and age invariant. Our purpose in leaving the body size in Eqn (2.10) to (2.12) is to isolate the effect of body size on individual consumption. Thus, isolating body mass on (Eqn 2.9) yields:

$$\frac{\partial \log(q)}{\partial \log(w)} = d \quad (2.13)$$

Thus, if we plot log (consumption) against log (body mass) during an individual's lifespan, the slope of the relationship is an estimate of parameter d . Although this result might appear trivial, our interest is in comparing the value of d obtained in this way with that assumed in the original formulation of the VBGF. As we will discuss later, parameter d is explained by von Bertalanffy in terms of dependence of mass-specific anabolism on surface area, and thus it may be derived from basic principles underlying the physiology of growth.

Now consider a collection of pairs of estimates of consumption and weight for each species at a particular point during their ontogeny, let us say q^* , w^* . For technical convenience, we assume, as Peters (1983) and Charnov (1993) did, that the transition

from species to species can be represented as a continuum in space, so that differential operators can be applied. In linear equations, the discrete slope ($\Delta y/\Delta x$) is an approximation of the continuous slope ($\partial y/\partial x$), regardless of the value of Δx . Thus, Eqn (2.10) yields:

$$\frac{\partial \log(q^*)_j}{\partial \log(w^*)_j} = d_j \quad (2.14)$$

Where q^* is the individual consumption evaluated at a particular body mass (w^*).

The ecological implications of this solution can be interpreted as follows: if we take individuals at a given point in their lifespan from j different fish species and plot their consumption against weight, the slope will be the parameter d of the VBGF. As we discuss later, d can be interpretable in terms of the basic principles which underpin the physiology of growth.

We now consider the theoretical basis for the allometric relationship between Q/B and asymptotic size found by Palomares and Pauly (1998) by comparing population consumption across j species at the asymptotic body size (w_∞, l_∞). The first term on the right-hand side of Eqns (2.11) and (2.12) is composed of the product between k and w_∞ or l_∞ . As these parameters are known to be highly correlated across species (Beverton and Holt, 1959; Pauly, 1980; Charnov, 1993), it is convenient to analyse the effect of one or the other in an isolated manner (Gallucci and Quinn, 1979). Charnov (1993) proposed that there was a trade-off $l_\infty = \mathfrak{S}k^{-h}$ between these three parameters that constrained k and l_∞ . In biological terms, that means that animals that grow faster (higher k) tend to reach a smaller asymptotic size and vice versa. Thus, it is possible to re-parameterise Eqn (2.11) and eliminate k . Taking into account the length-weight relationship $w_\infty = \alpha l_\infty^\beta$, we get $k = \mathfrak{S}^{\frac{1}{h}} l_\infty^{-\frac{1}{h}}$,

$k = \mathfrak{S}_j^{\frac{1}{h}} \alpha_j^{-\frac{1}{\beta h}} w_\infty^{-\frac{1}{\beta h}}$. Expressing Eqns (2.11) and (2.12) in terms of asymptotic body size we get:

$$\log \left[\frac{Q(w)}{B(w)} \right]_j = \left(1 - d - \frac{1}{\beta h} \right)_j \log[w_{\infty,j}] + \log \left[\frac{\beta_j \mathfrak{S}_j^{\frac{1}{h}} \alpha_j^{\frac{1}{\beta h}}}{A_j} \right] + \log \left[E(w^{(d-1)})_j \right] \quad (2.15)$$

$$\log \left[\frac{Q(w)}{B(w)} \right]_j = \left(\beta(1 - d) - \frac{1}{h} \right)_j \log[l_{\infty,j}] + \log \left[\frac{\beta \mathfrak{S}_j^{\frac{1}{h}}}{A_j} \right] + \log \left[E(l^{\beta(d-1)})_j \right] \quad (2.16)$$

Thus, the slope of the log-log plot of Q/B against w_∞ or l_∞ should be:

$$\frac{\partial \log(Q/B)_j}{\partial \log(w_\infty)_j} = \left(1 - d - \frac{1}{\beta h} \right)_j \quad (2.17)$$

$$\frac{\partial \log(Q/B)_j}{\partial \log(l_\infty)_j} = \left(\beta(1 - d) - \frac{1}{h} \right)_j \quad (2.18)$$

It is possible to drop the j subscript because parameters d , β and h are relatively constant across fish species. The parameter d is explained by Bertalanffy (1957) in terms of the dependence of mass-specific anabolism on surface area, and Bertalanffy (1957) assumed that $d = 2/3$. The specific value of β can be explained in terms of the cubic dimensional relationship between the length and weight of nearly homogeneous bodies; for most metazoan species β has a value of approximately three (Peters, 1983).

Note that solutions of the Eqns (2.17) and (2.18) rely on the independence between w_∞ and l_∞ with $E(w^{(d-1)})$ and $E(l^{\beta(d-1)})$, respectively. Although the assumption of independence is debatable in this chapter two alternative considerations were taken into account. First, $E(w^{(d-1)})$ and $E(l^{\beta(d-1)})$ are mostly determined by size/age-dependent mortality rate, variations in recruitment and increasing size variability

over time (growth depensation). This highlighted the fact that population size structure is greatly dependant on the dynamics of the population rather than on the asymptotic individual size (Pfister and Stevens, 2002). Second, (2.15) and (2.16) allowed the understanding of the underlying mechanism in the scaling of Q/B reported by Palomares and Pauly (1998) where asymptotic size was used as an independent variable.

Pauly (1980) noted that estimates of the dimensionless parameter h cluster around $1/2$. Therefore, we can drop the subscript j from the right-hand sides of Eqns (2.17) and (2.18). With a 'typical fish' having $d = 2/3$, $\beta = 3$ and $h = 1/2$, it is possible to predict the slopes resulting from Eqns (2.14), (2.17) and (2.18) across a large group of fish species:

$$\begin{aligned}\frac{\partial \log(q^*)_j}{\partial \log(w^*)_j} &= \frac{2}{3} \\ \frac{\partial \log(Q/B)_j}{\partial \log(w_\infty)_j} &= -\frac{1}{3} \\ \frac{\partial \log(Q/B)_j}{\partial \log(l_\infty)_j} &= -1\end{aligned}$$

However, we are interested in evaluating how variations of these parameters can help to explain the empirical observations. Eqns (2.15) and (2.16) yield further predictions. As $0 < d < 1$, the expected individual body size in the population is inversely related to Q/B . Furthermore, mortality rate is directly related to Q/B because it tends to reduce the expected body size in the population. In addition, the same allometric slope will hold for any body size that is a constant proportion of asymptotic body size. For instance, maximum body size and size at maturity are constant proportions of asymptotic body size (Charnov, 1993), making these quantities good

candidates for further empirical explorations. A further adjustment is necessary to account for the allometric relationship found by Palomares and Pauly (1998) in the relationship between Q/B and asymptotic size in fishes. Pauly (1980) argued that the surface rule of Bertalanffy (1957) very rarely applies in fish, so that d should take values other than $2/3$. To support this hypothesis, Pauly (1981) introduced the concept of a 'physiologically limiting surface' that determines anabolic rate. Pauly (1981) explained that in fish the synthesis of body substance is a matter of adequate food and oxygen supply because fishes derive the energy for the synthesis of body substances exclusively from the oxidation of energy-rich assimilates. Therefore, the physiologically limiting surface might be represented by the area of the gills, the surface area of the gut, or by the area of any other internal surface across which assimilates and/or oxygen have to be transported. Pauly (1981) concluded that the intrinsic properties of fish gills make them the most appropriate candidate for the physiological limiting surface because this is where oxygen is incorporated into the body. Pauly (1981) gathered data on gill area and mass for 40 species of fishes and calculated an average d value of 0.789 (s.d.=0.04). In contrast, Froese (2006) used a meta-analysis of 3929 mass-length relationships from 1773 species of fish to obtain a median value of 3.025 (95%CI=3.011, 3.036) for β . Palomares and Pauly's (1998) compilation of Q/B and VBGF parameters was used to estimate the trade-off parameter h in order to make theoretical predictions of the slopes for the relationship between Q/B and asymptotic body size. We followed Charnov's (1993) suggestion that h has to be estimated from a functional regression (Ricker, 1973) between $\log(l_\infty)$ and $\log(k)$ to obtain a value of $h = 0.700$ (s.d.=0.074). Using these values for d , β and h in Eqns (2.13) to (2.18) yields the following predictions:

$$\partial \log(q) / \partial \log(w) = 0.789$$

$$\partial \log(q^*)_j / \partial \log(w^*)_j = 0.789$$

$$\partial \log(Q/B)_j / \partial \log(w_\infty)_j = -0.261$$

$$\partial \log(Q/B)_j / \partial \log(l_\infty)_j = -0.790$$

2.5 Empirical predictions

Essington et al (2001) assembled consumption rate estimates for 36 fish species/location combinations. These results include a wide range of fish sizes with estimates coming from bioenergetics models. The average value for d (slope of log (individual consumption) v. log (body mass)) was 0.801 (s.d.=0.22). We used 23 estimates of d for different species of fish reared under laboratory conditions and fed until satiation (Grove and Crawford, 1980; Cui and Lui, 1990; Elliott and Hurley, 1998; Andersen and Riss-Vestergaard, 2003) to obtain a mean value for d under laboratory conditions of 0.733 (s.d.=0.16). The overall average of d from these two analyses is 0.774 (s.d.=0.202). We also compiled estimates of individual daily food consumption for 86 different species/locations of marine and freshwater fishes, chosen to include a wide range of adult fish sizes to evaluate the $\partial \log(q^*)_j / \partial \log(w^*)_j$ prediction. Three methodologies had been used to obtain these data: (i) laboratory studies; (ii) in situ field studies; and (iii) indirect estimates from bioenergetics and mass balance models. When the data came from laboratory experiments, we chose those estimates in which fish were fed until satiation and animals that were reared under a non-stressing thermal regime. For all methods, we chose estimates based on wet body mass. Overall, the mean value of $\partial \log(q^*)_j / \partial \log(w^*)_j$ was 0.804 (95%CI= 0.742, 0.867). Further details about these data are in Appendix (2.7). Finally, we used the compilation

of 108 population estimates of food consumption per unit of biomass of marine and freshwater fish reported by Palomares and Pauly (1998). The empirical slopes were:

$$\begin{aligned}\partial \log(Q/B)_j / \partial \log(w_\infty)_j &= -0.209 (95\%CI = -0.285, -0.135) \\ \partial \log(Q/B)_j / \partial \log(l_\infty)_j &= -0.747 (95\%CI = -0.974, -0.520)\end{aligned}\tag{2.19}$$

Our theoretical predictions match these empirical predictions remarkably well (Fig. 2.1, Table 2.5).

Slopes	Theoretical predictions			Empirical values		
	Values	References	Values	Independent Variable	References	
Intra-specific individual consumption	0.798 (0.776,0.800) ^A	Pauly (1981)	0.774 (0.721,0.825) ^A	Body mass	Several authors	
Inter-specific individual consumption	0.798 (0.776,0.800) ^A	Pauly (1981)	0.804 (0.742,0.867)	Average body mass	Appendix 2.7	
Inter-specific Q/B and body mass	-0.261 (-0.402,-0.150) ^A	β by Froese (2006) and d by Pauly (1981)	-0.209 (-0.285,-0.135)	Asymptotic body mass	Palomares and Pauly (1998)	
Inter-specific Q/B and body length	-0.790 (-1.125,-0.487) ^A	β by Froese (2006) and d by Pauly (1981)	-0.747 (-0.974,-0.520)	Asymptotic body length	Palomares and Pauly (1998)	

Table 2.1: Theoretical predictions and empirical values of the relationship between individual consumption (q) and population consumption to biomass ratio (Q/B) with body mass (w) or body length (l) for fish. Confidence intervals are shown in parentheses.

^A Confidence intervals computed by resampling

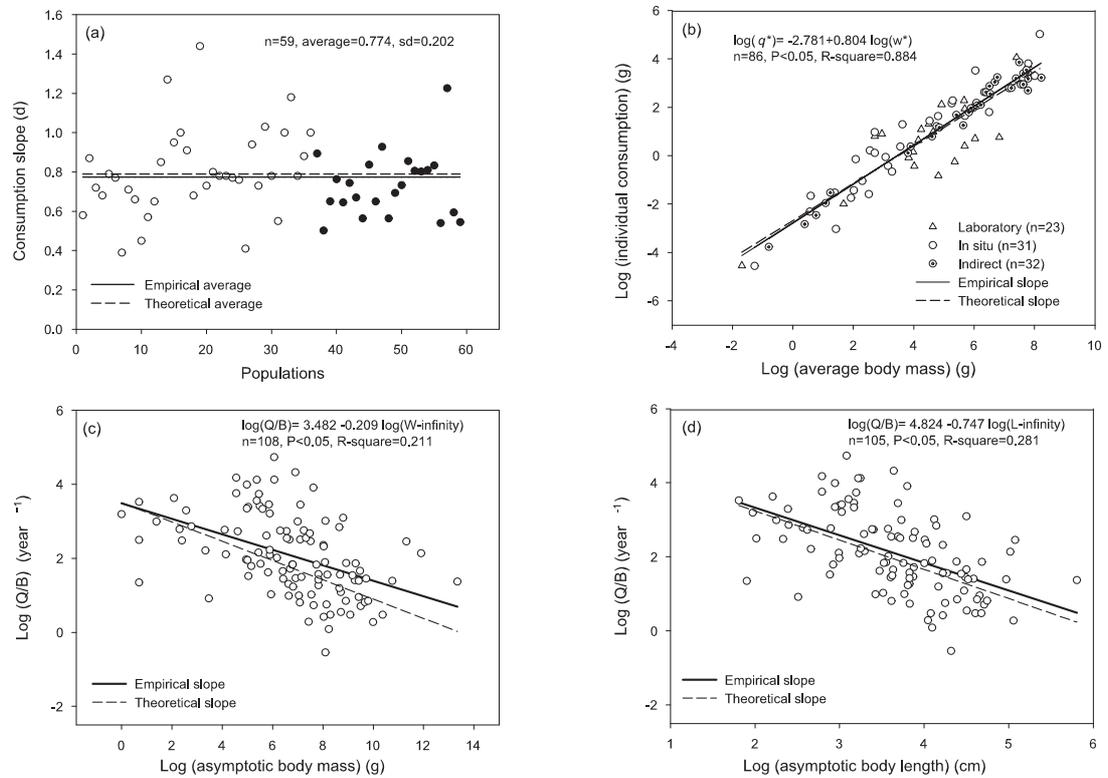


Figure 2.1: Empirical estimates and theoretical predictions of consumption for fish. The black and dashed lines show the empirical and theoretical predictions respectively. (a) Slopes (parameter d) resulting from a plot of log (individual consumption) v. log (body mass); the line indicates the average slope. Estimates of d from bioenergetics models (open symbols are the data from Essington et al (2001)) and laboratory studies (filled symbols are the data from Grove and Crawford (1980); Cui and Lui (1990); Elliott and Hurley (1998)). (b) log (daily individual consumption) v. log (average body mass); the line is the least-square regression of the data (Appendix 2.7). (c) log (population consumption-to-biomass ratio) (Q/B) v. log (asymptotic mass); the line is the least-square regression of the data (data from Palomares and Pauly (1998)). (d) log (population consumption-to-biomass ratio) (Q/B) v. log (asymptotic length); the line is the least-square regression of the data (data from Palomares and Pauly (1998)).

2.6 Discussion

We propose a quantitative framework to analyse the scaling of food consumption by fish within and among species at both the individual and population level. Regularities in consumption rates at these levels appear to be a consequence of the constraints imposed by anabolism, represented by the value of d in the VBGF. Our explanation depends on the invariance of the parameters d , β and h , and on the VBGF. It implies that allometric scaling can be entirely explained by the physiology of growth. This reductionist approach supports the idea that the same underlying process underpins within- and among-species relationships.

2.6.1 Invariance of d , β and h

Although the original formulation of the VBGF set d at $2/3$, consumption allometry in fish rarely scales to this value. We found that Pauly's (1981) gill area surface, which sets d at ~ 0.8 is appropriate to predict patterns in consumption rates in fish at both intraspecific and interspecific levels. In addition, Q/B allometry variations should be driven mostly by changes affecting the trade-off parameter h , because d and β show only small variations across fish species. Thus, species or populations with similar h values should fall on the same line of the Q/B -asymptotic body mass allometry. Beverton and Holt (1959) showed that h for most fish species is in the range 0.4-0.8. They seemed to believe that life-history invariants involving h would hold within specific groups (e.g. Clupeiformes). Charnov (1993) added that h is inversely related to the ratio of length at maturity to asymptotic length (l_m/l_∞). Populations with similar l_m/l_∞ should have similar values of h and therefore similar Q/B dependence with asymptotic body size. One explanation for the relationship that Palomares and Pauly (1998) found with asymptotic body size is that most of the species they analysed belonged to the same taxonomic group (order Perciformes), and should

show little variation in l_m/l_∞ and therefore h . Nevertheless, the predictive capacity of Q/B in the empirical equation of Palomares and Pauly (1998) might be improved by applying different regressions to taxonomic groups with similar l_m/l_∞ values, and therefore h . In conclusion, the regularity found by those authors is probably not a consequence of the demography or ecology of the populations that were studied, but rather of the invariance in: (i) the parameter of the process-limiting anabolism d ; (ii) the parameter of volumetric increase in body mass β ; and (iii) the dimensionless growth parameter h in the VBGF.

2.6.2 Growth model dependence

Our analysis is conditional on a specific model for growth. An alternative model based on constraints to transport energy and materials to the cell was developed by West et al (2001), although, ultimately, it is very similar to von Bertalanffy's model. The main difference is that the value of d is $3/4$ rather than $2/3$. The growth model in West et al (2001) with $\beta = 3$ and $h = 1/2$ yields the following predictions for allometric scaling in fish:

$$\begin{aligned}\partial \log(q^*)_j / \partial \log(w^*)_j &= \frac{3}{4} \\ \partial \log(Q/B)_j / \partial \log(w_\infty)_j &= -\frac{5}{12} \\ \partial \log(Q/B)_j / \partial \log(l_\infty)_j &= -\frac{5}{4}\end{aligned}$$

Debate continues (see Doods et al, 2001; Savage et al, 2004) about whether the universal metabolic scaling factor on which d is based should be $2/3$ or $3/4$. However, Makarieva et al (2005) and Kozłowski and Konarzewski (2004) have criticised the theoretical reasoning for the choice of $d = 3/4$ in the growth model of West et al (2001) on the grounds that it leads to mathematical inconsistencies. Nevertheless,

Economo et al (2005) recently proposed a theory to explain the relationship between the ratio of food assimilation to biomass (I/B) and body size in fish and mammals that is based on the model of West et al (2001). They were able to predict the I/B slope in fish, but not in mammals. This was probably because of the rigid dependence of the model of West et al (2001) on a value of $3/4$ for d , because anabolism in mammals appears to be surface dependent (Doods et al, 2001; White and Seymour, 2003). Growth models other than those of von Bertalanffy and West et al. have been applied to other species groups. For example, squid grow according to Schnute's (1981) model (Arkhipkin and Roa-Ureta, 2005). For those species, the theory in this paper might apply with modifications.

2.6.3 Factors affecting food consumption

A comprehensive understanding of food consumption by fish is difficult because it depends on a great number of internal (physiological) and external (environmental) factors (Silverstein et al, 1999). When food is continuously available, individual consumption patterns will be limited only by digestive constraints on how much food can be processed per unit of time Hall (1987). Feeding rates estimated under these conditions can be considered to be the physiological maximum for a species, setting a limit to the pressure a species can place on its food resource. Nevertheless, we did not find significant variations between the slopes in consumption patterns for fish reared under laboratory conditions and wild fish. This is consistent with Jobling's (1980) conclusion that fish fed a variety of diets appear to regulate their food consumption to maintain a relatively constant energy intake. Grant and Kott (1999) proposed that day-to-day variation in food intake might be independent of prey availability, suggesting that consumption rates of wild fish might be self-regulated and ultimately determined by factors that affect metabolic rates. Environmental temperature is one

of the most important abiotic factors affecting nearly all biological rates (Charnov and Gillooly, 2004), and has been identified as the most important factor shaping consumption rate patterns (e.g. Finstand, 2005). For example, the empirical equation of Palomares and Pauly (1998) relates Q/B to habitat temperature. However, Elliott and Hurley (1998) found that there were no statistical differences in the slopes of the relationship between daily consumption and body mass for fish of different body sizes reared under 15 different temperature regimes in the range 3.8 - 21.6 °C. The pooled value of these slopes (0.763) is close to our prediction of 0.798 (see Table 2.5).

2.6.4 Intraspecific and interspecific allometries

Most allometric studies assume that intraspecific and interspecific patterns are virtually identical, perhaps because interspecific comparisons are abundant, whereas empirical intraspecific allometries are scarce (Koziowski and Weiner, 1997). In the present paper, we show the conditions under which intraspecific and interspecific consumption allometries can be compared. Koziowski and Weiner (1997) concluded that interspecific allometries reflect some functional relationship between body size and physiological parameters. In this reductionist approach, interspecific allometries are seen as the statistical results of body size optimisation under constraints. This means that interspecific allometries per se do not reflect ecological processes in terms of population dynamics. In a related field, Andersen and Beyer (2006) showed that the slope of the interspecific plot of log (number of individual) on log (body size) was solely a consequence of processes at the individual level. Their work, and that of Koziowski and Weiner (1997) and Roa and Quiñones (1998), suggests that many complex ecological patterns might be a consequence of basic and purely individual phenomena. Our analysis follows the same philosophy and suggests that the allometry in population consumption/biomass ratio is determined by processes operating at the

individual level.

2.7 Appendix Chapter 2

Compilation of estimates of daily individual consumption and average body mass in fish. Superscript *FR* and *MA* in each method indicate Freshwater and Marine fishes, respectively.

Species	Average Mass (g)	Average consumption (g day ⁻¹)	Method	Locality	References
<i>Abramis brama</i>	298	5.180	In situ ^{FR}	Czech Republic	Vasek and Kubecka (2004)
<i>Alburnus alburnus</i>	37.5	3.640	In situ ^{FR}	Czech Republic	Vasek and Kubecka (2004)
<i>Ambassis notatus</i>	1.75	0.099	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Ambloplites rupestris</i>	116.394	3.384	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Amblypharyngodon melettinus</i>	1.800	0.189	In situ ^{FR}	Sri Lanka	De Silva et al (1996)
<i>Barbus chola</i>	6.850	0.174	In situ ^{FR}	Sri Lanka	De Silva et al (1996)
<i>Barbus dorsalis</i>	12.350	0.204	In situ ^{FR}	Sri Lanka	De Silva et al (1996)
<i>Barbus filamentosus</i>	12.800	1.239	In situ ^{FR}	Sri Lanka	De Silva et al (1996)
<i>Carcharinus plumbeus</i>	1900	19	In situ ^{MA}	USA (Virginia)	Medved et al (1988)
<i>Catostomus commersoni</i>	565.125	13.730	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Channa (Ophiocephalus) striata</i>	92.5	4.216	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Channa argus</i>	295.6	6.918	Lab. ^{FR}	China	Liu et al (1998)

Table 2.2: Appendix Chapter 2 (1/7)

Species	Average Mass (g)	Average consumption (g day ⁻¹)	Method	Locality	References
<i>Clupea harengus</i>	70	2.950	Lab. ^{MA}	Walles (UK)	Blaxter and Holliday (1958)
<i>Coregonus artedii</i>	49.250	1.459	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Coregonus clupeaformis</i>	672.575	17.697	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Coregonus clupeaformis</i>	598.093	13.729	Indirect ^{FR}	Caniapiscou Reservoir (North America)	Trudel et al (2000)
<i>Coregonus clupeaformis</i>	687.839	12.772	Indirect ^{FR}	Lac Rond-de-Poele (North America)	Trudel et al (2000)
<i>Coregonus clupeiformes</i>	363.206	7.062	Indirect ^{FR}	Lac Serigny (North America)	Trudel et al (2000)
<i>Cyclocheilichthys repasson</i>	7.5	0.238	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Cyprinus carpio</i>	1285	16.225	In situ ^{FR}	Mississippi River (USA)	Garcia and Adelman (1985)
<i>Cyprinus carpio</i>	224.217	5.381	Indirect ^{FR}	White Oak lake (North America)	Rowan and Rasmussen (1996)
<i>Dicentrarchus labrax L</i>	294	1.496	Lab. ^{MA}	Ionean Sea (Greece)	Kavadias et al (2003)
<i>Epinephelus costae</i>	123.672	0.436	Lab. ^{MA}	South Eastern Adriatic (Croatia)	Glamuzina et al (2003)

Table 2.3: Appendix Chapter 2 (2/7)

Species	Average Mass (g)	Average consumption (g day ⁻¹)	Method	Locality	References
<i>Esox lucius</i>	104.25	2.688	Lab. ^{FR}	England (UK)	Hart and Connellan (1984)
<i>Esox lucius</i>	2048.305	18.952	Indirect ^{FR}	Canapiscou Reservoir (North America)	Trudel et al (2000)
<i>Esox lucius</i>	1612.750	24.224	Indirect ^{FR}	Lac Rond-de-Poele (North America)	Trudel et al (2000)
<i>Esox lucius</i>	2404.375	24.166	Indirect ^{FR}	Lake Simcoe (North America)	Trudel et al (2000)
<i>Esox lucius</i>	799.3	21.005	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Esox lucius</i>	2048.305	18.952	Indirect ^{FR}	Great Slave Lake (North America)	Rowan and Rasmussen (1996)
<i>Etheostoma nigrum</i>	0.450	0.0023	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Fugu obscurus</i>	55.570	0.649	Lab. ^{MA}	China	Yan et al (2004)
<i>Gadus macrocephalus</i>	2600	28.6	Lab. ^{MA}	Alaska (USA)	Paul et al (1990)
<i>Gadus morhua</i>	2993	26.937	In situ ^{MA}	North Sea	Daan (1973)
<i>Gasterosteus aculatus</i>	0.28165	0.0105	In situ ^{FR}	Wales (UK)	Allen and Wootton (1982)
<i>Gasterosteus aculatus</i>	0.18484	0.0106	Lab. ^{FR}	Wales (UK)	Allen and Wootton (1982)
<i>Hampala dispar</i>	35	1.4525	In situ ^{FR}	Thailand	Kakkaeo et al (2004)

Table 2.4: Appendix Chapter 2 (3/7)

Species	Average Mass (g)	Average consumption (g day ⁻¹)	Method	Locality	References
<i>Henicorhynchus siamensis</i>	15	2.64	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Ictalurus punctatus</i>	63.850	1.883	Lab. ^{FR}	Arkansas (USA)	Silverstein et al (1999)
<i>Lepomis macrochirus</i>	99.9	2.208	Indirect ^{FR}	White Oak lake (North America)	Rowan and Rasmussen (1996)
<i>Limanda aspera</i>	212	0.784	Lab. ^{MA}	Alaska (USA)	Smith et al (1991)
<i>Limanda limanda</i>	89.810	3.682	Lab. ^{MA}	Scotland (UK)	Hall (1987)
<i>Macquaria ambigua</i>	925.8	2.129	Lab. ^{FR}	Wales (UK)	Collins and Anderson (1999)
<i>Megalops cyprinoides</i>	53.633	1.171	Lab. ^{FR}	India	Pandian (1967)
<i>Melanogrammus aeglefnus</i>	137.7	8.234	Lab. ^{MA}	Scotland (UK)	Hall (1987)
<i>Merlangius merlangus</i>	122.332	5.113	In situ ^{MA}	North Sea	Pedersen (2000)
<i>Merluccius gayi</i>	662.3	6.030	In situ ^{MA}	Chile	Cubillos et al (2003)
<i>Microgogonias furnieri</i>	23.34	0.653	In situ ^{MA}	Brazil	de Figueiredo and Vieira (2005)
<i>Micropterus dolomieu</i>	445.15	7.903	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Moxostoma macrolepidotum</i>	866.833	25.515	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)

Table 2.5: Appendix Chapter 2 (4/7)

Species	Average Mass (g)	Average consumption (g day ⁻¹)	Method	Locality	References
<i>Mystacoleucus marginatus</i>	4	0.216	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Negaprion brevirostris</i>	2417	44.876	In situ ^{MA}	Bahamas	Cortes and Gruber (1990)
<i>Negaprion brevirostris</i>	2420	42.834	Lab. ^{MA}	Bahamas	Cortes and Gruber (1990)
<i>Notropis antherinoides</i>	3.438	0.217	Indirect ^{FR}	River (North America)	Rowan and Rasmussen (1996)
<i>Notropis heterolepis</i>	2.150	0.0856	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Notropis hudsonius</i>	2.950	0.140	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Oncorhynchus kisutch</i>	9.936	0.351	In situ ^{FR}	Alaska (USA)	Ruggerone (1989)
<i>Oncorhynchus kisutch</i>	1789.1	47.411	Indirect ^{FR}	Lake Erie (North America)	Rowan and Rasmussen (1996)
<i>Oncorhynchus kisutch</i>	2279.45	34.42	Indirect ^{FR}	Lake Michigan (North America)	Rowan and Rasmussen (1996)
<i>Ophiocephalus striatus</i>	46.233	0.923	Lab. ^{FR}	India	Pandian (1967)
<i>Oreochromis niloticus</i>	26.567	0.515	In situ ^{FR}	Philippines	Richter et al (2004)
<i>Osteochilus hasseltii</i>	15	1.121	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Perca flavescens</i>	45.2	1.118	Indirect ^{FR}	Ottawa River (North America)	Trudel et al (2000)

Table 2.6: Appendix Chapter 2 (5/7)

Species	Average Mass (g)	Average consumption (g day ⁻¹)	Method	Locality	References
<i>Perca flavescens</i>	127.742	3.186	Indirect ^{FR}	Lake Michigan (North America)	Rowan and Rasmussen (1996)
<i>Perca fluviatilis</i>	5.353	0.136	Lab. ^{FR}	Belgium	Fiogbe and Kestemont (2003)
<i>Percina caprodes</i>	1.475	0.059	Indirect ^{FA}	River Ottawa (North America)	Rowan and Rasmussen (1996)
<i>Pleuronectes platessa</i>	191.825	8.651	In situ ^{MA}	Walles (UK)	Basimi and Grove (1985)
<i>Pseudopleuronectes americanus</i>	800	16	Lab. ^{MA}	Passamaquoddy Bay (North America)	Tyler and Dunn (1976)
<i>Puntioplites proctozysron</i>	21.5	0.943	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Puntius (systemus) orphoides</i>	8	0.864	In situ ^{FR}	Thailand	Kakkaeo et al (2004)
<i>Rasbora daniconius</i>	4.15	0.0484	In situ ^{FR}	Sri Lanka	De Silva et al (1996)
<i>Rutilus rutilus</i>	198.5	9.736	In situ ^{FR}	Czech Republic	Vasek and Kubecka (2004)
<i>Salvelinus namaycush</i>	2386.713	14.785	Indirect ^{FR}	Great Slave Lake (North America)	Rowan and Rasmussen (1996)
<i>Salvelinus namaycush</i>	3733.85	25.012	Indirect ^{FR}	Lake Memphremagog (North America)	Trudel et al (2000)

Table 2.7: Appendix Chapter 2 (6/7)

Species	Average Mass (g)	Average consumption (g day ⁻¹)	Method	Locality	References
<i>Salvelinus namaycush</i>	2053.143	29.908	Indirect ^{FR}	Lake Ontario (North America)	Trudel et al (2000)
<i>Sarda chiliensis</i>	3550	151.644	In situ ^{MA}	Peru	Pauly et al (1987)
<i>Sargochromis codringtonii</i>	420	33.6	In situ ^{FR}	Lake Kariba (Africa)	Moyo (2002)
<i>Scophthalmus maximus</i>	1640	57.85	Lab. ^{MA}	England (UK)	Bromley (1987)
<i>Serrasalminus nattereri</i>	19	2.459	Lab. ^{FR}	Brazil	Pauly (1994)
<i>Siniperca chuatsi</i>	288.7	9.813	Lab. ^{FR}	China	Liu et al (1998)
<i>Stizostedion canadense</i>	395	7.248	In situ ^{FR}	Watts Bar Reservoir (USA)	Minton and McLean (1982)
<i>Stizostedion vitreum</i>	281.010	3.505	Indirect ^{FR}	Lac Rond-de-Poele (North America)	Trudel et al (2000)
<i>Stizostedion vitreum</i>	1383	16.321	Indirect ^{FR}	Lake Simcoe (North America)	Trudel et al (2000)
<i>Stizostedion vitreum</i>	501.093	8.130	Indirect ^{FR}	Ottawa River (North America)	Trudel et al (2000)
<i>Stizostedion vitreum</i>	339.907	5.981	Indirect ^{FR}	Ottawa River (North America)	Rowan and Rasmussen (1996)
<i>Theragra chalcogramma</i>	416	2.038	Lab. ^{MA}	Alaska (USA)	Smith et al (1988)
<i>Trachurus trachurus</i>	15	2.227	Lab. ^{MA}	Denmark	Temming and Herrmann (2001)

Table 2.8: Appendix Chapter 2 (7/7)

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Chapter 3

Modelling food consumption-to-biomass ratio (Q/B)

3.1 abstract

Consumption-to-biomass ratio (Q/B) has a key importance in population energetics because it determines the amount (in mass) of preys eaten by each gram predator's biomass. Models proposed to estimate Q/B usually used ad-hoc methods or they rely on the empirical relationships between this quantity and other life history attributes. We propose a general quantitative framework for the estimation of the (Q/B) for fish populations. This framework is based on an explicit dependence of Q/B on body size, modelled with the von Bertalanffy growth function, in which all parameters have a clear biological meaning. Four models of different complexity that allow information from different sources to be combined were proposed. The statistical properties of a Q/B estimator based on length structure were assessed by resampling methods under several different scenarios of parameter uncertainty. The potential use of these models is illustrated by applying them to two commercial important fish species. The results were comparable to those obtained using standard

methods. Simulation results indicated that, individual growth parameter estimates should have a coefficient of variation of less than 15% if the estimate of Q/B is to have negligible bias, correct coverage probabilities of confidence intervals, and high precision. The models presented here offer a promising way to estimate Q/B for fish populations in which, new individuals recruit to the population in a discrete event every year and where this recruitment may vary among years.

3.2 Introduction

One of the key parameters required by ecosystem models is the ratio of a population's food intake rate (Q) to its biomass (B). The Q/B ratio can be seen as the number of times a population eat its own weight during a certain period of time (usually a year). Estimating Q/B in fish populations is a laborious and difficult task that is usually done using ad-hoc methods or empirical equations (Palomares and Pauly, 1998). Methods for estimating consumption rates at the individual level have been well studied (see Richter et al., 2004). However, estimating population consumption rates remains problematic for most fish species because the existing methods have important limitations. These methods fall roughly into two categories: (*i*) methods, like those of Pauly (1986), in which experimental and field data are combined to estimate Q/B by integrating consumption and biomass over age. (*ii*) methods that use an empirical relationship between Q/B and some body size attribute (Palomares and Pauly, 1998). Method in category (*i*) rely on the assumption of a stable age distribution, a continuously reproducing population where fishing mortality is independent of age or size. They also include parameters which cannot be interpreted biologically. The empirical methods in category (*ii*) are easier to apply, but they generally lack theoretical support and they cannot account for shifts in population structure. These limitations suggest that complementary approaches are needed.

The relationship between the growth rate of an individual fish and the amount of food it ingests has been noticed by several authors (e.g. Dawes, 1931; Paloheimo and Dickie, 1965; Condrey, 1982; Andersen and Riis-Vertergaard, 2003). The existence of this relationship implies that food consumption can be inferred from growth rate (Beverton and Holt, 1957; Ivlev, 1945). In this reductionist approach, food acquisition is primarily limited by properties of the organism and, consequently, growth rate is a feature of organism design. Thus, a number of authors (e.g. Temming, 1994; Pauly, 1986; Aydin, 2004) have proposed models to estimate food consumption from feeding experiment and size-based attributes derived from modelling growth. These models have been widely used to explain processes at the individual level. What is lacking, however, is a quantitative framework that connects individual processes to population attributes. Here we propose such a framework for estimating Q/B by modelling individual growth using the von Bertalanffy Growth Function (VBGF) and incorporating population attributes by using population size structure. This allows changes in Q/B due to shifts in population structure to be modelled. We propose four different models that involve different assumptions about population dynamics. Which model is most useful will depend on what data are available.

3.3 Formulation

In chapter 2 (section 2.3) we developed a model for instantaneous individual consumption rate, based on the principles underlying the VBGF. We will now use this model as starting point to develop an estimator for Q/B . Based on chapter 2, an expression for the instantaneous individual consumption rate, in which all parameters have a clear biological meaning is:

$$q(w) = \frac{\beta k w_{\infty}^{(1-d)}}{A} w^d \quad (3.1)$$

The instantaneous consumption rate $Q(w)$ of a cohort of size N in which all fish have weight w is:

$$Q(w) = \frac{N \beta k w_{\infty}^{(d-1)}}{A} w^d \quad (3.2)$$

The biomass $B(w)$ of such a cohort at age can be defined $B(w) = Nw$, so the instantaneous $Q(w)/B(w)$ ratio is:

$$C(w) = \frac{Q(w)}{B(w)} = \frac{\beta k}{A} \left[\frac{w}{w_{\infty}} \right]^{d-1} \quad (3.3)$$

If all individuals have identical growth parameters and all recruitment occurs at one point in time, then the consumption to biomass ratio $Q(w)/B(w)$ (hereafter $C(w)$) of a cohort is identical to that of an individual, and is dependent only on individual growth and assimilation rate. Unfortunately, Eqn (3.3) is not applicable to real populations because fish in a cohort do not all have the same weight and fish populations are composed of multiple overlapping cohorts.

We deal with this as follows: Let w_{t^*} be the body mass of a randomly selected individual in the population at time t^* and let $f_{t^*}(w_{t^*})$ be the probability density function (pdf) of w_{t^*} . We suppose that t^* is a pre-determined point in year y . For the sake of brevity, we drop the t^* and write the pdf of w at time t^* in year y as $f_y(w)$. $C(w)$ is then also a random variable and, the expected value of $C(w)$ at time t^* in year y can be written as:

$$\begin{aligned}
E[C_y(w)] &= \int_{w_0}^{w_\infty} C(w)f_y(w)dw \\
&= \frac{\beta k}{Aw_\infty^{(d-1)}} \int_{w_0}^{w_\infty} w^{(d-1)}f_y(w)dw \\
&= \frac{\beta k}{Aw_\infty^{(d-1)}} E_{f_y}[w^{(d-1)}]
\end{aligned} \tag{3.4}$$

Here we assume that the population is composed of individuals who share the same growth parameters (t_0, w_∞, d, k) and assimilation rate (A) . If length is treated as a deterministic function of weight, Eqn (3.3) can be recast in terms of body length (l) using a suitable length-weight relationship such as $w = \alpha l^\beta$, where α and β are parameters. Eqn (3.3) then becomes:

$$C(l) = \frac{\beta k}{A} \left[\frac{l}{l_\infty} \right]^{\beta(d-1)} \tag{3.5}$$

where l_∞ is the asymptotic body length. We can write the expected value of $C(l)$ at time t^* , in the year y , as follows:

$$\begin{aligned}
E[C_y(l)] &= \int_{l_0}^{l_\infty} C(l)f_y(l)dl \\
&= \frac{\beta k}{Al_\infty^{\beta(d-1)}} \int_{l_0}^{l_\infty} l^{\beta(d-1)}f_y(l)dl \\
&= \frac{\beta k}{Al_\infty^{\beta(d-1)}} E_{f_y}[l^{\beta(d-1)}]
\end{aligned} \tag{3.6}$$

where $f_y(l)$ is the pdf of lengths in the population at time t^* in year y .

Eqns (3.3) and (3.5) are based on the generalized VBGF. A particular solution can be found by using the specialized VBGF (where d is set at $2/3$) and isometric growth (where $\beta = 3$). In this case, Eqns (3.4) and (3.6) become:

$$E[C_y(w)] = \frac{3kw_\infty^{1/3}}{A} E_{f_y}[w^{(-1/3)}] \quad (3.7)$$

$$E[C_y(l)] = \frac{3kl_\infty}{A} E_{f_y}[l^{-1}] \quad (3.8)$$

For brevity, we will now use C_y to represent $E[C_y(w)]$ or $E[C_y(l)]$. It is apparent that estimation of C_y hinges on estimation of the expected value of the inverse of body size (weight or length). The modelled value of C_y represents the expected consumption to biomass ratio and it has units of $time^{-1}$. When age is measured in years (and thus k has units of $year^{-1}$), Eqns (3.7) and (3.8) represent the number of times a population consumes its own weight per year (assuming that C_y is constant throughout the year). In order to actually implement the model described in Eqn (3.8), it is necessary to have estimates of individual growth parameters (k and l_∞), assimilation rate (A) and the expected inverse of body size ($E_{f_y}[l^{-1}]$).

A can be estimated from the daily ration, in an analogous way to that which Pauly (1986) used to estimate parameters defining conversion efficiency. The best way to do estimate C_y depends on what data are available to estimate the expected inverse body size, and we will explore this in the next section.

3.4 Modelling $E_{f_y}[l^{-1}]$

3.4.1 No sampling bias: Exact length data

If exact lengths of sampled fish are available, and all fish are equally likely to be sampled, the mean value of l^{-1} in a sample of size n provides a simple, unbiased estimate of $E_{f_y}[l^{-1}]$:

$$\hat{E}_{f_y}[l^{-1}] = \frac{1}{n} \sum_{i=1}^n \frac{1}{l_i} \quad (3.9)$$

where l_i is the length of the i th sampled fish. Thus, an estimator of C_y of a sample at time t^* in the year y can be estimated as:

$$\hat{C}_y = \frac{3kl_\infty}{A} \frac{1}{n} \sum_{i=1}^n \frac{1}{l_i} \quad (3.10)$$

Variance and confidence intervals (conditional on k , l_∞ and A) can be estimated using standard results for the sample mean.

3.4.2 No sampling bias: Grouped length data

In fisheries where exact observations are not available, but there is information on the frequencies n_j in a number ($j = 1, \dots, J$) of length intervals spanning the observed lengths, the data can be considered as draws from a multinomial distribution with J classes in which the probability of a fish being in class j is given by:

$$p_j = \int_{c_{j-1}}^{c_j} f_y(l) dl \quad (3.11)$$

Here c_{j-1} and c_j are the lower and upper bands respectively of the j th length interval. The unknown $f_y(l)$ can be replaced by its empirical distribution function by using the plug-in principle (Pawitan, 2001). Thus, the nonparametric maximum likelihood estimator (MLE) of the cell probabilities in this case is:

$$\hat{p}_j = \frac{n_j}{\sum_{j=1}^J n_j} \quad (3.12)$$

Using this, we can estimate $E_{f_y}[l^{-1}]$ as follows:

$$\begin{aligned}
\hat{E}_{f_y}[l^{-1}] &= \sum_{j=1}^J \frac{n_j}{\sum_{j=1}^J n_j} l_j^{-1} \\
&= \frac{1}{n} \sum_{j=1}^J n_j l_j^{-1}
\end{aligned} \tag{3.13}$$

where l_j is the midpoint of the j th length interval ($j = 1, \dots, J$). The variance of $\hat{E}_{f_y}[l^{-1}]$ can be estimated by non-parametric bootstrap (Efron and Tibshirani, 1993) by sampling with replacement from the body length sample. C_y of a sample can be estimated from such data as follows:

$$\hat{C}_y = \frac{3kl_\infty}{A} \frac{1}{n} \sum_{j=1}^J n_j l_j^{-1} \tag{3.14}$$

If all individuals are equally likely to be sampled, the model of the equation (3.14), is an estimator of the population C_y . When there is length selectivity, this model is an estimator of C_y for the fraction of the total population that is caught.

3.4.3 Parametric $f_y(l)$, under sampling bias

An estimator of $E_{f_y}[l^{-1}]$ can be obtained by modelling the pdf of lengths $f_y(l)$ in the population at the time t^* in the year y . If we have knowledge of the functional form for $f_y(l)$, then $E_{f_y}[l^{-1}]$ can be estimated by:

$$\hat{E}_{f_y}[l^{-1}] = \int_{l_0}^{l_\infty} l^{-1} \hat{f}_y(l) dl \tag{3.15}$$

where $\hat{f}_y(l)$ is an estimator of the distribution of lengths in the population ($f_y(l)$). Usually we cannot estimate $f_y(l)$ directly using sampled lengths from commercial fisheries because these have been subject of size-biased selectivity. If we have knowledge

of the discrete age structure, $P_y(a)$, the probability mass function (pmf) of the age a of a randomly chosen fish in the population, $f_y(l)$ can be written as:

$$f_y(l) = \sum_a P_y(a)P_y(l | a) \quad (3.16)$$

where $P_y(l | a)$ is the pdf of length l given age a in the population of fish in the year y , and $P_y(a)$ is the age structure and can be seen as the relative abundance of a cohort of the age a in the population. $P_y(a)$ is determined by the magnitude of the recruitment and mortality rates experienced by a cohort up to the moment of observation. Accurately observations of this quantity are rarely available, and thus it is usually obtained using model-based approaches.

Substituting Eqn (3.15) in Eqn (3.16), the expected l^{-1} is then defined by:

$$E_{f_y}[l^{-1}] = \int_{l_0}^{l_\infty} l^{-1} \sum_a P_y(a)P_y(l | a)dl \quad (3.17)$$

3.4.3.1 Estimation

Suppose the ages and lengths of a random sample of caught fish from year y is available in a matrix $n_y(l, a)$, whose elements are the numbers of fish sampled at each discrete length l and age a . In this case $n_y(l, a)$ is multinomial:

$$\ln L(\Theta | n) = \sum_l \sum_a n_y(l, a) \ln [P_y(l, a | caught)] \quad (3.18)$$

The pdf $P_y(l, a | caught)$ has parameters θ can be expressed as the product of three factors: a size dependent selectivity function, $S_y(l)$, the relative abundance $P_y(a)$ of age- a fish, and the conditional probability $P_y(l | a)$ of being in the discrete length interval l at age a :

$$P_y(l, a \mid caught) = \frac{S_y(l)P_y(a)P_y(l \mid a)}{\sum_l P_y(l)S_y(l)} \quad (3.19)$$

We assume that selectivity is only size-biased and has a functional form with increasing selectivity-at-length, $S_y(l) = [1 + e^{-\omega(l-l_h)}]^{-1}$, where l_h is the length at 50% of selectivity and ω is a shape parameter that describes the slope of the curve. $P_y(l \mid a)$ can be modelled as:

$$P_y(l \mid a) = \frac{1}{\sigma_a \sqrt{2\pi}} \exp \left[\frac{-(E[l_a] - l)^2}{2\sigma_a^2} \right] \quad (3.20)$$

where $E[l_a]$ is the expected length l of a fish of age a according to the von Bertalanffy growth function, $E[l_a] = l_\infty(1 - e^{-k(a-t_0)})$ and σ_a^2 is the variance in length-at-age. In wild populations, σ_a^2 increases with age, a process known as growth depensation (Gurney and Veitch, 2007). Here we assume the coefficient of variation (CV_σ) is constant across ages: $\sigma_a = CV_\sigma \times E[l_a]$. Here parameters to be estimated are those related with selectivity and growth depensation, thus $\theta = \{\omega, l_h, CV_\sigma\}$.

3.4.3.2 Simplifying $E_{f_y}[l^{-1}]$

If the matrix $n_y(l, a)$ is not available, a simplification of Eqn (3.17) can be done by treating $P_y(l \mid a)$ as a deterministic function. A first simplifying assumption is to assume that there is no variability in the length-at-age relationship. Under this assumption, all individuals of the same discrete age have the exactly the same length. Thus $E_{f_y}[l^{-1}]$ can be simplified to:

$$\begin{aligned} E_{f_y}[l^{-1}] &= \int_{l_0}^{l_\infty} l^{-1} \sum_a P_y(a) P_y(l \mid a) dl \\ &= \sum_a l_a^{-1} P_y(a) \end{aligned} \quad (3.21)$$

where $l(a)^{-1}$ is the inverse of the unique length of all individuals. This can be expressed in terms of the von Bertalanffy growth model as $l(a) = [l_\infty(1 - e^{-k(a-a_0)})]$. In this case

$$E_{f_y}[l^{-1}] = \sum_a [l_\infty(1 - e^{-k(a-a_0)})]^{-1} P_y(a) \quad (3.22)$$

A second simplifying assumption is to model the expected l^{-1} assuming a stable age distribution which implies constant recruitment over time and the same mortality rate Z_y for all recruit ages. In this case, abundance decays exponential $N_y(a) = R e^{-Z_y a}$, where R is a constant recruitment. In this case $P_y(a) = N_y(a) / \sum_a N_y(a) = e^{-Z_y a} / \sum_a e^{-Z_y a}$. Thus, if there is no variability in length-at-age and constant recruitment, $E_{f_y}[l^{-1}]$ is given by:

$$E_{f_y}[l^{-1}] = \sum_a \left[[l_\infty(1 - e^{-k(a-a_0)})]^{-1} \frac{e^{-Z_y a}}{\sum_a e^{-Z_y a}} \right] \quad (3.23)$$

3.5 Estimators for C_y

To estimate C_y , we assuming that estimates of the von Bertalanffy growth parameters and the assimilation rate A is available. At least three models from the previous section 3.4 can be used to estimate population C_y when there is sampling selectivity. The choice, depends on what additional data are available. First, if a random sample of age-at-length and an independent estimate of the proportion at age $P(a)$ are available, we estimate C_y from:

$$C_y = \frac{3kl_\infty}{A} \int_{l_0}^{l_\infty} l^{-1} \sum_a P_y(a) P_y(l | a) dl \quad (3.24)$$

This model allows us to consider variation in recruitment and length-at-age (hereafter referred as “model with variable length-at-age”). If age and length data are not available but it is possible to get an independent estimate of $P(a)$, assuming that all individuals of each age will have the same length, we can estimate C_y by:

$$C_y = \frac{3kl_\infty}{A} \sum_a [l_\infty(1 - e^{-k(a-t_0)})]^{-1} \hat{P}_y(a) \quad (3.25)$$

We refer to this as “model with fixed length-at-age”.

In a data-limited situation, where no information on age and length nor an independent estimate of $P_y(a)$ is available, it is still possible to estimate C_y by assuming a stable age distribution. This implies constant recruitment, constant mortality rate across ages and the same length for each age:

$$C_y = \frac{3kl_\infty}{A} \sum_a \left[[l_\infty(1 - e^{-k(a-a_0)})]^{-1} \frac{e^{-Z_y a}}{\sum_a e^{-Z_y a}} \right] \quad (3.26)$$

This model is comparable to the model of Pauly (1986) because they are obtained from the same assumptions on age distribution. Hereafter, the model of equation (3.26) will be referred as “model under stable age distribution”.

Note that there are three sources of uncertainty in the estimator C_y : growth parameters, assimilation efficiency A , and $E[l^{-1}]$. In the following sections we will estimate the uncertainty in the estimator C_y by a resampling approach.

3.6 Model sensitivity

We chose Eqn (3.14) to evaluate the sensitivity of a model in which length samples are obtained with knife-edge selectivity (when all individual above certain length or age are selected). We implemented a simulation similar to that presented by Roa et

Parameter		Value	Reference
cv size-at-age	cv_σ	0.0773	Wiff et al. (2006)
Growth (mean values)			Wiff et al. (2007)
	$k(year^{-1})$	0.186	
	$l_\infty(cm)$	111.45	
	$t_0(year)$	-0.912	
Correlation coefficient	r_{k,l_∞}	-0.971	
Mortality	$M(year^{-1})$	0.24	Ojeda et al. (1986)
Daily ration	$D(grams * day^{-1})$	7.28	re-estimated from Pool et al. (1997)

Table 3.1: Parameters for pink cusk-eel (*Genypterus blacodes*) used to generate simulated data to test the statistical properties of the proposed model.

al. (1999) using a population with known age, growth, daily ration (amount of food consumption per fish per day), size structure and mortality rate, and therefore with known C_y . Parameter values (table 3.1) were chosen to mimic the population of the pink cusk-eel (*Genypterus blacodes*) off southern Chile. The known C_y was given by:

$$\begin{aligned}
C_{y,true} &= \sum_{a=1} P_y(a) \frac{N(a)G(a)}{B(a)} \\
&= \sum_{a=1} P_y(a) \frac{G(a)}{w(a)}
\end{aligned} \tag{3.27}$$

which is the deterministic core of the simulation. Here, N_a is the abundance of the age group a , $G(a)$ is the annual ration (daily ration scaled to a year), and $P_y(a)$ is the proportion of each cohort in a particular year.

The length structure was constructed as a mixture of normal probability distributions using $P_y(l | a)$ from Eqn (3.20), each distribution representing a specific age. The proportion of individuals at each length in year y , $f_y(l)$, can be calculated from

the marginal distribution of lengths as in Eqn (3.16). That equation represents the known and discrete length structure of a population (Roa et al., 1999) in which each cohort is represented by a Gaussian length distribution ($P_y(l | a)$, Eqn 3.20). $P_y(a)$ is the pmf of the age a of a randomly chosen fish in the population. The parameters k and l_∞ were fixed at the values shown in Table (3.1). Simulation stochasticity came from two sources. First, using the probability integral transform (Casella and Berger, 1990) we selected a uniform random number in the interval $[0,1]$ and mapped it back into the cumulative distribution function of the Eqn (3.16), thus selecting a length value for each trial. We repeated this process until we obtained a random length distribution of pre-defined size ($n_{sample} = 500, 1000, 3000, 5000, \text{ and } 10\,000$).

Based on the life history parameters reported for pink cusk-eel (Table 3.1), Eqn (3.16) was evaluated for ages 1-16 covering a length range of 10-1120 mm. The second source of stochasticity came from the pair of growth parameters $\{k, l_\infty\}$ which were drawn from a bivariate Gaussian distribution with mean vector equal to the population parameters and variance given by their reported covariance matrix. Three different levels of CV , namely 5%, 15%, and 30% for k were used.

The bivariate distribution of $\{k, l_\infty\}$ was truncated to produce positive values for both random variables. This is equivalent to assuming a strictly positive growth rate dl/da . Two scenarios for recruitment were evaluated to compute the proportion of a given age in a particular year, $P_y(a)$: constant recruitment; and uniform random variation in recruitment over the interval $[0.5R; 1.5R]$, where R is an arbitrary recruitment equal to 100.

The simulation described above involves six scenarios: all possible pairwise combinations of constant and variable recruitments and three different values of the CV

of k . The simulation can be divided into two iterative processes. First we sampled a random length distribution and growth parameters $\{k_j; l_{\infty,j}\}$ for a given sample size in each iteration j . Second, to incorporate uncertainty associated with estimation of $\{k, l_{\infty}\}$, the pair of growth parameters was resampled to obtain a pair $\{k_{j,i}; l_{\infty,j,i}\}$ using the constant CV of k defined in the iteration j . The uncertainty in the length structure on each i iteration was taken into account by using a simple non-parametric bootstrap (Efron and Tibshirani, 1993) sampling with replacement from the vector of body lengths. Iterations j and i were repeated 1000 and 3000 times respectively, giving a total of 30 000 runs for each sample size. 95% confidence intervals were computed using the percentile method (Efron and Tibshirani, 1993) in each j iteration. The simulation process is illustrated in Figure (3.1).

Four statistical properties were used to evaluate the performance of C_y , following the approach of (Roa et al., 1999). The first of these was, the proportion of times in which 95% of the simulated confidence interval contained the true $C_{y,true}$:

$$\text{coverage probability} = 1 - \epsilon \quad (3.28)$$

ϵ is the failure probability, described by $\epsilon = \frac{1}{n} \sum_{j=1}^n \varpi(j)$, where n is the total number of j iterations and ϖ is an indicator function as:

$$\varpi(j) = \begin{cases} 1, & \text{if } (true - lower) < 0 \\ 1, & \text{if } (upper - true) < 0 \\ 0, & \text{otherwise} \end{cases}$$

Second, was the bias:

$$\text{bias} = \text{resampled mean} - \text{true} \quad (3.29)$$

Third, the shape of the 95% confidence interval:

$$shape = \frac{upper - median}{median - lower} \quad (3.30)$$

Fourth, the length of the 95% confidence interval:

$$length = upper - lower \quad (3.31)$$

In equations (3.28)-(3.31), "true" is the value of C_y from equation (3.27), while "lower", "upper", and "median" refer to the lower and upper bounds, and the median of the 95% confidence interval from the resampling method described. The simulation algorithm was written in MATLAB 6.5.

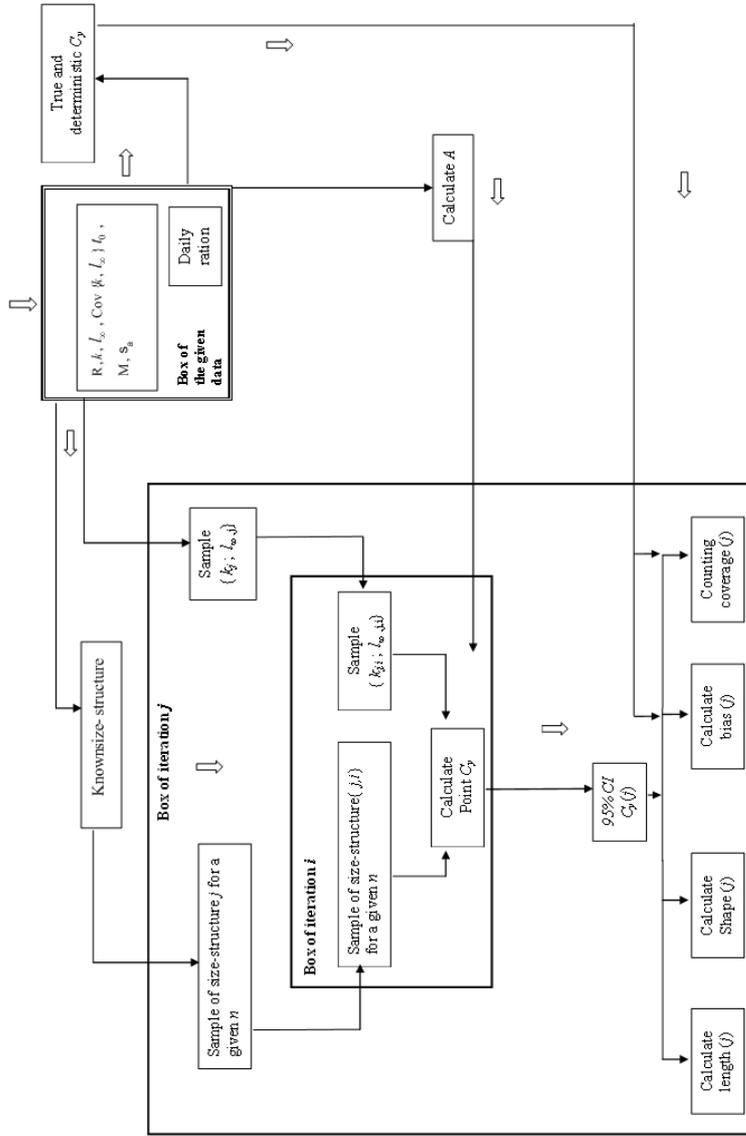


Figure 3.1: Diagram of the structure of the simulation used to assess the effect of sample size, uncertainty in growth parameters and recruitment on the statistical properties of the C_y estimator. R is recruitment, k , l_∞ and t_0 are the parameter of the von Bertalanffy growth function with covariance $cov(k, l_\infty)$ and σ_a is the standard deviation of the length at age.

3.7 Practical applications

To illustrate the method, we applied the models developed in the previous section to two fish species using data from the Chilean austral zone (41°28' - 57°00'S). The species considered were pink cusk-eel and southern hake (*Merluccius australis*). These species are intensely fished in the austral zone of Chile by a multispecies demersal fishery consisting of industrial vessels operating trawls and longlines. Length structures were taken from the routine sampling program of the Instituto de Fomento Pesquero (IFOP). A time series of annual average length structures (in which each fish was measured to the nearest cm) was constructed between 1982 and 2003 by combining data across fishing gears and genders for each species. Wiff et al. (2007) reported differences in growth for pink cusk-eel within areas in the austral zone and so the data were divided into two fishing zones: Northern-austral zone (41°28' - 47°00'S) and Southern-austral zone (47°00' - 57°00'S).

Estimates obtained using the methods described here were compared with estimates from a model proposed by Pauly (1986), in which C_y for a population with stable age distribution:

$$C_y = \frac{\int [(dw/da)e^{-Z_y(a-a_0)}K^{-1}]da}{\int [we^{-Z_y(a-a_0)}]da} \quad (3.32)$$

where K is the gross food conversion efficiency represented by $K(w) = 1 - (w/w_\infty)^b$, and b is a constant, and from the empirical equation proposed by Palomares and Pauly (1998):

$$\log_{10}(C) = 7.964 - 0.204\log_{10}(w_\infty) - 1.965T + 0.083\mu + 0.532\rho + 0.39\nu \quad (3.33)$$

where T is a temperature factor expressed as $T = 1000/(T^c + 273.15)$, and T^c is the mean annual temperature of the water body. μ is the aspect ratio of the caudal

fin, ρ and ν are binary variables indicating the types of food consumed: $h = 1$ for herbivores, $\nu = 1$ for detritivores, otherwise ρ and ν are equal to 0.

The mean temperatures registered during oceanographic surveys of the distribution of the species analyzed carried out between 2001 and 2004 was 5°C . A value of 1.6 of S for southern hake was taken from FISHBASE (Froese and Pauly, 2008), while μ for eel-like fish such as pink cusk-eel is 0. Both species are piscivorous (Pool et al., 1997) and therefore $\rho = 0$ and $\nu = 0$.

The estimates presented are based on the specialized VBGF (in which the anabolism term d is set at $2/3$). We also estimated C_y under the generalized VBGF to evaluate the effect of the choice of VBGF. Parameters of the generalized for both populations of pink cusk-eel were estimated using the age and growth data in Wiff et al. (2007). It was impossible to get a value for the parameter d from age and growth data (Pauly, 1981), so we fixed this parameter at $d = 0.789$ based on the theoretical considerations in discussed in chapter 2 (Wiff and Roa-Ureta, 2008). We then applied the generalized model of Eqn 3.4 with the stable age distribution assumption to both populations.

A matrix $n(l, a)$, containing a random sample of length and age, was available from data routinely collected by IFOP. More details of the sampling process can be found in Céspedes et al. (2007). Using the likelihood of Eqn (3.18), we obtained estimates of the parameters for the functional form of $P(l | a)$. The population value of \hat{C}_y for pink cusk-eel was evaluated for 1978 to 2004 for individuals between 3 and 16 years old, and for southern hake for the years 1977 to 2005, covering individuals between 4 and 24 years old. The estimated proportions at age by year ($\hat{P}_y(a)$) and total mortality \hat{Z}_y and their variances, were taken from the stock assessment program carried out by

IFOP -see Wiff et al. (2006) for pink cusk-eel and Quiroz et al. (2007) for southern hake. The VBGF parameters $\{\hat{k}, \hat{l}_\infty\}$ and their variances and correlations, were taken from Ojeda and Aguayo (1986) for southern hake and from Wiff et al. (2007) for pink cusk-eel. In the case of southern hake, no variances were available and instead we assumed a CV of 5% for each parameter. The parameters A and b parameter of Pauly's model were estimated from the daily ration G_d and the growth parameters as described by Pauly (1986). Following Ivlev (1945) the food growth conversion efficiency (K) was estimated as the growth increment per food ingested $K(w) = (dw/da)/G_d$, and then A was estimated from Temming's (1994) model ($K(w) = A[1 - (w/w_\infty)^{(1-d)}]$) and b was estimated from Pauly's (1986) models ($K(w) = 1 - (w/w_\infty)^b$). Daily rations of 7.12 and 5.72 $g \times d^{-1}$ for pink cusk-eel and southern hake, respectively, were re-estimated from the information provided by Pool et al. (1997).

We accounted for uncertainty in \hat{C}_y by resampling pairs of estimates of $\{\hat{k}, \hat{l}_\infty\}$ from a bivariate normal distributions with covariance matrices given by the asymptotic estimates of variances and correlation. Due to a lack of available information on the variance of the parameter A , we assumed it to have no error. For Eqn (3.14), uncertainty in $\hat{E}[l^{-1}]$ was introduced using a non-parametric bootstrap (Efron and Tibshirani, 1993), by sampling with replacement from the observed body lengths in different samples. For the model under sampling selectivity (Eqns 3.24 to 3.26), uncertainty was incorporated by resampling from a multivariate normal distribution using the parameter estimates from the fitting process described for $\hat{P}_y(l | a)$ and from the stock assessment output for $\hat{P}_y(a)$ and \hat{Z}_y . Uncertainty in the growth parameters and mortality rate in Pauly's model for C_y was accounted for as described above. Ninety-five percent confidence intervals (CI) were obtained by the percentile method (Efron and Tibshirani, 1993) based on 5000 iterations. The resampling algorithm was

written in MATLAB 6.5.

3.8 Results

3.8.1 Model sensitivity

All subsequent remarks about simulation results refer to figure (3.2), unless indicated otherwise, and sample size refers to number samples from the distribution of body lengths. The CIs for C_y based on Eqn (3.14) showed a coverage probability close to the nominal 95 % for all sample sizes and recruitment scenarios. For both recruitment scenarios and for all sample sizes, the CI for the bias estimator included 0. For all sample sizes, the median resampling bias was negligible when the CV of k was 5% and 15%. CI for shape included 1 in their range indicating that, on average, the estimator produced symmetric CIs. Median shape was close to 1 for $CV(k)$ of 5% and 15%, and tended to decrease with increasing sampling size. Median length also tended to decrease, stabilising at samples of 3000 or greater for $CV(k)$ of 5% and 15%. Length increased with bigger $CV(k)$. In the scenario with the highest variation in growth parameters ($CV(k) = 30\%$) the median bias tended to be higher with a larger CI and the shape parameter tended to be positive, indicating an asymmetric. This effect was probably a result of truncating the probability distribution to produce only positive values for growth rate. In general, the scenario with variable recruitment showed a smaller coverage probability, higher bias and more asymmetric CI than the constant recruitment scenario. Overall, the resampled C_y from Eqn (3.14) appeared to be reliable for reasonable low $CV(k)$ and it performed well under constant and variable recruitment scenarios.

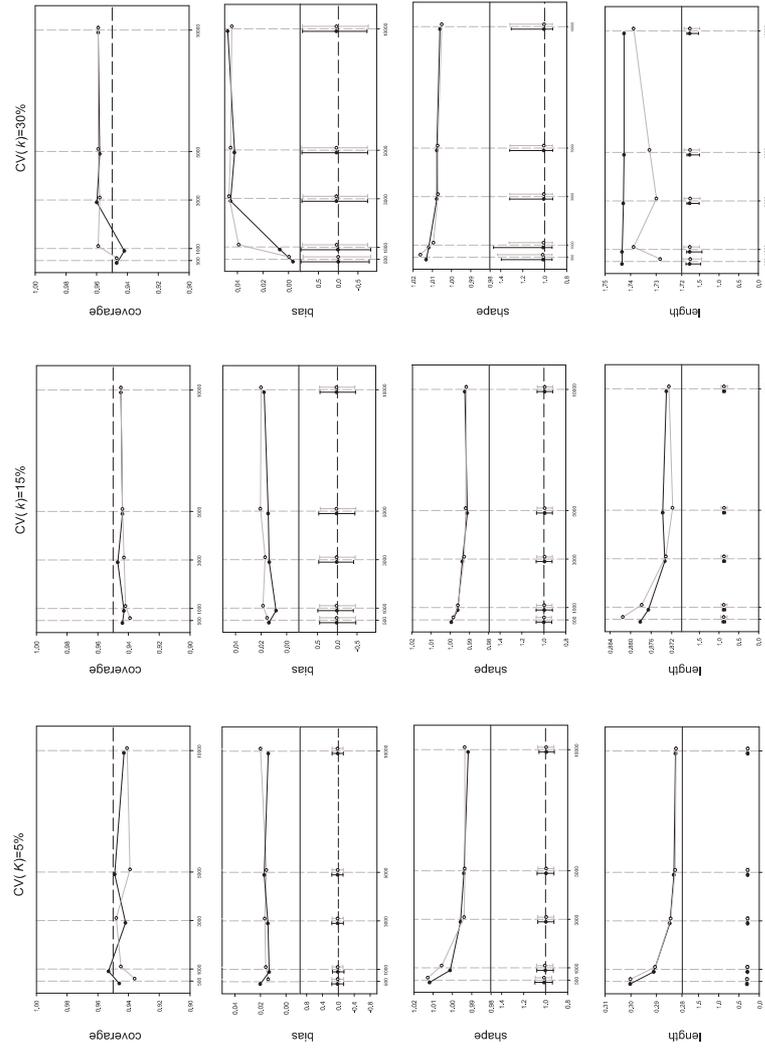


Figure 3.2: Effect of sample size, uncertainty in growth parameter (k) and recruitment on the statistical properties of the C_y estimator. Black dots= constant recruitment, white dots=variable recruitment (CV(R)=50%). The vertical lines represent the 95% confidence intervals. In the case of bias, shape and length the upper plots in each graphic represents the resampled median through sampled size.

3.8.2 Practical applications

When there was variable length-at-age (Eqn 3.24), \hat{C}_y was 1.1 yr^{-1} for the northern and population of pink cusk-eel, 0.9 yr^{-1} for the southern population and 0.87 yr^{-1} for southern hake. These values showed only small variations over the years analyzed (Fig. 3.3). \hat{C}_y for the caught fraction of the population increased monotonically across years in both species. For pink cusk-eel it increased from 0.85 yr^{-1} in 1982 to 1.1 yr^{-1} in 2003 for the northern population, and from 0.73 yr^{-1} to 0.93 yr^{-1} for the southern population (Fig. 3.3 a,b). In the case of southern hake, the increase was from 0.59 yr^{-1} in 1982 to 0.64 yr^{-1} in 2003. In all cases, C_y when length-at-age was fixed (Eqn 3.25) was on average 1% smaller than C_y from Eqn 3.24, although both time series showed the same pattern of variation. C_y under the stable age distribution assumption (Eqn 3.26) were higher than those from Eqn 3.24, and followed different trajectories through the time.

For both species, Pauly's model gave estimates that were on average 10-11% lower than the stable age distribution model estimates for pink cusk-eel. In the case of southern hake, estimates from Pauly's model were 8% lower than those from the stable age distribution model. C_y from the empirical equation of Palomares and Pauly (1998) was 1.3 year^{-1} for northern pink cusk-eel, 1.2 yr^{-1} for southern pink cusk-eel, and 1.6 yr^{-1} for southern hake. On average, C_y using the generalized VBGF was 4% lower than with the specialised VBGF for northern pink cusk-eel and 2% lower for the southern population (Fig. 3.3 b,e).

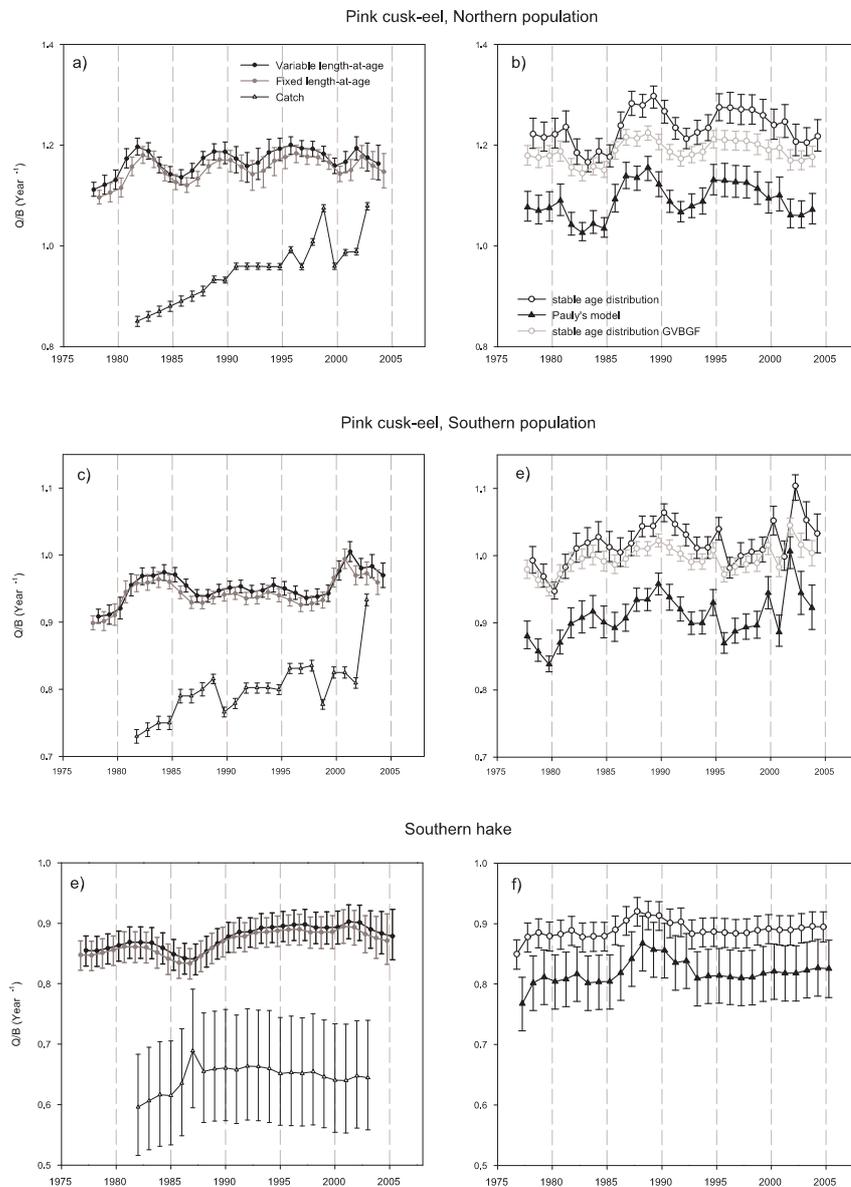


Figure 3.3: Results of the application of the different methods for estimating C_y for three fish populations off southern Chile. Left-hand plots include estimates for the caught fraction, and fixed and variable length-at-age. Right-hand size include estimates under stable age distribution and with Pauly's model. (a,b) Pink cusk-eel (*Genypterus blacodes*), northern population, (c,d) Pink cusk-eel, southern population, (e,f) Southern hake (*Merluccius australis*). In each case the vertical bars represent the 95% confidence intervals computed by resampling and dots are the median values.

3.9 Discussion

3.9.1 Comparison with Pauly's model

The models for estimating C_y proposed here contrast with the model proposed by Pauly (1986) in which the C_y is computed as a ratio of integrals and age distribution must be assumed constant in order to arrive at a tractable estimator. Pauly's model estimates the expected C_y at a defined point in time, assuming that age is a continuum variable (with an infinite numbers of age-classes between age-at-recruitment and terminal age). Thus Pauly's model applies to a continuously reproducing populations with constant recruitment. The main differences between Pauly's (1986) models and those presented here are: recruitment occurs in discrete events and may change through time; all parameter have a clear biological meaning; and there is an explicit dependence of C_y on body size. The assumption of a continuously reproducing population in Pauly's models does not naturally allow for any hypothesis other than constant recruitment, unless a function relating recruitment and time is available. Although, little is known about how recruitment varies over time for most fish stocks, the disadvantage in introducing variability in recruitment in this way is that it implies C_y also changes continuously in time. The model described here rest on the assumption of discrete recruitment and provide an estimate of C_y at a point in time. This is appropriate if recruitment is discrete, as is usually the case for fish populations inhabiting temperate environments, where population dynamics is commonly modelled by assuming that recruitment occurs at a pre-defined moment each year, that growth parameters are the same for all individuals in the population and remain invariants over time, and that average total mortality across ages \bar{Z} is constant within each year. These widely accepted assumptions in fishery modelling imply that the population value for $E[l^{-1}]$ and C_y will be constant between recruitment events.

Under this scenario, C_y estimates need to be updated in the same time interval as recruitment occurs. A continuous time model is more appropriate for tropical fish populations. In addition, many fish species at low latitudes have several reproductive events during the year (van Leeuwen et al., 2007), resulting in an age distribution that is almost continuous at any particular point in time.

The differences between Pauly's model and the ones presented here will also depend on the functional form used to define gross conversion efficiency (K), because this determines the value of b in Pauly's model or A in our models. In Pauly's approach the constant b has no clear biological meaning, whereas all of the parameters in Temming's gross conversion efficiency model (Temming, 1994; Temming and Herrmann, 2009) can be interpreted in this way.

3.9.2 Interpretation of C_y time series

The populations used to illustrate our method have been intensively fished, resulting in a considerable reduction in the average lengths of caught fish over time (Wiff et al., 2007). C_y is inversely related to average length, so exploitation is probably the main reason for the monotonic increase in C_y for the caught fraction of all of the populations we studied (Fig. 3.3). Only small differences were observed between the variable and fixed length-at-age models. This is a consequence of the small CV for the length-at-age in the analyzed species. Growth rate is known to vary between individual whiting cohorts, and this may be the result from genetic differences in growth rate potential or interactions with conspecifics (Smith and Fuiman, 2003). Mitton and Lewis (1989) have pointed out that genetic variability is associated with fish populations inhabiting less stable environments, with short generation time, quick maturation, small maximum size and small eggs. However, the species considered

here inhabit relatively a stable demersal environment and they are characterized by a long lifespan, late maturation and large maximum size. Therefore, we would expect low genetic variability and a small CV in the length-at-age. However, short-lived fish species, such as small pelagics, are likely to show a much higher variability in the length-at-age and this should be included in models of C_y , to avoid any potential bias.

Time series of C_y estimated with stable age distribution assumption (constant recruitment, constant mortality rate and fixed length-at-age) were higher and had a different trajectory compared with those obtained when length-at-age and recruitment were variable (Fig. 3.3). This is probably because the assumption of constant mortality result in an overestimation of total mortality, because the same fishing mortality for fully recruited fish is applied for all individual above a certain length or age. Mortality rate has a direct effect on C_y because it tend to reduce the expected body size in the population. For both species and all methods, Palomares and Pauly's (1998) empirical method resulted in an overestimation of C_y . This empirical method derives from data points estimated with a model with stable age distribution assumption, and thus an overestimation of C_y is expected for the reasons mentioned above.

3.9.3 Effect of the form of the VBGF

In the original formulation of the VBGF (Bertalanffy, 1938), the anabolism scaling parameter d is set at $2/3$; the resulting model is known as the specialized VBFG. However, Essington et al (2001) compiled estimates for d , and concluded that its value differs from $2/3$ for fish species. If d is allowed to take values other than $2/3$, we have the generalized VBGF. We have used the models proposed here to investigate

the effect of the choice of the VBGF on estimates of C_y . However, parameters for the generalized VBGF cannot be taken directly from published sources, because they refer almost exclusively to the specialized VBGF. This is probably due to the impossibility of obtaining estimates for d solely from size-at-age data (Pauly, 1981). In order to estimate the other parameters of the generalized VBGF, d has to be fixed to a priori defined value. Pauly (1981) proposed that for fish the slope of the linear relationship between gill area and body mass (0.789) can be used as an approximation for d , and Wiff and Roa-Ureta (2008) concluded that this assumption was adequate for modelling consumption in fish (for details see chapter 2). Thus, we set $d = 0.789$ in the generalized VBGF we used for pink cusk-eel. In practice, the estimates of C_y were hardly affected by the form of the VBGF, probably because both versions provided equally good descriptions of the age and growth data for pink cusk-eel.

3.9.4 Modelling environmental factors

One criticism of many population models, including those related with consumption, is that they do not account for environmental variation. Temperature is one of the most important environmental variables affecting nearly all biological rates (Charnov and Gillooly, 2004), and it has been identified as the most important factor shaping patterns of consumption (e.g. Finstand, 2005). For example, the empirical equation of Palomares and Pauly (1998) relates C_y to habitat temperature. Although in the methods developed here environmental factors are not explicitly incorporated, they can be considered as implicitly included because growth parameters and length structure can vary over time. Although the general framework of the VBGF (Bertalanffy, 1938) does not explicitly incorporate time-dependance in factors such as ambient temperature or food availability (Xiao, 2000), it can be modified to do so by modelling the seasonal growth (Xiao, 1999).

3.9.5 Dependence on mortality

The estimates of C_y are highly dependant on the mortality rate experienced by a population up to the moment of observation. Pauly (1986) made C_y explicitly dependent on mortality by modelling a continuous age distribution. In our models, we have used the population length-structure to estimate of C_y . This failure to account for mortality explicitly may seem counter-intuitive, but mortality rates are implicitly in $E_{f_y}[l^{-1}]$. Nevertheless, it is widely recognised that mortality rate is the most important, but least well-estimated, parameter in fisheries models (Hewitt and Hoening, 2005), and it is often one of the main sources of error in stock assessment (Hampton, 2000). Although, it is possible to estimate $E_{f_y}[l^{-1}]$ from fisheries data without assuming any value for natural mortality, this will only provide an unbiased estimate of C_y for the caught fraction of the population, which may not be useful in the context of ecosystem modelling. When the length structure is size-biased, an estimate of $E_{f_y}[l^{-1}]$ for the entire population can only be obtained if the proportion-at-age ($P_y(a)$) is known. Alternatively, an unbiased sample of the population's size-structures may be available from the results of size selection experiments (e.g Fryer et al., 2003) or by direct observation, as is done in shellfish fisheries (e.g Hartill et al., 2005).

3.10 Conclusions

We have proposed a quantitative framework for estimating the consumption to biomass ratio for fish populations that accounts explicitly for size. Using this framework, it is possible to take account of changes in this ratio that occur as a result of shifts in population size structure. Many models of aquatic ecosystems use a size-based approach (see Jennings and Blanchard, 2004; Hall et al., 2006), and the models

proposed here offer a promising avenue for extending single species fisheries models into an ecosystem context.

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Chapter 4

Modelling production-to-biomass ratio (P/B)

4.1 abstract

Production-to-biomass ratio (P/B) has assumed a fundamental role in the quantification population and ecosystem dynamics, since this ratio determines the renewal rate of the population biomass. Several methods have been proposed to estimate P/B , but they usually rest on strong assumption about population dynamics or they belong to empirical equation which attempt to predicts P/B from other more easy-to-obtain demographic attributes. Here, a simplified model for the P/B in fish population is proposed. The model considers an explicit dependence of P/B on individual length, which is modelled with the von Bertalanffy growth function (VBGF). Two models are proposed; their applicability depends on what data are available. The first model relies on the assumption of knife-edge selectivity (when all fish above certain length or age are sampled), while the second that there are no variation on the length-at-age (for each age there is just one length) and a stable age distribution (constant recruitment and mortality at age). The sensitive of P/B estimates to the different assumptions were assessed using a simulation approach with resampling. We illustrate the application of the model by applying it to data from 16 Chilean fish populations

which support important fisheries. In both models, P/B estimates show negative bias when assumptions about knife-edge-selectivity and fixed length-at-age are not met. Failures of the assumption of knife-edge selectivity may introduce significant bias, but violation of the assumption of fixed length-at-age causes negligible bias. Application of the model to real data indicates that P/B increases with mortality rate and the growth parameter of the VBGF. Fast-growing fish have a higher P/B than long-lived, slow-growing species. This model provides a simplification of the methods available for P/B estimation that allow a detailed exploration of the dependence of P/B on body size in fish.

4.2 Introduction

Biomass production is the total amount of somatic tissue accumulated in a population during a given time period (Allen, 1971). Production per unit of biomass (P/B) is an important indicator in population dynamics because it is the replacement rate of the population biomass. Widely applied methods for estimating P/B are based on empirical relations between this quantity and body size attributes such as observed mean or maximum body mass and average body mass at maturity (Banse and Mosher, 1980; Downing and Plante, 1993; Randall and Minns, 2000). A more direct approach is to use estimates of production and biomass to estimate the ratio. Methods for estimating production can be either aggregated or structured by age, length or another physiological variable. In aggregated models, no direct account is taken of recruitment, individual growth, mortality rate (e.g. Shaefer, 1954; Pella and Tomlinson, 1969; Fox, 1970), while in age-structured models all these factors are taken into account by considering the trajectory of numbers and body mass in the population over longitudinal observations (Hamilton, 1969; Allen, 1971). Despite

the extensive literature on production models, methods for estimating P/B have important limitations. Those derived from empirical relations are easy to apply but they are not useful for assessing shifts in population structure due to exploitation. Age-structured models have a solid theoretical background but they require extensive knowledge of individual and population parameters. These limitation suggest that alternative approaches would be useful.

Allen (1971) provided a family of equations for the expected P/B obtained by integrating separately production, then biomass and dividing the two. Thus, data supporting the modelling for production and biomass is explicitly accounting for time. This kind of data is usually refereed as “longitudinal”. The resulting longitudinal estimator of P/B in Allen (1971) have a varying degree of complexity depending on the chosen model for mortality and individual growth. Nevertheless, no analytical expression for P/B has been obtained with Allen’s longitudinal equation using the VBGF. This may have limited the application of Allen’s model to fish populations, because their growth is commonly described by the VBGF. An alternative to Allen’s approach is to consider the cohort production of biomass, and the biomass, at a fixed moment in time in order to model expected P/B directly (see for example Roa and Quiñones, 1998). We call this, the cross-sectional definition approach to estimating P/B . Cross-sectional analysis refers to those processes modelled at a given moment in time. It has the potential to simplify the estimation of this ratio in animal populations by adding explicit dependence of P/B on body size described by the VBGF. Therefore, here we propose such model for estimating P/B in fish populations where individual growth is described by the VBGF.

4.3 Formulation

Production rate is, by definition, a rate of change of a non-negative quantity with time. Instantaneous biomass production of a cohort of identical individuals from a population in which recruitment is concentrated at one point in the time is:

$$P(a) = N(a) \frac{dw}{da} \quad (4.1)$$

where $P(a)$ is production at age a , $N(a)$ is numerical abundance at age a ($N(a) = Re^{-Za}$ where R is recruitment and Z is the mortality rate), and w is body mass. Note here mortality is assumed constant through ages and thus, no density dependant variations are considered. We call $N(a)$ the “cohort size and decay term” because it reflects size with parameter R and decay with parameter Z . The biomass (B) of a cohort at age a can be defined by:

$$B(a) = N(a)w(a) \quad (4.2)$$

These models are simple deterministic definitions. For individuals which are all born on the same date, that grow at the same rate and whose number changes continuously through time, the cohort biomass is the product of individual body mass and the number of individuals. The production of biomass is the product of the instantaneous rate of individual growth and the number of individuals. The P/B ratio of a cohort of identical individuals that are born on the same date is:

$$\lambda(a) = \frac{P(a)}{B(a)} = \frac{1}{w} \frac{dw}{da} \quad (4.3)$$

This equation represents production-to-biomass ratio (or biomass turnover, $\lambda(a)$ hereafter), of a cohort at a particular age during its lifespan. This $\lambda(a)$ is the individual standardized growth rate, and it does not depend on mortality rate and cohort size only because all individuals are assumed to be exactly identical in growth, date of birth, and survival probability (Van Straalen, 1985). Expressions for $dw/(wda)$ can be found from specific growth functions. Here, we rely on the VBGF to describe the relationship between age and individual body size (see appendix 4.8). If length is treated as a deterministic function of weight, Eqn (4.3) can be recast in terms of body length (l) using a suitable length-weight relationship such as $w(l) = \alpha l^\beta$, where α and β are parameters. Then Eqn (4.3) becomes:

$$\lambda(l) = \beta k \left[\frac{l_\infty}{l} - 1 \right] \quad (4.4)$$

where l_∞ is the asymptotic length parameter of the von Bertalanffy growth model ($l(a) = l_\infty[1 - e^{-k(a-a_0)}]$). For details on the derivation of Eqn (4.4) from Eqn (4.3) see Appendix 4.8.

Similarly, as discussed in chapter 3 with Q/B estimator, Eqn (4.4) is not directly applicable to real populations because individuals of a cohort are not identical and because at any given point in time there are multiple co-existing cohorts. To make our equations useful for analysing populations, we adopt a stochastic representation of body length. So let l_{t^*} be a random variable representing body length of an individual at time t^* , and let $f_{t^*}(l_{t^*})$ be the probability density function (pdf) of l_{t^*} . We suppose that t^* is pre-determined in the year y and for brevity drop the t^* subscript on l_{t^*} and use year y instead of time t^* . We therefore write the pdf of l at the time t^* in the year y as $f_y(l)$. $\lambda(l)$ is then also a random variable. Thus if l is continuous, the expected value of $\lambda(l)$ at time t^* in the year y is written as:

$$\begin{aligned}
\lambda_y &= \int_{l_0}^{l_\infty} \lambda(l) f_y(l) dl \\
&= \int_{l_0}^{l_\infty} \beta k \left[\frac{l_\infty}{l} - 1 \right] f_y(l) dl \\
&= \beta k l_\infty \int_{l_0}^{l_\infty} f_y(l) l^{-1} dl - \beta k \int_{l_0}^{l_\infty} f_y(l) dl \\
&= \beta k \left[l_\infty E_{f_y} [l^{-1}] - 1 \right]
\end{aligned} \tag{4.5}$$

where l_0 is usually the length at born and E is the expectation operator. As mentioned in the introduction, this approach contrasts with Allen's (1971), in which λ is computed as a ratio of integrals and in which case, the cohort size and decay term ($N(a)$) becomes explicit in the formulation. Allen's ratio-of-integrals approach and related methods are longitudinal, whereas our integral-of-ratio approach is cross-sectional. λ modelled here has units of $time^{-1}$ which is consistent with the definition of biomass turnover.

Eqn (4.5) represents the expected biomass produced per gram of population biomass. It is apparent that estimation of λ depends on estimation of the expected value of the inverse of body size. If parameters β , k and l_∞ are assumed to be known, then data enters the estimation of λ in Eqn (4.5) via $E_{f_y} [l^{-1}]$ exclusively.

Since the estimator for C_y (chapter 3) and λ_y have the same dependence on expected length, any of the models described in chapter 3 for $E_{f_y} [l^{-1}]$ may be applied here. We chose two of these possible estimators. First, we use the model for $E_{f_y} [l^{-1}]$ with no sampling selectivity for non-grouped data (section 3.4.1) to evaluate the assumption of knife-edge selectivity (where all fish are caught after a certain length or age) on the estimation of λ_y . In order to produce the simplest possible estimator of λ_y , we chose the model for $E_{f_y} [l^{-1}]$ with stable age distribution (fixed length at age and constant

recruitment) in section (3.4.3). Accordingly, the first model is:

$$\hat{\lambda}_y = \beta k \left[\left(\frac{l_\infty}{n} \sum_{i=1}^n \frac{1}{l_i} \right) - 1 \right] \quad (4.6)$$

where l_i is the length of the i th sampled fish and n is the sample size.

For the model of Eqn (4.6) to be implemented, it is necessary to have a random sample of l_i from the population, estimates of individual growth parameters k and l_∞ , and β from the length-weight relationship. Eqn (4.6) is an unbiased estimator of λ_y if the l_i s are a random sample of lengths in the population. This assumption may be violated in fish populations, because usually the length sample is size-biased by the gear selectivity. Thus, to implement the model of Eqn (4.6) the length sample must not be biased by selectivity or at least, if there is selectivity, it should be a knife-edge selectivity (when all fish above certain length or age are sampled). In this case inferences concern only fish of selected ages.

The second model proposed under the assumptions of fixed length-at-age and stable age distribution. In this case $E_{f_y}[l^{-1}]$ is the same than in Equation (3.24) and thus λ_y can be expressed as follows:

$$\lambda_y = \beta k \left\{ \sum_a \left[\frac{1}{(1 - e^{-k(a-a_0)})} \frac{e^{-Z_y a}}{\sum_a e^{-Z_y a}} \right] - 1 \right\} \quad (4.7)$$

This estimate is deterministic because it assumes no variation in length-at-age, recruitment, nor mortality.

4.4 Simulation Tests

In this section we evaluate the potential bias caused by violation of two assumptions of the model. First, we evaluate the bias from violation of the assumption of fix

length-at-age of the model of Eqn (4.7). Second, we evaluated bias due to failure of the assumption of knife-edge selectivity on the model of Eqn (4.6).

27 populations of different lifespans were simulated. Life history parameters defining these populations were obtained from functional form constraining the relationship between two life history parameters (trade-off equations) reported for fish as follows: First, populations from 4 to 30 years old of maximum ages (a_∞) were generated. Then, for each population the natural mortality rate (M) was calculated as function of a_∞ by $M = 3/a_\infty$ (Hewitt and Hoening, 2005). Growth coefficient k was calculated as $k = (2/3)M$ (Charnov, 1993). Asymptotic length (l_∞) was deducted from k using the trade-off equation reported by Charnov (1993) for fish as $l_\infty = \mathfrak{S}k^{-h}$, where \mathfrak{S} and h were set up at 3.5 and 0.5 respectively. For simplicity, in all populations we assumed constant recruitment and constant mortality ($M = Z$), $a_0 = 0$ and $\beta = 3$. For each population true λ was calculated by:

$$\lambda_{true} = \beta k \left[l_\infty E_{true}[l^{-1}] - 1 \right] \quad (4.8)$$

where the true expectation was:

$$E_{true}[l^{-1}] = \int_{l_0}^{l_\infty} l^{-1} \sum_a P_y(a) P(l | a) dl \quad (4.9)$$

where $P_y(a) = e^{-Ma} / \sum_a e^{-Ma}$. $P(l | a)$ was modelled as a Gaussian distribution of length-at-age, in the same manner as it was modelled in chapter 3, Eqn (3.20). Here the standard deviation of the length-at-age σ_a is assumed to have a linear relationship with the expectation of the length-at-age ($E[l_a]$) where the coefficient of variation, CV_σ is the constant of proportionality.

The relationship between CV_σ and other life history parameters is poorly known in fish populations. This makes it difficult to define a trade-off equation a priori for CV_σ , as we did above for other parameters. However Mitton and Lewis (1989) pointed out that populations with shorter lifespans (smaller maximum size) show higher variability in sizes between individuals of the same cohort, in comparison with populations with longer lifespans. Thus, CV_σ is inversely related with a_∞ across populations. Here, we modelled the trade-off between CV_σ and a_∞ by a linear equation as $CV_\sigma = \phi/a_\infty$, where ϕ is a proportionality constant.

We evaluated the bias (in percentage) on the assumption of fixed length-at-age by the following equation:

$$bias_1 = 100 \left[\frac{\lambda_{fixed} - \lambda_{true}}{\lambda_{true}} \right] \quad (4.10)$$

where λ_{fixed} refers to λ with fixed length-at-age of the Eqn (4.7). The value of the constant ϕ is unknown and therefore we evaluated bias of the Eqn (4.10) under six values for ϕ namely 0.5, 1, 1.5, 2, 2.5 and 3.

To evaluate the knife-edge selectivity assumption we generated a population size structure for each one of the 27 population described. The pdf of length in each population was modelled by $f(l) = \sum_a P_y(a)P(l | a)$ under the same assumptions described above. For simplicity, ϕ was set at 2 for all populations. Using the probability integral transform (Casella and Berger, 1990) we selected a uniform random number in the interval [0,1] and mapped it back into the cumulative distribution function of $f(l)$, thus selecting in each trial a length value. Each length sample was chosen by applying a selectivity function. We repeated this process until we obtained a random length sample of 1000 individuals. Using this length sample we evaluate Eqn (4.6) generating a λ value under selectivity (λ_s) for each iteration. We repeat this process

for 1000 iterations. Then the median value of λ_s was computed for each one of the 27 population described. Then bias was computed as:

$$bias_2 = 100 \left[\frac{median(\lambda_s) - \lambda_{true}}{\lambda_{true}} \right] \quad (4.11)$$

The simulated selectivity was assumed to be size-biased only and it had a functional form with increasing selectivity-at-length, $S(l) = [1 + e^{-\omega(l-l_h)}]^{-1}$, where l_h is the length at 50% of selectivity and ω is a shape parameter that describes the slope of the curve. For each population, l_h was fixed to $E[l(a_1)]$, where l is the length described by the VBGF and a_1 is the age-at-first capture. a_1 increased with a_∞ as follows: populations were separated into groups of 3 according to their lifespan. Thus 9 groups were created for a_∞ of $\{4, 5, 6\}$ to $\{28, 29, 30\}$. For each one of these group the same a_1 was assigned. Group of a_∞ of $\{4, 5, 6\}$ a value of $a_1 = 2$ was assigned. Then, a_1 had increment of 1 in each one of the group of a_∞ . Thus, the last group of a_∞ of ages $\{28, 29, 30\}$ received a $a_1 = 10$. $bias_2$ was evaluated for each population under 6 scenarios for ω parameter namely 0.05, 0.1, 0.2, 0.3, 0.4, 0.5.

Thus, for $bias_1$ and $bias_2$ a total of 6×27 scenarios were evaluated each time, depending on the lifespan and ϕ or ω value chosen.

4.5 Applications

We illustrate the application of the model in Eqn (4.7) by applying it to 16 populations from Chile which support important fisheries. These populations are composed of 13 species of demersal and pelagic fish with different life history strategies. Although the model was proposed in principle for fish species, we also show its applicability by estimating λ for 3 species of crustaceans. The model was applied in two ways. First, we estimated the population λ with no fishing mortality ($Z = M$)

covering individual of ages 1+. These results were then compared with estimates for a 'typical fish' having $k = (2/3)M$, $\beta = 3$ and $a_0 = 0$.

In order to evaluate the effect of the fishing exploitation on λ estimates, we compiled yearly age-averaged fishing mortality estimates (\bar{F}) and then we computed λ under exploitation ($\bar{Z} = M + \bar{F}$), between the a_1 and a_∞ reported in each population. Only the last 5 years of average fishing mortality data in each population were used. A detail of the database used is in Table (4.1)

We also analysed four cases where the data in Table (4.1) were artificially impoverished to evaluate the sensitivity in the estimates of λ_M from Eqn (4.7). To compute λ_M , information about VBGF, M , β and a_∞ is needed. Case 1 represents the situation where all parameters needed to compute λ_M are unknown. Case 2,3 and 4 each assuming a further parameter is known. Case 2 is the same as case 1 but β is now known. Case 3 is the same as case 2 but M is now known. Case 4 is the same as case 3 but a_∞ is now known. When each of these parameters were considered unknown, we estimated them as follows. We used the procedure described in Froese and Binohlan (2003) to obtain estimates of the VBGF. Froese and Binohlan (2003) is an empirical method to derive preliminary parameters of the VBGF from other known life history traits such as maximum length (l_{max}) and age at first maturity (a_m). Thus, for each species in Table (4.1), parameters of the VBGF were obtained from l_{max} and a_m available in the IFOP database. For case 1, only information on l_{max} and a_m was available to obtain an estimate of λ_M . Once the VBGF was obtained, a_∞ was computed as the age where 95% of l_∞ is reached, M was derived from the trade-off equation described by Charnov (1993) where $M = (3/4)k$. For case 1, β was fixed to 3 for each species according to Froese (2006). Bias in the estimates of λ_M , when using real and derived parameters for the VBGF was computed for each case scenario and species. The bias

was computed as the difference (in proportion) between estimates of λ_M using real and simulated data.

4.6 Results

4.6.1 Bias evaluation

A negative bias was found when the assumption of fixed length-at-age was used ($bias_1$, Fig. 4.1a). The magnitude of the bias decreased with lifespan for any values of ϕ assumed. However, bias was also dependent of the value of ϕ applied. When ϕ was higher there was a relative higher CV_σ on the length-at-age relationship for each population simulated and thus the model became more biased. Bias was higher in species with relatively short lifespan. For populations with maximum ages between 4 and 10 years, there was a bias between -7 and -3% and for species with lifespans between 11 and 30 years, bias was almost negligible with values in the range of -2 to -0.5%.

We found also a negative bias when evaluating failure of the assumption of knife-edge selectivity ($bias_2$, Fig. 4.1b). When the selectivity function increased slowly across lengths, for $\omega = 0.05$ and $\omega = 0.1$, the bias was relatively constant across populations with values around -6% and -11%, respectively. When individuals were selected faster according to length ($\omega > 0.1$) the magnitude of the bias decreased with lifespan. For $\omega > 0.1$ and maximum ages between 4 and 15 years old, bias was around -25 and -10, respectively. On the other hand, for maximum ages older than 15 years, variations in bias between ω values became smaller, ranging between -6% and -11%.

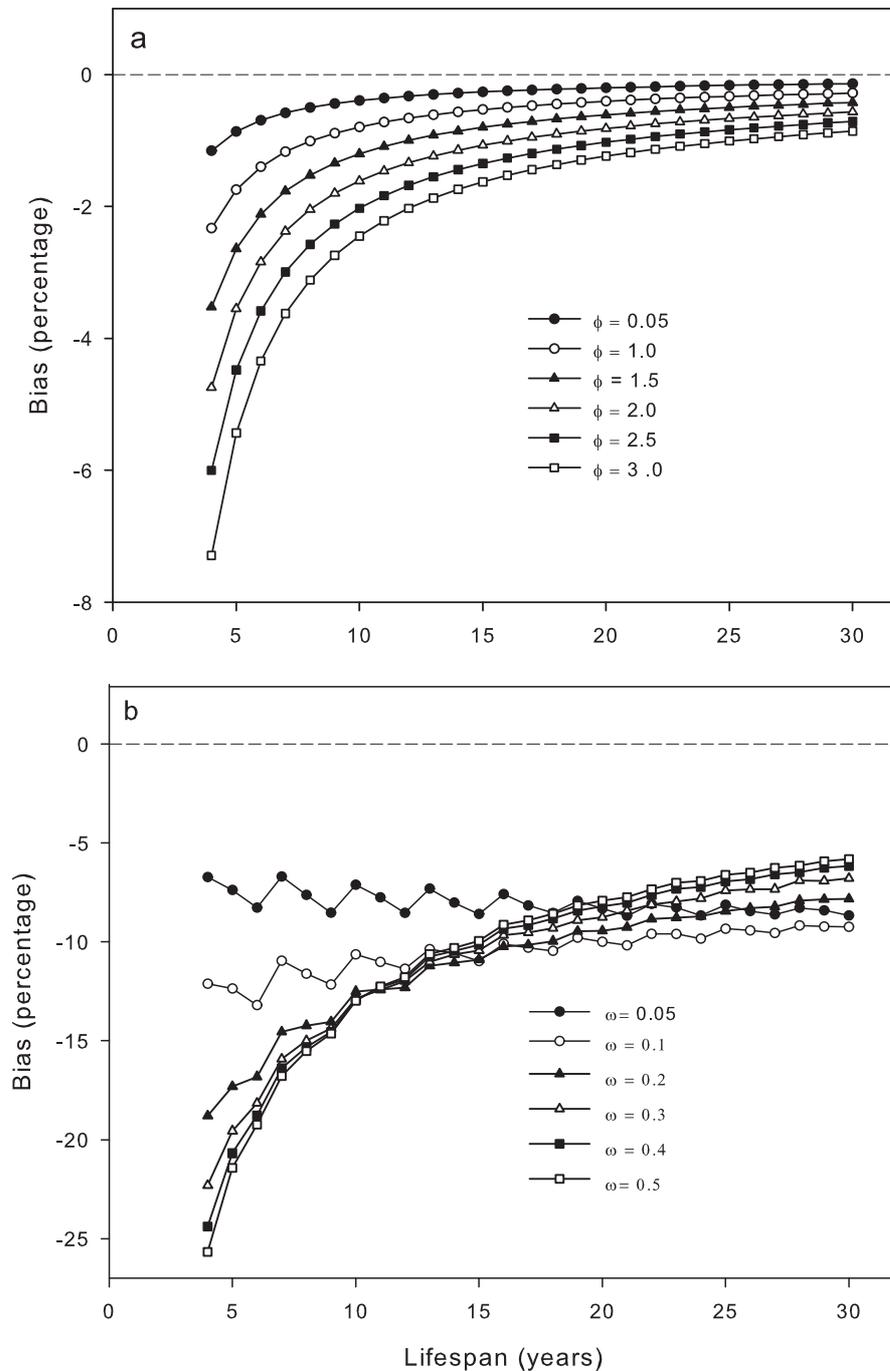


Figure 4.1: Estimated bias of the model proposed. In both cases the dashed line indicates an unbiased estimation. (a) Evaluating the assumption of fix length-at-age ($bias_1$). ϕ is the proportionality constant between coefficient of variation of the length-at-age (CV_σ) and maximum age (a_∞). (b) Evaluating the assumption of knife-edge selectivity ($bias_2$). ω is the slope parameter of the selectivity function.

4.6.2 Applications

Production-to-biomass ratio in populations not subject to exploitation (λ_M) increased when M and k values are higher (Fig. 4.2). For fast-growing fish with high natural mortality rate such as anchoveta and araucanian herring λ_M was 1.508 and 1.119 $year^{-1}$, respectively. These values were high in comparison long-lived, slow-growing species such as orange roughy and splendid alfonsino where λ_M was 0.242 and 0.347, respectively (Table 4.1). Crustaceans show higher λ_M in comparison with fishes of similar life history parameters (Table 4.1). In general, species agreed well to the theoretical line described for M , k and λ_M (Fig. 4.2).

Production-to-biomass ratio estimated with total mortality (λ_Z) was high in fast-growing species, although its decrease was not as clear as in λ_M when moving to slow-growing species (Fig. 4.4). λ_Z was bigger than λ_M in species where age-at-first capture (a_1) is 1, such as anchoveta, araucanian herring, patagonian grenadier, swordfish, yellownose skate, splendid alfonsino and southern hake (Fig. 4.4). Bigger differences between λ_Z and λ_M were produced in species with low age-average fishing mortality, such as yellow and red squat lobster and orange roughy (Table 4.1, Fig. 4.4).

Specie name	Mortalities				Growth parameters					λ_M (year^{-1})
	M (year^{-1})	\bar{F} (year^{-1})	β	a_1 (year)	a_∞ (year)	l_∞ (cm)	k (year^{-1})	t_0 (year)		
Fish										
Orange roughy	0.050	0.070-0.119 (2002-2006)	2.90	30	90	52.13	0.031	-1.716	0.242	
Southern hake	0.210	0.163-0.198 (2001-2005)	3.46	1	24	121.00	0.081	-1.457	0.617	
Patagonian toothfish	0.150	0.029-0.082 (2000-2004)	3.10	3	24	152.19	0.085	-0.471	0.682	
Splendid alfonsino	0.157	0.173-0.571 (2001-2005)	3.08	1	19	63.39	0.093	-2.567	0.347	
Jack Mackerel	0.230	0.163-0.209 (2002-2006)	3.08	2	12	74.20	0.111	-0.809	0.735	
cardinalfish	0.200	0.375-0.867 (2002-2006)	2.95	7	13	45.20	0.112	-0.775	0.667	
Yellownose skate	0.149	0.012-0.086 (2001-2005)	3.14	1	34	118.05	0.123	-0.668	0.571	
Swordfish	0.220	0.214-0.614 (1999-2003)	3.15	1	20	327.00	0.126	-2.590	0.364	
Pink cusk-eel	0.260	0.043-0.131 (2000-2004)	3.15	3	14	123.18	0.147	-1.779	0.489	
Patagonian grenadier	0.350	0.098-0.195 (2002-2006)	2.96	1	14	101.30	0.173	-0.812	0.756	
Common hake	0.300	0.064-0.786 (2002-2006)	2.97	2	13	67.75	0.220	-0.510	0.785	
Araucanian herring	1.200	0.489-0.920 (2003-2007)	3.21	1	4	18.10	0.745	-0.330	1.119	
Anchoveta	1.300	0.220-0.990 (2002-2006)	3.14	1	4	18.72	0.910	-0.010	1.508	
Crustaceans										
Yellow Squat lobster	0.279	0.055-0.213 (2001-2005)	3.29	3	19	4.92	0.163	0	1.263	
Red Shrimp	0.280	0.069-0.542 (2000-2004)	2.89	3	13	4.45	0.187	-0.659	0.709	
Red squat lobster	0.315	0.014-0.002 (2003-2007)	2.89	2	7	6.00	0.245	-0.056	1.275	

Table 4.1: Parameters used to illustrate the production to biomass ratio model of equation (4.7). Range on fishing mortality indicates the minimum and maximum of the last five years of available data (years shown in parentheses). Range of age indicates the age-at-first capture (a_1) and maximum ages observed (a_∞) reported by the Instituto de Fomento Pesquero (IFOP). For references of parameters used see appendix 4.9

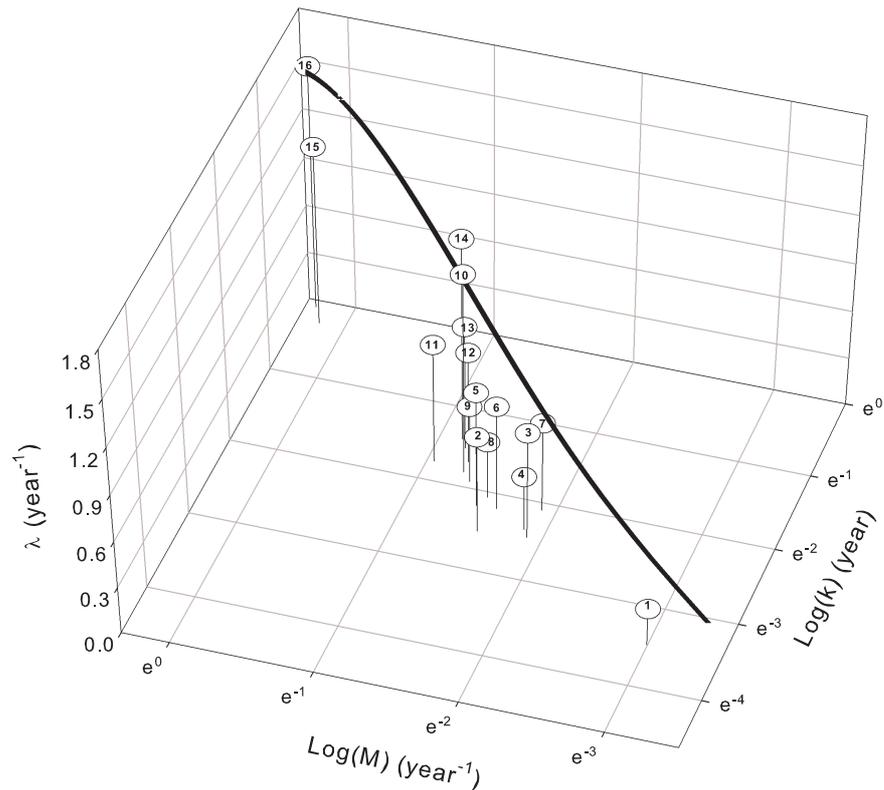


Figure 4.2: Estimation of production-to-biomass ratio with no fishing mortality (λ_M) according to the von Bertalanffy growth parameter (k) and natural mortality (M) for the 16 species describes in Table (4.1). Solid line indicates the λ of a 'typical fish' ($k = (2/3)M$, $\beta = 3$, $a_0 = 0$). Numbers inside each symbol indicate the species: (1) O. roughy (2) S. hake (3) P. toothfish (4) S. alfonsino (5) J. mackerel (6) Cardinalfish (7) Y. skate, (8) Swordfish (9) P. cusk-eel (10) Y.S. lobster (11) P. grenadier (12) R. shrimp (13) C. hake (14) R.S. lobster (15) A. herring (16) Anchoveta.

Results for the sensitivity analysis of artificially impoverished data sets are shown in Figure 4.3. The lack of different pieces of information needed to estimate λ_M produces a different behaviour across species. For the scenario where all pieces of information were unknown (case 1), estimates of λ_M were highly affected in species such as southern hake, splendid alfonsino and swordfish. In these species, λ_M values were twice as large as those estimated with the real parameters. On the other hand, estimates of λ_M in species such as cardinalfish, common hake and araucanian herring were almost unaffected when impoverished data sets were used. For all crustacean species impoverished data sets produced underestimation of λ_M . When knowledge of parameters was increasingly improved (case 1 to case 4), bias decreased accordingly in most fish species. Conversely, in crustacean species an opposite bias behaviour is observed; when information is improved the bias increased.

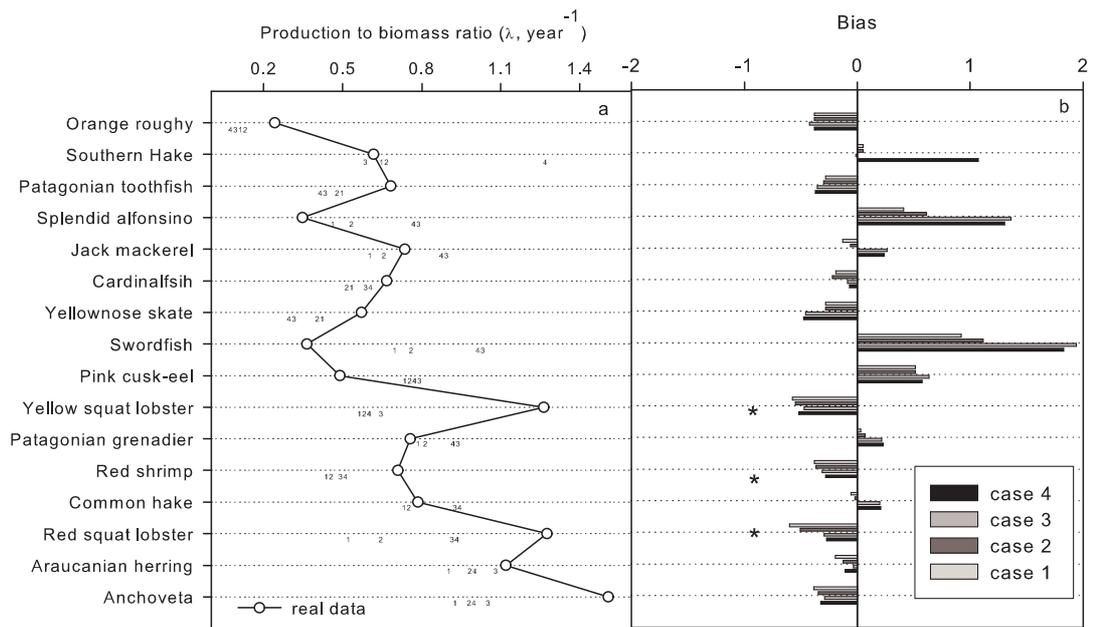


Figure 4.3: Sensitivity analysis for impoverished data sets. Case 1 represents the situation where all parameters needed to compute λ_M are unknown. Case 2,3 and 4 each assuming a further parameter is known. Case 2 is the same as case 1 but β is now known. Case 3 is the same as case 2 but M is now known. Case 4 is the same as case 3 but a_∞ is now known. (a) Production-to-biomass ratio with no fishing mortality (λ_M). The numbers indicate the cases and the circles and solid lines represent the real data estimates. (b) Relative bias for each case scenario.

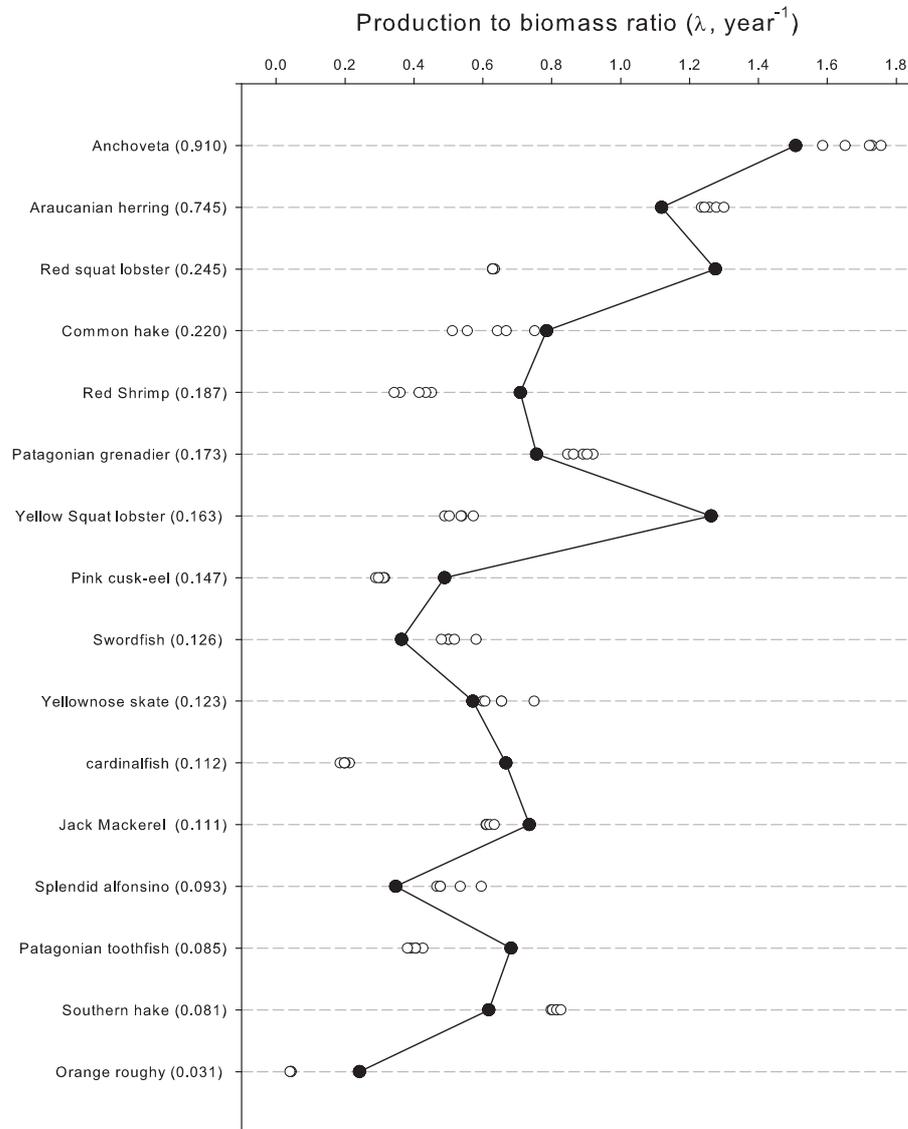


Figure 4.4: Estimation of production-to-biomass ratio (λ) for the 16 species described in Table (4.1). Open symbols indicate estimation with age-average total mortality (λ_Z) for the last five years of available data in each species (Table 4.1). Filled symbols represents production-to-biomass ratio estimates with no fishing mortality (λ_M). Species on the abscissa are sorted according to their growth rate parameter k (in parenthesis).

4.7 Discussion

Production-to-biomass ratio is an important quantity in assessing harvested populations because it determines the population capacity for exploitation and recovery (Peters, 1983). In theory, to maintain a stock under steady-state condition, all mortality must be compensated by the total renewal and thus $\lambda_y = Z_y$, (Allen, 1971). Consequently, a λ_y estimator modelled in this manner is equivalent to the total mortality rate that could have been applied in a given year that would have left a stock at equilibrium. Therefore, production-to-biomass ratio is directly proportional to the mortality rate. Indeed, short-lived species that are characterized by high natural mortality rate and high values for the individual growth parameter (k) will present high production to biomass ratio as demonstrated here (Fig. 4.2). This is also supporting a well known idea that short-lived species can support more fishing mortality in a sustainable way in comparison with slow-growing species (Beddington and Kirkwood, 2005). Here, we explored the effect of introducing fishing mortality on λ_y for species with different life histories. Although fast-growing species show high λ_y of the exploited fraction (Fig. 4.4), the effect of fishing mortality is not easily interpretable. For the species analyzed, fishing mortality does not necessarily reflect the population renewal because it is regulated by a total allowable catch according to the Chilean general law of fishing and aquaculture which does not require $\lambda_y = Z_y$. Each species has its own age at first capture which makes that λ_Z is aggregated over a different age interval. Nevertheless, the model presented here could be useful as an independent indicator of the total mortality needed to maintain a stock under steady-state (where all renewal is compensated by mortality). Our methods might also be useful for stocks which are not closely monitored (e.g. Paramo and Roa, 2003) or whose exploitation is incipient.

For those species where the data available is particularly poor, estimates of λ_M can be obtained using only information on l_{max} and a_m . In these cases, estimation of λ_M can be divided in three steps: first, parameters of the VBGF can be derived from l_{max} and a_m using the method described in Froese and Binohlan (2003). Second, values for M and a_∞ can be derived from parameters of the VBGF. Third, β of the length-at-weight relationship can be either fixed to 3 or estimated by empirical method described in Froese (2006). Bias in λ_M estimates using such a procedure may vary across species. For the species of interest, bias in λ_M is highly dependent on how reliably the growth parameters are estimated by the method in Froese and Binohlan (2003). Such method was proposed for a 'typical fish' inhabiting temperate waters. This may be the reason why the data-poor case produces considerable bias in fish species such as southern hake, splendid alfonsino and swordfish which are species with particular life histories. On the other hand, estimates of λ_M for crustacean species were underestimated in all data-poor cases presented. Thus, we think Froese and Binohlan (2003) method can be a useful manner to obtain parameters needed to estimate λ_M in data-poor situations, as long as the study species behaves as a 'typical' temperate fish. Nevertheless, the application of the Froese and Binohlan (2003) method may cause severe bias for crustaceans and fish with these particular life histories.

4.7.1 Longitudinal vs cross-sectional estimators

Models proposed here for λ are based on observations at a given point in time. Models for such observations are usually named as cross-sectional estimators. Historically, most of the models proposed to estimate λ are longitudinal, which mean they attempt to model processes occurring on the time scale. This implies that production-to-biomass ratio models have included time explicitly (Allen, 1971) or

implicitly (Mertz and Myers, 1998). Predominance of longitudinal models for λ probably obey to the axiom summarized by Beverton and Holt (1957) in which changes in biomass production are studied during a period of time in a form of a conservation equation which counted new individuals and individual growth as positive terms and natural mortality and catch as negative terms.

In practice, the incorporation of time is generally not feasible in estimating biomass production, because model are usually implemented using time-average information of dynamics processes. Thus, longitudinal models for λ usually use time-averaged number-at-age and growth-at-age (Mertz and Myers, 1998). Production is a rate quantity and thus it can be defined over time by longitudinal models. However, biomass is not a rate quantity and therefore it only admits a point in time definition and thus it can be naturally defined by cross-sectional models. Longitudinal models for λ necessarily need to treat separately production and biomass by turning biomass on an longitudinal quantity by using the average biomass over a time period. Time introduces an extra complication in modelling λ because then production and biomass need to be computed separately before calculating their ratio. Considering λ at a point in time however, the cohort size and decay term cancel out during intermediate stages of analysis. The analysis then is simplified, and the cross-sectional population information is recovered by the expected inverse body length in the population ($E[l^{-1}]$) at some particular point in time. Although this approach provides a non-dynamical estimation for λ , when available, the dynamical behavior can be recovered by simply ordering in time the separate estimates.

Under some assumptions, longitudinal and cross-sectional estimators for λ are comparable. For a population where recruitment occurs on discrete events, say every Δt time period, size structure will remains constant inside this Δt in case that individual

growth parameters and mortality rate are constant and age-invariant for Δt . Under these particular conditions, λ will remain constant between recruitment events at any point in time during this Δt , basically because growth parameters and $E_{f_y}[l^{-1}]$ will be constant between recruitment events. Thus, if $E_{f_y}[l^{-1}]$ is constant for Δt only one observation is needed to get the expected value of λ during Δt .

Note that production and well as biomass will change between recruitment events when they are analyzed separately. Both quantities depend on the number of individual at age which is certainly a quantity which decreases between recruitment event. In closed populations (with no immigration/emigration) increases of abundance are only giving by recruitment at the beginning of the year, but inside recruitment event it will be noted a decreased in abundance due to mortality. Thus when analyzed separately, production and biomass are quantities that change continuously inside recruitment events. Considering λ at a point in time however, the cohort size and decay term cancel out during intermediate stages of analysis, when equations derived apply to individuals and single cohorts as demonstrated by Van Straalen (1985). Thus, in cross-sectional models, λ does not dependent on abundance. It is only depending in the expectation of the inverse body length.

4.7.2 Model assumptions

To implement the model presented here, an estimate of the von Bertalanffy growth parameters, length-at-weight parameter (β) and the expected inverse body length ($E[l^{-1}]$) are required. In the context of fisheries science, growth-related parameters are relatively easy to obtain, while unbiased estimates of $E[l^{-1}]$ may not be readily available in data-sparse situations. Here, we propose two ways of estimating $E[l^{-1}]$. First, we proposed a design-based approach where $E[l^{-1}]$ can be estimated simply

and unbiasedly from a sample of lengths in the population. Second, a model-based approach was proposed by modelling the length distribution in the population. The first approach, relies on the assumption of knife-edge selection in the fisheries at the length at first capture (l_c). One can thus sample the commercial catch to estimate $E[l^{-1}]$ for those fish above l_c . In this approach, we may not need to have knowledge of population processes such as recruitment, total mortality and variability of the length-at-age, because they are implicitly on the length sample. This approach, may be important in the context of fisheries science where estimation of such processes are particularly difficult to obtain. Nevertheless, if the fishing gear is size-selective, biased estimates of $E[l^{-1}]$ (and thus biased estimates of λ) may be obtained. Unbiased samples of lengths may be available from research surveys (Gedamke and Hoening, 2006). If the survey fully selects individuals larger than a certain length, say l_c , and the fish recruited to the fishery are bigger or equal to l_c , one can simply compute unbiasedly ($E[l^{-1}]$) for those fish in the survey above l_c .

For those cases where gear selectivity plays a key role in determining the length sample, a second approach for modelling $E[l^{-1}]$ was proposed. In order to ensure to a tractable equation for $E[l^{-1}]$, the size distribution was modelled by assuming stable age distribution (constant recruitment and mortality across ages) and fixed length-at-age. Both these assumptions are routinely used in ecological modelling as the mathematics is simple and they imply an important reduction on the parameters needed to implement the models. Nevertheless, stable age distribution is rarely realized in nature, except perhaps as an average over several generations (Charnov, 1993), because recruitment and mortality are likely to vary with time. Although recruitment variability will not cause bias in the average size in the population (Gedamke and Hoening, 2006), it may lead to autocorrelated errors in a time series of estimates.

A more realistic approach is to assume that recruitment varies with time. Variations in recruitment can be easily introduced if results of an stock assessment models are available. In other cases, a stock-recruitment (S-R) relationship is needed. There is a large literature relating to stock size and recruitment in fish populations. Two popular models have been widely used to define the S-R relationship namely the Beverton-Holt (Beverton and Holt, 1957) and Ricker models (Ricker, 1954). If pairs of estimates of stock size and recruitment are available, S-R relationship can be easily fitted to this data and thus a functional form between stock and recruitment is known. If such data is available, variation in recruitment can be easily inferred from stock size and thus λ estimates under variable recruitment can be computed.

In many cases, however, such data are absent and it is then difficult to obtain realistic values for parameters of the S-R functional forms. An alternative is to reparameterize the S-R relationship in terms of pristine condition (before any fishing mortality has been applied in the population) on stock size and recruitment as done by Francis (1992) in case of Beverton-holt's model and Cubillos (1994) for Ricker model. The advantage of these formulations depends on one dimensionless parameter, namely "steepness", which characterized the shape of the S-R relationship and it is unaffected by the actual stock size. Thus, density dependent variability in recruitment can be parameterized in terms of the steepness parameter. Although, in practice, steepness is a difficult parameter to estimate reliably, it has been shown to have a relationship with other life history attributes such as the VBGF (Beddington and Kirkwood, 2005). Thus, is possible to "guess" a value for steepness from other more readily obtainable parameters. Beddington and Kirkwood (2005) have demonstrated that steepness parameter can be used to relax the assumption of constant recruitment in case of data-poor situations. A similar approach can be implement to extent the model

proposed here for case where recruitment is allow to vary with density-dependant processes.

4.8 Appendix 1 Chapter 4

How to derive Eqn (4.5) from Eqn (4.4)

Here we will show how production to biomass ratio (P/B) in age: $\frac{P(a)}{B(a)} = \frac{1}{w(a)} \frac{dw}{da}$ (Eqn 4.3) can be expressed in terms of length as: $\frac{P(l)}{B(l)} = k\beta(\frac{l_\infty}{l} - 1)$ (Eqn 4.4).

The von Bertalanffy growth model in mass is described by:

$$w(a) = w_\infty [1 - e^{-k(a-a_0)}]^\beta \quad (4.12)$$

where k is the growth rate coefficient, w_∞ is the asymptotic weight, a_0 is the age at $w = 0$ and β is the exponent of the length-weight relationship.

Finding the derivative dw/da by the chain rule:

$$\frac{dw}{da} = \beta w_\infty [1 - e^{-k(a-a_0)}]^{\beta-1} k e^{-k(a-a_0)} \quad (4.13)$$

Solving the growth function in Eqn 4.12 for $e^{-k(a-a_0)}$ yield:

$$\frac{w(a)}{[1 - e^{-k(a-a_0)}]} = w_\infty [1 - e^{-k(a-a_0)}]^{\beta-1} \quad (4.14)$$

and

$$1 - \left[\frac{w(a)}{w_\infty} \right]^{\frac{1}{\beta}} = e^{-k(a-a_0)} \quad (4.15)$$

therefore, we can write dw/da in terms of:

$$\frac{dw}{da} = k\beta \frac{w(a)}{[1 - e^{-k(a-a_0)}]} \left(1 - \left[\frac{w(a)}{w_\infty} \right]^{\frac{1}{\beta}} \right) \quad (4.16)$$

Thus, P/B of a cohort can be expressed in terms of body weight as:

$$\frac{P(w)}{B(w)} = \frac{k\beta}{[1 - e^{-k(a-a_0)}]} \left(1 - \left[\frac{w}{w_\infty} \right]^{\frac{1}{\beta}} \right) \quad (4.17)$$

by assuming that length is describing by the von Bertalanffy growth function ($l(a) = l_\infty(1 - e^{-k(a-a_0)})$), and the body mass being a deterministic function of mass by $w(l) = \alpha l^\beta$, P/B can be written in terms of the body length as:

$$\frac{P(l)}{B(l)} = k\beta \frac{l_\infty}{l} \left(1 - \left[\frac{\alpha l^\beta}{\alpha l_\infty^\beta} \right] \right) \quad (4.18)$$

$$= k\beta \left(\frac{l_\infty}{l} - 1 \right) \quad (4.19)$$

4.9 Appendix 2 Chapter 4

References for parameter in table 4.1.

References by species are organized by (a) Natural Mortality, (b) Fishing Mortality (c) weight at length parameter (d) Growth parameters.

- (1) **Orange roughy** (*Hoplostethus atlanticus*) (a,d) Gili et al (2000) (b) Costa-Feltrim (2008a) (c) Lillo et al (1999). (2) **Southern hake** (*Merluccius australis*) (a) Ojeda et al. (1986) (c,b) Ojeda and Aguayo (1986) (d) Quiroz et al (2007) (3) **Patagonian toothfish** (*Dissostichus eleginoides*) (a,b) Wiff et al (2006a) (c,d) Oyarzun et al (2003) (4) **Splendid alfonsino** (*Beryx splendens*) (a,d) Gili et al (2000) (b) Wiff et al (2006b) (c) Lillo et al (1999). (5) **Jack mackerel** (*Trachurus symmetricus murphy*) (a,b) Serra and Canales (2007) (c) Froese and Pauly (2008) (d) Kochkin (1994). (6) **Cardinalfish** (*Epigonus crassicaudus*) (a,c,d) Galvez et al (2000) (b) Wiff et al (2005). (7) **Yellownose skate** (*Dipturus chilensis*) (a) Quiroz and Wiff (2005) (b,c) Wiff and Quiroz (2007) (d) Licandeo et al (2006)(average value between genders). (8) **Swordfish** (*Xiphias gladius*) (a,d) Cerna (2009) (b,c) Serra et al (2007). (9) **Pink cusk-eel** (*Genypterus blacodes*) (a) Ojeda et al. (1986) (b,c) Wiff et al (2006c) (d) Wiff et al (2007). (10) **Patagonian grenadier** (*Macruronus magellanicus*) (a,b) Canales et al (2006) (c,d) Chong et al (2007). (11) **Common hake** (*Merluccius gayi*) (a) Arancibia and Cubillos (1993) (b) Canales et al (2007a) (c) Froese and Pauly (2008) (d) Aguayo and Ojeda (1987) (average value between genders). (12) **Araucanian herring** (*Strangomera bentincki*) (a,c) Costa-Feltrim (2008b) (d) Cubillos et al (2001). (13) **Anchoveta** (*Engraulis ringens*) (a,d) Canales and Leal (In press) (b) Canales et al (2007b) (c) Froese and Pauly (2008). (14) **Yellow squat lobster** (*Cervimunida Johni*) (a,b) Montenegro et al (2008a) (c) Acuna et al (1998) (d)

Arancibia et al (2005) (average between genders). (15) **Red shrimp** (*Heterocarpus redii*) (a,b) Montenegro and Zilleruelo (2008) (c) Acuna et al (1998) (d) Arancibia et al (2005) (average between genders). (16) **Red squat lobster** (*Pleuroncodes monodon*) (a) Quiroz et al (2006) (b,c) Montenegro et al (2008b) (d) Arana (1990).

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Chapter 5

A simple formulation for production per unit of food consumed

5.1 abstract

Production-to-consumption ratio (P/Q) is usually named as ecological efficiency, because it reflects how efficiently a population can transform ingested food into biomass. Usually this ratio is estimated by computing production and consumption separately, introducing an extra complexity in the estimation. We proposed a simple approach to estimate this ratio by modelling simultaneously P and Q . The model assumes that populations are made up of multiple co-existing cohorts, in which individual growth can be described by the specialized von Bertalanffy growth function (VBGF). Although models with different complexity can be explored, we focus on the simplest possible estimator, which rests on the assumption that the population has a stable age distribution (constant recruitment and mortality rate). We applied this model to two species, Pink cusk-eel (*Genypterus blacodes*) and the Southern hake (*Merluccius australis*), that are targets of commercial fisheries in the south-east Pacific. Uncertainty in the estimates was evaluated using a resampling approach. We

propose an approximate estimator for calculating P/Q , based on the assumption that some physiological and growth parameters ratios are invariant across species. On average, P/Q was around 0.3 for both species. The rule-of-thumb indicates that, in the absence of exploitation, P/Q is 0.35 for carnivorous and 0.26 for herbivorous fish. This model provides unbiased estimates for P/Q in fish that may improve population and ecosystem models.

5.2 Introduction

The ratio between biomass production and food consumption (P/Q) is an important quantity in ecosystem modelling because it reflects how efficiently a population can transform ingested food into biomass. This quantity is usually estimated by computing production and consumption separately. However, production and consumption are difficult quantities to estimate accurately in fish populations, because they require knowledge about individual growth rate, number of individuals at different ages and the amount of food ingested-at-age. In a different approach, P/Q has been computed by estimating the efficiency with which individuals convert ingested food into body tissue and then, using the average of these values as an unbiased estimate for the whole population (e.g Tang et al, 2007).

Pauly (1986) proposed a model for the estimation of P/Q in which production was replaced with total mortality, thus simplifying the estimation. This model, however, relies on the assumptions that population biomass is at steady-state (all the renewal is compensated by mortality) and the parameters defining individual consumption have no clear biological meaning. These limitations suggest that alternative approaches need to be explored. In this paper we propose a simplified method for estimating P/Q in fish populations in which P and Q are modelled simultaneously and it is assumed

that individuals grow according to the von Bertalanffy growth function (Bertalanffy, 1938). The von Bertalanffy growth function is particularly convenient for modelling P/Q because it is commonly used to describe fish growth, and consumption rates can be inferred from first principles discussed in chapter 2 (Wiff and Roa-Ureta, 2008). The resulting provides an unbiased estimator of P/Q for fish populations in which all parameters have a clear biological meaning.

5.3 P/Q for a cohort

By definition, the population production-to-consumption ratio (P/Q , hereafter designated ρ) is the biomass production per unit of food consumed (Pauly, 1986). Here we propose a model for ρ where a population is composed of cohorts of identical individual and which recruitment is discrete and occurs at one point in time. As in chapter 4, and according to Allen (1971), under these conditions P for a cohort of age a can be expressed as the product between individual growth rate and number at age. Under the same assumptions as were discussed in chapter 3, consumption Q of a cohort is simply the production of this cohort divided the the size-specific gross efficiency K . Thus, is a cohort is composed by identical individuals in terms of grow parameters and gross efficiency and recruitment occurs at one point in time, ρ is the same for all individual in the cohort:

$$\rho(w) = \frac{P(w)}{Q(w)} = K(w) \quad (5.1)$$

This equation represents ρ for a cohort at a particular weight during its lifespan. Gross efficiency in this terms can be explained as the individual efficiency in transforming ingested food into biomass. Note that if individuals have the same growth rate and they are all recruited at the same point in time, the value of ρ for the cohort is the

same as the value of ρ for an individual, because $N(a)$ cancels out in P and Q when taking the ratio (Eqn 5.1). Therefore, a model for ρ in a cohort can be obtained if a functional form for $K(w)$ is known. In this case, the population can be represented by simply overlapping multiple cohorts at a particular time t^* . In the next section we explore possible functional forms for $K(w)$, and then we extend the cohort estimate of ρ to incorporate population structure.

5.4 Gross food conversion efficiency

Gross food conversion efficiency (K) is the growth increment in weight per unit of food consumed. K is an interval quantity because increments in growth are not instantaneous with the amount of food ingested. However, K can be approximated as an instantaneous quantity by using continuous individual growth models. This relationship implies that food consumption can be inferred from growth rate.

Empirical estimates confirm that K declines with increasing body size, but it is also affected by other factors such as ration size (Condrey, 1982), type of food (Pandian and Marian, 1985), temperature and salinity (Kinne, 1960).

A basic formula for modelling K comes from the allometric model:

$$K(w) = \alpha_2 w^{b_2} \quad (5.2)$$

where w is a growth function with unit of mass. The parameters α_2 and b_2 are usually estimated by linearizing Eqn (5.2) by log transformation, and regressing empirical values of K against body weight. This model has three clear problems: (1) the parameters have no biological meaning, (2) the model implies $K > 1$ when $\alpha_2^{-1/b_2} > w > 0$, which is nonsensical. $K > 1$ implies that production is bigger than consumption, but animals cannot grow more than they eat, (3) it implies that, except when $w = 0$, K is

always > 0 implying that animals never stop growing during their (infinite) lifespan. In the light of these problems, Pauly (1986) proposed a model that constrains K using the asymptotic weight (w_∞):

$$K(w) = 1 - \left[\frac{w}{w_\infty} \right]^b \quad (5.3)$$

However, this is still a purely phenomenological description of K . The parameter b cannot be interpreted biologically and the model still has an important boundary problem: it implies a K value near to 1 when w is near 0, which is thermodynamically impossible.

Temming (1994) proposed a simplification of Pauly's model based on the theoretical concepts behind the generalized von Bertalanffy growth function (VBGF). They use the definition of gross conversion efficiency, $K = \text{growth}/\text{consumption}$ to establish a link between K and the VBGF.

In Temming's formulation, anabolism is assumed to be directly proportional to the consumption rate q , with A the proportionality constant:

$$q = \frac{1}{A} \times \text{anabolism} \quad (5.4)$$

from growth rate from the VBGF defined in chapter 2, $dw/da = Hw^d - cw$, in which cw reflects catabolism (energy losses) and Hw^d is the anabolism term (energy assimilation), d determines the allometric scaling of consumption. Expressing K in

terms of VBGF:

$$\begin{aligned}
 K(w) &= \frac{\textit{growth}}{\textit{consumption}} \\
 &= \frac{dw/da}{q} \\
 &= \frac{Hw^d - cw}{\frac{1}{A}Hw^d}
 \end{aligned} \tag{5.5}$$

Note in chapter 2 the anabolism term can be expressed by $\textit{anabolism} = \beta kw_\infty^{(1-d)}w^d$ when $k = c/\beta$. Under these definitions, Temming's model is defined by:

$$K(w) = A \left[1 - \left(\frac{w}{w_\infty} \right)^{1-d} \right] \tag{5.6}$$

where A is a parameter defining the fraction of ingested food that is available for the build up of body substance. Note that this equation is closely related to (Eqn 5.3) when $b = (1 - d)$ and $A = 1$. However, Temming's model avoids the boundary problems associated with this equation. In addition, all parameters have a clear biological interpretation, A and d can be estimated from a variety of sources of information.

It is impossible to get meaningfully estimation of d from age and growth data (Pauly, 1981), so this parameter must be estimated using empirical methods, as described in chapter 2 (Wiff and Roa-Ureta, 2008). Temming (1994) suggested that the nitrogen content of the organism's diet could also be used to obtain an independent estimate of A , because it is strongly correlated with absorption efficiency (Pandian and Marian, 1985). Another option for estimating A is to use the daily ration of food consumed, in an way analogous to the method proposed by Pauly (1986) for estimating b for equation (5.3) (see Cubillos et al (2003) for further details).

If weight is a deterministic function of length, Eqn (5.6) can be recast in terms of body length using a suitable length-weight relationship such as $w(l) = \alpha l^\beta$, where α

and β are parameters. Eqn (5.6) can be parameterized in terms of body length as:

$$K(l) = A \left[1 - \left(\frac{l}{l_\infty} \right)^{\beta(1-d)} \right] \quad (5.7)$$

5.5 ρ for a population

From Eqn (5.1) it is clear that $\rho(l) = K(l)$ for a cohort of identical individuals. If the cohort estimator $\rho(l)$ is to represent $\rho(l)$ for the population we need to incorporate population attributes. We can deal with this as follows: let l_{t^*} be the body length of a randomly selected individual in the population at time t^* and let $f_{t^*}(l_{t^*})$ be the probability density function (pdf) of l_{t^*} . We suppose that t^* is pre-determined in the year y and for brevity drop the t^* subscript of l and index t^* by year y . We therefore write the pdf of l as $f_y(l)$. Then, $K(l)$ is a random variable, and if l is continuous, the expected value of $\rho(l)$ at time t^* in year y can be written as:

$$\begin{aligned} \rho_y(l) &= \int_{l_0}^{l_\infty} K(l) f_y(l) dl \\ &= \int_{l_0}^{l_\infty} A \left[1 - \left(\frac{l}{l_\infty} \right)^{\beta(1-d)} \right] f_y(l) dl \\ &= \int_{l_0}^{l_\infty} A f_y(l) dl - \int_{l_0}^{l_\infty} \frac{A}{l_\infty^{\beta(1-d)}} l^{\beta(1-d)} f_y(l) dl \\ &= A \left[1 - \frac{E_{f_y}(l^{\beta(1-d)})}{l_\infty^{\beta(1-d)}} \right] \end{aligned} \quad (5.8)$$

where l_0 is the length at recruitment and l_∞ is the asymptotic length. Since this model is based on the generalized VBGF, a particular solution for it can be obtained by using the specialized VBGF in which d is set at $2/3$, and growth is assumed to be isometric ($\beta = 3$). In this case Eqn (5.8) becomes:

$$\rho_y(l) = A \left[1 - \frac{E_{f_y}(l)}{l_\infty} \right] \quad (5.9)$$

It is apparent that the estimation of ρ now hinges on the estimation of the expected value of body length. To implement the model of Eqn (5.9), it is necessary to have estimates of l_∞ , A and the expected body length ($E_{f_y}(l)$) in the population in year y .

There is more than one way of estimating ρ . The choice depends on what data are available to estimate $E_{f_y}(l)$. As we have shown in chapter 2, if the exact lengths of sampled fish have been observed, and all fish are equally likely to be sampled, an unbiased estimate of $E_{f_y}(l)$ can be obtained from the mean l in a sample of size n . However, most fisheries use gear that is selective and so the sampled lengths are likely to be size-biased. $E_{f_y}(l)$ can be obtained from samples of this kind, by modelling the probability density function (pdf) of lengths $f_y(l)$ in the population at time t^* in the year y .

A similar modelling approach implemented in chapter 3 (section 3.4) for the expected inverse body length can be used here for modelling $E_{f_y}(l)$. Note that equations in section 3.4 were proposed to model $E_{f_y}(l^{-1})$, and thus they should be modified to include the expected length. These modifications can be obtained by replacing length, instead of inverse length, in Eqns (3.9, 3.13, 3.15, 3.15).

Here, we assume that no data are available to define processes such as recruitment, variability of the length at age or mortality rate at age. Our purpose is so doing this is to propose the simplest possible estimator for ρ_y with least demanding on data knowledge. Accordingly, we modelled $E_{f_y}(l)$ with fixed length at age and stable age distribution. According to chapter 3, under this assumptions, abundance in

each successive age class decays exponentially so that $N_y(a) = Re^{-Z_y a}$, where R is (constant) recruitment and Z_y is the average total mortality across all ages. In this case the abundance proportion of each age in year y is $P_y(a) = N_y(a) / \sum_a N_y(a) = e^{-Z_y a} / \sum_a e^{-Z_y a}$. Thus $E_{f_y}(l)$ with no variability in length-at-age and a stable age distribution is given by:

$$\begin{aligned}
 E_{f_y}(l) &= \sum_a l_\infty (1 - e^{-k(a-a_0)}) \frac{e^{-Z_y a}}{\sum_a e^{-Z_y a}} \\
 &= l_\infty \sum_a \frac{e^{-Z_y a} - e^{-a(Z_y+k)+ka_0}}{\sum_a e^{-Z_y a}} \\
 &= l_\infty \left[1 - \sum_a \frac{e^{-a(Z_y+k)+ka_0}}{\sum_a e^{-Z_y a}} \right] \tag{5.10}
 \end{aligned}$$

To estimate ρ_y we start by assuming that estimates of the von Bertalanffy growth parameters (l_∞, a_0, k) , Z_y and A are available. In this case, we can estimate ρ_y by combining Eqns (5.9) and (5.10):

$$\begin{aligned}
 \rho_y(l) &= A \left[1 - \frac{E_{f_y}(l)}{l_\infty} \right] \\
 &= A \left[1 - \frac{l_\infty \left(1 - \sum_a \frac{e^{-a(Z_y+k)+ka_0}}{\sum_a e^{-Z_y a}} \right)}{l_\infty} \right] \\
 &= Ae^{ka_0} \left[\sum_a \frac{e^{-a(Z_y+k)}}{\sum_a e^{-Z_y a}} \right] \tag{5.11}
 \end{aligned}$$

There are three sources of uncertainty in the estimator ρ_y , namely growth parameters, assimilation parameter and total mortality. In the following section we will show some applications of the model and determine likely uncertainty using a resampling approach.

5.6 Approximate estimator for ρ

We can derive an approximate value for ρ under certain assumptions about population dynamic if we define the likely trade-off between mortality and growth parameters. First, since the categories in Eqn (5.11) can be made as narrow as desired, we replaced the sum with a more mathematically tractable integral to get:

$$\rho_y(a) = Ae^{kt_0} \left[\int_0^\infty \frac{e^{-a(Z_y+k)} da}{\int_0^\infty e^{-Z_y a} da} \right] \quad (5.12)$$

This equation represents the gross efficiency for the population in year y for all individuals recruits (age 0) to those in the infinite age. Here, age 0 is taken to be the onset of feeding in the larval stage, which is the point at which tissue growth commences. For simplicity, we assume that mortality rate is constant across ages. Solving the integral in the denominator of Eqn (5.12) by substitution yields:

$$\int_0^\infty e^{-Z_y a} da = \left. \frac{-e^{-Z_y a}}{Z_y} \right|_0^\infty = \frac{-1}{Z_y} [e^{-Z_y \infty} - e^{-Z_y 0}] \quad (5.13)$$

with $e^{-Z_y 0} = 1$ and $e^{-Z_y \infty} = 0$, then:

$$\int_0^\infty e^{-Z_y a} da = \frac{1}{Z_y} \quad (5.14)$$

$$\rho_y(a) = Ae^{ka_0} Z_y \left[\int_0^\infty e^{-a(Z_y+k)} da \right] \quad (5.15)$$

solving by substitution the integral of the righthand side of the Eqn (5.15):

$$\int_0^\infty e^{-a(Z_y+k)} da = \left. \frac{-e^{-a(Z_y+k)}}{(Z_y+k)} \right|_0^\infty = \frac{-1}{(Z_y+k)} [e^{-\infty(Z_y+k)} - e^{0(Z_y+k)}] \quad (5.16)$$

with $e^{-Z_y 0} = 1$ and $e^{-\infty(Z_y+k)} = e^{-Z_y \infty} e^{-ka} = 0$ since $e^{-Z_y \infty} = 0$, then:

$$\int_0^{\infty} e^{-a(Z_y+k)} da = \frac{1}{(Z_y + k)} \quad (5.17)$$

replacing Eqn (5.17) on Eqn (5.15):

$$\rho_y = \frac{Ae^{ka_0} Z_y}{(Z_y + k)} \quad (5.18)$$

At age zero, the VBGF can be expressed as $(1 - \frac{l_0}{l_\infty}) = e^{ka_0}$, where l_0 is the length at age 0. Mertz and Myers (1998) deduced that $l_\infty \gg l_0$ for fish species. Thus $l_0/l_\infty \approx 0$ and $e^{ka_0} \rightarrow 1$. Therefore an approximation version of Eqn (5.18) can be written as:

$$\rho_y \approx A \frac{Z_y}{(Z_y + k)} \quad (5.19)$$

Average total mortality across all ages (Z_y) can be expressed as the sum of natural (M_y) and fishing mortality (F_y). A similar simplification for ρ is done by Aydin (2004), although it is was proposed only for cases considering steady-state condition (where all mortality is compensated by renewal).

The way in which natural mortality rate may vary between years is poorly known, and therefore it is often assume to be time-invariant (i.e. $M_y = M_{y+1} = M$). If M is assumed to be constant across years and the population is not under exploitation $F_y = 0$, ρ is also time-invariant and can be defined by:

$$\rho \approx A \frac{M}{(M + k)} \quad (5.20)$$

This equation can be simplified further if there is a relationship (trade-off) between M and k . Beverton and Holt (1959) pioneered the comparative study of fish life-histories and showed the existence of patterns of growth and mortality across species. These patterns were reviewed by Charnov (1993), who found that M/k tends to be constant with a dimensionless value of $3/2$. Accordingly, we can write $k = (2/3)M$ and Eqn (5.20) becomes:

$$\rho \approx A \frac{3}{5} \quad (5.21)$$

In this case ρ is completely dependant on the value of A . Temming (1994) defined this parameter as the "fraction of ingested food that is available for the build up of body substance". Indeed, this parameter serves to scale the anabolism term in the VBGF to give the net food (energy) ingested. According to Temming and Herrmann (2009) A must be the proportion of food consumption that is not lost as faeces (f), excretion (u) and apparent specific dynamic action (s_2 , the increased metabolic rate a fish experiences following ingestion of a meal) (Brett and Groves , 1979; Andersen and Riss-Vestergaard, 2003). Thus, A can be expressed as:

$$A = 1 - (f + u + s_2)$$

$\{f + u + s_2\}$ appears to be a relatively constant proportion of the food ingested across a wide range of fish species (Brett and Groves , 1979) within the same trophic group (carnivorous/herbivorous)(Turner, 1970). According to Brett and Groves (1979) f , u and s_2 for carnivorous fish have average values of 0.2, 0.07 and 0.14. Thus, for carnivorous fish

$$\begin{aligned}
A &= 1 - (0.2 + 0.07 + 0.14) \\
&= 0.59
\end{aligned}$$

Herbivorous fish have received less attention than carnivorous fish, but they are characterized by a generally low absorption efficiency of the food because large fraction of their normal diet is indigestible (Wootton, 1990). On average, faecal loss is about 0.4 and excretion about 0.03 (Brett and Groves, 1979). According to Jobling (1981) specific dynamic action does not vary significantly different between herbivorous and carnivorous fish and it is about 0.14. Therefore a general value of A in herbivorous fish is:

$$\begin{aligned}
A &= 1 - (0.4 + 0.03 + 0.14) \\
&= 0.43
\end{aligned}$$

Using these values for A , we can therefore estimate that ρ is around 0.35 for carnivorous fish and approximately 0.26 for herbivorous

If a fish population is exploited, fishing mortality can be introduced explicitly into Eqn (5.19). A convenient way to evaluate the effect of fishing mortality in ρ_y , is expressing the age-average fishing mortality as a proportion of natural mortality ($\bar{F}_y = \psi_y M$).

Using again the Beverton-Holt's trade-off between M and k we get:

$$\rho_y \approx A \frac{(M + \bar{F}_y)}{(M + \bar{F}_y + k)} \approx A \frac{(M + \psi_y M)}{(M + \psi_y M + \frac{2}{3}M)} \approx A \frac{(1 + \psi_y)}{(\frac{5}{3} + \psi_y)} \quad (5.22)$$

where ψ_y is a proportionality constant linking fishing and natural mortality. Incorporation of exploitation is directly related with population gross efficiency because a

higher value \bar{F}_y produce higher values of ψ_y . Furthermore, mortality rate produces a non-linear increment in ρ_y because it tends to reduce the expected body size in the population. For example, in highly exploited population we can assume that the fishery remove the same amount of biomass that natural mortality (Pauly, 1996), thus $\bar{F}_y = M$. Under this condition $\psi_y = 1$ and $\rho_y \approx A\frac{3}{4}$. Figure (5.1) shows this non-linear behavior of ρ_y according to increments in ψ_y for carnivorous and herbivorous fish.

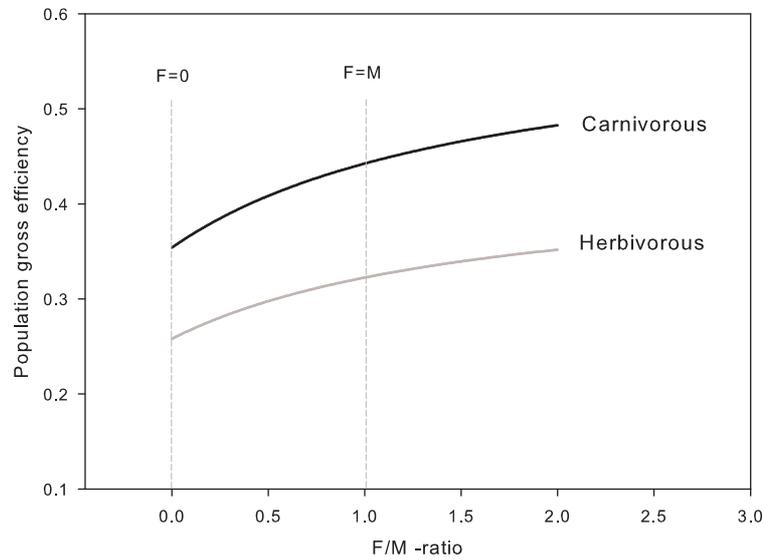


Figure 5.1: Production per unit of food consumed (ρ) in carnivorous and herbivorous fish population in relation to the relative increments in fishing mortality (F) with respect to the natural mortality (M).

5.7 Applications

To illustrate the model, we applied Eqn (5.11) for pink cusk-eel (*Genypterus blacodes*) and southern hake (*Merluccius australis*). The parameters $\{\hat{k}, \hat{a}_0\}$, \hat{A} and a time series of Z_y were taken from the same database used in chapter 3 (section 3.6). Conversely, uncertainty on ρ estimates was incorporated using the same resampling procedure described in chapter 3.

5.8 Results of applications

Results from the application of the models are shown in Figure (5.2). Pink cusk-eel from the northern population has an average ρ_y of 0.306 with a 95%CI of [0.295,0.318]. The southern population of pink cusk-eel has an average ρ_y of 0.328 and a 95%CI of [0.319,0.338]. In case of Southern hake the average ρ_y and 95%CI were 0.308 and [0.286,0.331], respectively. Time-series of ρ_y estimates for both species can be divided into three periods. The first period, from 1977 to 1984, has relative low estimated for ρ_y . Between 1985 and 1993 there was a significant increment in ρ_y . From 1993 to 2005 the values ρ_y oscillated around the average value of the time series.

5.9 Discussion

The model presented here differs with that proposed by (Pauly, 1996) in two main aspects: 1. We incorporated Temming's gross efficiency model, which allows all parameters relating to food consumption to be interpreted in biological terms. 2. We relaxed the assumption of steady-state conditions for the biomass. The use of Temming's model allowed us to propose a rule-of-thumb estimator for ρ , by defining an a priori value for A as done in Temming and Herrmann (2009). Relaxing the steady-state assumption allowed us to consider a non-equilibrium relationship between

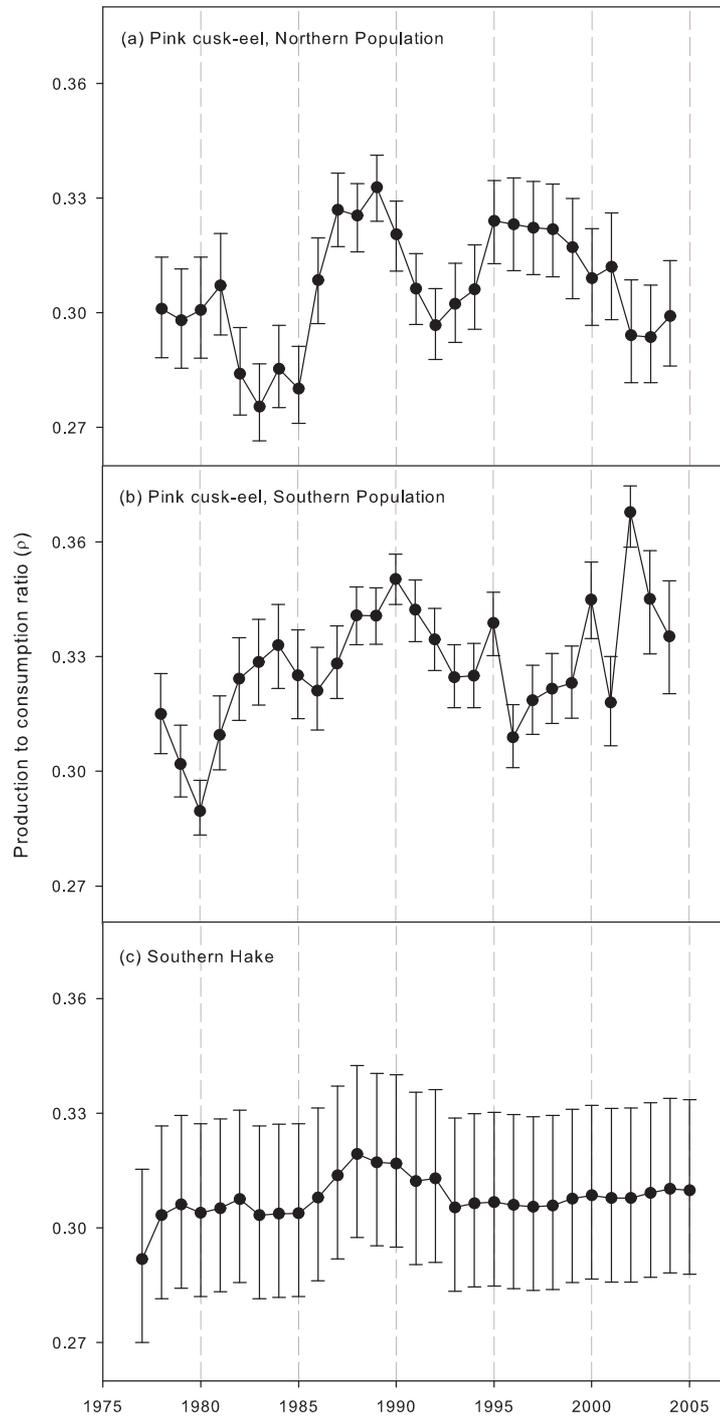


Figure 5.2: Estimates of production per unit of food consumed in three populations of Chile. (a) Pink cusk-eel (*Genypterus blacodes*), northern population, (b) Pink cusk-eel, southern population, (c) Southern hake (*Merluccius australis*). In each case vertical bars represent the 95% confidence intervals computed by resampling and dots are the median values.

the renewal and decay of biomass. As a result, variations in age structure can be incorporated via total mortality. Thus, if a time-series of total mortality estimates is available, dynamical behaviour in ρ can be incorporated by ordering the estimates of this quantity at different points in time. Smaller individuals have higher ρ because they are more efficient in transforming the ingested food into biomass. Thus, mortality has a direct effect on ρ because it tends to reduce the expected body length in the population. Incorporation of dynamic behaviour on ρ may improve the evaluation of time-dependant perturbations in ecosystem models, such as ECOPATH (Polovina, 1984; Christensen and Pauly, 1992), because this parameter is often assumed to be time- and species-invariant (Walters et al, 1997; Ainsworth et al, 2008).

The simplest models proposed here rest on the assumption of a stable age distribution. Nevertheless, stable age distributions are rarely realized in nature, except as an average over several generations (Charnov, 1993), because recruitment and age-specific mortality are likely to vary over time. Whether or not it is possible to relax this assumption depends, on what data are available to model the proportion of each age in each year ($P_y(a)$) and length at a given age ($P_y(l | a)$). Estimates of $P_y(a)$ can be obtained, for example, from the output of a fisheries stock assessment models. In addition, $P_y(l | a)$ can be modelled from age and growth, if it can be assumed that the population is made up of a mixture of co-existing cohorts, each of which has a length-at-age that can be represented by a Gaussian distribution (Fournier et al, 1990).

Several authors have noticed that production per unit of food consumed remains constant across species (Slobodkin, 1960; Welch, 1968; Turner, 1970). No theoretical analysis has yet been proposed to explain this constancy, although it has been hypothesized that it may be a consequence of compensation between the efficiency with which

food can be assimilated and the efficiency with which energy can be channeled into growth (Welch, 1968). Here we proposed a theoretical explanation for this constancy which depends on processes that occur within and among individuals. Individual fish of the same trophic habits (carnivorous/herbivorous) seem to absorb the same proportion of their food ingested, and thus A is relatively constant across individuals of different species. Among individuals, the trade-off between natural mortality and growth, tends to result in ρ being constant across populations. Although this model presents a new avenue for exploring this constancy, the assumption of stable age distribution makes that the constancy found here for ρ should be interpreted as the expected value for fish of the same trophic habits averaged across several generations.

In general, carnivorous fish absorb their food relatively efficiently, because protein, which is a large component of their prey, is usually assimilated to a greater degree than other dietary components (Brett and Groves, 1979). Welch (1968) used experimental data to show that carnivorous animals have a higher ρ than herbivorous. Here, we have used theoretical analysis to show that ρ is approximately 0.35 for an unexploited population of carnivorous fish and 0.26 for herbivorous species. Although the results of these empirical and theoretical analyses coincide, we found that empirical values for ρ (0.32 and 0.30) for two fish species were smaller than the predicted theoretical value. Tang et al (2007) reported values of ρ , for four carnivorous fish populations that ranged from 0.13 to 0.3. These lower than expected values may be because theoretical value of ρ is calculated across the entire lifespan from the onset of larval feeding until the terminal age. A value of ρ calculated for only older and/or larger individuals will have smaller than the theoretical value, because ρ decreases exponentially with age or size (Slobodkin, 1960).

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Chapter 6

General Discussion

6.1 Extending the allometry in food consumption to mammals

Birds, mammals and insects show determinate growth, in which adult body size is more or less unchanging. For example, mammals mature upon reaching adult size. Although the VBGF was originally proposed for animals such as fish and reptiles that do not cease growing after they have reached maturity, this growth function has also been used to describe growth in mammals (e.g. Griffiths and Brook, 2005). If the VBGF does apply to mammals, the allometric theory for food consumption proposed in previous chapters, may also be applied, with modifications, to this taxon. First, the physiological considerations that determine the parameter d in fish (chapter 2) need to be modified. Mammals are warm-blooded organisms. Heat output takes place through the body surface, and heat output must be balanced to maintain the body temperature constant. Thus, according to the principles underlying the von Bertalanffy equation, the body surface in mammals is physiologically limiting and the relationship between surface area and mass can be used as a proxy for d .

Reynolds (1997) compiled data on the relationship between surface area and body mass for 56 aquatic and terrestrial species of mammals, and found no statistical differences in the mass-specific surface area relationship between marine and terrestrial mammals. The overall slope resulting from this inter-specific analysis was $\sim 2/3$. Further theoretical predictions of Q/B allometry for mammals need an estimation for weight at length parameter β and the trade-off parameter h . Calder (1996) noticed that β for mammals is close to 3. No estimates of h have been made for mammals, so we assume that it has the same value as for fish, $h = 1/2$. Inserting this values into Eqns (2.14) and (2.17), yields the predictions: $\frac{\partial \log(q^*)_j}{\partial \log(w^*)_j} = 2/3$ and $\frac{\partial \log(Q/B)_j}{\partial \log(w^*)_j} = -1/3$ where w^* is any weight which is a constant proportion the asymptotic body size.

Although available empirical information from mammals to support this theoretical results is less extensive than that for fish, Farlow (1976) compiled a large data set of daily consumption estimates (expressed in kcal/day) for 85 herbivorous and 102 carnivorous mammals. The slope of the relationship between $\log(\text{daily individual consumption})$ and $\log(\text{average mass})$ across species and populations provided an estimate for $\frac{\partial \log(q^*)_j}{\partial \log(w^*)_j}$, of 0.728 (95%IC=0.689, 0.768) for herbivores and 0.697 (95%IC=0.672, 0.722) for carnivores. Humphreys (1981) compiled estimates of daily Q/B (expressed as assimilation) for 47 species and/or populations of mammals. These provide an estimate $\frac{\partial \log(Q/B)_j}{\partial \log(w^*)_j}$, of -0.336 (95%IC=-0.384,-0.289). The theoretical prediction matches the data well, offering an interesting opportunity to extend the allometric model in food consumption to mammals. Although both compilations involved transformation of the data, (either into kcal, in the case of individual consumption, or from assimilation in the case of population consumption), this is not an impediment to using the equations in Chapter 2, because both transformations only affect the intercept of the allometric relations and not the slope. This is supported by the work of Pandian

(1967) and Pandian and Marian (1985) who reported that ingestion is proportional to consumption, and that the proportionality constant linking these values is related to the parameter A in Chapter 2.

6.2 Latitudinal versus cross-sectional estimators

Latitudinal data refer to observations of a given unit made over time and thus, such data can be represented as a time-series. On the other hand, cross-sectional data refer to observations of many individuals at a given point in time. Models presented here, use size structure at a given point in time and thus they can be referred as cross-sectional models. On the historical context, most of the estimators proposed for the trio $\{P/B, Q/B, P/Q\}$ have been based on latitudinal models.

General principles, like those proposed in this thesis, provide a broader context for modelling this trio. In the case of P and Q , different methods have been proposed to cope with their application at the individual and population levels. Some authors use the value of P or Q to define an instantaneous rate (Kimmerer, 1987; Pauly, 1986), or a rate average over a time interval (Clarke, 1946; Majkowski and Waiwood, 1981), or a quantity integrated over a time interval (Allen, 1971; Majkowski and Hearn, 1984). In each case, the first reference relates to production and the second to food consumption. Different authors have also considered the case of discrete and continuously reproducing populations (Kimmerer, 1987; Pauly, 1986), and the need to explicitly account for mortality rate in the model's formulation (Kimmerer, 1987; Buckel et al, 1999). P and Q can also be inferred from individual growth principles and thus mathematical models for these quantities are similar. This is probably the reason why both processes have been modelled by a variety of divergent approaches.

The different approaches used to model P/B and Q/B are, in part, a consequence of the basic mathematical nature of these processes. P and Q are rate quantities, and therefore they accept a longitudinal (interval of time) definition. However, population biomass B is not a rate quantity and thus it does not make much sense to define it over an interval of time. It only admits a “point in time” definition and thus cross-sectional estimators can be applied. Allen (1971) tackled this problem, by turning the denominator in P/B into an interval quantity, by using the average biomass over a time period and calculating production over the same interval. This approach has two clear disadvantages: using averages result in a loss of information on biomass and production changes within the time period; and the resulting model is hardly tractable analytically and thus the explicit dependence of P/B and Q/B on body size is lost. The other option is to convert P and B into point in time quantities and treat both as cross-sectional estimators, as we have done here. Fortunately, P and Q admit a point in time definition. Changes over time can be introduced by simply ordering the discretised cross-sectional estimates of P/B and Q/B . Time-average properties on these estimators can also be obtained by considering the time-average expected inverse body length in the population ($E[l^{-1}]$). This flexibility in mathematical definition for P and Q also makes it possible to formulate ecological efficiency P/Q explicitly in terms of body size. Thus, by using point definitions for P and Q the trio $\{P/B, Q/B, P/Q\}$ can be made explicitly dependant on body size.

6.3 Life history invariants and the regularity of P/B , Q/B and P/Q across species

In this thesis, I have demonstrated that the across-species regularities in Q/B and P/Q depend on specific dimensionless quantities. Q/B allometry depends on the invariance across species of the parameter h , which defines the trade-off between

asymptotic length l_∞ and the growth parameter k (chapter 2). At the population level, P/Q remains invariant across species if the ratio between the natural mortality rate M and k is constant for the taxa involved. Similarly, Roa and Quiñones (1998) demonstrated that allometric scaling in P/B holds if the ratio between length at maturity l_m and l_∞ remains constant across species. As I pointed out in chapter 2, invariance in h is ultimately caused by the constancy of l_m/l_∞ across species. Therefore, the allometry of the trio $\{P/B, Q/B, P/Q\}$ is, at least in part caused by the invariance of the two dimensionless numbers l_m/l_∞ and M/k . Accordingly, the emerging question is: are these numbers invariants across species?

As pointed out on the introduction, “the Beverton-Holt life history invariants” indicates that three quantities did appear to be constant across species: the ratio between the instantaneous mortality rate (M) and the parameter k of the VBGF, the product of M and the age at sexual maturity (a_m), and the ratio between the length at maturity (l_m) and the asymptotic length (l_∞). The Beverton-Holt life history invariants have been obtained by maximization of evolutionary fitness through optimization of the net reproductive rate (Charnov, 1993) or by a simple ecological trade-off between survival and mortality (Jensen, 1996). Therefore, the across-species constancy of the trio $\{P/B, Q/B, P/Q\}$ is ultimately a consequence of the Beverton-Holt life history invariants. This result enables us to make a theoretical connection between population level energetics, namely the trio $\{P/B, Q/B, P/Q\}$, and the basic principles governing the the Beverton-Holt life history invariants.

6.4 Applicability of the models

In recent years, the emphasis in fisheries science has shifted single-species assessment to more holistic multi-species and ecosystem-based approaches (Essington,

2007). The trio $\{P/B, Q/B, P/Q\}$ has a key importance in ecosystem modelling, because it determines population energetics in terms of food intake by predation and the transformation of this energy into the population biomass of predators. A diversity of analytical tools for evaluating fisheries on an ecosystem context have been proposed. Two of these tools have been widely applied in the recent years and they can be divided into two main groups: the multispecies virtual population analysis (MSVPA) (Anderson and Ursin, 1977) and the trophic mass-balance models (Walters et al, 1997). MSVPA are deterministic models based on the seminal work of Anderson and Ursin (1977). They represent an explicit extension of the age-structured single species stock assessment models to include multiple species through predator-prey interactions. In MSVPA models, natural mortality for prey species is extended by explicitly including another source of mortality related with predation. On the other hand, mass-balance model is a simpler approach for analysis of trophic interactions in fisheries resource systems. These models facilitate the calculation of ecosystem indicators and the exploration of management policies implications of the food web interactions (Essington, 2007). Thus, they are a valuable complement to the experimental and observational approaches that are traditionally used to investigate ecosystem function. One of the most popular software for mass-balance model is named ECOPATH. Originally proposed by Polovina (1984), and further developed by Christensen and Pauly (1992), ECOPATH is a mass balance model which provides a static picture of ecosystem trophic structure. Nowadays, a common practice is to implement ECOPATH altogether with ECOSIN which is a dynamic food web model that simulates food web responses over time to natural and anthropogenic disturbances (Walters et al, 1997).

MSVPA utilizes extensive time series of catch-at age data and it needs to estimate complex parameters such as the suitability coefficients in order to extent the natural mortality for preys species. Suitability is a parameter reflecting the diet composition of the predator relative to the available food (Jurado-Molina et al, 2005). On the other hand, ECOPATH with ECOSIN (EwE) requires estimates of P/B and Q/B for each member of the food web and it provides an estimate of P/Q as an output. P/Q values are usually used as an indicator to constrain an acceptable global solution for the model (Kavanagh et al, 2004). Models developed on this thesis may improve both approaches for evaluating fisheries on an ecosystem approach. First, predation mortality models in MSVPA can be directly derived from Q/B model presented here, because it represents the global mortality a predator put on their preys. Thus, predation mortality can be inferred from Q/B rates which is driven by basic principles underpinning VBGF and dynamics of size/age structure of predators. Second, in order to implement EwE, P/B is assumed to be equivalent to the total mortality, while Q/B is usually obtained from the empirical allometric equation proposed by Palomares and Pauly (1998). The estimation of P/B in this way rest on the assumption that the system is at a steady-state (where all biomass renewal is compensated by mortality), while deriving Q/B from an empirical equation does not allow for the effects of variation in the age and/or size distribution of the population. Underlying assumptions of EwE is that fishing mortality does not allow surplus production of the biomass, whereas single-species fishing theory implies that fishing leads to surplus by leaving on the water smaller and younger fish which are highly efficient in transformed their ingested food into biomass. Model proposed here for the trio $\{P/B, Q/B, P/Q\}$ can cope with this inconsistency between single and multispecies fishing theory, because they are size/age dependant models who explicit accounted for shifts in population structure due fishing exploitation.

Exploitation affects surplus production as fishing gear is highly size-selective. Fishing constantly removes larger, less-efficient fish, leaving in the water smaller and more “hungry” individuals. Since P/B , Q/B decay exponentially with size, smaller fish have higher P/Q which means they are highly efficient in transforming their ingested food into biomass. The EwE model does not take into account this shift in population structure, of the species to be modelled, due to fishing (Walters et al, 1997). In developing ECOSIM Walters et al (1997) assume that changes in surplus production are entirely driven by changes in predator/prey functional responses. In other words, ECOSIN considers changes in population structure but these are only effects of the vulnerability function of the predator/prey dynamics. Thus ECOSIN incorporates phenomenological shifting of the population structure where all possible causes (including fishing exploitation) are confounded on the predator/prey functional responses. Aydin (2004) noted the same inconsistencies in EwE and he tackled this problem by making the trio $\{P/B, Q/B, P/Q\}$ explicitly dependant on age structure. He extended the model of Pauly (1986) for Q/B and Allen (1971) for P/B to include age structure. He integrated biomass, consumption and production of a single recruit over its lifespan, assuming equilibrium conditions on recruitment and total mortality, in a similar manner yield-per-recruit is computed in single species fishing theory (Quinn and Deriso, 1999). Aydin (2004) derived similar equations for consumption per recruit as those proposed by Pauly (1986) and the same equations as those derived by Allen (1971) in case of production. In this thesis, I deal with these inconsistencies between between single and multispecies fishing theory. However, there are still several fundamental differences between the models proposed by Aydin (2004) and those developed in this thesis. First, Aydin (2004) studied both Q/B and P/B as latitudinal models whereas in this thesis they are treated as cross-sectional models. Second,

models proposed by Aydin (2004) underpin a phenomenological description for surplus production. As discussed above, latitudinal models introduce time-complexity in to the analyse when relationships between the trio $\{P/B, Q/B, P/Q\}$ and body size/age are difficult to determine. Latitudinal models are easily tractable only by assuming a stable age distribution. For these models, the exploration of alternative hypotheses on age distribution are only suitable when difficult-to-obtain quantities such as the number of recruits per year and/or a stock recruitment relationship are available. On the other hand, the phenomenological description for surplus production in Aydin (2004) makes it difficult to connect the processes occurring at individual level with basic principles governing the physiology of growth. Cross-sectional models based on first principles, like those presented here, may cope with these difficulties. The modelling framework presented here permits explicit connections between the trio $\{P/B, Q/B, P/Q\}$ and body size where all parameters are derived for first principles governing individual growth. This framework allows also the exploration of hypotheses others than the stable age distribution. This framework naturally allows the exploration of fishing exploitation in EwE, as fishing mortality is well known to be highly size dependant. Thus, incorporating size-dependence in P/B and Q/B allows an exploration of the way in which size-based metrics respond to the effect of fishing. These models may help make community ecology, rather than population ecology, the fundamental ecological science underlying fisheries (Harwood, 2007).

Recently, Gascuel and Pauly (2009) proposed a model called ECOTROPH which is a trophic-level based ecosystem model. ECOTROPH assigns the biological production of all the ecosystem components onto trophic levels, regardless of species or body size. This model treats all ecosystem functions as a continuous flow of biomass from lower to higher trophic levels. In the assumptions of ECOTROPH, P/B is seen as a measure

of the speed of the flow and it is equal to the total mortality. In the model, biomass is accessible to fishing exploitation by considering a selectivity coefficient as a function of trophic level. Thus, ECOTROPH can be used to simulate virtual ecosystems facing various exploitation patterns. The main difference between ECOTROPH and models such as EwE, is the latter is based on energy flow between boxes representing species, while ECOTROPH considers continuous trophic classes only, regardless of species or groups thereof. However, in both modelling approaches, the ecosystem is represented as a trophic flow moving from lower to upper trophic levels, with losses due to non-predatory mortality, catches, excretion and respirations. Overall, the two approaches differ more in their parameterisation than in their conceptualisation of predation and related processes. For EwE, a value is based on the knowledge of P/B and Q/B for each (group of) species with trophic levels estimated as outputs. Conversely, ECOTROPH is based on trophic level estimates and it does not require either P/B or Q/B values. This leads to a reduction in the number of parameters needed to implement ECOTROPH but also to a loss in flexibility and realism. Models proposed in this thesis are based on single species fishing theory where variations on population structure are caused by recruitment and size-dependant fishing mortality. Therefore, these models attempt to improve input parameters of ecosystem models based on species like those discussed above. Nevertheless, the ecosystem model approximations based on species or trophic level should be seen as a complementary tool to understand the ecosystem functioning (Gascuel and Pauly, 2009).

The allometric theory for the trio $\{P/B, Q/B, P/Q\}$ discussed in this thesis has other applications in ecosystem modelling. For example, Brose et al (2006) demonstrated that allometric scaling at the population level might explain the stability and

persistence of complex food webs. This stability is a consequence of the fact that individual and populations processes are not random across species. Instead, they are determined by allometric scaling relationships. Thus, the across-species regularities presented here for $\{P/B, Q/B, P/Q\}$ may enhance the stability of ecosystem models by constraining general solution to the underlying rules described by the allometric theory.

The same quantitative framework also makes it possible to identify the underlying mechanism that produce allometric scaling, and it provides simplified models for estimating these quantities. As a result, it has which the potential to be widely applied in fisheries science.

6.5 Further generalizations

The allometric theory for food consumption proposed here can be generalized in, at least, two different ways. First, it can be extended to cover taxa other than fish, in which the physiological constraints that determine d may be different (as I discussed in section 6.1). Traditionally, a distinction has been made between the value of $3/4$ predicted by nutrient distribution networks (West et al, 1997) and the value of $2/3$ predicted by Euclidean surface-area-to-volume considerations (Heusner, 1982). However, these approaches exclude the possibility that d is neither $3/4$ nor $2/3$ and that its value may differ between taxa. White et al (2007) presented empirical arguments against the dogmatic idea of adopting a single value for d . Here I follow the same philosophy, and argue against the concept that there is a single exponent for food consumption. By allowing more flexibility in this parameter we are able to explore the way in which physiological processes might determine the value of d for different taxa.

Second exploration of this allometric theory deals with the intercept of this relationship. The allometric scaling that I described in Chapter 2, only explored the mechanisms that might determine the slope of the relationship between food consumption and body size. However, Economo et al (2005) have shown the slope and intercept of allometric scaling can be predicted from theory.

The applicability of the models presented here for estimating the trio $\{P/B, Q/B, P/Q\}$ depends mostly on what data are available to estimate of the expected length in the population. Two different approaches can be implemented to estimate this value. One is a design-based approach, which can be used if an unbiased sample of length is available. The other is model-based approach that is more appropriate to estimate the expected length in the population. The model that is least demanding on data, relies on the assumption of stable age distribution. An unbiased sample of fish lengths can only be obtained from a specially design experiment for gear selectivity (Gedamke and Hoening, 2006), while stable age distribution is rarely realized in nature (Charnov et al, 1993). However, Gedamke and Hoening (2006) noticed that an unbiased estimator of expected length can be obtained by combining length data from survey-design experiment with length data from commercial fisheries. The stable age distribution assumption can be relaxed by re-parameterizing the stock-recruitment relationship (Beddington and Kirkwood, 2005), in a way that does not require extensive data knowledge (as discussed in chapter 4).

The approximate estimator for P/Q that is developed in Chapter 5 considers individuals of all ages from the onset of larval feeding to the terminal age together. However, practical application of this rule may require an estimation of P/Q with a starting age other than the larval stage, for example the age at recruitment. Chapter 5 can be generalized for this rule-of-thumb by integrating from ages other than 0.

An elegant way to deal with this is to express the lower limit of age integration as a proportion of terminal age.

6.6 Concluding remarks

The main purpose in this thesis has been to propose a quantitative framework for analysing food consumption. This framework allows the mechanism underlying the allometric scaling of food consumption be identified and provides a predictive models for Q/B in fish populations. A similar quantitative framework was then used to produce models for P/B , which naturally allows for across-species comparison. Once functional forms for production and food consumption had been identified, a third model was proposed for ecological efficiency, the ratio of production to consumption. From a theoretical point of view, the results presented here allow the first quantitative explanation for the existence of the allometry for Q/B and invariance for P/Q across fish species. These results, together with those of Roa and Quiñones (1998), provide an explanation for allometry in P/B , and suggest that the regular across-species patterns in the trio $\{P/B, Q/B, P/Q\}$ can be explained by basic principles which are connected with the Beverton-Holt life history invariants. This result is particularly important because it connects previously separated fields in theoretical ecology. The development of a quantitative framework for the trio $\{P/B, Q/B, P/Q\}$ clarified their explicit dependence on body size, and simplified the estimation of these quantities. The resulting estimators were applied to real data and their statistical properties evaluated using a computer-intensive resampling approach. These quantities have a key importance in ecosystem modelling and thus, these new models have the potential to be widely applied in fisheries science. This thesis bring together disciplines, such as physiology, macroecology and fisheries science, that have traditionally been viewed as distinct. I hope that their integration might improve both population and ecosystem

models.

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Appendix A

Age and Growth in pink cusk-eel

Appendix based on: Wiff. R, V. Ojeda and J.C Quiroz. 2007.– “Age and growth in pink cusk-eel (*Genypterus blacodes*) off the Chilean austral zone: evaluating differences between management fishing zones” Journal of Applied Ichthyology. **23**, 270-272

A.1 abstract

The pink cusk-eel (*Genypterus blacodes*) is a benthic-demersal fish which support an important fishery in Chile. However, there is a lack on basic fishery and biological information for this specie. Here, the von Bertalanffy (vB) growth parameters for pink cusk-eel (*Genypterus blacodes*) were estimated for the Chilean austral zone (41°28-57°00 S) by gender and management fishing zones. A total of 47 026 samples were collected between March 1982 and May 2004, with total length ranging from 19 to 154 cm. Age determinations, based on the reading of saggital otoliths, were between 1 and 14 years in males and between 1 and 16 years in females. Statistical differences in growth were found between the sexes and management fishing zones. For the combined sexes the vB growth parameters for the northern-austral zone (41°28 - 47°00'S) were: $l_{\infty} = 111.452$ cm, $k = 0.186$ year⁻¹, $a_0 = -0.912$ year; and for the southern-austral zone (47°00' - 57°00'S): $l_{\infty} = 123.447$ cm, $k = 0.147$ year⁻¹,

$a_0 = -1.779$ year.

A.2 Introduction

The species forming the genus *Genypterus* are benthic-demersal fishes inhabiting the continental shelf and slope in the southern hemisphere. Although five or six species are caught for commercial purposes, most are considered bycatch. The pink cusk-eel (*Genypterus blacodes*) is the most important in terms of catch amounts and target intentions, supporting important fisheries in Australia, New Zealand, Argentina and Chile. Knowledge about the ecological processes in this species is fragmentary at best, due to a lack of basic biological and fishery information. Nevertheless, it is still possible to characterize these individuals according to their average life-span, relative low fecundity and sedentary behaviour, in which the adults spend most of their time buried in the soft bottom sediments (Ward et al, 2001). According to the compiled logbooks, in Chilean waters the pink cusk-eel fishery is developed between Talcahuano (36°44'S) and south of Cabo de Hornos (57°00'S). Nevertheless, catches are mostly in the austral zone (41°28' - 57°00'S). Historically, the pink cusk-eel has been caught as an incidental species in the demersal multispecies fishery off southern Chile, where the fishing effort is mainly directed to southern hake (*Merluccius australis*). Catches are carried out by industrial vessels operating with bottom trawls and longlines as fishing gear. As of 1992 the pink cusk-eel fishery has been managed by total allowed catch (TAC) in the austral zone. These TACs have fluctuated around 5000 tonnes per year and are divided by two management fishing zones (MFZ): the northern-austral zone (41°28' - 47°00'S) and the southern-austral zone (47°00' - 57°00'S).

Although Chong and Aguayo (1990) reported preliminary results on growth parameters for *G. blacodes* in Chile, these parameters are questionable principally because

of the shorter temporal and spatial scales covered. For actual stock assessment framework the representative growth parameters throughout the years as well as the sex and MFZ are required (Wiff et al, 2005). By using the extensive data made available by the Instituto de Fomento Pesquero (IFOP), the principal aim of this manuscript was to estimate the von Bertalanffy (vB) growth parameters for sex and MFZ.

A.3 Materials and methods

The process included a total of 47 026 sagittal otoliths aged from March 1982 to May 2004. Total length (TL) of each fish was measured to the nearest centimetre. The samples came from two fleets and the two MFZs. Experienced readers determined the ages from the external surface whole otolith. To determine age the otoliths were remoistened in water at least 24 h before reading and their proximal surface polished. They were then immersed in water or oil on a black background and read with reflected light under a stereomicroscope at $10x$. An annulus or annual ring consisted of an opaque and translucent ring or band. The translucent rings were formed principally during the southern winter (April to September, Chong and Aguayo (1990)). For each MFZ and sex, a relationship between otolith radius (τ) and TL was described by back calculation using the Fraser-Lee method (Francis, 1990). Fitted back calculation equations for the northern-austral zone were: males $TL = 1.25\tau - 9.1$ ($r^2 = 0.65$); females $TL = 1.45\tau - 22.3$, ($r^2 = 0.74$). For the southern-austral zone: males $TL = 1.03\tau + 7.8$ ($r^2 = 0.48$); females $TL = 1.30\tau - 8.9$, ($r^2 = 0.60$). The VBGF was used to describe fish length as a function of age of pink cusk-eel corresponding to:

$$l(a) = l_{\infty} [1 - e^{-k(a-a_0)}] \quad (\text{A.1})$$

where $l(a)$ is the total length at age a ; l_{∞} is the asymptotic length; k is the growth

coefficient that determines how fast l approaches l_∞ and a_0 is the theoretical age for $l = 0$. These parameters were estimated by using the minimum squares method. The differences between vB growth parameters for MFZs and sex were assessed by the Hotelling test (Zar, 1984), under the null hypothesis of $H_0 : \Theta_1 = \Theta_2$ where Θ_1 y Θ_2 are particular vector parameters coming from the fitted models to n_1 and n_2 data sets.

A.4 Results

The fitted parameters are summarized in Table (A.4). In both MFZs, the oldest ages observed corresponded to 14 and 16 years for males and females respectively. At any given age, the individuals from the northern-austral zone were smaller and had higher growth rates than those from the southern-austral zone (Fig. A.1). In both MFZs, the females were larger and had smaller growth coefficients compared with males at the same age (Table A.4). By using the Hotelling test we determined that the differences between vB parameters were statistically significant ($P < 0.05$) between sexes in the same MFZ as well for the same sex between MFZs. Comparing length at a given age, an average difference of 4.6 cm of TL was found for combined sexes between MFZs. These differences show a decrease with age. At lower ages (1-3 years) we found greater differences (8.6-5.1 cm) followed by a stabilization difference of around 4 cm from ages 4-16.

	Northern-Austral Zone			Southern-Austral zone		
	Males (N=12311)	Females (N=7270)	Both sexes (N=19581)	Males (N=13154)	Females (N=14291)	Both sexes (N=27445)
l_{∞} (cm)	97.166 (0.249)	117.409 (0.392)	111.452 (0.273)	101.007 (0.260)	123.184 (0.292)	123.447 (0.287)
k ($year^{-1}$)	0.241 (0.002)	0.184 (0.002)	0.186 (0.001)	0.209 (0.002)	0.165 (0.001)	0.147 (0.001)
a_0 ($year$)	-0.844 (0.010)	-0.591 (0.011)	-0.912 (0.009)	-1.756 (0.016)	-1.248 (0.010)	-1.779 (0.010)
Oldest age recorded (years)	14 (N=1)	16 (N=1)		14 (N=2)	16 (N=4)	
Length range sampled (cm)	29-125	19-141		31-127	11-154	

N=number of otoliths read and used for fitting the model. Standard errors shown in brackets.

Table A.1: von Bertalanffy growth parameters fitted by management zones and sexes in pink cusk-eel, *Genypterus blacodes*.

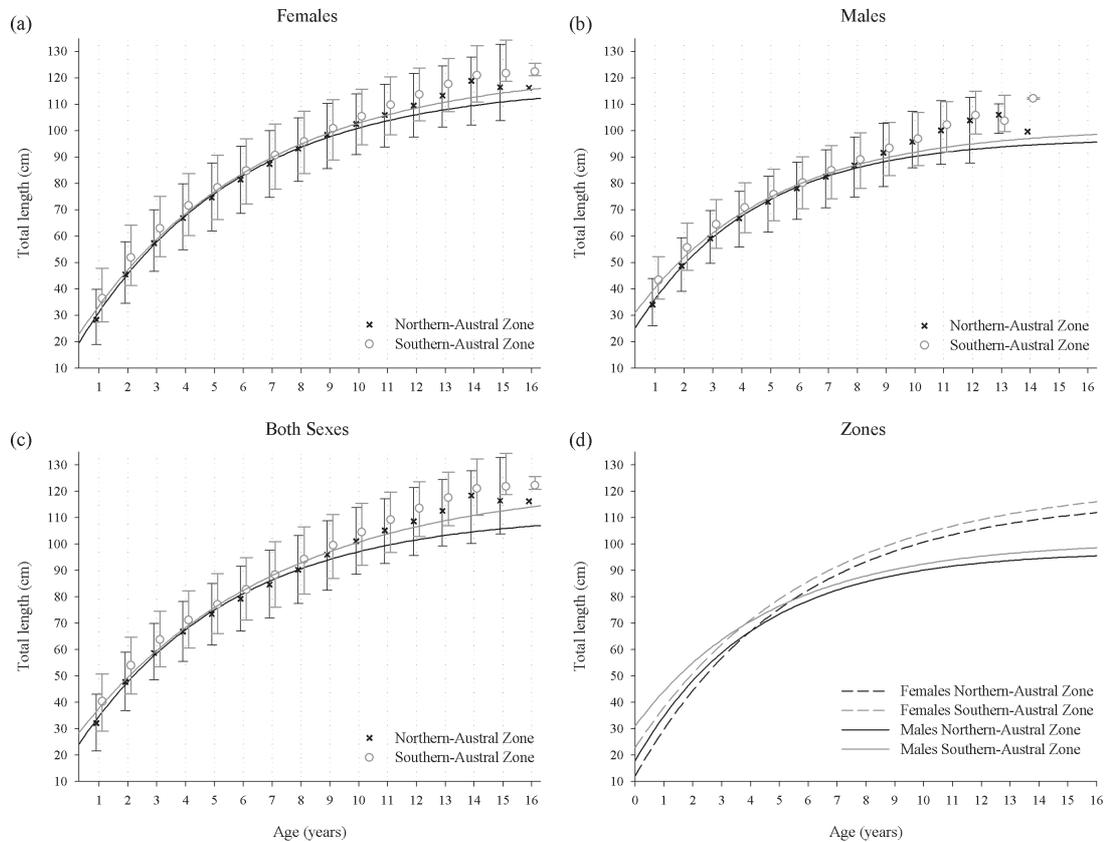


Figure A.1: von Bertalanffy curve fitted to pink cusk-eel, *Genypterus blacodes*, in Chilean austral zone. Continuous line = model fitted; vertical lines = 5-95% percentile of length-at-age; symbol = median length-at-age. (a) females; (b) males; (c) both sexes combined; (d) fitted curves by sexes and management zones.

A.5 Discussion

The differential growth by sexes is also demonstrated for *G. blacodes* off both Argentina (Renzi, 1986) and New Zealand (Horn, 1993). The asymptotic lengths and maximum ages estimated here were smaller than those reported for *G. blacodes* in Australia and New Zealand. In Australia the maximum age appearing routinely in the fishery is 21 years (Withell and Wankowski, 1989); in New Zealand it is 26 years

in males and 27 years for females (Horn, 1993). In Chilean waters for both MFZs, we found significant proportions of 3- to 4-year-old individuals vulnerable to trawling. Although the same ages are vulnerable in New Zealand waters (Horn, 1993), in Chile it appears likely that that full recruitment does not occur until about age 6 (Wiff et al, 2005), while in New Zealand the full recruitment is around 14 years old.

Significant differences were found between our parameter estimations and those estimated by Chong and Aguayo (1990), who used samples registered during 1984 and non-considering separation between MFZs. In fact, the asymptotic lengths for each sex found by Chong and Aguayo (1990) are higher (134.8 cm for females; 117.5 cm for males) and the growth coefficient slightly lower (0.141 year^{-1}) for females; (0.179 year^{-1} for males) in comparison with our estimated values. Over time, a decrease in size is often observed in heavily exploited species, which may be what is being observed in the pink cusk-eel fishery. Supporting this point, Wiff et al (2005) showed a decrease in average length through the years in the trawl fishery. Between 1982 and 2004 the average length decreased from 95 to 80 cm *TL* in the southern-austral zone and from 85 to 78 cm *TL* in the northern-austral zone. For the same fishing gear and period the proportion of catch (in weight) under the length at maturity increased between 1982 and 2004, from 0.1 to 0.45 in the southern-austral zone and from 0.2 to 0.5 in the northern-austral zone. These results give an idea of the high exploitation rates of the pink cusk-eel population off southern Chile.

Differences in growth rates of *Genypterus* species from adjacent areas have been demonstrated for fishes off South Africa (Payne, 1985) and New Zealand (Horn, 1993). Off the Chilean austral zone, Wiff et al (2005) estimated and compared by MFZs the population attributes such as average individual length, cohort dynamics, resilience and sex ratios. Wiff et al (2005) concluded that the population dynamics for these

MFZs exhibited extremely different patterns. Here we provide further evidence for this difference, showing that individual growth traits can vary by zones.

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