# Modelling production per unit of food consumed in fish populations 

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## H I G H L I G H T S

- We developed a general framework to estimate production-to-consumption ratio ( $p / Q$ ).
- This framework is based on the generalised von Bertalanffy growth function.
- This modelling framework relates $p / Q$ directly to population length or age-structure.
- Models proposed were assessed using simulated populations.
- Models proposed were applied to three harvested fish populations.


## A R T I C L E I N F O

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#### Abstract

The ratio of production-to-consumption $(\rho)$ reflects how efficiently a population can transform ingested food into biomass. Usually this ratio is estimated by separately integrating cohort per-recruit production and consumption per unit of biomass. Estimates of $\rho$ from cohort analysis differ from those that consider the whole population, because fish populations are usually composed of cohorts that differ in their relative abundance. Cohort models for $\rho$ also assume a stable age-structure and a constant population size (stationary condition). This may preclude their application to harvested populations, in which variations in fishing mortality and recruitment will affect age-structure. In this paper, we propose a different framework for estimating $(\rho)$ in which production and consumption are modelled simultaneously to produce a population estimator of $\rho$. Food consumption is inferred from the physiological concepts underpinning the generalised von Bertalanffy growth function (VBGF). This general framework allows the effects of different age-structures to be explored, with a stationary population as a special case. Three models with different complexities, depending mostly on what assumptions are made about age-structure, are explored. The full data model requires knowledge about food assimilation efficiency, parameters of the VBGF and the relative proportion of individuals at age $a$ at time $y\left(P_{y}(a)\right)$. A simpler model, which requires less data, is based on the stationary assumption. Model results are compared with estimates from cohort models for $\rho$ using simulated fish populations of different lifespans. The models proposed here were also applied to three fish populations that are targets of commercial fisheries in the south-east Pacific. Uncertainty in the estimation of $\rho$ was evaluated using a resampling approach. Simulation showed that cohort and population models produce different estimates for $\rho$ and those differences depend on lifespan, fishing mortality and recruitment variations. Results from the three case studies show that the population model gives similar estimates to those reported by empirical models in other fish species. This modelling framework allows $\rho$ to be related directly to population length- or agestructure and thus has the potential to improve the biological realism of both population and ecosystem models.


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## 1. Introduction

The ratio between biomass production and food consumption (hereafter designated $\rho$ ) is an important parameter in ecosystem modelling because it reflects how efficiently a population can transform ingested food into biomass. This ratio is usually estimated by computing production $(p)$ and consumption $(Q)$ to biomass ( $B$ ) ratio separately, in a cohort per-recruit analysis. In addition, production and consumption to biomass ratio are difficult to estimate accurately in fish populations, because they require knowledge about individual growth rate, the number of individuals at different ages in the population and the amount of food ingested by individuals in these age classes. In a different approach, $\rho$ is computed by estimating the efficiency with which a number of different individuals convert ingested food into body tissue and using the average of these values as an unbiased estimate for the whole population (e.g., Tang and Guo, 2007).

Pauly (1986) proposed a model for the estimation of $\rho$ in which food consumption is modelled in a cohort per-recruit analysis. Pauly's model relies on the assumption of stable age-structure and constant size (stationary condition) and the parameters defining individual consumption have no clear biological meaning. Aydin (2004) extended Pauly's model to incorporate biological parameters which describe consumption but this model still relies on the assumption of stationary conditions. The cohort analysis framework used in Pauly (1986) and Aydin (2004) has three main drawbacks for estimating $\rho$ in fish populations. First, an analytical solution is only achieved when a specialised von Bertalanffy growth function (VBGF) is used. Von Bertalanffy's principle states that an individual's growth is determined by the difference between anabolism and catabolism (von Bertalanffy, 1938). When the scaling parameter for anabolism is set to $d=2 / 3$, the specialised VBGF is achieved. However, Essington et al. (2001) concluded that $d=2 / 3$ is unusual for teleost fishes, suggesting the generalised VBGF (in which $d$ may takes values other than $2 / 3$ ) provides a better representation of fish growth. Second, the assumption of stationary condition may not be useful for harvested populations because fishing exploitation often produces inter-annual variations on age-specific mortality and recruitment (Hidalgo et al., 2014). Third, and most important, several authors have indicated that cohort and populations models of the production-to-biomass ratio $(p / B)$ estimate different quantities (see France, 2011). Models for $\rho$ proposed in Pauly (1986) and Aydin (2004) are based on Allen's integrated $p / B$ models (Allen, 1971), which provides a biased estimator of population $p / B$, as demonstrated in Van Straalen (1985). Thus, cohort estimators for $\rho$ do not represent population $\rho$ (France, 2011). These limitations indicate that alternative approaches need to be explored.

In this paper, we propose a general framework for estimating $\rho$ in fish populations in which $p$ and $Q$ are modelled simultaneously, and individuals grow according to the generalised VBGF. Although there are few models to describe animal growth, the generalised VBGF is particularly convenient for modelling $\rho$ because it is the standard formula for describing growth in fish (Pardo et al., 2013), the parameter $d$ can takes values other than $2 / 3$ and consumption rates can be inferred from first principles (Wiff and Roa-Ureta, 2008). This modelling framework also allows the exploration of the effect of variability in age-structures, so that the stationary population assumption could be treated as a particular case of the
general theory. Exploring the effects of variation in age-structure result in an estimator for $\rho$ that is more suitable for harvested fish populations. The framework proposed here allows a population value of $\rho$ be estimated, whereas published models only provide a cohort-specific estimator for $\rho$. It also allowed us to explore the use of different models that take account of the available data. Here we explore three situations: the full data model, which requires population attributes usually available from an integrated stock assessment model; partial data model, which does not require all of the outputs from an integrated stock assessment, but does require knowledge of age-specific mortality rate; and a model that assumes a stable age-structure and only requires knowledge of basic life history parameters.

## 2. Theory

We develop the theory by modelling the processes that determine $\rho$ at three different levels of complexity. First, we define the instantaneous $\rho$ of a cohort in one point in time. Then, we analyse the processes occurring at the individuals level and how consumption can be inferred from an individual's growth using the generalised VBGF. Finally, we incorporate population processes to provide a population estimator for $\rho$.

## 2.1. $\rho$ for a cohort

By definition, production ( $p$ ) of a cohort of age $a$ can be expressed as $p(w)=(N(w)) d w / d a$, where $N(w)$ is the number of individuals with body weight $w$. In cohort analysis, age and body weight are considered continuous variables. According to Pauly (1986) $Q$ for this cohort can be represented by $Q(w)=(N(w) / K(w)) d w / d a$, where $K(w)$ is the individual production-to-consumption ratio, known as gross food conversion efficiency (Pauly, 1986). Thus, if a cohort is composed by identical individuals in terms of grow parameters and gross efficiency and recruitment occurs at one point in time, $\rho$ is the same for all individual in the cohort:
$\rho(w)=\frac{p(w)}{Q(w)}=K(w)$.
This equation represents $\rho$ for a cohort at a particular body weight during its lifespan. Note that if individuals have the same growth rate and they are all recruited at the same point in time, the value of $\rho$ for the cohort is the same as the value of $\rho$ for an individual. Therefore, a model for $\rho$ 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 the multiple cohorts present in the population at a particular point in time.

In the next section we explore a functional forms for $K(w)$, and then we extend the cohort estimate of $\rho$ to incorporate population structure. The incorporation of population structure will allow us to relax the assumption regarding individuals and recruitment attributes.

## 2.2. $\rho$ of an individual

The individual production-to-consumption ratio, also known as gross food conversion efficiency $(K)$ is the growth increment in body weight per unit of food consumed. Temming (1994a)

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