



Modelling production per unit of food consumed in fish populations



Rodrigo Wiff^{a,*}, Mauricio A. Barrientos^b, Andrés C. Milessi^{c,d}, J.C. Quiroz^{e,f},
John Harwood^a

^a Centre for Research into Ecological and Environmental Modelling, School of Mathematics and Statistics, University of St. Andrews, The Observatory, Buchanan Gardens, St. Andrews KY16 9LZ, Scotland, UK

^b Instituto de Matemáticas, Pontificia Universidad Católica de Valparaíso, Blanco Viel 596, Cerro Barón, Valparaíso, Chile

^c Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo No. 1, 7600 Mar del Plata, Argentina

^d Comisión de Investigaciones Científicas de la Provincia de Bs.As (CIC), Calle 526, 1900, La Plata, Buenos Aires, Argentina

^e Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001, Australia

^f División de Investigación Pesquera, Instituto de Fomento Pesquero (IFOP), Blanco 839, Valparaíso, Chile

HIGHLIGHTS

- 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.

ARTICLE INFO

Article history:

Received 5 May 2014

Received in revised form

30 September 2014

Accepted 3 October 2014

Available online 18 October 2014

Keywords:

Consumption

Von Bertalanffy growth function

Population energetics

ABSTRACT

The ratio of production-to-consumption (ρ) 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 ρ 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 ρ 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 (ρ) in which production and consumption are modelled simultaneously to produce a population estimator of ρ . 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 ($P_y(a)$). A simpler model, which requires less data, is based on the stationary assumption. Model results are compared with estimates from cohort models for ρ 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 ρ was evaluated using a resampling approach. Simulation showed that cohort and population models produce different estimates for ρ 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 ρ to be related directly to population length- or age-structure and thus has the potential to improve the biological realism of both population and ecosystem models.

* Corresponding author. Tel.: +56979894828; fax: +56412225400.

E-mail addresses: rodrigo.wiff@gmail.com, rowiff@udec.cl (R. Wiff).

¹ Current address: COPAS Sur-Austral, Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile. Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Av. Alameda 340, Santiago, Chile.

1. Introduction

The ratio between biomass production and food consumption (hereafter designated ρ) 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, ρ 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 ρ 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 ρ 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 take 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 ρ 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 ρ do not represent population ρ (France, 2011). These limitations indicate that alternative approaches need to be explored.

In this paper, we propose a general framework for estimating ρ 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 ρ because it is the standard formula for describing growth in fish (Pardo et al., 2013), the parameter d can take 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 ρ that is more suitable for harvested fish populations. The framework proposed here allows a population value of ρ be estimated, whereas published models only provide a cohort-specific estimator for ρ . 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 ρ at three different levels of complexity. First, we define the instantaneous ρ 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 ρ .

2.1. ρ for a cohort

By definition, production (p) of a cohort of age a can be expressed as $p(w) = (N(w))dw/da$, 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 $Q(w) = (N(w)/K(w))dw/da$, 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 growth parameters and gross efficiency and recruitment occurs at one point in time, ρ is the same for all individual in the cohort:

$$\rho(w) = \frac{p(w)}{Q(w)} = K(w). \quad (1)$$

This equation represents ρ 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 ρ for the cohort is the same as the value of ρ for an individual. 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 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 ρ to incorporate population structure. The incorporation of population structure will allow us to relax the assumption regarding individuals and recruitment attributes.

2.2. ρ 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)

proposed a model for K based on the theoretical concepts underpinning the generalised VBGF. He indicates that the individual consumption rate (q) is directly proportional to the anabolism (energy assimilation):

$$q = \frac{1}{A} \times \text{anabolism}, \tag{2}$$

where A is a parameter defining the fraction of ingested food that is available for the build up of body substance. [Temming \(1994a\)](#) pointed out that anabolism can be taken from the general VBGF such $dw/da = Hw(a)^d - cw(a)$, in which $cw(a)$ reflects catabolism (energy losses) and $Hw(a)^d$ is the anabolism term, d determines the allometric scaling of consumption. H and c are positive proportionality constants for anabolism and catabolism, respectively.

In Temming's formulation, K is expressed as the growth rate divided by consumption rate, both defined as instantaneous quantities in a continuous space, and the growth and consumption rates are taken from the general VBGF thus:

$$K(w) = \frac{\text{growth}}{\text{consumption}} = \frac{dw/da}{q} = \frac{Hw^d - cw}{\frac{1}{A}Hw^d}. \tag{3}$$

According to [Temming \(1994b\)](#), H can be recast in terms of the generalised VBGF as $H = k/[1 - d)w_\infty^{(d-1)}]$. Thus, anabolism term can be expressed by $\text{anabolism} = \beta k w_\infty^{1-d} w^d$ with $k = c/\beta$, where β is a parameter from the length-at-weight relationship and w_∞ is the asymptotic weight. Under these definitions, Temming's models is given by

$$K(w) = A \left[1 - \left(\frac{w}{w_\infty} \right)^{1-d} \right]. \tag{4}$$

Here, all parameters have a clear biological interpretation, A and d can be estimated from a variety of sources of information, such as nitrogen absorption ([Pandian and Marian, 1985](#)) and from experimental measurements of daily ration and growth rate ([Cubillos et al., 2003](#)).

If weight is a deterministic function of length, Eq. (4) 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. Eq. (4) can be parameterised in terms of body length as

$$K(l) = A \left[1 - \left(\frac{l}{l_\infty} \right)^\psi \right], \tag{5}$$

where $\psi = \beta(1 - d)$.

2.3. ρ for a population

From Eq. (1) 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 structure. We can deal with this as follows: let t^* be a particular point in time t , then l_{t^*} is 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

$$\begin{aligned} \rho_y(l) &= \int_l K(l) f_y(l) dl = \int_l A \left[1 - \left(\frac{l}{l_\infty} \right)^\psi \right] f_y(l) dl \\ &= \int_l A f_y(l) dl - \int_l \frac{A}{l_\infty^\psi} l^\psi f_y(l) dl \\ &= A \left[1 - \frac{E_{f_y}(l^\psi)}{l_\infty^\psi} \right], \end{aligned} \tag{6}$$

where l is the length and l_∞ is the asymptotic length. Also, E is the expectation operator defined in general as $E[g(x)] = \int_{-\infty}^{\infty} g(x) f(x) dx$ which represent the expected value of an arbitrary function of x , $g(x)$, with respect to the pdf $f(x)$.

It is apparent that the estimation of ρ_y now hinges on the estimation of the expected value of l^ψ . To implement the model of Eq. (6), it is necessary to have estimates of l_∞ , A , ψ and the expected function of body length ($E_{f_y}(l^\psi)$) in the population in year y .

There is more than one way of estimating ρ_y . The choice depends on what data are available to estimate $E_{f_y}(l^\psi)$. When ψ is known and a exact lengths of sampled fish are available where all fish are equally likely to be sampled, an unbiased estimate of $E_{f_y}(l^\psi)$ can be obtained from the mean l^ψ in a sample of size n . However, most fisheries use gear that is selective and thus, the sampled lengths are likely to be size-biased. Those cases are explored in the next sections.

3. Calculation

3.1. Full data model

$E_{f_y}(l^\psi)$ can be modelled by using the probability density function (pdf) of lengths $f_y(l)$ in the population at time t^* in the year y . Suppose we have some suitable functional form $f_y(l)$ for this pdf, then $E_{f_y}(l^\psi)$ can be estimated by

$$E_{f_y}(l^\psi) = \int_l l^\psi f_y(l) dl, \tag{7}$$

where $f_y(l)$ is an estimator of the marginal distribution of l in the population. If parameters for the general VBGF are known and an estimation of $f_y(l)$ is available, for example, from a length-based stock assessment model, ρ_y can be estimated by replacing Eq. (7) onto Eq. (6). In other cases, such in age-structured stock assessment models, it is useful to write $f_y(l)$ in terms of the probability mass function of age a ($P_y(a)$) as follows:

$$f_y(l) = \sum_a P_y(a) P_y(l|a), \tag{8}$$

where $P_y(l|a)$ is the pdf of a function of length l given age a in the population of fish in the year y . Note we assume that a population at time t^* is composed of cohorts of discrete ages but continuous body length. $P_y(a)$ is 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 the mortality rate experienced by a cohort up to the moment of observation. Accordingly, the expected function of length in the population is defined by

$$E_{f_y}(l^\psi) = \int_l l^\psi \sum_a P_y(a) P_y(l|a) dl = \sum_a P_y(a) E[l(a)^\psi]. \tag{9}$$

Then, $P_y(a)$ can be obtained from population models output and $E[l(a)^\psi]$ can be modelled from the growth parameters by assuming that a population is a mixture of overlapping cohorts each one represented by a Gaussian distribution of the length-at-age ([Roa-Ureta, 2010](#)). Therefore, if $P_y(l|a)$ is normally distributed, then the expected length at age can be described by the general VBGF as $E[l(a)^\psi] = l_\infty^\psi (1 - e^{-\psi k(a - t_0)})$, where t_0 is the theoretical age at length 0 and k is the growth coefficient. Thus, $E_{f_y}(l^\psi)$ is defined by

$$E_{f_y}(l^\psi) = l_\infty^\psi \sum_a (1 - e^{-\psi k(a - t_0)}) P_y(a). \tag{10}$$

Thus, a full data model to estimate ρ_y in a population can be written by combining Eqs. (6) and (10) as follows:

$$\rho_y(a) = A \left[1 - \sum_a (1 - e^{-\psi k(a - t_0)}) P_y(a) \right]. \tag{11}$$

Note that model in Eq. (11) can be implemented if the von

Bertalanffy parameters and $P_y(a)$ are known. The later can be available from a age-structured stock assessment model outputs.

3.2. Partial data model

Here we will model an intermediate situation in which we do not need knowledge of $P_y(a)$ from a integrated stock assessment, but we do need some knowledge of the way in which age-specific fishing mortality varies across time. Partial data model presented here relies on the assumption that recruitment is constant across years and thus $P_y(a)$ can be estimated by only using a total mortality matrix across ages and years. $P_y(a)$ is the relative abundance of each cohort and it is defined by $P_y(a) = N_y(a) / \sum_a N_y(a)$ being $N_y(a)$ the abundance of age a at the time y . $N_y(a)$ can be modelled by a decay exponential function such as $N_y(a) = N_{y-1}(a-1)e^{-Z_{y-1}(a-1)}$, where the first age ($N_y(a=1)$) is defined by the recruitment (R) such as $N(a=1) = R_y$. Here Z represents the total mortality rate and can be defined by $Z_y(a) = M + F_y s(a)$, where M is the natural mortality rate, F is the fishing mortality rate of the full recruited ages and s is a function of the selectivity at age. Considering these simplifying assumption, ρ_y for partial data yield

$$\rho_y(a) = A \left[1 - \sum_a (1 - e^{-\psi k(a-t_0)}) P_y(a) \right], \quad (12)$$

with

$$P_y(a) = \begin{cases} \frac{e^{-S_1(a-1)}}{\sum_{a=1}^y e^{-S_1(a-1)} + \sum_{a=y+1}^n e^{-[S_2(a-y) + S_1(a-y+1)]}} & a \leq y, \\ \frac{e^{-[S_2(a-y) + S_1(a-y+1)]}}{\sum_{a=1}^y e^{-S_1(a-1)} + \sum_{a=y+1}^n e^{-[S_2(a-y) + S_1(a-y+1)]}} & a > y, \end{cases} \quad (13)$$

where $S_i : \mathbb{N} \rightarrow \mathbb{R}$; $i = 1, 2$ are functions defined as

$$S_1(n) = \sum_{j=1}^n Z_{y-j}(a-j) \quad (14)$$

and,

$$S_2(n) = \sum_{j=1}^n Z_1(j). \quad (15)$$

The values of $Z_{y-j}(a-j)$ where $j \leq y$ were considered as zero. From the equation above, it can be seen that when we observed less ages than years (complete cohorts, $a \leq y$), $P_y(a)$ is easily computed as the accumulation of mortality up to age a . When dealing with uncompleted cohorts ($a > y$), the estimation of $P_y(a)$ is more complicated because we must assume that age-specific fishing mortality has remained constant during the period of exploitation that have led to the available $P_y(a)$ matrix. The $P_y(a)$ matrix can be constructed in different ways, and thus further simplified assumptions on $P_y(a)$ can be explored. For example, the way in which natural mortality rate may vary between years is poorly known, and therefore it is often assumed to be constant across time. In addition, a functional form for $s(a)$ is usually unknown in data-poor situations. Nevertheless we may have a roughly idea about the age, say a_r , at which fish became fully available for the fishing gear. If a_r is known, a useful way to model selectivity is with a knife-edge function, that assumes that all age groups above a_r experience the same fishing mortality rate. In those cases $Z_y(a) = M$ for $a < a_r$ while for all other ages $Z_y(a) = M + F_y$. Incorporating these assumptions simplifies $P_y(a)$ in Eq. (12).

3.3. Stationary model

Our main purpose here is to provide an estimator for ρ which is comparable, to the cohort estimate of ρ in Aydin (2004). A population model for ρ , assuming stationary condition, can provide the simpler estimator for ρ in data poor-situations. In a stationary population, the age-structure is stable and proportional to the survival function (Van Straalen, 1985). Thus, $P_y(a) = e^{-Ma} / \sum_a e^{-Ma}$. Note the model assuming stable age-structure does not allow the inclusion of fishing mortality. In harvested populations, fishing mortality is likely to vary over time producing changes in the age-structure.

To compute a more tractable analytical model, we tackled the partial data model of Eq. (12) with stable age-structure and we replaced the sum with an integral as follows:

$$\rho(a) = A e^{\psi k t_0} \int_0^{a_\infty} \frac{e^{-a(M+\psi k)}}{\int_0^{a_\infty} e^{-Ma} da} da. \quad (16)$$

This equation represents the gross efficiency for the population in year y for all individuals from recruits (age 0) to those in the terminal age (a_∞). Here, age 0 is taken to be the onset of feeding in the larval stage, which is the point at which tissue growth commences.

Now, by direct integration we have

$$\int_0^{a_\infty} e^{-Ma} da = \frac{1}{M} [1 - e^{-a_\infty M}] \quad (17)$$

and,

$$\int_0^{a_\infty} e^{-a(M+\psi k)} da = \frac{1}{M+\psi k} [1 - e^{-a_\infty(M+\psi k)}]. \quad (18)$$

Then, replacing Eqs. (17) and (18) on Eq. (16), we obtain

$$\rho = \frac{A e^{\psi k t_0} M [1 - e^{-a_\infty(M+\psi k)}]}{M+\psi k [1 - e^{-a_\infty M}]} \quad (19)$$

The simpler model for estimating ρ in Eq. (19) can be implemented if we have knowledge about the assimilation parameter A , parameters of the VBGF and the natural mortality.

4. Simulations

In this section we evaluate the differences, in terms of deviation, between ρ_y estimates from the three models presented above (full data, partial data and stationary models) and the model proposed by Aydin (2004):

$$\rho_{Aydin} = [3k w_\infty] \times \left[\frac{e^{k t_0}}{Z_y + k} - \frac{2(e^{2k t_0})}{Z_y + 2k} + \frac{e^{3k t_0}}{Z_y + 3k} \right] + w_0 \times \left[\frac{3k w_\infty}{A} \right]^{-1} \times \left[\frac{1}{Z_y} - \frac{2(e^{k t_0})}{Z_y + k} + \frac{e^{2k t_0}}{Z_y + 2k} \right]^{-1}, \quad (20)$$

where Z_y is total mortality in the year y and the other parameters are already defined. Note that the underlying assumption of Aydin's model is that $\psi = 1$, there is constant recruitment and total mortality Z_y affects all ages from 0+ equally.

Five populations representing fishes of different life histories were simulated to evaluate the differences between the three models presented, and model in Eq. (20). Firstly, five populations with lifespans of 5, 10, 15, 20 and 25 years (a_∞) were generated. Afterwards, the natural mortality rate (M) in each population was calculated as function of a_∞ by $M = 4.22/a_\infty$ (Hewitt and Hoenig, 2005). Growth coefficient, k was calculated as $k = (2/3)M$ (Charnov, 1993). t_0 was assumed to be proportional to the lifespan so that $t_0 = -0.05 a_\infty$. Likewise, we assumed a knife-edge selectivity (s) proportional to the lifespan so that $s = a_\infty/3$. This resulted in a fixed fishing mortality rate for all age groups above s .

Each population was subjected to a fishing mortality (F) between 0 and 1.1 (year^{-1}). In order to match the life history assumptions of our model with that of Aydin, we set $\psi = 1$ for all individuals from age 0.

The full data model described in Eq. (11) considers variability in the relative recruits over time. Thus, to evaluate the differences between this model and Aydin’s model, we simulated variable recruitment over a 25 year period for the five populations described above, by resampling from a uniform random distribution in the range [0.8–1.2]. The time span we chose ensured the observation of at least one cohort in the oldest population simulated. For each year and population, fishing mortality was set equal to natural mortality (i.e. $F_y = M$) in order to evaluate model performance for a fully exploited population (Pauly, 1996).

In a second simulation, we compared the performance of the partial data model (Eq. (12)) and Aydin’s model. In this case, the simulated populations described above were assessed across different fishing mortalities. However, recruitment was kept constant, to match the assumption of the partial data model. Thus, it was not necessary to evaluate the model performance using time series. Instead, each simulated population was assessed at different fishing mortalities.

A third simulation was used to compare the performance of the stationary model in Eq. (19) with Aydin’s model. In the case of Aydin’s model, only natural mortality was considered in order to match the assumptions of our model of a stationary population.

The relative deviation between our models and Aydin’s model was computed as follows:

$$\text{deviation} = \frac{\rho_y - \rho_{\text{aydin}}}{\rho_y} \tag{21}$$

ρ_y represents the full, partial or stationary model, Eqs. (11), (12) and (19). ρ_{aydin} is the model in Eq. (20).

Fig. 1 shows the results of the first set of simulations, in which we compared the full data model and Aydin’s model. The effects of variation in recruitment on the estimates of ρ_y depends on the lifespan of the populations being modelled. In a population with a lifespan of 5 years, the relative deviation between models fluctuated around 0, and these fluctuation followed a similar pattern to that of recruitment time series. In populations with a lifespan between 10 and 25 years, the relative deviation centre around 0.1, indicating that estimates from the full data model are around 10% higher than those from Aydin’s model. In addition, the variation in deviation depended on the lifespan of the population being modelled. Populations with longer lifespan showed smoother variations across time with recruitment than those with a shorter lifespan. This is probably related to buffering effect that the number of age classes has on the effects of variations in fishing mortality and recruitment.

Results for the second set of simulations are show in Fig. 2. Here we note that the deviation between the estimates from the partial data model and Aydin’s model decreases with fishing mortality across all simulated populations. At the point of full exploitation (marked with dots in Fig. 2) all populations presented positive deviations of around 0.1, similar to those observed in Fig. 1. Relative deviation decreased faster in populations with longer lifespans, and it became negative after a fishing mortality of 0.3 (year^{-1}) in the older population simulated.

Fig. 3 shows the deviation between the stationary model and Aydin’s model. It was around 0.37 across all populations, coinciding with the deviation at $F=0$ in Fig. 2. Thus, the stationary model predicts values of ρ 37% higher to those computed with Aydin’s model if the population has constant recruitment and stable age-structure is only affected by natural mortality. Because both models rely on the same population dynamic assumptions, this value can be seen as the intrinsic deviation between the method

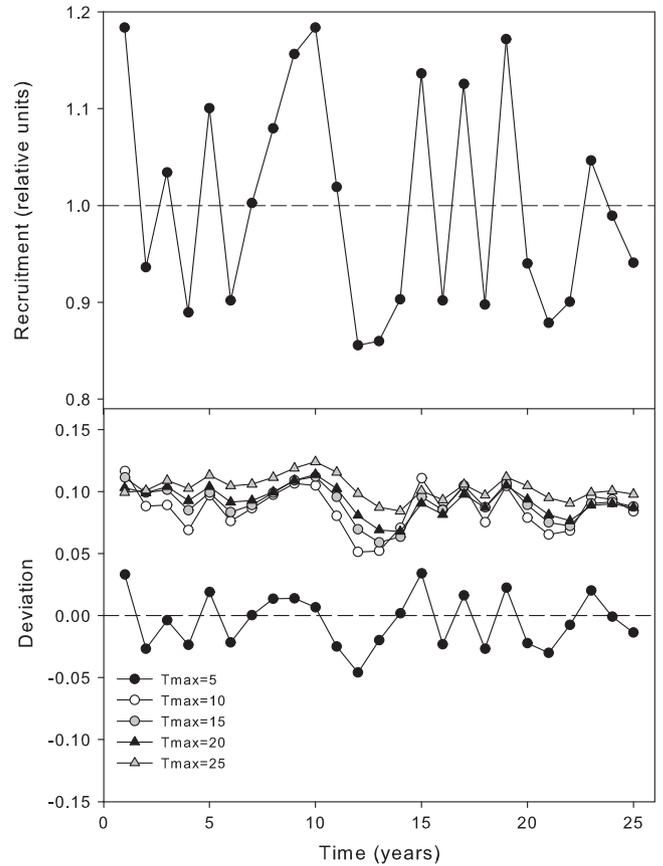


Fig. 1. Simulated recruitment variability and the deviation between full data model (Eq. (11)) and Aydin’s model for populations of different maximum ages (T_{max}).

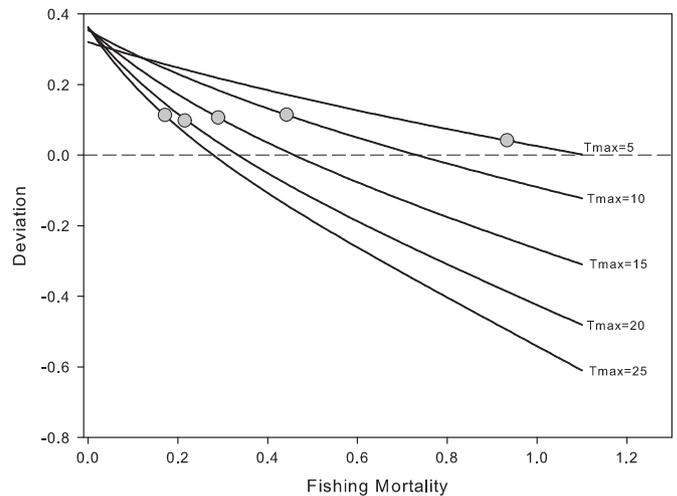


Fig. 2. Simulated deviation between partial data model (Eq. (12)) and Aydin’s model across fishing mortality and maximum ages (T_{max}). Grey dots represent when fishing mortality equals natural mortality ($F=M$).

proposed and Aydin’s model. This difference is a result of the fact that the models estimate different quantities. Our model estimates ρ_y for the population, whereas Aydin’s model computes ρ_y for a cohort.

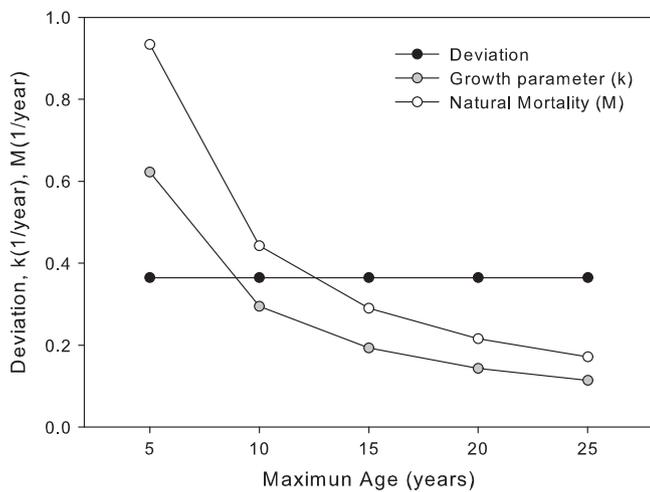


Fig. 3. Simulated deviation between the stationary model (Eq. (19)) and Aydin's model (with $F=0$), growth parameter (k) and natural mortality (M) across populations of different maximum ages (T_{max}).

5. Applications

To illustrate the model, we use the available data for the life history parameters and integrated stock assessment for two species fished in the Chilean austral zone. The species considered were pink cusk-eel (*Genypterus blacodes*) and southern hake (*Merluccius australis*). These species are intensely exploited by a multispecies demersal fishery consisting of industrial vessels operating trawls and longlines. Available data consisted in proportion of abundance at age ($P_y(a)$), fishing mortality (F_y) and recruitment time series between 1978 and 2004. Those estimates come from a statistical catch-at-age stock assessment models from the stock assessment program carried out by the Instituto de Fomento Pesquero (IFOP-Chile). In order to compare the estimates of the three models presented here with those from Aydin's model, we used estimated of abundance from 0 to 14 years in case of pink cusk-eel (both populations) and from 0 to 24 years in case of southern hake. Details of the stock assessment of these species this can be found in Wiff et al. (2006) and Quiroz et al. (2007). The VBGF parameters $\{\hat{k}, \hat{t}_0\}$ for southern hake were taking from Ojeda and Aguayo (1986) and these parameters for pink cusk-eel from Wiff et al. (2007). A of 0.72 and 0.59 for pink cusk-eel and southern hake, respectively, were estimated from daily ration using information provided by Pool et al. (1997). ψ was estimated considering $\beta=3$ and for cases were $d=2/3$ and $d=3/4$. Using the described information, ρ was computed using the full data model (Eq. (11)), the partial data model (Eq. (12)) and stationary model (Eq. (19)) assuming natural mortality reported in each the stock assessment. All the comparison with Aydin's model were done assuming the specialised VBGF and β of the length-at-weight relationship equal to 3 (thus, $\psi=1$). We accounted for uncertainty in ρ_y by resampling $\{\hat{k}, \hat{t}_0\}$ from a bivariate normal distribution. Due to a lack of available information on the variance of the parameter A , we assumed it to have no error. Variability in from $\hat{P}_y(a)$ and \hat{Z}_y was taken from the stock assessment outputs. Ninety-five percent confidence intervals (CI) were obtained by the percentile method (Efron and Tibshirani, 1993) based on 5000 iterations.

Fig. 4 shows point estimates of ρ from the application of the full data model (Eq. (11)), the partial data model (Eq. (12)), the stationary model (Eq. (19)) and Aydin's model (Eq. (20)). Average estimates of ρ from the three case studies were similar to the populations assessed. Across these three models, the average value of $\rho=0.37$ for the pink cusk-eel north population and $\rho=0.35$ in

the pink cusk-eel south population. Likewise, an average $\rho=0.39$ was estimated across the three models for southern hake. Estimates from Aydin's model gives higher estimates in all three populations and for most of the year analysed, these estimates were also more variable across time as a result of variations in fishing mortality.

In Fig. 5 we present estimates from the full, partial and stationary models with their 95% confidence intervals made using values of the anabolism parameter defining the specialised VBGF $d=2/3$ and the alternative $d=3/4$ (the value of the general scaling for metabolism (Brown et al., 2004)). In the three populations assessed here and across models, we found that increasing d resulted in a higher value of ρ_y but did not change its behaviour across time. The full data model provided a good representation of the changes in ρ across time according to the changes in recruitment and fishing mortality. The inter-annual variations in ρ estimates provided by the partial data model are smoother than those from the full data model because of the assumption of constant recruitment. Estimates of ρ from the stationary model are constant across time and do not capture the effects of inter-annual variations in recruitment and fishing mortality. Uncertainty in the stationary model is only dependent on the life history parameters, and uncertainty in these parameters for the pink cusk-eel populations is very narrow (Wiff et al., 2007).

6. Discussion

Aydin (2004) improved the model presented by Pauly (1986) by allowing all parameters related to food consumption to be interpreted in biological terms. The models we propose here, rely on a similar assumption to that used by Aydin (2004): consumption is inferred from the principles underpinning the VBGF. However, Aydin (2004) followed Allen (1971) in integrating cohort per-recruit production (p) and consumption (Q) to biomass (B) ratio, considering both Q/B and p/B as longitudinal estimates (estimators of observations of a given unit made over time). Here, we assume that estimates of ρ are cross-sectional (estimators of observations of many individuals at a given point in time). Longitudinal models such as those used by Pauly (1986) and Aydin (2004) are only likely to be realistic in the context of cohort models using stable age-structure. In these models, alternative hypotheses for age-structure can only be explored when difficult-to-obtain quantities, such as the number of recruits per year and/or a stock-recruitment relationship, are available. In addition, analytical solutions to longitudinal models can only be obtained if a specialised form of the VBGF is used. We modelled production and consumption simultaneously, and this enable us to compute an instantaneous estimator for ρ . This allow us to propose a general model for population ρ based on the generalised VBGF. This framework also allowed us to relax the assumption of cohort per-recruit analysis and stable age-structure, and to establish an explicit connections between ρ and body size. This allowed us to explore the implications of the value of ρ in harvested populations.

Although the formulation of our estimator of ρ using the stationary model (Eq. (19)) is similar to that of Aydin (2004), the two models actually estimate different quantities. Aydin's estimator represents the ρ of a cohort during its entirely lifespan whereas our estimator represents ρ for the entire population at one point in time. Models for ρ 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), because a population is usually composed of several cohorts of different relative abundance. Several authors (e.g. France, 2011) have suggested that the whole idea of cohort values should be abandoned when population estimators are

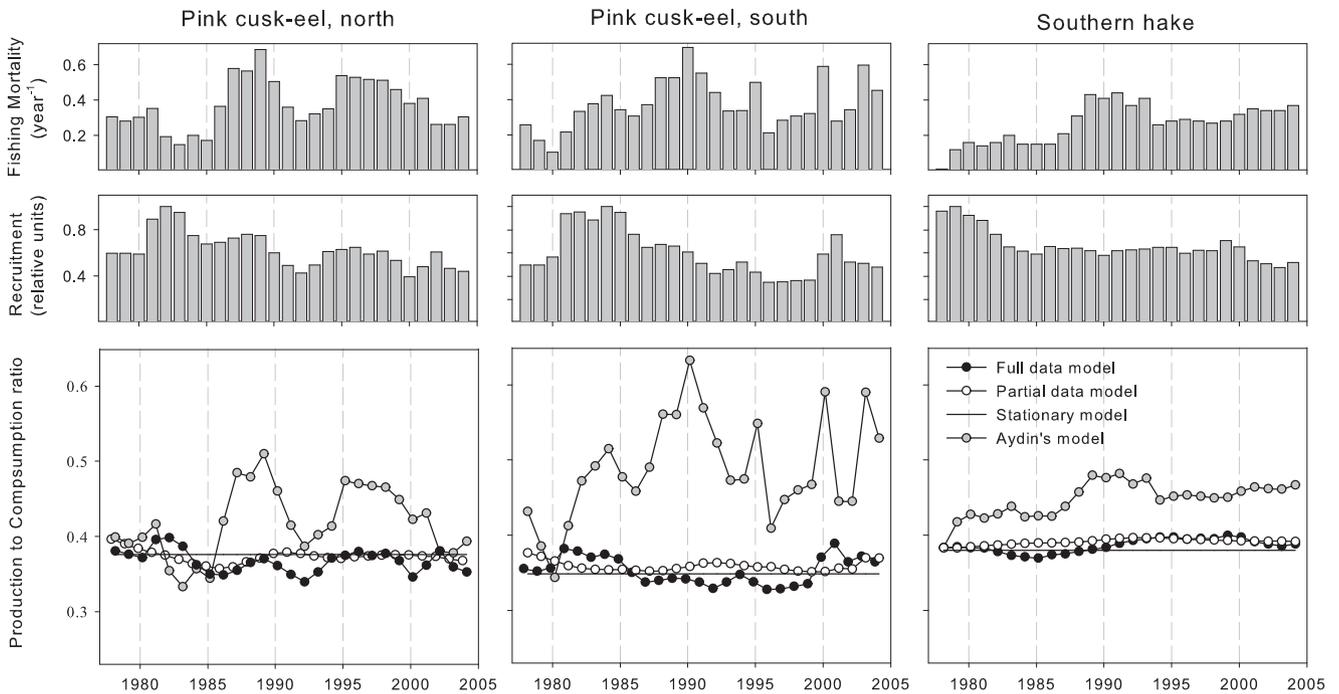


Fig. 4. Estimates of production per unit of food consumed (ρ), fishing mortality and recruitment in three fish populations of Southern Chile. Estimates of ρ from the full data model (Eq. (11)), partial data model (Eq. (12)) and stationary model (Eq. (19)) were compared with estimates from Aydin's model. (a) Pink cusk-eel, northern population, (b) Pink cusk-eel, southern population, (c) Southern hake.

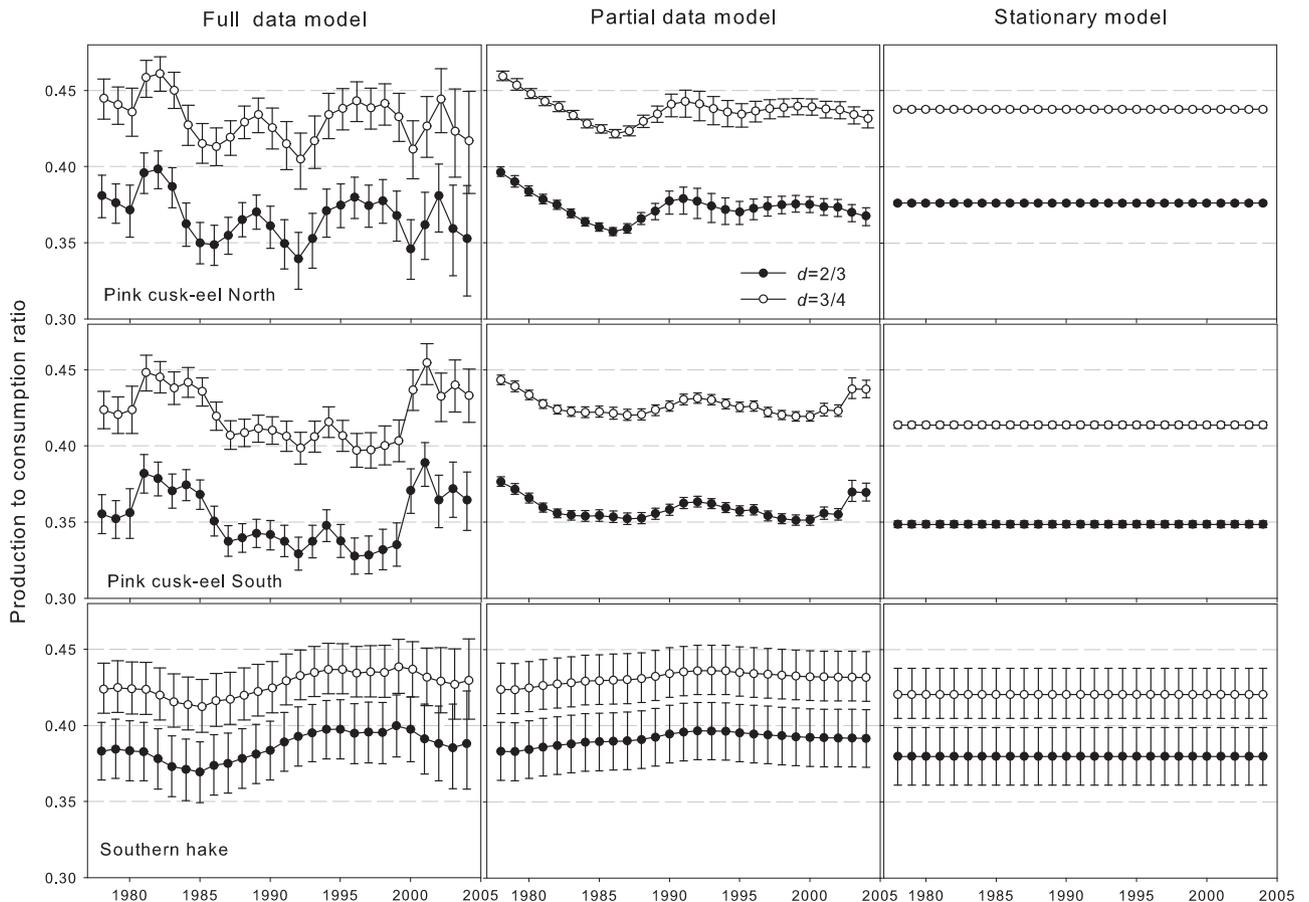


Fig. 5. Estimates of production per unit of food consumed (ρ) in pink cusk-eel (northern and southern population) and southern hake for full data model (Eq. (11)), partial data model (Eq. (12)) and stationary model (Eq. (19)) using two values for the anabolism parameter ($d = 2/3, d = 3/4$). Vertical lines indicates the 95% confidence intervals.

available. This primary difference between Aydin's model and the framework presented here, explains the deviation showed in Fig. 3. We expect estimates of ρ made using Aydin's model to be about 37% lower than those made using the model proposed here for a stationary population. However, the differences between cohort and population estimators of ρ became more complicated in harvested populations. They will depend, at least, on the lifespan of the population, the fishing mortality it experiences and variability of the recruitment, as shown in Figs. 1 and 2.

Models developed in this paper give a snapshot estimator of ρ in fish populations. These estimates can be interpreted as the potential production-to-consumption ratio of a fish population at a particular point in time. However, if a time series for $P_y(a)$ is available, the dynamic behaviour in ρ can also be determined by ordering estimates of this quantity at different points in time. Assuming that the VBGF for the species is time-invariant, the dynamic behaviour of ρ will depend on variations of $P_y(a)$ across time. As we have shown, $P_y(a)$ is determined by the relationship between recruitment and age-specific fishing mortality. Integrated stock assessment models usually provide an estimate of $P_y(a)$ on each assessed year. Such estimates can be interpreted as averaged age-structures between recruitment events. Thus, estimates of ρ using such outputs from stock assessment models should be interpreted accordingly as representative ρ between recruitment events. The differences between full and partial data models depend on how variable recruitment is across time and the number of age classes composing a population. For example, we expected large differences between full and partial data models in species where populations are composed of few age classes and highly variable recruitment, such as small pelagic fishes. For such species, the use of best available data for estimating ρ should be encouraged and estimates using partial data model should be interpreted with caution.

For the models presented here, the scale of ρ estimates is directly related to the values of A that are used. Temming (1994b) defined A as the “fraction of ingested food that is available for the build up of body substance”. This parameter serves to scale the anabolism term in the VBGF to give the net food (energy) ingested. It can be estimated from growth and feeding studies (Temming and Herrmann, 2009). In theory, the value of A must be the proportion of food consumption that is not lost as faeces, excretion and apparent specific dynamic action (the increased metabolic rate a fish experiences following ingestion of a meal). Turner (1970) and Brett and Groves (1979) suggest that A appears to be relatively constant across a wide range of fish species within the same trophic group. 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 carnivores have a higher ρ than herbivores. Tang and Guo (2007) reported values of ρ for four carnivorous fish populations that ranged from 0.13 to 0.43. The application of the model here to three carnivorous fish populations demonstrated that, when using the specialised VBGF, ρ varies between 0.35 and 0.4, matching the empirical range reported in Tang and Guo (2007). Note that the estimates of ρ presented are for individuals from a starting age of 0 years. ρ estimates for any other starting age yielded lower values, because ρ decreases exponentially with age and size (Slobodkin, 1960). Thus, special attention should be paid to the range of ages considered in the population when comparing estimates from theoretical and empirical models.

In recent years, the emphasis in fisheries science has shifted from single-species assessment to more holistic multi-species and ecosystem-based approaches (Christensen et al., 1996). The incorporation of dynamical behaviour in ρ into such models would

improve the way time-dependent perturbations are represented. ρ has a key importance in ecosystem modelling, because it defines population energetics in terms of food intake by predation and the transformation of this energy into their population biomass. One of the most utilised tools for ecosystem modelling is the trophic mass-balance models (Christensen and Pauly, 1992). ECOPATH, the most popular software implementation of this tool, originally proposed by Polovina (1984), provides a static picture of ecosystem trophic structure. A common practice is to implement ECOPATH together with ECOSIM, a dynamic food web model that simulates food web responses over time to natural and anthropogenic disturbances (Walters et al., 1997). ECOPATH with ECOSIM (EwE) requires estimates of population production-to-biomass ratio (p/B) and consumption-to-biomass ratio (Q/B) for each member of the food web and it provides an estimate of ρ as an output. ρ values are usually used as an indicator to constrain an acceptable global solution for the model (Kavanagh et al., 2004), and are usually assumed to be time-invariant. The model developed here should help to improve these ecosystem models by incorporating variation in population ρ . It may also make it easier to obtain realistic solutions of ecosystem models because these solutions can be constrained to match independent estimates of population ρ , such as those provided by the framework we described here.

Acknowledgments

We are sincerely grateful to two anonymous reviewers for all their valuable comments and constructive criticism that greatly improved an early version of this manuscript. We also thank Dr. Charles Paxton, Professor Jason Matthiopoulos for their comments and suggestions. JC Quiroz was supported by BECAS-CHILE scholarships program sponsored by the Chilean government. Rodrigo Wiff was supported by CONICYT (Chile) scholarship for postgraduate studies abroad (“Beca Presidente de la Republica para Estudios de Postgrado en el Extranjero”) and by CONICYT/FONDECYT post doctoral project number 3130425.

References

- Allen, K.R., 1971. Relation between production and biomass. *J. Fish. Res. Board Can.* 28, 1573–1581 (<http://dx.doi.org/10.1139/f71-236>).
- Aydin, K.Y., 2004. Age structure or functional response? Reconciling the energetics of surplus production between single-species models and ECOSIM. *Afr. J. Mar. Sci.* 26 (1), 289–301 (<http://dx.doi.org/10.2989/18142320409504062>).
- Brett, J.R., Groves, T.D.D., 1979. Physiological energetics. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), *Fish Physiology*, vol. 8. Academic Press, New York, pp. 279–352 ([http://dx.doi.org/10.1016/S1546-5098\(08\)60029-1](http://dx.doi.org/10.1016/S1546-5098(08)60029-1)).
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85 (7), 1771–1789 (<http://dx.doi.org/10.1890/03-9000>).
- Charnov, E.L., 1993. *Life History Invariants*. Oxford University Press, London.
- Christensen, V., Pauly, D., 1992. ECOPATH II— a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Model.* 61 (1–2), 169–185 ([http://dx.doi.org/10.1016/0304-3800\(92\)90016-8](http://dx.doi.org/10.1016/0304-3800(92)90016-8)).
- Christensen, N.L., Bartuska, M., Brown, J., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J., MacMahon, J., Noss, R., Parsons, D., Peterson, C., Turner, M., Woodmansee, R., 1996. Report of the Ecological Society of American Committee on the scientific basis for ecosystem management. *Ecol. Appl.* 6, 665–691 (<http://dx.doi.org/10.2307/2269460>).
- Cubillos, L.A., Rebolledo, H.P., Hernández, A.F., 2003. Prey composition and estimation of Q/B for the Chilean hake, *Merluccius gayi* (Gadiformes, Merlucciidae), in the central-south area off Chile (34°–40°S). *Arch. Fish. Mar. Res.* 50 (3), 271–286.
- Efron, B., Tibshirani, R.J., 1993. *An Introduction to the Bootstrap*. Chapman and Hall, New York.
- Essington, T.E., Kitchell, J.F., Walters, C.J., 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. *Can. J. Fish. Aquat. Sci.* 58, 2129–2138 (<http://dx.doi.org/10.1139/CJFAS-58-11-2129>).
- France, R.L., 2011. Conversion confusion—Does annual P/B equal cohort P/B for multi-year organisms? A cautionary tale for ecotoxicology studies. *Int. J. Environ. Sci.* 1 (7), 1379–1394.

- Hewitt, D.A., Hoenig, J.M., 2005. Comparison of two approaches for estimating natural mortality based on longevity. *Fish. B-NOAA* 103 (2), 433–437.
- Hidalgo, M., Olsen, E.M., Ohlberger, J., Saborido-Rey, F., Murua, H., Piñeiro, C., Stenseth, N.C., 2014. Contrasting evolutionary demography induced by fishing: the role of adaptive phenotypic plasticity. *Ecol. Appl.* 24, 1101–1114 (<http://dx.doi.org/10.1890/12-1777.1>).
- Kavanagh, P., Newlands, N., Christensen, V., Pauly, D., 2004. Automated parameter optimization for Ecopath ecosystem models. *Ecol. Model.* 172 (2–4), 141–149 (<http://dx.doi.org/10.1016/j.ecolmodel.2003.09.004>).
- Ojeda, V., Aguayo, M., 1986. Edad y crecimiento de merluza del sur *Merluccius australis* (Gadiformes-Merlucciidae). *Investig. Pesq.* 33, 47–59.
- Pandian, T.J., Marian, M.P., 1985. Nitrogen content of food as an index of absorption efficiency in fishes. *Mar. Biol.* 85, 301–311 (<http://dx.doi.org/10.1007/BF00393251>).
- Pardo, S.A., Cooper, A.B., Dulvy, N.K., 2013. Avoiding fishy growth curves. *Methods Ecol. Evol.* 4, 353–360 (<http://dx.doi.org/10.1111/2041-210x.12020>).
- Pauly, D., 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. *Fish. B-NOAA* 84 (4), 827–840.
- Pauly, D., 1996. One hundred million tonnes of fish, and fisheries research. *Fish. Res.* 25, 25–38 ([http://dx.doi.org/10.1016/0165-7836\(95\)00436-X](http://dx.doi.org/10.1016/0165-7836(95)00436-X)).
- Polovina, J.J., 1984. Model of a coral reef ecosystem. Part. I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3 (1), 1–11 (<http://dx.doi.org/10.1007/BF00306135>).
- Pool, H., Balbontín, F., Montenegro, C., Cortés, N., Arriaza, M., 1997. Interacciones tróficas en recursos demersales en la zona sur-austral. Reporte del fondo de investigación pesquera. Documento 94-32. FIP-Chile.
- Quiroz, J.C., Canales, C., Ojeda, V., 2007. Investigación evaluación de stock y CTP Merluza del sur 2007. Reporte tecnico Instituto de Fomento Pesquero Documento BIP-2007. IFOP-Chile.
- Roa-Ureta, R., 2010. A likelihood-based model of fish growth with multiple length frequency data. *J. Agric. Biol. Environ. Stat.* 15, 416–429 (<http://dx.doi.org/10.1007/s13253-009-0009-7>).
- Slobodkin, L.B., 1960. Ecological energy relationships at the population level. *Am. Nat.* 94 (876), 213–236 (<http://dx.doi.org/10.1086/282124>).
- Tang, Q., Guo, X., 2007. Ecological conversion efficiency and its influencers in twelve species of fish in the Yellow Sea Ecosystem. *J. Mar. Syst.* 67 (3–4), 282–291 (<http://dx.doi.org/10.1016/j.jmarsys.2006.04.013>).
- Temming, A., 1994a. Food conversion efficiency and the von Bertalanffy growth function Part II and conclusion: extension of the new model to the generalized von Bertalanffy growth function. *Naga, WorldFish Center Q.* 17 (4), 41–45.
- Temming, A., 1994b. Food conversion efficiency and the von Bertalanffy growth function I: a modification of Pauly's model. *Naga, WorldFish Center Q.* 17 (1), 38–39.
- Temming, A., Herrmann, J.P., 2009. A generic model to estimate food consumption: linking von Bertalanffy's growth model with Beverton and Holt's and Ivlev's concepts of net conversion efficiency. *Can. J. Fish. Aquat. Sci.* 66 (4), 683–700 (<http://dx.doi.org/10.1139/F09-028>).
- Turner, F.B., 1970. The ecological efficiency of consumer populations. *Ecology* 51 (4), 741–742 (<http://dx.doi.org/10.2307/1934059>).
- Van Straalen, N.M., 1985. Production and biomass turnover in stationary stage-structured populations. *J. Theor. Biol.* 113, 331–352 ([http://dx.doi.org/10.1016/S0022-5193\(85\)80231-9](http://dx.doi.org/10.1016/S0022-5193(85)80231-9)).
- von Bertalanffy, L., 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). *Hum. Biol.* 10, 181–213 (on <http://www.jstor.org/stable/41447359>).
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fisher.* 7 (2), 139–172 (<http://dx.doi.org/10.1023/A:1018479526149>).
- Welch, H.E., 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. *Ecology* 49 (4), 755–759 (<http://dx.doi.org/10.2307/1935541>).
- Wiff, R., Quiroz, J.C., Ojeda, V., 2006. Investigación evaluación de stock y CTP congrio dorado 2006. Reporte tecnico Instituto de Fomento Pesquero. Documento BIP-2006. IFOP-Chile.
- Wiff, R., Ojeda, V., Quiroz, J.C., 2007. Age and growth in pink cusk-eel (*Genypterus blacodes*) off the Chilean austral zone: evaluating differences between management fishing zones. *J. Appl. Ichthyol.* 23 (3), 270–272 (<http://dx.doi.org/10.1111/j.1439-0426.2007.00854.x>).
- Wiff, R., Roa-Ureta, R., 2008. Predicting the slope of the allometric scaling of consumption rates in fish using the physiology of growth. *Mar. Freshw. Res.* 58 (10), 912–921 (<http://dx.doi.org/10.1071/MF08053>).