

UNIVERSIDAD DE CONCEPCION  
ESCUELA DE GRADUADOS  
MAGISTER EN CIENCIAS MENCION PESQUERIAS

TESIS

EXTENSION TEORICA DE LA RAZON PRODUCCION-BIOMASA, Y EL DESARROLLO DE UNA  
APLICACIÓN EN PRODUCCION SECUNDARIA



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Concepción, Chile, Junio de 2003.

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Tesis Presentada a la

ESCUELA DE GRADUADOS  
DE LA UNIVERSIDAD DE CONCEPCION



Para optar al Grado de

MAGISTER EN CIENCIAS MENCION PESQUERIAS

CONCEPCION-CHILE

2003

UNIVERSIDAD DE CONCEPCION  
ESCUELA DE GRADUADOS

Esta tesis ha sido realizada en el Departamento de Oceanografía de la Facultad de Ciencias Naturales y Oceanográficas

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Para quienes me hubiese gustado que la mortalidad se les cancelara, como se cancela en las ecuaciones de esta tesis.

A la memoria de mi abuela Adriana Lizama y mi amigo José Benito, ambos Q.E.P.D



## **AGRADECIMIENTOS**

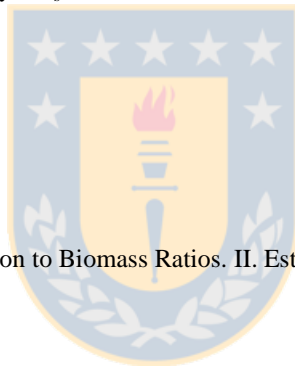
Mis primeras palabras de agradecimiento son para mi amigo y tutor Rubén Roa quien ha sido fundamental en mi formación. Agradezco la entera no-jerarquización en la enseñanza y poner las cosas de una forma “decente” cuando todo parecía oscuro.

Deseo agradecer también a las personas de la cabina 10: A la extinta Ely, quien hacía que todo funcionara, a mis compañeros de maestría quienes hicieron muy grato my paso por la cabina, al Dr. Renato Quiñones quien me apoyó sustancialmente durante el primer año en esta maestría. Especialmente debo agradecer al Dr. Ricardo Galleguillos quien siempre me ha tendido una ayuda desinteresada y quien fue pieza fundamental en mi pasantía en el Reino Unido. También al Dr. Franklin Carrasco y Dr. Ciro Oyarzun quienes me apoyaron en dicha pasantía. Deseo agradecer al Mathematical Ecology Group, University of Stirling, Scotland, UK, donde terminé esta tesis y en especial al Dr. Tim Benton quien me brindó hospitalidad y un apoyo incondicional durante mi estadía en aquellas frías latitudes. También agradezco al DEFAO por hacer los almuerzos diarios más amenos durante estos tres años, en especial a mis amigos Dante Figueroa, Alberto Foppiano y Freddy Echeverría. Agradezco los valiosos comentarios matemático-teóricos de mi amigo y colega Ricardo De Pol, como también a los siempre acertados comentarios del Profesor Luis Cubillos. Por ultimo no puedo dejar de agradecer el apoyo incondicional de mi familia y mis amigos de El Cortijo, Conchalí.

Esta tesis fue financiada por el FONDECYT N° 1010903 y la Escuela de Graduados de la Universidad de Concepción.

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## CAPITULO II.

Fig. 1.- Results of Monte Carlo simulation to assess the effects of body-length distribution sample size, uncertainty in growth parameter  $K$ , and uncertainty in biomass  $B$ , on statistical properties of the production estimator in eq. 1.6.  $CV$ : coefficient of variation. Black triangles:  $CV(B) = 10\%$ ; black squares:  $CV(B) = 20\%$ ; black dots:  $CV(B)=50\%$ . 55



## RESUMEN GENERAL

Los invariantes de la historia de vida, son cantidades demográficas que permanecen constantes bajo transformaciones taxonómicas. La razón entre la talla de madurez y la longitud asintótica ( $l_s/l_\infty$ ) ha mostrado ser invariante para peces y reptiles, pero no se ha demostrado para invertebrados, necesitándose una extensión taxonómica. Una de las principales invarianzas que engloba tanto a taxos vertebrados como invertebrados es la razón producción-biomasa (P/B) contra  $l_s$ . Análisis teóricos previos sugieren que la invarianza  $P/B-l_s$  es una consecuencia de  $l_s/l_\infty$  invariante. Este análisis depende de dos supuestos: (1) El intervalo de la razón P/B es una aproximación a la razón instantánea de P/B y (2) El crecimiento individual es descrito por el modelo de von Bertalanffy. En el primer capítulo, para extender la invarianza de  $l_s/l_\infty$  a otros taxos que cubren la invarianza  $P/B-l_s$  se somete a prueba (1) mediante el examen de las predicciones utilizando las estimaciones de parámetros publicados de historias de vida, y (2) por generalización de la razón P/B mediante el modelo general de crecimiento. La prueba empírica para (1) resulto exitosa, mientras que la generalización (2) confirma la dependencia del modelo de crecimiento de von Bertalanffy en la teoría de la razón P/B. Se muestra que la razón  $l_s/l_\infty \approx 0.63$ , lo que esta de acuerdo a compilaciones previas. En el segundo capítulo de esta tesis se desarrolla un método de estimación de producción desde un punto de vista no dinámico, basado en la teoría razón P/B instantánea. Este método requiere una observación de la estructura de talla, biomasa del stock y una estimación de los parámetros de crecimiento individual. El intervalo de confianza para esta estimación es obtenido a través de técnicas de remuestreo. Este método es aplicado a una población real

y probado para muchos escenarios de incertidumbre en los parámetros. Los resultados de la aplicación obtenidos aquí son comparables con los obtenidos a través de dinámica de stock.



## GENERAL ABSTRACT

Life-history invariants are demographic quantities remaining unchanged upon taxonomical transformation. The ratio body size at maturity to asymptotic body size ( $l_s/l_\infty$ ) has been shown invariant for fish and reptiles, though not for invertebrates, so it necessitates taxonomical extension. A further invariant covering invertebrate and vertebrate taxa relates the production/biomass ratio ( $P/B$ ) of populations with  $l_s$ . A previous theoretical analysis suggested that the  $P/B-l_s$  invariant is a consequence of the  $l_s/l_\infty$  invariant. The analysis depended on two assumptions: (1) interval  $P/B$  ratios are approximations to instantaneous  $P/B$  ratios, and (2) growth is described by von Bertalanffy's model. In the first chapter, in order to extend the  $l_s/l_\infty$  invariant to taxa covered by the  $P/B-l_s$  invariant, we tested (1) by examining a prediction using published estimations of life-history parameters, and (2) by generalizing instantaneous  $P/B$  ratios with a general growth model. The empirical test of (1) was successful while the generalization of (2) confirmed the dependence of the argument on von Bertalanffy's model. A further compilation of life-history parameters yielded  $l_s/l_\infty \approx 0.63$ , in agreement with previous compilations. In the second chapter, we introduce here a non dynamical production estimation method derived from the theory of instantaneous  $P/B$  ratios. It requires one observation of the length structure and the stock biomass, and estimates of individual growth parameters. Point and interval estimates of production are obtained by means of resampling statistical techniques. The method is applied to real data from a research survey and tested with simulated data under several scenarios of parameter

uncertainty. The application produced results which were comparable to those obtained by using dynamical stock assessment procedures.



## I INTRODUCCION GENERAL.

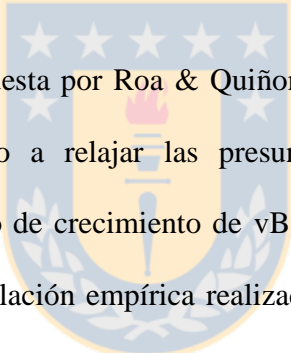
Cuando los biólogos piensan en el concepto de simetría, regularmente se refieren a la arquitectura corporal de los individuos (e.g radial, bilateral). Pero la simetría es un concepto mucho más general, que indica que los atributos de un objeto de interés permanecen invariantes bajo transformaciones específicas (Charnov, 1993). Un grupo particular de simetría es llamada por Charnov (1993) “invariantes de la historia de vida de Beverton & Holt”, donde la simetría se mantiene en los parámetros de historia de vida a través de las especies y poblaciones. Tres casos importantes de invariantes de la historia de vida son: (i) La razón entre la tasa de mortalidad instantánea ( $M$ ) y el parámetro ( $k$ ) de la ecuación de crecimiento de von Bertalanffy (vB) (ii) El producto entre  $M$  y la edad de madurez ( $a_s$ ). (iii) La razón entre la talla de madurez ( $l_s$ ) y el tamaño de crecimiento asintótico ( $l_\infty$ ) de vB.  $M$  proviene del modelo de decaimiento exponencial de una cohorte  $N(t) = R e^{-Mt}$ , donde  $N$  es el número de individuos a tiempo  $t$  y  $R$  es el reclutamiento; los parámetros de crecimiento provienen del modelo de crecimiento asintótico de vB  $l(t) = l_\infty (1 - e^{-k(t-t_0)})$ . La existencia de estos tres invariantes han sido investigados mayormente en peces (Beverton & Holt 1959; Charnov 1993, Jensen 1996, 1997), también en reptiles (Charnov & Berrigan, 1993) e invertebrados acuáticos (Ebert, 1975; Charnov 1979).

Beverton (1963), Charnov (1993) y Roff (1984) indican que estas relaciones invariantes son el resultado de la selección natural y adaptación, donde se maximiza la contribución de nuevos individuos a la futura generación, por otra parte Jensen (1996)

obtiene estos tres invariantes razonando desde un punto de vista ecológico, donde se realiza un balance entre sobrevivencia y fecundidad. De esta forma, los tres invariantes de Beverton & Holt han sido investigados desde un punto de vista evolutivo y ecológico, apoyados por resultados empíricos obtenidos para algunos taxa, mayormente peces.

Banse & Mosher (1980) realizan una compilación extensiva de resultados empíricos de producción secundaria anual (P), biomasa poblacional (B) y el parámetro  $l_s$  a través de un amplio espectro de especies y phyla del reino animal. Estos autores encuentran que cuando se gráfica  $\log(P/B)$  en contra de  $\log(l_s)$  los puntos siguen una ecuación lineal decreciente con pendiente cercana a  $-1/3$ . De esta forma, podemos señalar que existe una cuarta relación invariante (diferencial de primer orden), llamada  $\partial \log(P/B) / \partial \log(l_s)$ , que contiene a la mayoría de los taxa animales de ambientes templados. En este contexto la pregunta emergente es: ¿se encuentra esta cuarta invariante relacionada con alguna de las otras tres invariantes de Beverton & Holt?. Roa & Quiñones (1998) muestran que si sólo una condición crítica es reunida, esta cuarta invarianza es consecuencia de la invariante  $l_s/l_\infty$ , para animales que crecen acorde al modelo vB. Por otra parte la condición crítica necesaria en esta teoría fue, que las mediciones de los intervalos de P/B colectadas por Banse & Mosher (1980) fuesen una aproximación a la razón P/B instantanea. Además  $l_s/l_\infty$  invariante presenta un limitado soporte empírico y teórico en comparación con las otras dos invariantes de Beverton & Holt. Sin embargo Charnov (1993) señala que esta razón es constante dentro de cada taxón animal, donde los peces típicamente poseen  $l_s/l_\infty \approx 0.65$  y en los

reptiles  $0.62 < l_s/l_\infty < 0.68$ . En el argumento teórico a la relación  $l_s/l_\infty$ , Jensen (1985) indica que la madurez ocurre en, o levemente después del punto de inflexión del modelo de vB en peso, desarrollando una teoría para explicar la regularidad encontrada sólo en base al crecimiento en peso de los animales. A la luz de los resultados empíricos y teóricos que soportan los invariantes de Beverton & Holt y agregando los resultados empíricos obtenidos por Banse & Mosher (1980) y la explicación para estos resultados por parte de Roa & Quiñones (1998), podemos estar frente a una de las pocas leyes “firmes” de la ecología que puede beneficiar a los investigadores del área en cuanto a construir teoría y desarrollar aplicaciones.



Sin embargo, la teoría propuesta por Roa & Quiñones (1998) puede ser sujeta a una extensión teórica en cuanto a relajar las presunciones iniciales, principalmente referidas a asumir el modelo de crecimiento de vB. Esto indicaría que esta teoría es robusta en explicar la compilación empírica realizada por Banse & Mosher (1980) y por otro lado se abre un amplio campo de construcción y aplicación de modelos de producción derivados de la razón P/B instantánea. De esta forma en el primer capítulo de esta tesis, se encuentra una teoría robusta a la razón P/B. Se muestra que los resultados encontrados por Banse & Mosher (1980) entregan una base empírica firme y que la relación  $l_s/l_\infty$  es invariante no solo para peces y reptiles, como ya era demostrado, sino que abarca un amplio espectro de taxones del reino animal. En base a los descubrimientos teóricos del primer capítulo, se deriva una ecuación de producción en poblaciones animales, particularmente para poblaciones de peces y crustáceos de importancia pesquera desde un punto de vista no dinámico. Un planteamiento similar

es usado recientemente por Mertz & Myers (1998), aunque difiere del planteamiento propuesto aquí, en cuanto a usar un modelo para la totalidad del crecimiento y mortalidad, estudiando la producción desde un punto de vista dinámico. En esta tesis se plantea la existencia de un estimador independiente de biomasa y frecuencia de tallas, donde no es estrictamente necesario el uso de modelos clásicos de dinámica de poblaciones. Esta aproximación puede ser útil para data proveniente de cruceros de investigación, mientras que la de Mertz & Myers (1998) son apropiados bajo criterios de dinámica poblacional. Por lo tanto el objetivo principal de esta tesis es realizar una extensión teórica de la razón P/B instantánea y desarrollar un modelo no dinámico de estimación de producción en poblaciones animales.





## OBJETIVOS, HIPOTESIS, MATERIALES Y METODOS

### Objetivos Específicos

Los objetivos específicos pueden ser divididos en tres líneas de investigación: teoría, modelación y aplicación.

#### Línea 1. Extensión teórica

**Objetivo 1-** Extensión teórica del planteamiento de Roa & Quiñones (1998).

#### Hipótesis

La derivación de la invarianza empírica de primer orden  $\partial \log(P/B)/\partial \log(l_s)$  es explicada por la invarianza  $l_s/l_\infty$ , suponiendo el modelo general de crecimiento de Schnute & Richard (1990).

El análisis teórico realizado por Roa & Quiñones (1998) dependen de un modelo particular de crecimiento (modelo de vB). El uso de este modelo se justifica, ya que representa el crecimiento de muchos phyla del reino animal, abarcando desde gorgonidos a mamíferos (ver Roa & Quiñones, 1998). Por otra parte los planteamiento teóricos realizados por Charnov (1993); Charnov & Berrigan (1993); Roff (1984); Jensen (1985,1996, 1997), dependen fuertemente de un modelo particular de

crecimiento. Sin embargo, existe un modelo general de crecimiento propuesto por Schnute & Richard (1990), que incluye como casos particulares los modelos de crecimiento de Weibull, Gompertz, vB, logístico y otros menos conocidos modelos de crecimiento asintóticos, lineales o exponenciales. Aquí se demuestra mediante análisis matemático que es posible expandir la teoría de Roa & Quiñones (1998) al modelo de crecimiento de Weibull. Por otra parte, mediante revisión bibliográfica se prueba que la invarianza  $l_s/l_\infty$  y  $\log(P/B)/\log(K)$ , para un amplio espectro de phyla del reino animal.

#### Línea 2. Modelación.

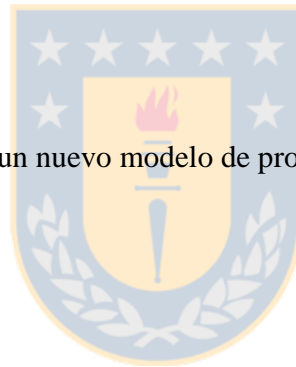
**Objetivo 2** – Derivación de un nuevo modelo de producción.

#### Línea 2. Modelación.

#### Hipótesis

La teoría de la razón P/B instantánea, en asociación a un estimador independiente de biomasa poblacional, permiten generar un método no dinámico de estimación de producción secundaria.

Se desarrolla aquí un método de estimación no dinámico de producción, basado en la teoría de la razón P/B instantáneo, generalizando desde una ecuación uni-cohorte al caso multi-cohorte a través del modelo estocástico de crecimiento de vB propuesto por



Prajneshu & Venugolopan (1999). El modelo de producción propuesto aquí, requiere la observación de la estructura de talla, biomasa del stock y una estimación de los parámetros de crecimiento. Esta aproximación puede ser útil para data proveniente de cruceros de investigación o pesquerías incipientes, entregando un modelo paralelo al propuesto de Mertz & Myers (1998) el cual es más apropiados bajo criterios de dinámica poblacional.

**Objetivo 3** - Desarrollo de un procedimiento estadístico para el estimador de producción y su aplicación.

#### Hipótesis

El procedimiento de remuestreo permite obtener una estimación de producción secundaria con criterios estadísticamente consistentes de: éxito, sesgo, forma y longitud del intervalo.

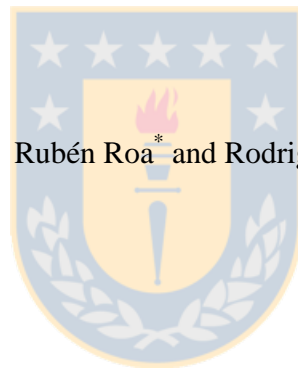
El modelo derivado del objetivo 2 presenta una forma no-lineal, debido principalmente a la alta no-linealidad del modelo de crecimiento y la distribución normal. Desde un punto de vista estadístico, se piensa que el procedimiento más adecuado para determinar las propiedades de estos estimadores es a través de la estadística de remuestreo (ver Manly 1994). El modelo de producción propuesto presenta tres fuentes de incertidumbre: distribución de frecuencia de talla, biomasa y parámetros de crecimiento. La incertidumbre fue analizada mediante bootstrap no-paramétrico en la

estructura de talla, Monte Carlo para la Biomasa y Monte Carlo de distribución bivariada para los parámetros de crecimiento. El comportamiento estadístico del estimador se evalúa mediante los criterios de éxito, sesgo, forma y longitud del intervalo de confianza, propuestos por Roa et al. (1999) y muchos escenarios de variación para la biomasa poblacional y parámetros de crecimiento. El algoritmo de simulación fue implementado para FORTRAN 90. Por ultimo, mediante este método se estima la producción para la población de langostino colorado (*Pleuroncodes monodon*) de Chile central en el año 1997.



**CAPITULO I: Submitted to Canadian Journal of Fisheries and Aquatic Science.**

**Instantaneous Production to Biomass Ratios. I. Relation to Beverton-Holt Invariant**



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Key words: Invariants, life-history, maturity, Production/Biomass ratios, Beverton-Holt

Running head: P/B ratios and life-history invariants

## Abstract

Life-history invariants are demographic quantities remaining unchanged upon taxonomical transformation, having the potential to best express the forces at work in evolution. The ratio body size at maturity to asymptotic body size ( $l_s/l_\infty$ ) has been shown invariant for fish and reptiles, though not for invertebrates. A further invariant covering invertebrate and vertebrate taxa relates the production to biomass ratio ( $P/B$ ) of populations with  $l_s$ . A previous analysis suggested that the  $P/B-l_s$  invariant is a consequence of the  $l_s/l_\infty$  invariant. The analysis depended on two assumptions: (1) interval  $P/B$  ratios are approximations to instantaneous  $P/B$  ratios, and (2) growth follows von Bertalanffy's model. To extend the  $l_s/l_\infty$  invariant to taxa covered by the  $P/B-l_s$  invariant, we tested (1) by examining the conditions under which it is true and by testing a further prediction using published estimations, and we studied (2) by generalizing instantaneous  $P/B$  ratios with a general growth model. The test of (1) was successful while the generalization of (2) confirmed the dependence of the argument on von Bertalanffy's model. We conclude that the  $l_s/l_\infty$  invariant can be extended to many new invertebrate and vertebrate taxa.

## Introduction

Evolution leads to results which are common to many or even all species. Some of those results may occur at the level of demography rather than in basic biology or biochemistry. Charnov (1993) coined the term 'life-history invariants' for demographic quantities which do not change from species to species. Invariants are quantities which remain unchanged under certain transformations; they allow identifying the conditions under which two objects are equivalent (Olver 1995). These quantities appear in mathematics, science and engineering because the basic processes involved can conveniently be defined in terms of invariants and their relations. Beverton and Holt (1959) considered three dimensionless life-history invariants: (a) the ratio between the instantaneous mortality rate  $M$  and the growth rate coefficient  $K$ , (b) the product between  $M$  and the age at sexual maturation  $a_s$ , and (c) the ratio between body size at sexual maturity  $l_s$  and asymptotic body size  $l_\infty$  (or alternatively, in mass units  $m_s/m_\infty$ ). The existence of these three invariants has been investigated mainly for fish (Roff 1984, Beverton 1992, Charnov 1993, Jensen 1996) although the constancy of the  $M/K$  and  $l_s/l_\infty$  ratios has been extended to reptiles by Charnov et al. (1993) and Charnov (1993), respectively. Beverton (1992) presented the theory linking the 3 invariants and compiled empirical evidence from the literature for 4 groups of fish. He seemed to believe that life-history invariants would hold within specific groups (e.g. clupeiformes) rather than for all groups or more generally among different phyla. Accordingly, while testing for sex, inter-population, and geographic effects he found that in general the ratio  $l_s/l_\infty$  remained fixed within those 4 groups despite wide variations in both  $l_s$  and  $l_\infty$ . Charnov (1993)

showed that the three invariants can be obtained by maximization of evolutionary fitness (as represented by net reproductive rate) with respect to  $a_s$  and  $K$  under conditions of long-term equilibrium. Roff (1984) also justified the general correlation among life history parameters along evolutionary terms, by defining and analyzing a reproductive output function. Finally, Jensen (1996) used Roff's (1984) reproductive output function and assumed that the age at maturity occurs at the inflection point of the growth curve in mass to deduce the three invariants and their values from an ecological, rather than evolutionary, perspective.

From another branch of research, Banse and Mosher (1980, hereafter B&M) compiled empirical results of annual production ( $P$ ) and biomass ( $B$ ) of field populations and the  $m_s$  parameter of individuals composing those populations across a wide spectrum of animal phyla. They found that when plotting the annually accumulated  $\log(P/B)$  against  $\log(m_s)$  the points fell along a straight line with slope around  $-1/3$ . That is, they found an additional invariant, namely  $\partial \log(P/B) / \partial \log(m_s) \approx -1/3$ , which covered most animal taxa of temperate environments.

Is this empirically found invariant related to some of the other three invariants? Does it provide support to Beverton and Holt (1959), Roff (1984), Jensen (1996), and Charnov (1993) views on life-history parameters? Roa and Quiñones (1998, hereafter R&Q) suggested that B&M's result was a consequence of the  $l_s/l_\infty$  invariant for animals growing according to the von Bertalanffy model, although this suggestion was not framed in the context of life-history theory. In this paper we re-examine R&Q's instantaneous  $P/B$  ratio



analysis from theoretical and empirical viewpoints, by generalizing it and testing assumptions and a new prediction.

Our only purpose in this paper is to show that B&M's result provides a firm empirical basis to the hypothesis that the Beverton-Holt  $l_s/l_\infty$  invariant holds true across a wide spectrum of animal phyla, not just fish and reptiles. In an accompanying paper (Wiff and Roa, this issue) we study the related topic of the estimation of production of field populations.

### **1. Explaining B&M's Empirical Regularity using Instantaneous $P/B$ Ratios**

In this section we consider the problem of deriving B&M's empirical result by a bottom up approach. We start by considering the  $P/B$  ratio of an individual and a cohort, then of a population, then of a compilation of populations such as B&M's. Consider first a single cohort moving through the age dimension,  $a=t-t_0>0$ , where  $t$  is time and  $t_0\geq 0$  is a constant representing the date of birth of all members of the cohort, so that  $da=dt$ . According to production and biomass definitions (Allen 1971), instantaneous  $P/B$  ratio is the mass ( $m$ ) specific growth rate of the individual ( $R\&Q$ ), or alternatively the logarithmic individual growth rate

$$1.1. \quad \frac{P}{B} = \frac{1}{m} \frac{dm}{da} = \frac{d}{da} \log(m)$$

On an instantaneous basis, the ratio does not depend on mortality rate or cohort size but only on individual growth, because the cohort size and decay term  $N(a)$  cancels out in taking the ratio. In other words, the cohort size and decay term  $N(a)$  affects the biomass

and the production of a cohort in the same way on an instantaneous basis. It might appear that this result runs counter to biological intuition, but it only applies to the  $P/B$  ratio and not to  $P$  or  $B$  separately. The cancellation of the cohort size and decay term,  $N(a)$ , does not occur when the  $P/B$  ratio is computed on an interval, by integrating  $P$  and  $B$  separately over the interval and then computing the ratio (Allen 1971). In section 2 we discuss the conditions under which instantaneous and interval ratios are similar or even equivalent.

By adopting a particular growth model in mass, namely von Bertalanffy's (1957)

$$1.2. \quad m(a) = m_{\infty}(1 - \alpha e^{-Ka})^3$$

the instantaneous ratio becomes

$$1.3. \quad \frac{P}{B} = 3k \frac{\alpha e^{-Ka}}{1 - \alpha e^{-Ka}}, \quad \alpha < 1$$

In eq. 1.3 the instantaneous  $P/B$  ratio depends on the time that has passed since the cohort was born, its age  $a$ , and growth parameters  $K$  and  $\alpha$ . B&M's pattern was found on the body mass continuum so a change of variable is called for. By solving eq. 2 for the exponential terms and replacing in eq. (3), we can map the age-dependent  $P/B$  ratio into mass space

$$1.4. \quad \frac{P}{B} = 3k(\gamma^{-1/3} - 1)$$

where  $\gamma = m/m_{\infty}$  is a relative measure of body mass (a fraction of asymptotic body mass).

By taking logs and pooling together constant terms, we get

$$1.5. \quad \log\left(\frac{P}{B}\right) = \log(3Km_{\infty}^{1/3}) - \frac{1}{3}\log(m) + \log(1 - \gamma^{1/3})$$

For a cohort, the instantaneous  $P/B$  ratio is scaled up or down by the product of growth parameters  $K$  and  $m_\infty$  and then decreases nonlinearly as body mass increases. This latter effect can be seen by finding out the partial derivative of  $\log P/B$  with respect to  $\log m$

$$1.6. \quad \frac{\partial \log(P/B)}{\partial \log(m)} = -\frac{1}{3} + \frac{\partial \log(1 - \gamma^{1/3})}{\partial \log(m)} = -\frac{1}{3} + \frac{\partial \log(1 - (m/m_\infty)^{1/3})}{\partial m} m = -\frac{1}{3} \left( \frac{l_\infty}{l_\infty - l} \right)$$

where  $l < l_\infty$  is a 1-dimensional measure of body size (i.e. the cubic root of mass), say length. At the origin ( $l=0$ ) the slope of the relation is  $-1/3$  and in the limit as  $l \rightarrow l_\infty$  the slope tends to  $-\infty$ . So the larger the individuals composing the cohort the less production per unit biomass. We can also reach this conclusion but in a somewhat more general way by taking the partial derivative of  $\log(P/B)$  with respect to the log of relative body mass  $\gamma$

$$1.7. \quad \frac{\partial \log(P/B)}{\partial \log(\gamma)} = -\frac{1}{3} \frac{\gamma^{1/3}}{1 - \gamma^{1/3}} = -\frac{1}{3} \frac{\lambda}{1 - \lambda}, \quad 0 \leq \lambda < 1$$

where  $\lambda$  is relative body length (i.e.  $\lambda = l/l_\infty$ ).

A result similar to eqs. 1.3-1.7 applies to populations if growth parameters remain constant on the time scale of the lifespan of individuals composing the population. To see this, assume that the population is observed at a moment in time and that recruitment is periodic so that the population is composed of a discrete collection of cohorts, all of strictly different age. To simplify matters further, assume as above that all individuals belonging to a cohort are born in the same date,  $t_0$ . These same set of assumptions, among a few others, were used by Beverton and Holt (1957) in demonstrating that the yield from a cohort during its fishable lifespan was the same as the yield of a population in equilibrium in a moment in time. In our case we need a milder version of the equilibrium assumption (namely, short term stability of growth parameters) because the cohort size

and decay term does not enter in the formalism of instantaneous  $P/B$  ratios. The cumulative  $P/B$  ratio of a population as a function of its age distribution will thus be

$$1.8. \quad \frac{P}{B}(a) = 3\alpha K \sum_{i=0}^a \frac{e^{-Ki}}{1 - \alpha e^{-Ki}}$$

which can be compared with the equivalent function for a cohort up to age  $a$

$$1.9. \quad \frac{P}{B}(t) = 3\alpha K \int_{t_0}^{a+t_0} \frac{e^{-Kt}}{1 - \alpha e^{-Kt}} dt$$

It is clear then that eqs. 1.3-1.7 provide a continuous approximation to the instantaneous  $P/B$  ratio of a population at a moment in time. An example of the fit of eq. 1.5, in particular, to several aggregated observations of a fish population at a point in time, is shown in Fig. 2 of R&Q. The model built for cohorts provided a good fit, better than a simple allometric fit, to these population data from northern Chile.

Now let's move from the single-species cohort/population to a multi-species scenario. This is done to achieve our purpose of explaining B&M's empirical regularity, and as will be seen, to show that this regularity supports the  $l_s/l_\infty$  invariant. Thus we now handle a collection of instantaneous  $P/B$  trajectories for populations from different species,

$$1.10. \quad \log\left(\frac{P}{B}\right)_j = \log(3k_j m_{\infty,j}^{1/3}) - \frac{1}{3} \log(m_j) + \log(1 - \lambda_j)$$

where growth parameters and absolute and relative body mass are indexed by species  $j$ . Assume now that  $\lambda_j = \lambda$ , i.e. the ratio of body length to asymptotic body length (and therefore of body mass to asymptotic body mass) is a constant which does not vary across species, so that  $m_j$  can now be called  $m_j'$  to signify that it is a body mass which is taken at a fixed relative distance from asymptotic mass for all species. For technical correctness,

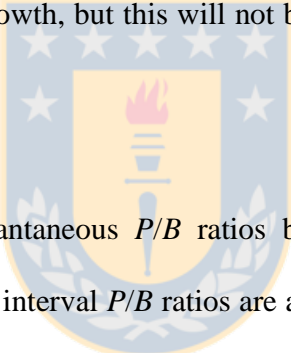
assume also that the jump from species to species can be represented by a continuum in parameter space ( $m_j' = m'$ ) so that differential operators can be applied. Then

$$1.11. \quad \frac{\partial \log(P/B)}{\partial \log(m')} = -\frac{1}{3}$$

because the first and third summands of the right-hand side of eq. 1.10 do not vary across the  $\log(m')$  continuum. This result provides a theoretical explanation of B&M's empirical regularity. Its main feature is that it is purely based on individual growth. This might seem counter intuitive: a pattern observed at the level of populations, involving two processes that are certainly affected by cohort size and decay rate, turns out to be explained by individual growth and nothing else. For example, van der Meer (1998) expressed his incredulity by presenting a possible counter-example of animals growing linearly,  $\gamma = Ka$  ( $K$  was called  $c$  by van der Meer), to a terminal age  $a = A$  ( $a$  in van der Meer). For this particular case,  $P/B = d\gamma/\gamma dt = K/Ka = 1/a$ , so it seems that the instantaneous  $P/B$  ratio is independent of growth. However, by mapping from the time-based  $P/B$  ratio to relative body size we get that  $P/B = K/\gamma$ . So the instantaneous  $P/B$  ratio of a cohort of animals growing linearly or of a population of animals which have grown linearly, still is solely determined by growth through the growth rate  $K$ . This is not surprising since the cohort size and decay term  $N(a)$  is cancelled out in taking the instantaneous  $P/B$  ratio.

The previous result applies to the  $P/B$  ratio across the relative body size dimension in the case of a cohort or across the relative body size distribution in the case of a population. Both for cohorts and populations we can also identify a reference body size and compute the  $P/B$  ratio with respect to that reference body size. This is what B&M did in selecting the body mass at sexual maturity. If we select the mean or expected relative body size, as

reference body size, for a population of animals growing linearly we arrive at the result quoted by van der Meer,  $P/B=2/A$ . To see this note that  $E(a)=A/2$ , where  $E$  is the expectation operator. Since  $P/B=1/a$  then at the reference body size  $P/B=2/A$ . However, this does not mean that growth is not involved in the  $P/B$  ratio of the population with reference to relative mean body size. Since  $a$  and  $\gamma$  are linearly related, the mean, or expected body size, is  $E(\gamma)=E(Ka)=KE(a)$ , from which we get  $E(a)=E(\gamma)/K$ , so that when using  $E(\gamma)$  as a reference body size we get  $P/B=2/A=K/E(\gamma)$ , the ratio between the individual growth rate and the mean relative body mass in the population. In this simplest of cases, using twice the reciprocal of longevity allows to circumvent the relation between the  $P/B$  ratio and growth, but this will not be the case for more complex growth models (see eq. 1.3).



B&M did not compile instantaneous  $P/B$  ratios but interval ones, usually measured during a whole year. B&M's interval  $P/B$  ratios are adimensional (Banse 1984) while our instantaneous  $P/B$  ratios have units of  $T^{-1}$ . Thus R&Q claimed to have found a theoretical explanation for B&M's result provided 3 conditions are met: (1) interval  $P/B$  ratios estimated in the works compiled by B&M are approximations to instantaneous  $P/B$  ratios, (2) the von Bertalanffy growth model is an appropriate mathematical description of growth for most metazoans, and (3) body mass or body length at maturity is a constant fraction of asymptotic body mass or body length for most metazoans. We now believe condition (3) is the significant implication of B&M's results, because it extends the Beverton-Holt invariant  $l_v/l_\infty$  to a wider spectrum of animal phyla than previously known. But we also believe that condition (1) must be studied further because in general,

instantaneous and interval ratios are different. The robustness of the explanation with respect to the growth model can also be studied by adopting a more general model. So in the next sections we explore conditions (1) and (2) and then we present a new compilation of  $l_t/l_\infty$  ratios to test the hypothesis of constancy and to approximate its actual value.

## **2. Interval $P/B$ ratios as Approximations to Instantaneous $P/B$ ratios**

In B&M,  $P/B$  ratio ‘measurements’ were done on a interval (annual) scale and our theory is based on instantaneous  $P/B$  ratios. There is an assumption of interchangeability between these two types of  $P/B$  ratios, our condition (1) above. In this section we present simple mathematical analyses intended to show the conditions under which instantaneous and interval  $P/B$  ratios can be interchangeable. Then we test a further prediction from the instantaneous theory of  $P/B$  ratios with interval measurements collected from the literature.

It is well known in statistics that in general the average ratio (what we call instantaneous ratio) gives a different estimate of the relative value of two variables than does the ratio of averages (or interval ratio) of those variables. Say we have  $X$  and  $Y$  and their ratio  $Z=X/Y$  ( $Y>0$ ), and  $n$  elements composing a set which has the property that for each element and any non-empty subset, the ratio  $Z$  can be computed. An example could be the organism density measure in a heterogeneous landscape, as in Lewontin and Levins

(1989). In that example the  $n$  elements are  $n$  habitat patches of density  $x_k/y_k$  each. The two manners of computing the average relative value of  $X$  and  $Y$  are

$$2.1. \quad \bar{Z} = \begin{cases} (1/n) \sum_{k=1}^n \frac{X_k}{Y_k} = \overline{\left( \frac{X}{Y} \right)} & \text{average ratio} \\ \frac{(1/n) \sum_{k=1}^n X_k}{(1/n) \sum_{k=1}^n Y_k} = \frac{X_T}{Y_T} & \text{ratio of averages} \end{cases}$$

where the subscript  $T$  stands for the sum total. When are these two computations equivalent? A trivial case is the set with one element,  $n=1$ . Equivalences of the average ratio and ratio of averages estimators also arise under special conditions when  $n>1$ .

Lewontin and Levins (1989) considered several interesting cases in population ecology.

Let us define ratio homogeneity of a set as the property under which the ratio does not change when computed across all levels of aggregation of elements in the set. For example, homogeneous spatial density of a biological population implies that the density ratio of the population is the same if we compute it by counting individuals in a small region of space and dividing the count by the area of the small region, or by counting the total number of individuals in the population and dividing that number by the entire population area, or if we do the same for any other region in between. Formally, the ratio homogeneity of a set is the property under which

$$2.2. \quad \frac{X_T}{Y_T} = \frac{X_k}{Y_k}$$

for all ways of subdividing the set into mutually exclusive subsets whose elements are indexed by  $k$ . When the homogeneity property is met the average ratio and the ratio of averages are the same:

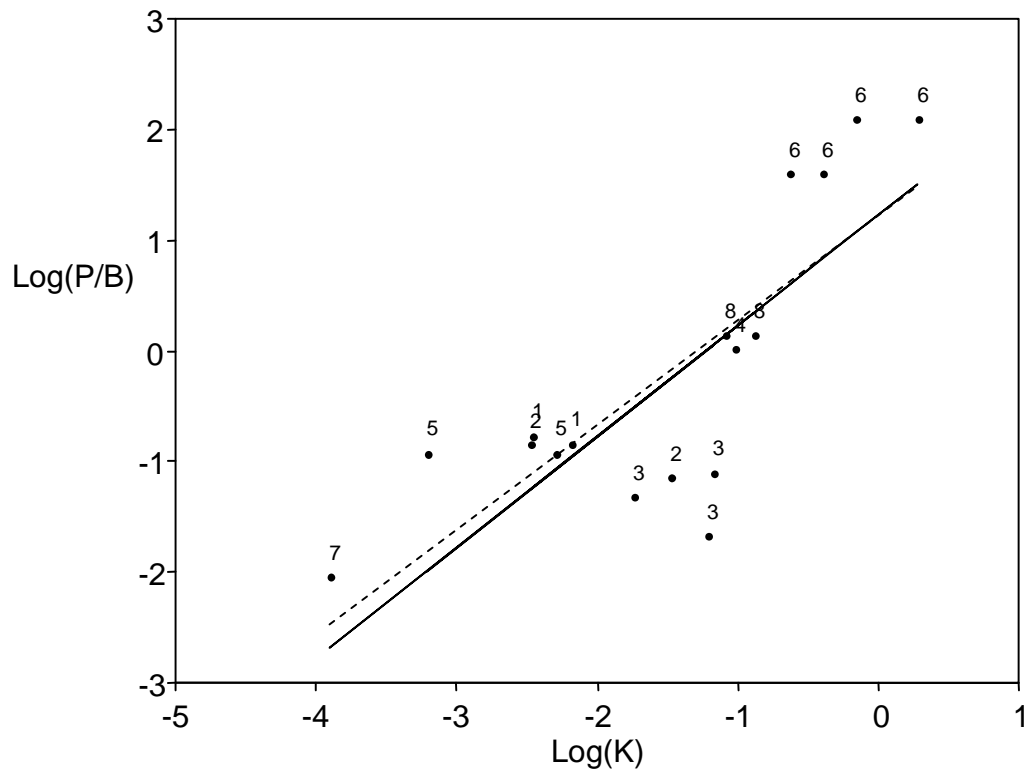


$$2.3. \quad \left( \frac{\overline{X}}{\overline{Y}} \right) = \frac{1}{n} \sum_{k=1}^n \frac{X_k}{Y_k} = \sum_{k=1}^n \frac{X_k}{Y_k} \frac{\overline{X}}{X_T} = \sum_{k=1}^n \frac{X_T}{Y_T} \frac{\overline{X}}{X_T} = \frac{n\overline{X}}{Y_T} = \frac{X_T}{Y_T}$$

We use the terms instantaneous ratio and interval ratio for the average ratio and ratio of averages modes, respectively, because the latter only makes sense when measured across a number of elements in the set, while the former is a property of each element, which is averaged *after* it is computed for each element.

Instantaneous and interval ratios are the same when the ratio homogeneity property is met. For continuous functions, the function must be smooth at least within the interval used to make the interval ratio measurements. B&M collected *annual* measurements of the interval  $P/B$  ratio. Therefore, our analysis based on instantaneous  $P/B$  ratios requires that both production and biomass varied smoothly within the year for those populations in B&M's compilation.

The appropriateness of considering empirical interval  $P/B$  ratios as approximations to theoretical instantaneous  $P/B$  ratios can also be tested by examining predictions of the theory in addition to the  $-1/3$  invariant in  $\log(P/B)/\log(I_s)$ , and test these predictions when using interval  $P/B$  ratios. For instance, according to eq. 1.10 (or its generalized version, see eq. 3.5 below),  $\partial \log(P/B)/\partial \log(K)=1$ , so that a plot of interval estimations of the  $\log(P/B)$  versus the  $\log$  of the growth parameter  $K$  should produce a slope of  $+1$  if interval  $P/B$  ratios are a proper approximation to instantaneous  $P/B$  ratios.



**Fig. 1.-** Empirical relation between interval estimations of  $\log(P/B)$  and estimations of  $\log(K)$  from the von Bertalanffy growth model (dots) collected from the literature, least-squares fitted line of the cloud of points (dashed line, slope=0.944, standard error=0.18), and the line predicted by the theory of instantaneous  $P/B$  ratios (continuous line, slope=1). Numbers indicate taxa and reference as follows: 1, mollusc (Brey and Hain 1992); 2, ophiuran (Dahm 1993); 3, mollusc (Urban and Campos 1994); 4, mollusc (Lopez-Gappa and Tablado 1997); 5, pleuronectiforme (Mackinnon 1973); 6, perciformes (Mattson and Kauda 1997); 7, gorgonian (Mistri and Ceccherelli 1994); 8, cypriniformes (Ostrovsky and Walline 1999).

In Fig. 1 we have plotted 17 paired estimations of interval  $P/B$  ratios for populations against the  $K$  parameter of their constituent individuals in log-log scale for vertebrate and invertebrate aquatic species collected from the literature. The slope does turn out to be extremely close to 1 as predicted by the theory of instantaneous  $P/B$  ratios. Visual inspection shows there is a non-random pattern in the residuals. The points cluster

according to reference as well as to taxa. Hence this pattern probably reflects methodological differences.

### 3. Generalized Instantaneous $P/B$ Ratios

Condition (2) can be studied by adopting a generalized growth model. Schnute and Richards (1990) proposed the model

$$3.1 \quad \begin{aligned} \lambda^{-b} &= (1 - \alpha e^{-Ka^c}) && \text{length units} \\ \gamma^{-b} &= (1 - \alpha e^{-Ka^c})^3 && \text{mass units} \end{aligned}$$

where  $\alpha$ ,  $K$ ,  $c$ , and  $b$  are parameters. The first two parameters are the same as in von Bertalanffy's model (eq. 1.2) and they have biological interpretation, while  $c$  and  $b$  are more mathematical in nature: they determine the particular shape the model may take. It contains as particular cases most historical versions by setting appropriate values for  $b$  and  $c$ . For example, if  $b=-1$  and  $c=1$  (and  $\alpha < 1$ ) we have von Bertalanffy's growth model. Under the general growth model the instantaneous  $P/B$  ratio for a cohort as their constituent individuals grow or for a population at any given moment in time (in continuous approximation) is

$$3.2. \quad \frac{P}{B} = \frac{\frac{3cK}{-b} (\alpha e^{-Ka^c}) a^{c-1}}{1 - \alpha e^{-Ka^c}}$$

By noting from eqs. 3.1 that

$$3.3. \quad \begin{aligned} \gamma^{-b/3} &= 1 - \alpha e^{-Ka^c} \\ 1 - \gamma^{-b/3} &= \alpha e^{-Ka^c} \end{aligned}$$

we can map the instantaneous  $P/B$  ratio into body-mass space

$$3.4. \quad \frac{P}{B} = \frac{\frac{3cK}{-b} a^{c-1} [1 - \gamma^{-b/3}]}{\gamma^{-b/3}}$$

Now we take logarithms to arrive at

$$3.5. \quad \log\left(\frac{P}{B}\right) = \begin{cases} \log\left(\frac{3cKm_{\infty}^{-b/3}}{-b}\right) + (c-1)\log(a) + \frac{b}{3}\log(m) + \log(1 - \gamma^{-b/3}) & b < 0 \\ \log\left(\frac{3cKm_{\infty}^{-b/3}}{b}\right) + (c-1)\log(a) + \frac{b}{3}\log(m) + \log(\gamma^{-b/3} - 1) & b > 0 \end{cases}$$

the generalized instantaneous  $P/B$  ratio of a cohort as their constituent individuals grow and in continuous approximation, the  $P/B$  ratio of a population at any given moment in time, the generalized version of eq. 1.10. Note that under the generalized growth model the instantaneous  $P/B$  ratio may also depend on age, depending on the value of  $c$ , even after mapping from time to body mass. On the other hand, the generalized rate of change of  $\log(P/B)$  versus  $\log(m)$  for a cohort is

$$3.6. \quad \frac{\partial \log(P/B)}{\partial \log(m)} = \frac{b}{3} \left( \frac{l_{\infty}^{-b}}{l_{\infty}^{-b} - l^{-b}} \right) \quad b \neq 0$$

In analogy with the argument for the specialized instantaneous  $P/B$  ratios (eq. 1.10), for a multi-species compilation we have

$$3.7. \quad \log\left(\frac{P}{B}\right)_j = \begin{cases} \log\left(\frac{3c_j K_j m_{\infty,j}^{-b/3}}{-b_j}\right) + (c_j - 1)\log(a_j) + \frac{b_j}{3}\log(m_j) + \log(1 - \gamma_j^{-b_j/3}) & b < 0 \\ \log\left(\frac{3c_j K_j m_{\infty,j}^{-b/3}}{b_j}\right) + (c_j - 1)\log(a_j) + \frac{b_j}{3}\log(m_j) + \log(\gamma_j^{-b_j/3} - 1) & b > 0 \end{cases}$$

and if  $\gamma_j = \gamma$  so that the fraction of asymptotic size is the same for all taxa ( $m_j = m_j'$ ) and if the discrete multi-species stance can be translated into a continuum in life-history parameter space ( $m_j' = m'$ ), then

$$3.8. \quad \frac{\partial \log(P/B)}{\partial \log(m')} = \frac{b}{3}$$

because the first, second, and fourth summands on the right-hand side of eq. 3.7 do not vary along the  $\log(m')$  continuum.

B&M's (1980) empirical results are predicted by our analysis of instantaneous  $P/B$  ratios when  $b=-1$  (given that conditions (1) and (3) are met). This is true for two special growth models: von Bertalanffy and Weibull. Therefore we have 'generalized' our previous results (R&Q) to the Weibull growth model. As it will be discussed later, von Bertalanffy and Weibull are the most widely used growth models in fishery and forestry, respectively.

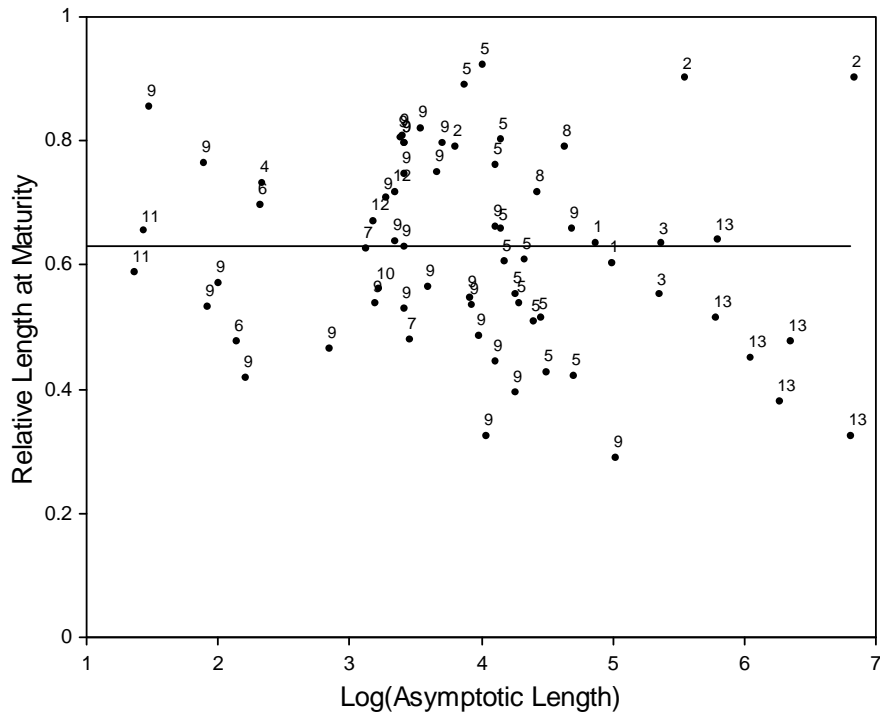
### **Re-testing the Constancy of $l_s/l_\infty$**



In Fig. 2 we have plotted 77 instances of the  $l_s/l_\infty$  ratio for a broad assortment of animal taxa collected from the literature. This set encompasses 3 orders of magnitude in body size and includes representatives from 4 phyla. The ratio does indeed appear as a constant centered around 0.63 when computed from length measurements (Fig. 3) or around 0.25 when computed from mass measurements. This result corroborates what has been found for some groups of fish (Beverton 1992) and reptiles (Charnov 1993).

## Discussion

Naturalists are usually interested in variation and change. This might be the reason why Beverton-Holt invariants went unnoticed for decades, as pointed out by Charnov (1993, p. 85). However, if evolution is the unifying principle in biology (Dobzhansky 1973), then regularities should underlie the variation at levels at which evolutionary forces can operate. A property of these regularities is that they should explain data coming from different ways of observing nature. Consistent with this view, our main purpose here is to show that B&M's empirical results with production to biomass ratios actually support a hypothesis of invariance from life-history research. Namely, that the ratio between size at maturity and asymptotic size ( $l_s/l_\infty$ ) is a constant across species. In achieving this purpose we would show that the  $l_s/l_\infty$  invariant holds true for a wider spectrum of animal taxa than previous compilations have demonstrated (Beverton 1992, Charnov 1993).



**Fig. 2.-** Empirical relation between relative length at maturity ( $\lambda=l_s/l_\infty$ ) and asymptotic length (cm) with estimations collected from the literature. A log scale is used on the X-axis to facilitate visual inspection. Numbers indicate taxa and reference as follows: 1, squaliformes (Avsar 2001); 2, mammals (Beverton 1992); 3, perciformes (Bullock et al. 1992); 4, octocorallia (Cordes et al. 2001); 5, perciformes (Charnov 1993, Table 4.1); 6, cephalopoda (Jackson et al. 1997); 7, perciformes (Mattson and Kaunda 1997); 8, squaliformes (Mammarck et al. 1985); 9, perciformes, pleuronectiformes, clupeiformes, scorpaeniformes, cypriniformes, gadiformes, gasterosteiformes, perciformes, salmoniformes, rajiformes (Roff 1984); 10, cypriniformes (Ostrovsky and Walline 1999); 11, decapod crustacean (Roa and Tapia 1998); 12, rajiformes (White et al. 2001); 13, cypriniformes, clupeiformes, siluriformes, perciformes, scorpaeniformes, pleuronectiformes (Winemiller and Rose 1992).

We tested the theory on two fronts. First, we derived the conditions under which interval  $P/B$  ratios are approximations to instantaneous ones and we tested a new prediction from instantaneous  $P/B$  ratios about their relation with the growth rate coefficient  $K$ . This was aimed at showing that a theory based in instantaneous  $P/B$  ratios was relevant to explaining a pattern found at the level of interval  $P/B$  ratios. These two ways of

computing the ratio are equivalent when both the numerator and denominator vary smoothly within the interval used to compute the interval ratio. For our case this means that populations should not show wild fluctuations within a year, which probably is a reasonable assumption for most vertebrate and invertebrate populations of metazoans in temperate environments. Furthermore, empirical support was found for the particular additional prediction of our theory when using published interval  $P/B$  ratio estimations. Since the theory is based on a reasonable assumption and it predicts two results obtained with interval  $P/B$  ratios, namely the relation with the body mass at maturity and the relation with the growth rate coefficient  $K$ , it is natural to conclude that this theory is a useful guide to understanding phenomena measured through interval  $P/B$  ratios. Then we maintain our claim in R&Q that the pattern with interval  $P/B$  ratios shows an underlying relation taking place at the level of instantaneous  $P/B$  ratios, and at that level  $P/B$  ratios are controlled by individual growth exclusively. In other words, something that appeared to be a complex ecological pattern turned out to be a more basic purely individual phenomenon. Second and less successfully, we attempted to make the predicted slope of the  $\log(P/B)$  versus  $\log(\text{mass at maturity})$  independent of a particular growth model by generalizing our results with Schnute and Richards' (1990) general growth equation. Only for two classical models, von Bertalanffy and Weibull, the theory of instantaneous  $P/B$  ratios is unambiguously able to predict the specific value of the slope found by B&M. Interestingly, these two models have been extensively used in two disciplines of applied biology, fisheries and forestry, respectively. In fact, von Bertalanffy's model has been shown to be an adequate description of growth for species representing a wide range of animal phyla (see references in R&Q). On the other hand, the Weibull distribution in



extensively used in forestry because it fits tree diameter frequency data (Schreuder and Swank 1974), with parameters having ecological interpretation (Stauffer 1979). Another interesting growth equation which is a particular case of Schnute and Richards' (1990) generalized version is the ontogenetic model of West et al. (2001). What is interesting about this model is that it was developed from basic physical principles governing cellular proliferation. Mathematically the model is very similar to von Bertalanffy's, although the exponent in eq. 1.2 is 4 instead of 3. The difference in the exponent leads to a value of  $b=-4/3$ , instead of  $-1$  as in von Bertalanffy's and Weibull's. Thus when plugging this model into the theory of instantaneous  $P/B$  ratios it predicts a slope of  $-4/9$  for B&M's plot of  $\log(P/B)$  versus  $\log(\text{mass at maturity})$ , instead of  $-1/3=-3/9$  as predicted by von Bertalanffy's and Weibull's, and observed by B&M. So our theory would only be approximately correct if West et al.'s (2001) ontogenetic growth model was the best mathematical description of growth for most animal metazoan taxa as claimed by its proponents. In summary then, our theory of instantaneous  $P/B$  ratios appears appropriate to explain phenomena measured through interval  $P/B$  ratios but remains dependent on the choosing of particular growth models in order to explain B&M's empirical regularity and to make the connection with the Beverton-Holt  $l_s/l_\infty$  invariant, though those particular growth models are the ones most widely used for animals and trees.

What is the meaning of having a correct explanation for B&M's empirical result which links it to Beverton-Holt  $l_s/l_\infty$  invariant?: taxonomical extension. Previous compilations have included reptiles and many fish species (Beverton 1992, Charnov 1993) while

B&M's compilation includes several invertebrate taxa such as annelids, hirudineans, chaetognatha, gastropods, bivalves, branchiopods, crustaceans and echinoids, which have not been previously shown to follow  $l_s/l_\infty$  invariance. It seems then that the Beverton-Holt  $l_s/l_\infty$  invariant holds true for a wide spectrum of invertebrate phyla as well as many vertebrate groups. The questions then are why it is invariant and what is its value? Charnov (1993) developed an evolutionary theory which explains the three Beverton-Holt invariants. It is based on three main assumptions: (1) evolutionary fitness can be measured by the net reproductive rate with a maximum of 1 (population in equilibrium), (2) lifetime fecundity is an increasing power function of body size, and (3) asymptotic size is a decreasing power function of the growth rate coefficient  $K$ . Under those conditions, maximization of the net reproductive rate with respect to the age at maturity and  $K$  yields the three invariants. In our view the first assumption is the critical one in the argument. It suggests that  $l_s/l_\infty$  would be constant when averaged over several generations, with population fluctuations on short time scales considered as noise. However, there are populations in which  $l_s/l_\infty$  rapidly adjust to short time scale fluctuations. For instance, consider the case of a population of benthic crustaceans in which two branches share the same nursery ground (Roa and Tapia 2000). Presumably, recruits leaving the nursery ground migrate to one or the other branch at random so that they share a common gene pool, i.e. they share the same average history over the last few generations. However, due to reasons which have only been hypothesized individuals from the southern branch grow to smaller sizes, mature earlier, and die younger than individuals from the northern branch; nonetheless, their  $l_s/l_\infty$  is about the same (Roa and Tapia 1998). Their age at maturity and their  $K$  parameter have not been differently

adjusted through several generations but rather ‘on the spot’. It seems then that at least for some cases long- or medium-term explanations are not appropriate. Jensen (1985) argued that fish have evolved life-history flexibility to changing environments rather than optimal life-history parameters to the average environment. The author also showed that the value of the  $l_s/l_\infty$  was close to  $l^*/l_\infty=0.66$ , where  $l^*$  is the body size at the inflection point of the von Bertalanffy growth model in mass units. Later Jensen (1996) proposed an ecological theory which predicted the existence of the three Beverton-Holt invariants. The theory started with Roff’s (1984) fecundity function and assumed that  $l_s/l_\infty$  was actually the same as  $l^*/l_\infty$ . This theory did account for short-term, rapid adjustment of life-history parameters to fluctuations. We believe Jensen’s theory should be explored further by deriving the equivalence between  $l^*/l_\infty$  and  $l_s/l_\infty$  from first principles. If we succeed then we may be closer to discover the “*very general features of life history trade-offs*” that seem to govern evolution (Charnov 1993, p:85), a thesis for which we have added new data by way of deducing a connection with B&M’s (1980) empirical regularity.

*Acknowledgements.* This work was funded by FONDECYT grant 1010903 to RR. RR also wishes to thank the University of Otago, New Zealand for support under an NZODA Doctoral scholarship. RW was also supported by Escuela de Graduados, Universidad de Concepción, under a M. Sc. Thesis scholarship.

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**CAPITULO II. Submitted to Canadian Journal of Fisheries and Aquatic Science.**

**Instantaneous Production to Biomass Ratios II. Estimation of Production**



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Key words: Production/Biomass ratio, Production, length structure, resampling statistics.

Running head: Size-structured production estimation.



## Abstract

Biomass production by fish and invertebrate populations in a period of time provides a measure of the catch that can be taken from that stock in a sustainable way. Methods for its estimation include theoretical dynamical procedures and empirical relations based on life-history or population average properties. We introduce here a non dynamical production estimation method derived from the theory of instantaneous  $P/B$  ratios. It requires one observation of the length structure and the stock biomass, and estimates of individual growth parameters. Point and interval estimates of production are obtained by means of resampling statistical techniques. The method is applied to real data from a research survey and tested with simulated data under several scenarios of parameter uncertainty. The application produced results which were comparable to those obtained by using dynamical stock assessment procedures. Simulation results indicated that in using the method, biomass and individual growth parameter estimates should have coefficients of variation of less than 20% and 10% respectively, in order to have negligible bias, correct coverage probabilities of confidence intervals, and high precision. The method may be particularly useful in the context of research survey data.

## Introduction

Production is the change of some positive quantity with time. We are interested here in the estimation of biomass production by animal populations, and in particular of fish and invertebrate populations of fisheries importance, from a non dynamical point of view. Biomass production is related to the catch that can be taken from a stock in a period of time in a sustainable way (Quinn and Deriso 1999). Ideally, fishermen may want to take all the newly produced biomass or less so that the stock does not decrease solely as a result of exploitation. Beverton and Holt (1957) unified previous work in setting their axiom of biomass change, as the balance between recruitment and individual growth, and natural and fishing deaths, in the absence of migration. In production estimation all those factors need be taken into account.

Dynamical methods of production estimation consider the trajectory in time of numbers and body mass at different times/ages (Hamilton 1969, Allen 1971, Mertz and Myers 1998, Quinn and Deriso 1999). Non dynamical methods are generally derived from empirical relations between production and population attributes such as cohort lifespan, observed mean body mass and average body mass at maturity (Banse and Mosher 1980, Plante and Downing 1989, Brey et al. 1996). Observing the population structure at a moment in time allows still other options for production estimation. Dynamical methods have a solid theoretical background but require a quite complete knowledge of individual and population parameters while non dynamical methods are easier to apply but generally lack in theoretical support. In this work we propose and apply a theoretically-based

equation to estimate production methods using one observation of the size structure of a population and a minimum number of population and individual parameters. This equation is a derivation of the analysis of instantaneous production to biomass ratios ( $P/B$  ratios hereafter) presented in the accompanying paper (Roa and Wiff, this issue).

Allen (1971) provided a family of equations for the  $P/B$  ratio by first integrating production and then biomass and then calculating the ratio. The resulting equations have a varying degree of complexity depending on the assumed mortality and individual growth models. An alternative approach is to integrate the ratio to cancel out the mortality model thereby simplifying the analysis. This alternative, ‘instantaneous ratio’ approach yielded a theoretical explanation (Roa and Quiñones 1998) for an empirical regularity found by Banse and Mosher (1980). The instantaneous ratio approach to  $P/B$  ratios has the added potential to simplify the estimation of production in animal populations. With instantaneous  $P/B$  ratios however, the same formulas apply to an individual and a single cohort, and in continuous approximation to a population (Roa and Wiff, this issue). Then the key aspect when solving for production in the theory for instantaneous  $P/B$  ratios lies in the incorporation of features which only populations can possess. Consequently we develop here a population equation derived from  $P/B$  ratios to solve for production with one observation of population body length distribution. Our results are useful for one-time observation of populations such as research surveys, thus we believe they complement those of Mertz and Myers (1998) which consider production in dynamical population models.

## 1. Formulation

From eq. 3 in Roa and Quiñones (1998), the integrated instantaneous  $P/B$  ratio of an individual and a single a cohort, and in continuous approximation to a population, from an initial age ( $a$ )  $a_0$  to a terminal age  $a_p$ , is

$$1.1. \quad \left. \frac{P}{B} \right|_{\Delta a} = \int_{a_0}^{a_p} \frac{dm(t)}{m(t)} dt$$

where  $m$  is body mass and  $t$  is time and the relation  $a=t-t_0$  holds, with  $t_0$  the fixed date of birth, so that  $da=dt$ . As pointed out in the Introduction, this approach contrasts with Allen's (1971), in which the interval  $P/B$  ratio is computed as a ratio of integrals (as in the ratio estimator of statistics),

$$1.2. \quad \left. \frac{P}{B} \right|_{\Delta a} = \frac{\int_{a_0}^{a_p} \frac{N(t)dm(t)}{dt} dt}{\int_{a_0}^{a_p} N(t)m(t)dt}$$

and the cohort size and decay term  $N(t)$  becomes relevant as well. Returning to the instantaneous  $P/B$  ratio approach of eq. 1.1., the adoption of von Bertalanffy's individual growth model, changing of the variable of integration from age to body length ( $l$ ), and solving for production, yields the integrated instantaneous production

$$1.3. \quad P = 3BK \int_{l_0}^{l_q} \left[ \frac{l_\infty}{l} - 1 \right] dl$$

where  $K$  and  $l_\infty$  are the growth rate coefficient and asymptotic length parameters in von Bertalanffy's model (see. eq. 1.4 in Roa and Wiff, this issue) and  $l_q$  is the terminal body

length. For simplicity we have dropped the time interval sub-index which remains implicit.

Because of (1) the cancelling out of the cohort size and decay term in eq. 1.1, and (2) the deterministic, one-to-one mapping from age to body length (so that  $l(a)=E[l(a)]$ , with E the expectation operator), eq. 1.3 does not apply to any real population at a moment in time. Both problems can be solved at once if a probability distribution reflecting population structure as a function of body length were incorporated into eq. 1.3. This stochastic representation need consider at least three factors affecting the structure of real populations, as observed once. First, recruitment occurs in periodic pulses and is variable in magnitude from cycle to cycle. Each pulse of individuals may also experience different levels of mortality during their lifetime up to the moment of observation. This results in a collection of discrete or at least identifiable cohorts that can have different relative contributions to global abundance. Let there be  $p+1$  such cohorts. Second, for any cohort individuals of the same age may not have the same body length and for all cohorts individuals of different age may have the same body length. Prajneshu and Venugolopan (1999) showed that when the differential equation leading to von Bertalanffy's model is taken as a stochastic process with additive Gaussian noise, the analytical solution for the probability density function of length of fish of fixed age is Gaussian. Third, the observation of the body length distribution is affected by relative vulnerability of individuals to the observation apparatus (or fishing gear). Accordingly, a stochastic version of 1.3 is,

$$1.4. \quad P = 3BK \sum_{i=0}^p \eta_i \int_{l_0}^{l_a} \frac{v(l) \exp(-z_i^2 / 2)}{\sqrt{2\pi} \sigma_i} \left[ \frac{l_\infty}{l} - 1 \right] dl, \quad \sum_{i=0}^p \eta_i = 1, \quad v(l) \leq 1$$

where  $z=(l(a)-E[l(a)])/σ$ , with  $σ$  the variance of length-at-age,  $v(l)$  is the relative vulnerability function of individuals of length  $l$  to the observation apparatus, and  $η_i$  is the proportion of cohort  $i$  in terms of numbers with respect to the population, whose value is determined by the magnitude of recruitment and the mortality rates experienced by the cohort up to age  $a=i$ . Note that in model 1.4, production ( $P$ ) has units of mass per unit of time (since  $B$  has units of mass and  $K$  has units of  $\text{time}^{-1}$  and the rest is adimensional) which is consistent with the general definition of production as the change of some quantity with time. The amount of time involved depends on the amount of time covered by the  $K$  growth parameter. Usually  $K$  has units of  $\text{year}^{-1}$  and in that case eq. 1.4 represents predicted production for a period of 1 year. Note also that in comparing eq. 1.3 and 1.4, it is clear that we have introduced a probability distribution for body length as a random variable. Each term in the sum is a cohort, spanning the complete body length range according to a Gaussian distribution and whose contribution to the body length distribution in the population is weighted by the cohort size and decay term and the vulnerability of its body length range.

Assuming that growth parameters are the same for the  $p+1$  cohorts composing the population, the model of production in eq. 1.4 contains  $3p+2$  plus the parameters in  $v(l)$ . From a statistical point of view, more than one approach that can be followed to estimate production and its estimation variance. Our preferred approach is to use resampling statistics such as bootstrap and Monte Carlo techniques (Manly 1994). With this in mind we make use of the plug-in principle (Efron and Tibshirani 1993) to replace the probability distribution with the empirical distribution of body length as observed from

the population, even though the theoretical distribution could be considered as known.

Under this principle, the model for production in eq. 1.4 can be represented as

$$1.5. \quad P = B \left( 3K \left[ \frac{\sum_{j=l_0}^{l_q} f_j}{\sum_{j=l_0}^{l_q} f_j} \left( \frac{l_\infty}{l_j} - 1 \right) \right] \right)$$

where  $f_j$  is the numeric frequency in a sufficiently small and discrete length category  $j$ . To estimate production, this particular equation requires observation of the body length distribution, the biomass, and knowledge of individual growth parameters. Recruitment, mortality and relative vulnerability of different cohorts enter implicitly in the frequencies  $f_j$ .



## 2. Estimation and Application

It can be noted in eq. 1.5 that there are three sources of uncertainty in the estimator of production, namely biomass, growth parameters, and length frequency distribution. We illustrate our methods by showing an application with real data from the squat lobster (*Pleuroncodes monodon*) population off central Chile. For this we use data collected in 1996 when we performed a research cruise covering the complete population in a chartered commercial vessel. Details of the cruise and the sampling of the body length distribution sample can be found in Roa and Tapia (2000).

The biomass was estimated using the theory of intrinsic geostatistics (Matheron 1971) as reported in Roa et al. (1997). The variance of the biomass estimator was computed from

the concept of extensive variances (Journel and Huijbregts 1978). The geostatistical estimator of biomass and its estimation variance were used to define a Gaussian density function from which uncertainty in biomass was considered by means of Monte Carlo resampling. For the second source of uncertainty, we used individual growth parameter estimates for the northern branch of the population from Roa and Tapia (1998). The pair of estimates  $\{\hat{K}, \hat{l}_\infty\}$  was considered as coming from a bivariate Gaussian distribution with covariance matrix given by asymptotic estimates of variances and correlation, and then their uncertainty was taken into account by resampling from the bivariate distribution using the Monte Carlo method (Roa et al. 1999, eq. 10). For the third source of uncertainty we used simple non-parametric bootstrap (Efron and Tibshirani 1993) by sampling with replacement from the univariate vector of observed body lengths in the sample. Since males and females have different growth parameters (Roa and Tapia 1998) we performed two separate production estimations, one for each sex, using size specific length distributions and  $\{\hat{K}, \hat{l}_\infty\}$  pairs. In addition, we partitioned the biomass into female and male fractions using the body-mass weighted sex proportion. The variance for male and female biomass was computed from the global extensive variance and the variance of sex proportion by using the delta method (Seber 1982). The three sources of uncertainty were considered as independent so that each realization of resampled biomass, the  $\{\hat{K}, \hat{l}_\infty\}$  pair, and the vector of body lengths were independently combined in each run of the resampling procedure using eq. 1.5. 95% confidence intervals were built by the percentile method (Efron and Tibshirani 1993). There were  $N_{iter}=5000$  thousand iterations in this application. The resampling algorithm (ND\_ProDest) was written in FORTRAN 90. Source codes and executables are available from the authors.



### 3. Resampling Estimation and Monte Carlo Simulation

To evaluate statistical behaviour of the chosen production estimator (eq. 1.5) under our resampling estimation approach, we simulate a population with known biomass, age and size structure, mortality and individual growth parameters, and therefore with known production. The values were chosen to mimic the squat lobster population off central Chile (Table 1). Methods are similar as those employed in a previous simulation with the same real population as reference (Roa et al. 1999). True production was given by

$$3.1. \quad P = B \left[ 3K \sum_{a=0}^{a_p} \eta(a) \frac{e^{-Ka}}{1 - e^{-Ka}} \right]$$

which is the deterministic core of the simulation. The cohort decay term was modelled as the exponential decay model with constant recruitment

$$3.2. \quad \eta(a) = \frac{\int_0^{a+1} e^{-Mt} da}{\int_0^{a_p} e^{-Mt} da} = e^{-Ma} - e^{-M(a+1)}$$

since the denominator is 1 by definition in reaching the terminal age. We considered that the condition of constant recruitment in the simulation was not critical to evaluate the quality of the production estimator under the resampling approach. Since our estimator in eq. 1.5 is based on discrete length distributions, we turned the deterministic and continuous age distribution in 3.2 into

$$3.3. \quad \eta_j = \frac{\sum_{a=0}^9 \frac{\eta_a}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{1}{2}\left(\frac{l_j - l_a}{\sigma}\right)^2\right]}{\sum_{j=0}^{40} \sum_{a=0}^9 \frac{\eta_a}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{1}{2}\left(\frac{l_j - l_a}{\sigma}\right)^2\right]}$$

which represents the deterministic and discrete size structure of a population composed of 10 cohorts and 41 length categories, where each cohort is represented by a Gaussian length distribution with mean individual length  $l_a$  given by a von Bertalanffy growth function, and all cohorts have the same variance of size-at-age,  $\sigma$ . Biomass was fixed at 1 and growth parameters  $K$  and  $l_\infty$  were fixed at the values shown in Table 1.

Simulation stochasticity came from three sources. First, using the probability integral transform (Casella and Berger 1990) we randomly selected a uniform random number in the interval  $[0, 1]$  and mapped it back into the cumulative distribution function of model 3.3, thus selecting a length value  $l_j$ , for fixed natural mortality coefficient  $M$ . We repeated this until we got a random length distribution of pre-defined sizes ( $N_{sample}=500, 1000, 3000, 5000, \text{ and } 10000$ ). The distribution was truncated to lengths greater than 2 arbitrary units (mm of carapace length if considering the squat lobster as reference). The second source of stochasticity came from the pair of growth parameters  $\{K, l_\infty\}$  which were collected from a bivariate Gaussian distribution by assuming with mean vector and correlation as in Table 1, and three levels of coefficient of variation, namely 2.5, 20 and 50%. This bivariate distribution also was truncated to produce positive values for both random variables. This amounts to assuming a strictly positive growth rate  $dl/dt$ . The third source of stochasticity was population biomass  $B$ , which was collected from a Gaussian distribution with mean 1 and coefficient of variation of 10, 20 and 50%, and once again truncated to produce only positive biomass. The simulation described above thus defined 9 scenarios of uncertainty in parameter knowledge: all possible pairwise combinations of 2.5, 20, and 50% coefficient of variation in  $K$ , and 10, 20 and 50%

coefficient of variation in  $B$ . The collection of random length distributions, growth parameters, and biomass was repeated  $N_{run}=5000$  times for each sample size in the length distribution, giving a total of 25000 runs, and to each one of these iterations the resampling estimation method of section 2 was applied, with  $N_{iter}=5000$  resampling iterations.

Table 1.- Parameters used to generate simulated data to test the statistical properties of the resampling estimation method of section 2. Parameters taken to represent the squat lobster population off central Chile (Roa and Tapia 1998).

Parameter	Value
Variance of size-at-age (constant for all ages)	4 (mm <sup>2</sup> )
Growth rate coefficient, $K$	0.286 (year <sup>-1</sup> )
Asymptotic body length, $l_{\infty}$	42.6 (mm)
Correlation coefficient, $r(K, l_{\infty})$	-0.998
Natural mortality, $M$	0.6 (year <sup>-1</sup> )
Biomass, $B$	1 (mass)

Four quality criteria were considered as it was done in Roa et al. (1999). First, the proportion of times in which the 95% confidence interval from section 2 contained the true production:

$$3.4. \quad success = 1 - failure = 1 - \frac{\#\{(true - lower)(upper - true) < 0\}}{\#iterations}$$

Second, the bias:

$$3.5. \quad bias = \frac{resampled \ median}{true}$$

Third, the length of the 95% confidence interval:

$$3.6. \quad length = upper - lower$$

Fourth, the shape of the 95% confidence interval:

$$3.7. \quad shape = \frac{upper - median}{median - lower}$$

In all eqs. 3.4-3.7 *true* means the true production value from eq. 3.1, while *lower*, *upper*, and *median* refer to the lower and upper bounds, and the median of the 95% confidence interval from the resampling method in section 2. The simulation algorithm (ND\_ProDest\_VL) was written in FORTRAN 90. Source codes and executables are available from the authors.

#### 4. Results

We estimated the total production of the squat lobster population off central Chile as it was observed in 1996, in the order of 26 thousand tons (Table 2). A strong imbalance between sexes was obtained, with most of the production (about 80%) coming from males (Table 2). Since the growth rate coefficient had units of year<sup>-1</sup>, the estimated production was the expected production during 1 year. The 95% confidence interval spanned the range of about 14 to 36 thousand tones (Table 2).

All subsequent remarks about simulation results are done with reference to Fig. 1 and sample size always refers to the size of the sample of the body length distribution. Nominally 95% confidence interval for the resampling production estimator based on eq.

1.5 showed coverage probabilities close to 95% for all sample sizes when the coefficient of variation in the  $K$  estimate was equal or less than 10% and the coefficient

of variation in the  $B$  estimate was less or equal than 20%. With 50% coefficient of variation in the  $B$  estimate coverage probabilities were always a little higher than the nominal 95%. Bias was very close to negligible when the coefficients of variation in  $B$  and  $K$  were 20% or less or 10% or less, respectively, for all sample sizes. When the coefficient of variation in  $K$  was 10% or more, the production estimator tended to negligible bias, showing the property of statistical consistency. Bias could be a serious problem for the worst case scenario, low sample size and high coefficients of variation of the  $B$  and  $K$  estimates. Length of the confidence interval increased with the coefficient of variation in the  $B$  and  $K$  estimates but it seemed unaffected by sample size above 500. Similarly, the production estimator tended to be positively asymmetric with increasing

Table 2.- Parameters used and production estimation using eq. 1.5 and the resampling estimation method of section 2, for the squat lobster population off central Chile as observed in 1996. The length structure data was presented in Roa and Tapia (2000, Fig. 4). Growth parameters in Roa and Tapia (1998) and total biomass in Roa et al. (1997).

Parameter	Females	Males	Total
Growth rate coefficient, $K$ (year <sup>-1</sup> )	0.199 (0.003)	0.200 (0.002)	
Asymptotic body length, $l_{\infty}$ (mm)	41.298 (0.369)	50.039 (0.311)	
Correlation coefficient, $r(K, l_{\infty})$	-0.996	-0.998	
Biomass, $B$ (ton)	16523	73546	90069
Point Production Estimate (ton*year <sup>-1</sup> )	4636	21339	25975
95% Confidence Interval (ton*year <sup>-1</sup> )	[2408, 6445]	[11254, 30079]	[13662, 36524]

of variation in the  $B$  estimate was less or equal than 20%. With 50% coefficient of variation in the  $B$  estimate coverage probabilities were always a little higher than the nominal 95%. Bias was very close to negligible when the coefficients of variation in  $B$  and  $K$  were 20% or less or 10% or less, respectively, for all sample sizes. When the coefficient of variation in  $K$  was 10% or more, the production estimator tended to negligible bias, showing the property of statistical consistency. Bias could be a serious problem for the worst case scenario, low sample size and high coefficients of variation of the  $B$  and  $K$  estimates. Length of the confidence interval increased with the coefficient of variation in the  $B$  and  $K$  estimates but it seemed unaffected by sample size above 500. Similarly, the production estimator tended to be positively asymmetric with increasing

coefficients of variation in the  $B$  and  $K$  estimates but remained unchanged with increasing sample size. This latter effect most likely results from truncating probability distributions to produce only positive values of biomass and growth rate. Overall, the resampling production estimator based on eq. 1.5 appeared statistically reliable for reasonably low coefficients of variation in  $B$  and  $K$  and reasonably high sample size, under the specified population model of eqs. 3.1-3.3.



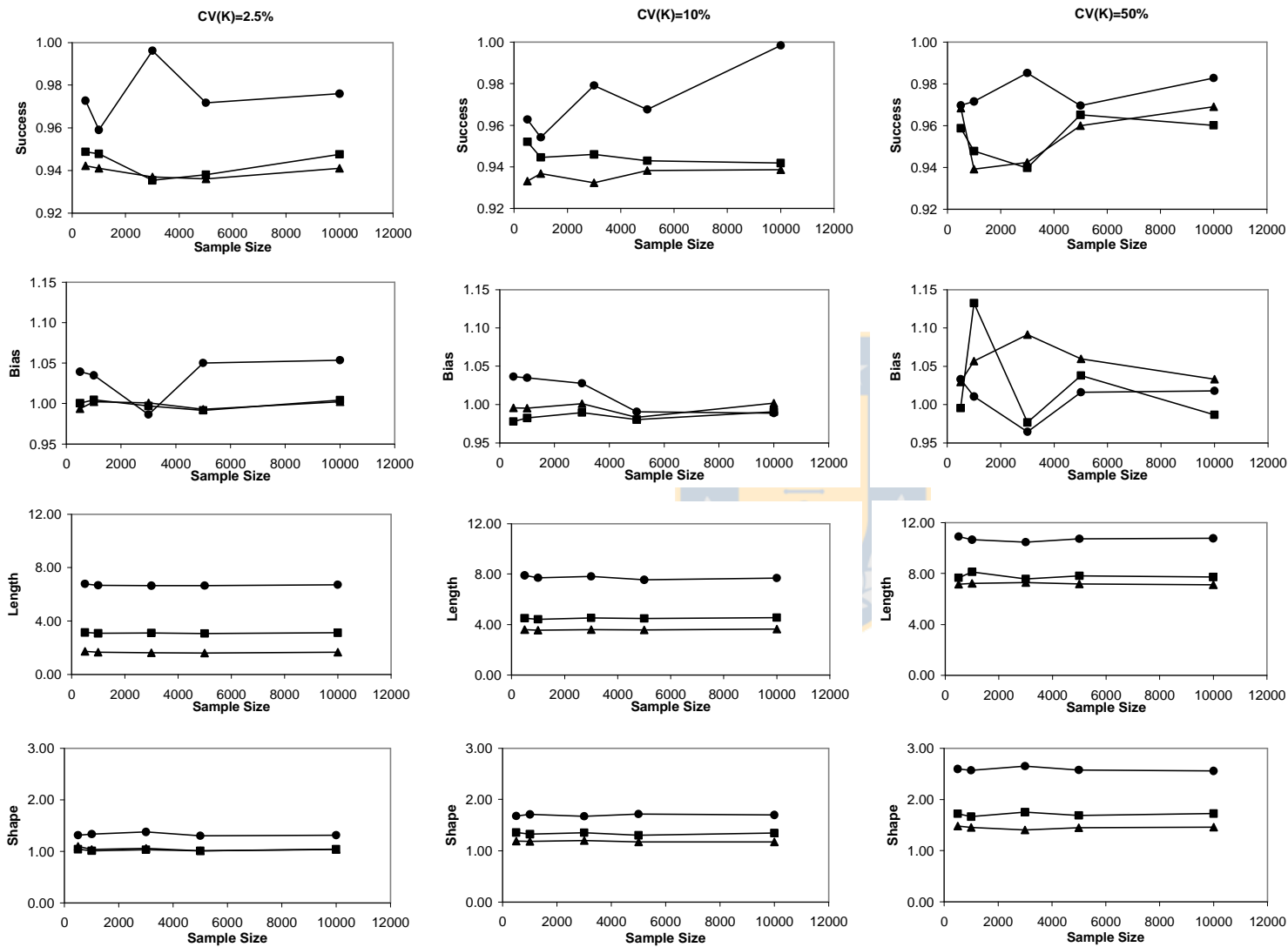


Fig. 1.- Results of Monte Carlo simulation to assess the effects of body-length distribution sample size, uncertainty in growth parameter  $K$ , and uncertainty in biomass  $B$ , on statistical properties of the production estimator in eq. 1.6.  $CV$ : coefficient of variation. Black triangles:  $CV(B) = 10\%$ ; black squares:  $CV(B) = 20\%$ ; black dots:  $CV(B)=50\%$ .

## Discussion

Intuitively, any theoretically-sound biomass production estimator should explicitly contain terms related to mortality, recruitment (and relative vulnerability). In the axiom of biomass change summarized by Beverton and Holt (1957, p. 26) this was given explicit form in a conservation equation which counted new individuals and individual growth as positive terms and natural mortality and catch as negative terms, during a period of time. Thus relatively old (Hamilton 1969) and new (Mertz and Myers 1998) production estimation methods explicitly include cohort size and decay terms in a dynamic fashion. With instantaneous  $P/B$  ratios however, the cohort size and decay term cancel out and the equations derived thereafter apply to individuals, single cohorts, and in continuous approximation to populations (Roa and Wiff, this issue). In following Beverton and Holt's axiom the key to utilize instantaneous  $P/B$  ratios lies in the incorporation of recruitment and mortality (and relative vulnerability), but this need not be done dynamically as in classical approaches but rather, taking into account population size and structure as observed only once. In our particular approach we relied on the plug-in principle (the interchangeability of theoretical distribution functions and empirical frequency distributions) to replace the theoretical population structure with length distributions as observed in a sample. Mortality rates are implicit in the length distribution (Van Sickle 1977), as are relative recruitment magnitude and relative vulnerability, and the biomass estimator scales the production estimator to population size. Our purpose in so doing is to provide the simplest possible production estimator with the least demand of knowledge on population parameters and the easiest to obtain



sampling information. Such an approach may also be advantageous when considering that the natural mortality-rate parameter is usually one of the main sources of error in stock assessment (Hampton 2000). Furthermore, the method proposed here lends itself easily to one of the most important sources of information on stock status, namely research surveys, and as such we believe is a complement to methods based on population dynamics such as Mertz and Myers' (1998). Our methods might be useful for stocks which are not closely monitored (e.g. Páramo and Roa 2003) or whose exploitation is incipient.

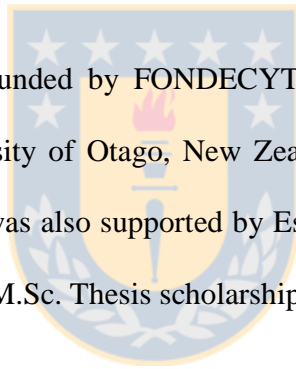
Based on a research survey done in 1996 (Roa and Tapia 2000), we estimated a total production of about 26 thousand tons/year for the squat lobster population off central Chile, with a 95% confidence interval which spanned the range between ca. 14 to 37 thousand tons/year. This is the expected production up to 1997. Its validity relies on the assumption of relative constancy in all relevant parameters during one year. It can be compared with the estimation by Canales et al. (1998) whom used traditional stock assessment methods based on population dynamics. They estimated 19 thousand tons/year. The discrepancy, though not statistically significant, can be entirely attributed to the biomass estimation, since the  $P/B$  ratio in Canales et al.'s and in this work amounted to about 0.26. We can think of the production estimation as a 'yield surplus' and use its value as a reference in suggesting reasonable catch quotas (e.g. Quinn and Deriso 1999) after the observation of length distribution and biomass has been done.

We evaluated our resampling production estimator derived from instantaneous  $P/B$  ratios by simulation. Our results regarding coverage probabilities of confidence intervals, bias, length of confidence intervals (related to precision), and shape are encouraging but they are contingent on the chosen population model. This model is for a population composed of cohorts of homogeneous magnitude, entering the population at regular intervals of time, and whose length distribution is Gaussian. Probably the most important shortcoming is in assuming recruitment which is constant in magnitude. This assumption makes the size structure to be more regular than is the case in most real populations, and is probably the cause of the almost negligible effect of sample size (the number of individuals whose length was measured in the sample) on precision as measured by the length of confidence intervals. Nevertheless, for the application that we have in mind for our methods, namely research surveys, sample size can usually reach very high values, in the order of thousand of individuals. Thus the uncertainty related to the size structure would probably be within reasonable bounds. We rather seek to emphasize the importance of having precise estimations of growth parameters and biomass. With coefficients of variation of the order of 10-20% or less for both, the production estimator introduced here will probably produce unbiased and precise estimates with confidence intervals whose coverage probabilities are close to nominal.

It is well known that environmental variables affect production (Stockwell and Johannsson 1997) as well as biomass (Ricciardi and Bouget 1999). In models of surplus yield environmental effects have been principally introduced in one of two ways: (i) through deterministic environmental functions (Freon 1998) and (ii) stochastic processes

giving rise to environmental variability (Fox 1971). Although in the methods developed here the environmental effects are not explicitly incorporated, they can be considered as implicitly included in the uncertainty due to growth parameters, biomass, and size structure. This same approach for stochastic effects of environment on individual and population models has been proposed by Fox (1971) and Prajneshu and Venugolopan (1999), among others. In the same spirit, generalized methods derived from those developed here may make some parameters explicitly dependent on environmental variables. For instance, the growth parameter  $K$  can be made a function of temperature (Ursin 1963, Akamine 1986).

*Acknowledgements.* Work funded by FONDECYT grant 1010903 to RR, whom also wishes to thank the University of Otago, New Zealand, for support under an NZODA Doctoral Scholarship. RW was also supported by Escuela de Graduados, Universidad de Concepción, Chile, under a M.Sc. Thesis scholarship.



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## DISCUSIÓN GENERAL.

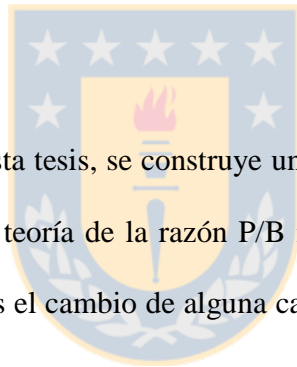
Las historias de vida invariantes reflejan el trabajo más básico de la evolución. Una propiedad de estas invarianzas es que se pueden explicar desde diferentes formas de observar la naturaleza. Así uno de los propósitos de esta tesis fue mostrar que la regularidad empírica encontrada por Banse and Mosher (1980), se soporta actualmente en la hipótesis de invariantes en las historias de vida de Beverton and Holt. Se alcanzó este propósito mostrando que la relación  $l_y/l_\infty$  es constante para muchos más taxas del reino animal, de los que ya se habían demostrado (Beverton 1992, Charnov 1993). Nosotros pusimos a prueba esta teoría en dos frentes: (i) Si los intervalos de la razón P/B son una aproximación a la razón instantánea, la predicción  $\partial \log(P/B)/\partial \log(K)=1$  debiese cumplirse. Así se encuentra el soporte empírico adicional a la teoría planteada a través de la revisión bibliográfica de intervalos de razón P/B publicados, concluyendo que esta teoría es una útil guía para entender los fenómenos de medición a través de intervalos de razones. Derivado de este análisis también se demuestra que la razón P/B es controlada exclusivamente por el crecimiento individual. En otras palabras algo que algunas veces parece un proceso ecológico complejo, es el resultado del más puro y básico proceso individual. Por otra parte, también se trata de predecir la pendiente entre  $\log(P/B)$  versus el  $\log$  (masa en la madurez) independiente de un modelo de crecimiento particular, generalizando nuestros resultados mediante el modelo general de crecimiento propuesto por Schnute and Richard (1990). La teoría instantánea de la razón P/B predice el valor de la pendiente encontrada solo para dos modelos de crecimiento: von Bertalanffy y Weibull. Interesantemente, estos dos modelos han sido ampliamente usados en dos ramas de la ecología aplicada: pesquerías y forestal, respectivamente. En resumen, la

teoría para la razón P/B instantánea parece apropiada para explicar el fenómeno de medición a intervalos, sin embargo, para explicar la regularidad empírica encontrada por Banse and Mosher (1980), aun depende de la elección de un modelo de crecimiento particular, aunque ampliamente usados para animales y arboles.

Los resultados empíricos encontrados por de Banse and Mosher (1980) se une a la teoría de historias de vida invariantes a través de la extensión taxonómica de la invarianza  $l_s/l_\infty$ . Compilaciones previas incluyen a reptiles y muchas especies de peces (Beverton 1992, Charnov 1993) mientras que la compilación de Banse and Mosher (1980) incluye muchas especies de invertebrados y vertebrados para los cuales la invarianza  $l_s/l_\infty$  no había sido mostrada. En este contexto la pregunta emergente es ¿por qué esta cantidad es constante y cual es valor?, Charnov (1993) explica la existencia de esta invarianza desde un punto de vista evolutivo, maximizando la tasa reproductiva neta bajo equilibrio poblacional. Jensen (1985) muestra que el valor de  $l_s/l_\infty$  es muy cercano a  $l^*/l_\infty = 2/3$ , donde  $l^*$  es el punto de inflexion en masa en el modelo de crecimiento de von Bertanffy, entregando una explicación a través de la teoría de drenaje reproductivo. Mas tarde Jensen (1996) propone una teoría ecológica para explicar los tres invariantes de Beverton & Holt. Sin embargo Pauly (1984) sugiere que la hipótesis de drenaje reproductivo no es correcta debido a que no puede unir la constancia en la razón  $l_s/l_\infty$  con una serie de eventos fisiológicos que conducen al desove, y propone que esta invarianza es el resultado de la constancia en la razón de consumo relativo de oxigeno a la madurez, respecto del consumo relativo de oxigeno a la longitud asintótica.



A la luz de estos resultados, Charnov (1993) sugiere que la razón  $l_s/l_\infty$  debería ser constante cuando se promedian muchas generaciones, donde las fluctuaciones de escala de tiempo pequeñas son consideradas como ruido. Nosotros creemos que las poblaciones ajustan esta razón en escalas de tiempo pequeñas. Esto en base a los resultados encontrados por Roa and Tapia (2000) para la población de langostino de Chile central. Esta población comparte el mismo pool genético pero los individuos de la rama norte presentan diferencias significativas en los parámetros de crecimiento con respecto a los individuos de la rama sur. Sorprendentemente, la relación  $l_s/l_\infty$  se mantiene constante para estas dos ramas de la población indicando un ajuste a esta relación en solo pocas generaciones.



En el segundo capítulo de esta tesis, se construye un modelo no dinámico para el cálculo de producción basado en la teoría de la razón P/B instantánea. Como ya se ha definido anteriormente, producción es el cambio de alguna cantidad positiva en el tiempo. De esta forma la producción de biomasa es un proceso sencillo de imaginar como un cambio de biomasa en un espacio de tiempo. Así, este cambio de biomasa debe contabilizar a los nuevos individuos que entraron en la población (reclutas), el cambio de masa por crecimiento individual y la pérdida en masa de los individuos que salen de la población (mortalidad). Por esto que desde los primeros métodos para estimar producción (Hamilton 1969) hasta los más recientes (Mertz and Myers 1998) incluyen explícitamente la mortalidad en su cálculo. En la teoría propuesta por Roa and Quiñones (1998) se utiliza la integral de la razón P/B con lo cual la mortalidad es cancelada, reflejando que esta razón es el resultado del más puro proceso individual. Este es el punto básico de división

entre el método de producción propuesto aquí y otros métodos de producción dinámicos ampliamente usados, que incluyen la mortalidad de forma explícita en la modelación. Ahora bien, la razón P/B es un proceso individual, pero la producción poblacional no lo es. En este modelo la mortalidad se encuentra intrínseca en la estructura de tallas (Van Sickle 1977) y la biomasa poblacional, lo que evita la necesidad de una estimación de mortalidad para poder obtener producción poblacional. Esto nos entregaría, en comparación a los otros métodos, una estimación más precisa debido a que la mortalidad natural es un parámetro difícil de obtener y es una de las principales fuentes de error en la evaluación de stock (Hampton 2000). Nuestro propósito aquí fue desarrollar un modelo de producción que demande el mínimo conocimiento de los parámetros de la población y sea de fácil muestreo. En resumen si se dispone de una estimación de los parámetros de crecimiento, un muestreo representativo de la estructura de talla y una estimación de biomasa, podremos predecir la producción poblacional en un año siguiente. Este procedimiento podría ser más adecuado bajo el enfoque de cruceros de investigación para la evaluación de stock, mientras que el modelo de Mertz and Myers (1998) puede ser más adecuado cuando se dispone de dinámica poblacional. Además este modelo puede ser útil en pesquerías incipientes o donde no se disponga de muchos años de investigación como las pesquerías tropicales.

La estimación de producción secundaria puede ser uno de los puntos más relevantes, en el manejo sustentable de los recursos naturales. En este contexto, la razón P/B puede ser considerada como un indicador del máximo rendimiento sostenible de una población, debido a que la razón P/B declina con respecto a la talla de los individuos (Roa and Wiff

(capítulo 1). Así las especies pequeñas pueden ser explotadas a tasas mayores que los individuos más grandes, debido a que presentan una tasa de renovación más alta pudiendo reemplazar la biomasa en un corto tiempo. Esta característica también permite que las especies sean más resilientes a las perturbaciones ambientales y en consecuencia pueden ser más exitosas ante un escenario de sobreexplotación.



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