UC Davis
UC Davis Previously Published Works

Title
Modeling growth and mortality of red abalone (Haliotis rufescens) in northern California.

Permalink
https://escholarship.org/uc/item/48d1r1gw

Journal
J. Shellfish Res., 26

Author
Rogers-Bennett, Laura, Dr.

Publication Date
2007

Peer reviewed

MODELING GROWTH AND MORTALITY OF RED ABALONE (*HALIOTIS RUFESCENS*) IN NORTHERN CALIFORNIA

LAURA ROGERS-BENNETT,[1,2]* DONALD W. ROGERS[3] AND STEVEN A. SCHULTZ[4]

[1]*California Department of Fish and Game and* [2]*Bodega Marine Laboratory University of California, Davis, P.O. Box 247, Bodega Bay, CA 94923* [3]*Chemistry Department, Long Island University, Brooklyn, NY 11201;* [4]*32200 Simpson Lane, Fort Bragg, CA 95437*

ABSTRACT We estimate annual growth and mortality of red abalone, *Haliotis rufescens*, in northern California using tag recapture data applied to multiple growth and mortality models. We investigate seven growth models of the form, $L_{t+1} = L_t + f(L_t)$, where L_t is the shell length at tagging (time t), L_{t+1}, is the shell length one year later, and the function $f(L_t)$ is a model of the change in length ΔL. Abalone are drawn from a broad range of sizes (shell lengths 5–222 mm) tagged and recaptured one year later ($n = 231$) in the Point Cabrillo Reserve in northern California. We present the results for seven growth models, rank the fit of the models (using the sum of the squared residuals) selecting the Richards, Gaussian, Ricker, and von Bertalanffy models (in that order) as most appropriate for these variable growth data. The von Bertalanffy model yields the shortest time to fishery (recreational legal size is 178 mm) as it slightly overestimates early growth. The Ricker model yields the longest time to enter the fishery underestimating early growth. We present a table of abalone sizes as a function of time for the Gaussian model, from which we estimate the number of years to grow into the fishery (12.0 ± 1 y). Because differences among the applicable models are not great, we use the growth parameters generated by the simple von Bertalanffy model (L_∞ and K) to estimate mortality. The results are consistent among our five mortality estimates ranging from 0.11–0.23 per year. Estimates of the number of years to enter the fishery and mortality estimates, as well as knowledge of how model selection can influence these estimates, is important for fishery management. Informed fishery management for red abalone is critical because the fishery in northern California is the last open abalone fishery in the state.

KEY WORDS: red abalone, Richards, logistic, Gaussian, von Bertalanffy, growth parameters, mortality parameters, northern California, fishery management

INTRODUCTION

Abalone populations have declined around the world, forcing the closure of many fisheries (Campbell 2000, Karpov et al. 2000, Shepherd et al. 2001). In California, the commercial and recreational abalone fishery, which once landed in excess of 3,000 metric tons in the 1960s, has collapsed (CDFG Code 5521) after the expansion of the sea otter's range (Vogel 2000) and the serial depletion of five species within the abalone complex (Dugan & Davis 1993, Karpov et al. 2000). Estimates of white abalone populations are so low that this species was placed on the federal endangered species list in May 2001 (Hobday et al. 2001). The black abalone is now a candidate species as a result of the combined pressures from fishing and the disease-withering syndrome (Haaker et al. 1992, Moore et al. 2002). Several other species in the genus *Haliotis* are proposed as species of concern (M. Neuman pers. comm.).

One exception to this pattern of declining abalone stocks in California has been populations of red abalone north of San Francisco that support a recreational fishery. An estimated 35,000 fishers caught 264,000 red abalone in 2002 (Kalvass & Geibel 2007) and landings in this fishery seem to be stable. The stability of the fishery in the north may be a consequence of unique management policies that combine traditional fishery management (size limits and season closures) with a prohibition of commercial fishing and the use of SCUBA. This contrasts sharply with southern California, where these additional restrictions were not in place and where history has shown abalone populations succumbed to multiple factors including

overfishing, sea otters, and disease. Population declines in the south highlight the need for precautionary management of the last abalone fishery in northern California.

Growth models and mortality estimates are needed to understand the population biology of abalone in California. Despite the need for growth information, modeling efforts have been hampered by (1) problems with model selection (Ebert & Russell 1993, Hernandez-Llamas & Ratkowsky 2004); (2) lack of data from a wide range of abalone sizes; and (3) lack of data from northern California where the recreational fishery is based. The von Bertalanffy function, which is commonly used to model abalone growth (Day & Fleming 1992), has been shown to overestimate juvenile growth for invertebrates (Yamaguchi 1975, Rogers-Bennett et al. 2003) including abalone, so other models such as the Gompertz model have been used (Day & Fleming 1992, Nash 1992, Matsuishi et al. 1995, Troynikov & Gorfine 1998). Several growth models should be examined to determine which fit growth data from red abalone in northern California best. Once parameter estimates have been made, they can be used to predict the time required to grow to legal size and instantaneous natural mortality rates. Previous growth estimates for red abalone in southern California have ranged widely from 5.6–11.3 y to reach minimum legal size (Tegner et al. 1989, Haaker et al. 1998) frustrating attempts to manage stocks in the north. Knowledge of the number of years required for wild abalone to grow into the fishery is essential for establishing sustainable take limits. Growth and mortality rates are also required to construct population models such as matrix models (Ebert 1999, Caswell 2001, Rogers-Bennett & Leaf 2006).

In this study, we estimate growth and mortality rates for red abalone, (*Haliotis rufescens*), in northern California. We use data from a tag-recapture study of red abalone growing for one

*Corresponding author: e-mail: rogersbennett@ucdavis.edu

year in northern California and input these data into seven growth models. We augment the size range of the tagging study using growth data from juvenile red abalone stocked into the tagging sites. We generate growth curves and estimate the number of years to reach minimum legal size in northern California. The models are ranked according to goodness of fit to the data, and appropriateness of each of the models for the data set is discussed. Selected models are tested for their sensitivity to changes (10%) in the parameter values. Mortality estimates are determined using the von Bertalanffy parameters and five methods of determining mortality estimates. The implications of these growth and mortality estimates as well as the choice of model are discussed in relation to their population biology and susceptibility to over-exploitation.

MATERIALS AND METHODS

Abalone Growth Data

A red abalone tag-recapture study was conducted in northern California (Shultz & DeMartini unpubl data). As part of this large growth study, changes in abalone length were determined after one year of growth in the Point Cabrillo Reserve at the Mendocino Headlands ($39°21'49''$N, $123°49'47''$W), California, USA. All fishing including recreational abalone fishing has been prohibited in the Point Cabrillo Reserve since 1975, and before this there may have been light fishing pressure in the northern portion of the reserve only. The subtidal area is a high energy exposed headland, dominated by high relief, rocky reefs with crevices and seasonally dense beds of kelp, excessive drift, *Nereocystis*, and annual laminarians.

Red abalone were tagged and recaptured over a five year period starting in summer 1971. The growth data presented here examined growth over one year. Shell length was measured at the time of tagging and then again 12 mo later when the tagged abalone were recaptured. Divers collected red abalone and brought them to the boat for tagging. Abalone were tagged using numbered stainless disc tags attached with stainless wires inserted into the first two open respiratory pores and then twisted tight. Of all the tagged abalone that were recaptured over this time period (>5,000) we used 208 in this study, because these were recaptured at or close to one year. We used only data from abalone that were recaptured one year after tagging at the north and south Point Cabrillo Cove site and most of these abalone were >100 mm in length. Fewer intermediate size abalone <100 mm were tagged in this study as smaller size classes were less common. A total of 38 abalone 50–100 mm in length were included in the data set and these abalone were recaptured 8–16 mo after tagging. For these intermediate size abalone, growth was determined per month then adjusted to estimate growth for one year. Months were assumed to equal 30 days.

To supplement growth information for juvenile abalone (<50 mm) we included growth of juveniles from a stocking study. Juvenile abalone and other invertebrates occupy deep crevices under large rocks, avoid light, feed on microalgae and are difficult to find. Little growth information for these small size classes exists. Stocking of large numbers ($n = 10,000$) of hatchery produced juvenile red abalone made it possible to follow juvenile red abalone growth at the Mendocino headlands over one year in the field. The shells of the juveniles were turquoise or pale green from the hatchery diet distinguishing them from wild stock. Stocking took place in October 1995 at the Mendocino headlands just north of the Point Cabrillo Reserve (near Caspar Cove), and the abalone were recaptured one year later. Growth data was obtained from red abalone ranging in size at the time of stocking from 5–30 mm (Rogers-Bennett & Pearse 1998). Of more than 10,000 juveniles stocked, positive identification of recaptured hatchery reared juveniles was made for 23 abalone from this site. The pale blue/green coloration allowed for the measurement of shell length at the time of stocking and then the final shell length (red shell) was measured at the time of recapture.

Growth Models

We investigated seven models, the Richards, logistic dose-response, Gaussian, Tanaka, Gompertz, Ricker, and von Bertalanffy models of red abalone growth. Each model yields a different $f(L_t)$, which approximates ΔL, the annual change in shell length of a representative member of the population. Here $f(L_t)$ is a function fitted to a data set consisting of measured individual annual growth $\Delta L = L_{t+1} - L_t$ *versus* size at tagging, L_t. Eqs. 8–15 later were input as user defined functions into a curve-fitting program. In certain cases, additive parameters in the model equations making a negligible contribution to the final fit were dropped. This curve-fitting program uses the Levenburg-Marquardt procedure for finding the minimum of the squared sum of deviations. During the least-squares minimization, local minima were occasionally found and were discarded in favor of the global minima. Matrix inversion was done using the Gauss-Jordan method (Carnahan et al. 1969).

We ranked the models according to the fitting criterion of the sum of squared residuals (SSR), called "Error Sum of Squares" in the output from the Table Curve fitting program. Rankings from other fitting criteria were also calculated including both the AIC information criterion, $AIC = \kappa \ln(RSS) - \kappa \ln \kappa + 2m$ and the Schwartz-Bayesian criterion $SBC = \kappa \ln(RSS) - (\kappa - m) \ln(\kappa)$ where κ is the number of data points and m is the number of parameters in the fitting equation (Akaike 1979). These tests of curve fitting quality were used to bring out substantive differences between the 2-parameter and 3-parameter equations. The results show that differences between the 2- and 3-parameter cases are swamped out by the data set, as might be anticipated from the disparity between the number of data points ($\kappa = 231$) and the number of parameters. For the present data set, in applying either of these criteria, one is essentially seeking the smallest SSR.

Growth as a Function of Time

Having $\Delta L = f(L_t)$ from Figure 1, one can assume a small (essentially zero) initial size at settlement and determine the size 1, 2, 3, … y after settlement using a simple loop in BASIC or by any similar recursive calculation. Growth curves $L = f(t)$ shown in Figure 2 yield an estimated time to fishery unique to each model. The Richards, Gompertz, and von Bertalanffy functions are members of the same mathematical family and are shown as the Richards group in Figure 2.

Mortality Estimates

Mortality estimates can be made without knowledge of age if K is known. Mortality estimates using tag recapture data
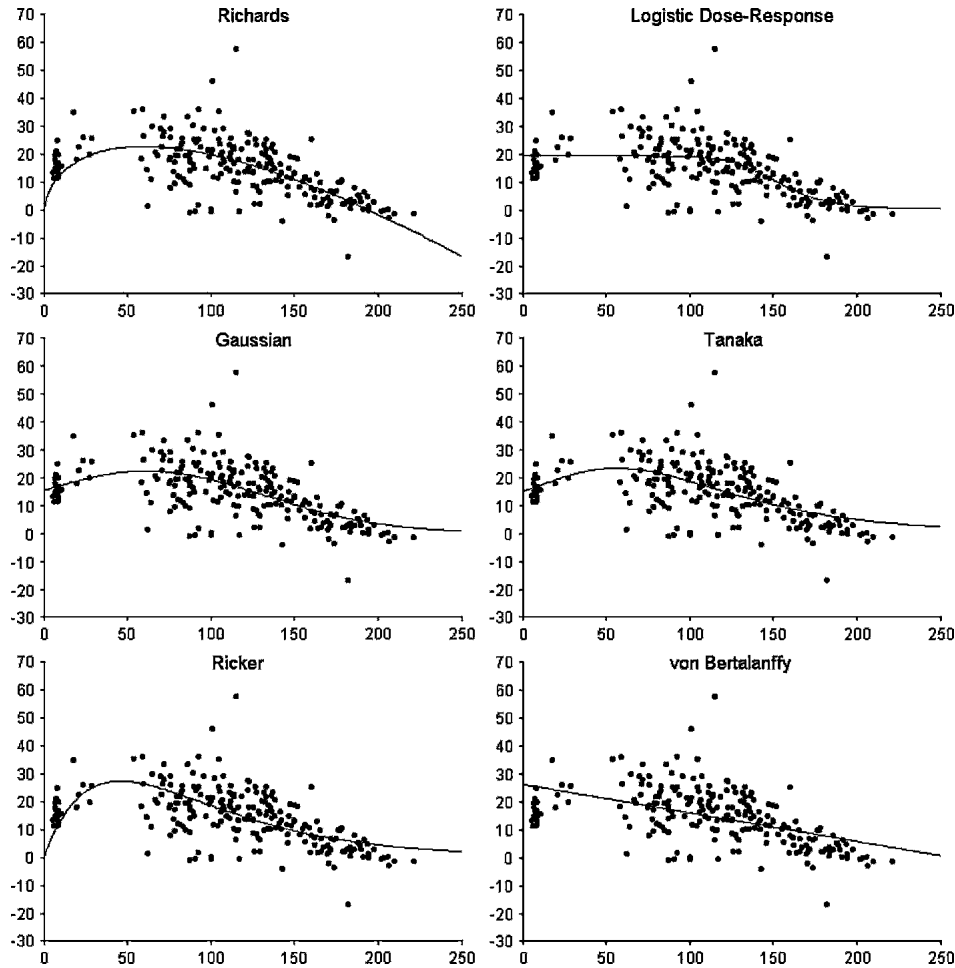
Figure 1. Growth (change in length) as a function of shell length for red abalone growing for one year in northern California. Growth of juvenile abalone <50 mm are from juveniles stocked in the wild for one year. Six growth models are fitted to the same data using the Richards, Logistic dose-response, Gaussian, Tanaka, Ricker, and von Bertalanffy models.

alone have been shown to agree closely with estimates generated when ages are known (Ssentongo & Larkin 1973). Mortality has been estimated for abalone, *H. iris*, using von Bertalanffy parameters by a number of different methods (Sainsbury 1982). The instantaneous total mortality rate Z is equal to the instantaneous total mortality rate M when no fishing is allowed such as inside the Point Cabrillo Reserve where these data were collected. Total mortality Z is estimated as follows:

Method 1: Beverton Holt (1956)

$$Z = \frac{K(L_\infty - \bar{l})}{\bar{l} - l_c} \tag{1}$$

where L_∞ = asymptotic abalone length, $\bar{l}$ = the mean length of abalone in the sample and l_c = length of smallest abalone in the sample. The derivation assumes that mortality and recruitment are constant, the population has a stable age distribution, and individual growth is described by the von Bertalanffy model.

Method 2: Ssentongo & Larkin (1973)

$$Z = \frac{n}{n+1} \frac{K}{\log_e(1 - l_c/L_\infty) - \log_e(1 - \bar{l}/L_\infty)} \tag{2}$$

where n = sample size.

Method 3. Alverson & Carney (1975)

$$Z = M = \frac{3K}{e^{KTmb} - 1} \tag{3}$$

where T_{mb} = critical age

Method 4. Pauly's empirical mortality equation (Pauly 1984).

$$\text{Log(M)} = -0.0066 - 0.279 \log(L_\infty) + 0.6543 \log(K) + 0.4634 \log(T) \tag{4}$$

Method 5. Jolly Seber

A Jolly-Seber tag and recapture model was used to estimate the instantaneous rate of total mortality (Jolly 1965, Seber 1965) of red abalone from surveys of the North Point Cabrillo Cove Reserve population. Model assumptions include equal probability of dying for all individuals, equal catchability and closed population. Red abalone were sampled after one year (±60 days). The Jolly-Seber model was used in the MARK program in which the parameters were held constant (White & Burnham 1999).

RESULTS

We present growth data for 170 adult, 38 juvenile (50–100 mm) and 23 young of the year (5–30 mm) red abalone growing
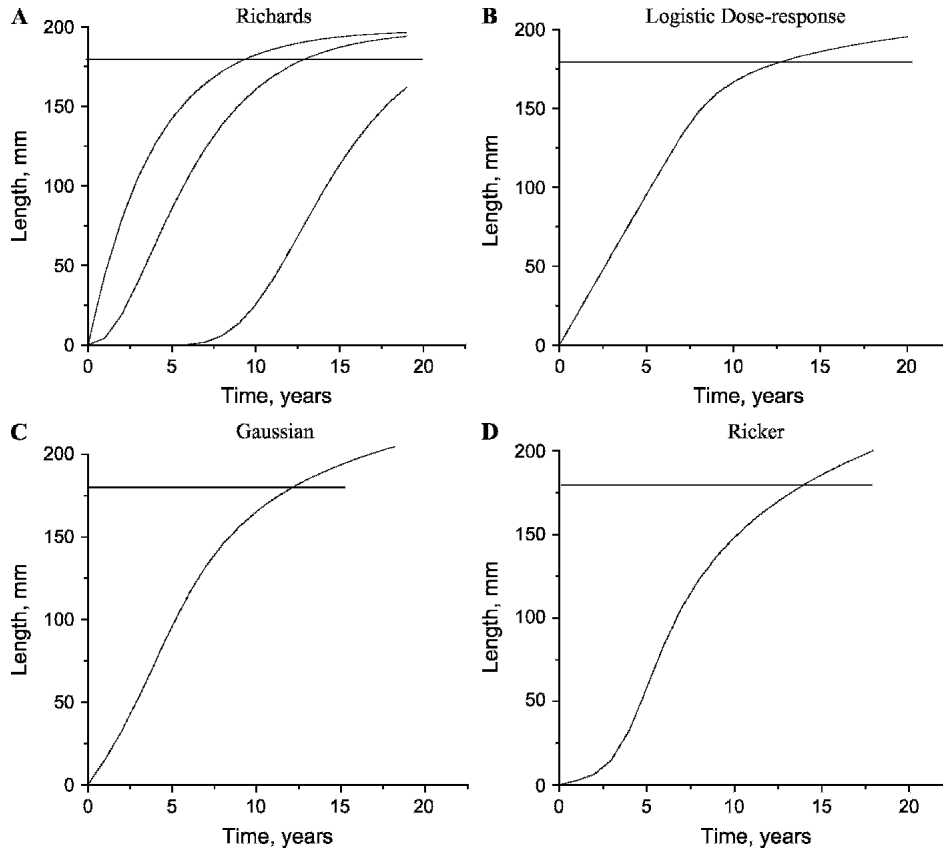
Figure 2. Length as a function of time in years according to selected growth models. The Richards model includes the Gompertz (rightmost curve) and the von Bertalanffy (leftmost curve) models as special cases. Horizontal lines indicate the minimum legal size (178 mm) of red abalone in northern California.

near the Mendocino headlands, in northern California for one year. Recaptured red abalone ranged in size from 5–222 mm at the time of tagging. Growth was greatest for red abalone in the 50–100 mm size class and least for the largest abalone although there was individual variation. Outliers and cases in which final measurements (after 12 mo) were less than initial measurements (negative growth) were not discarded. It is interesting to note that the six largest abalone had either negative or zero growth after one year, which may have been caused by measurement error or shell infestations.

Using the Jolly Seber methods we estimate the probability of recapture to be $P = 0.334$ (SE = 0.018).

Length-weight Relationship

The relationship between the length (L) and the weight (W) of an organism can be expressed

$$W = a \times L^b \qquad (5)$$

For red abalone, as for many other species, $b = 3$ or is not significantly different from 3 and $a =$ is very small. We used a large sample ($n = 576$) of red abalone from the recreational fishery at Van Damme State Park (near the reserve tag site) in 2000–2002 to determine the relationship between length and weight. We find that $W = 0.0001 \times L^{3.03}$. Because growth is isometric ($b = 3$), we can also determine that the condition factor ($c.f.$) is related to a as $c.f. / 100 = a$ so $c.f. = 0.01$.

Estimating Asymptotic Size

Estimates of L_∞, have been made by simply taking the largest length recorded from a given stock. The record is $L_{max} = 313.18$ mm for a red abalone taken by J. Pepper in Humboldt County, northern California. Taylor (1958) suggests that $\frac{L_{max}}{0.95} \cong L_\infty$, therefore, L_∞ would be larger than the largest abalone taken. For red abalone this would be $L_\infty = 329.66$ mm.

Growth conditions experienced by the record abalone, however may not be typical for the entire north coast. Therefore, it may be more appropriate to average several large abalone from multiple stocks or populations rather than use the record individual for the species as a whole. The 14 largest red abalone recorded from the recreational fishery average 287.8 mm (Macias 1999).

$$\text{Mean } \frac{L_{max}}{0.95} \cong L_\infty \qquad (6)$$

Using the mean of the 14 largest red abalone for L_{max}, $L_\infty = 303$ mm.

Growth Models

We modeled red abalone growth using seven growth models, the Richards, logistic dose-response, Gaussian, Tanaka, Gompertz, Ricker, and von Bertalanffy models (Table 1), and we rank them in order of quality of fit (Fig. 1 and Table 2) according to the sum of squared residuals (SSR). In each of the following equations, $f(L_t)$ is a model of growth as a function of L_t fitted to measured annual growth of abalone tagged at

<div align="center">

TABLE 1.

Parameter values for the red abalone size *versus* time growth curves. Models are ordered according to goodness of fit (see Table 2). Time to fishery (TTF) in years (minimum legal size) and sensitivity of TTF in years to 10% changes in the parameter values are presented. Functions are for length at $t + 1$.

</div>

Functions		Parameters	TTF	Sensitivity
Parameters		SSE		t_f, y
Richards	$[L_i^{-1/n}(1 - e^{-K}) + L_t^{-1/n}e^{-K}]^{-n}$	Li = 201.0 mm K = 0.254 y^{-1} n = −2.76	13.0 y	13.9–20 y
Logistic D R	$a/(1 + (L_t/b)^c)$	a = 19.1 b = 153.2 c = 10.2	12.2 y	
Gaussian	$Ae^{-(L-m)^2/2s^2}$	A = 22.0 mm m = 62.0 mm s = 70.3 mm	12.0 y	10.8–12.8 y
Gompertz	$[L_i^{-1/n}(1 - e^{-K}) + L_t^{-1/n}e^{-K}]^{-n}$	Li = 193.1 K = 0.316 y^{-1} N = 8.88 e^{+9}	15.5 y	
Tanaka	$1/\%f \; \ln\|2G + 2\%G^2 + fa\| + d$ $G = E/4 - fa/E + f$ $E = \exp(\%f \, (L_t - d))$	f = 0.0001 d = 453.6 a = 0.002	11.6 y	
Ricker	$BL_t \, e^{-K \, Lt}$	B = 1.59 mm K = 0.0216 y^{-1}	13.5 y	11.5–15.2 y
von Bertalanffy	$L_{inf}(1 - e^{-K}) - L_t(1 - e^{-K})$	L_{inf} = 254.2 mm K = 0.108 y^{-1}	11.3 y	10.3–14 y

length L_t. If L_t were known at some time t, adding $f(L_t)$ to it would yield the length at time $t + 1$ y. In tag-recapture studies, however, the age is not known. Curves in Figure 2 were generated by assuming the size of the animal to be near zero at $t = 0$, building the growth curve year by year by adding sequential annual increments $f(L_t)$.

There is more growth information for large abalone and so the statistical parameters are dominated by the larger abalone (see especially the Tanaka model). There is a good deal of scatter, which leads to rather poor statistical fitting parameters. Growth curves in Figure 1, especially the one corresponding to the Gaussian model, are, in our opinion, the best that can be extracted from the data set. There is redundancy among the Richards, Gompertz, and von Bertalanffy models, which are shown to be mathematically equivalent in the discussion relating to Figure 2.

Richards

As Ebert (1999) points out, the Richards function (time-to-fishery estimate = 13.0 y) incorporates the von Bertalanffy (time-to-fishery = 11.2 y)

<div align="center">

TABLE 2.

Fitting criteria for seven functions used to model red abalone growing in northern California.

</div>

	R^2	SSR	AIC	BIC	# Parameters
Richards	0.408	13444	933	955	3
Logistic	0.407	13460	933	955	3
Gaussian	0.391	13836	939	961	3
Gompertz	0.377	14137	944	967	3 (or 4)
Tanaka	0.370	14305	947	969	3
Ricker	0.330	15215	961	984	2
von Bertalanffy	0.273	16515	982	1003	2

$$L_t = L_\infty(1 - e^{-kt}) \qquad (7)$$

and Gompertz (time-to-fishery = 15.5 y where n is large) models

$$f(L_t) = \left[L_\infty^{-1/n}(1 - e^{-K}) + L_t^{-1/n}e^{-K}\right]^{-n} \qquad (8)$$

according to the value of a "shape parameter" n allowing for an inflection in the curve of L *versus*. t (Richards 1959, Ebert 1980, 1999).

$$L = L_\infty(1 - be^{-Kt})^{-n} \qquad (9)$$

When $n = -1$ this equation is the von Bertalanffy model, and when n is very large and negative, the expression for L converges on the Gompertz model. Strictly, the term Gompertz should be used when $n = \infty$ leading to

$$L(t) = e^{-e^{g(t-t_i)}}$$

where t_i is the time at which the inflection point is reached. Ebert (1999) refers to the "Richards family of growth curves," which include von Bertalanffy, logistic, and Gompertz curves as special cases.

Minimization of the fitting parameters in Eq. 8 leads to $L_\infty = 201$ mm, $K = 0.254$ y^{-1}, and $n = -2.76$ (unitless) with SSR = 13,444. In general, there is another parameter, b, to be determined

$$b = \frac{(L_\infty - L_{settle})}{L_\infty} \qquad (10)$$

where L_{settle} is the shell length at settlement. In the present case, L_{settle} is very small relative to L_∞, therefore b is essentially 1.

Minimization is difficult because of the singularity at $n = 0$ and the existence of multiple minima. Minimization of the Richards function from small negative values of n (which is not a linear parameter) and reasonable guesses as to L_∞ and K, leads to a curve with diminishing slope as L_t increases (Fig. 1).

The SSR is better than it is for the true von Bertalanffy case (leftmost curve, Richards, Fig. 2) because there is one more fitting parameter. The equation with n taking on negative values, which may be large from $-1, -10, -100, \ldots, -1\,000\,000$ tending to ∞ yields a family of quasi-sigmoidal Gompertz curves spaced at equidistant intervals from the origin with vertical inflection points from 8 to about 75 y. These impossibly long induction periods preceding growth is often compensated for by means of a negative additive parameter (Matsuishi et al. 1995), Gompertz curves are not strictly sigmoidal; for example, the curve at $n = -100\,000$ first rises above $f(L_t) = 0$, the *Length* axis, at 38 y and attains L_∞ at about 70 y; but the vertical inflection point is at only 47 y, in contrast to the vertical inflection at 56 y that one would expect of a truly sigmoidal curve, for example, the cumulative Gaussian distribution (Rogers 1983). Adjusting the base of the Gompertz curve (rightmost curve in, Richards, Fig. 2) using an additive constant of -7 y, moving the curve toward the origin, gives a time-to-fishery = 15.5 y. We do not consider this procedure optimal.

Logistic Dose-Response

The logistic dose-response curve (time-to-fishery estimate 12.2 y)

$$f(L_t) = a/(1+(L_t/b)^c) \qquad (11)$$

(Hastings 1997) fits our data with $a = 19.1$, $b = 153.2$, $c = 10.2$ and SSR = 13,460. It is a reverse sigmoidal transition function (TableCurve Windows V 1.0 User's Manual, Jandel Scientific Corp.). Although the fit is good, leading to a small sum of squared residuals, we reject the logistic dose-response model because it implies a long period of constant growth followed by a rather sharp drop to low growth (Fig. 1). This produces a linear portion of the growth curve, followed by a short transition to another linear growth function (Fig. 2). We believe that this is unrealistic and that this behavior does not accurately reflect individual red abalone growth or the average growth of a population of abalone. We do not select the logistic dose-response curve because of this unusual transition behavior and the fact that the time-to-fishery estimate is comparable to that of the Gaussian.

Gaussian

The Gaussian function (time-to-fishery estimate 12.0 y),

$$f(L_t) = Ae^{-(L_t-\mu)^2/2\sigma^2} \qquad (12)$$

fits the data well, having an SSR = 13,836, which is comparable to that of the Richards (time-to-fishery 13.0 y) and logistic dose-response (time-to-fishery 12.2 y) models. It is a three-parameter model (Rogers 1983) for which the parameters are well defined including maximum growth ($A = 22.0$ mm y^{-1}), size at maximum growth ($\mu = 62.0$ mm), and standard deviation ($\sigma = 70.2$ mm) of the distribution of maximum growth *versus* size. The initial annual growth rate is $\Delta L = 15.0$ mm y^{-1}. A strength of the Gaussian model, aside from its good fit, is that it provides a plausible growth model (Figs. 1 and 2) with maximum ΔL, at a shell length about one third that of legal size (as opposed to other models which predict a maximum ΔL at settlement near the Y axis, which seems biologically unrealistic), and that the parameters are mathematically well-defined. In this model,

annual growth is randomly distributed, according to shell length, about the maximum in ΔL.

Tanaka

The Tanaka equation (time-to-fishery estimate 11.6 y)

$$f(L_t) = \frac{1}{\sqrt{f}}\ln\left|2G + 2\sqrt{G^2 + fa}\right| + d - L_t \qquad (13)$$

where $G = \dfrac{E}{4} - \dfrac{fa}{E} + f$ and $E = \exp(\sqrt{f}(L_t - d))$ can be obtained from its differential form (Tanaka 1982, Ebert 1999). In this equation the variables do not have a biological interpretation.

$$\frac{dL}{dt} = \frac{1}{\sqrt{f(t-c)^2 + a}} \qquad (14)$$

using a standard integral (Barrante 1998).

The Tanaka equation has been used to model sea urchin growth (Tanaka 1982, Ebert & Russell 1993) and is discussed in Ebert (1999). Although the curve fit in Figure 1 appears to be good (SSR = 14,305), and the curve shape is reasonable, one cannot generate a reasonable growth curve from this function because the estimated length at infinite time is 453 mm, quite unrealistic for abalone (140 mm over the world's record), which are not found to exceed 222 mm in length in this data set. We reject this curve as well. Translation of the Tanaka model into a growth curve to yield size at age is unsuccessful owing to generation of very small and very large parameters in the model.

Ricker

The Ricker function (time-to-fishery 13.5 y) for population growth (Hastings 1997) translated into terms of abalone growth is

$$f(L) = BL_t e^{-KL} \qquad (15)$$

(Ricker 1954). This model also yields a maximum in $f(L_t)$ the growth function and an asymptotic approach to zero that characterize the data set (Fig. 1). The empirical fitting parameters are, maximum growth rate constant, $B = 1.59$ (unitless) and $K = 0.0216$ mm^{-1}, a constant, which controls decrease in growth rate as the animal gets larger. Fit to the present data set, it gives SSR = 15,215. Initially, L_t is very small and $\Delta L = BL_t$. At larger L_t, annual ΔL passes through a maximum as the negative exponential becomes important. Growth, though never zero, will eventually be too small to measure over a one-year period. This model requires an arbitrary specification of the shell size at settlement (e.g., 0.1 mm) to which the resulting $f(L_t)$ curve is quite sensitive.

von Bertalanffy

The von Bertalanffy function (von Bertalanffy 1938), time-to-fishery estimate is found by substituting the legal limit, 178 mm for L_t in Eq. 16 and solving for $t = 11.2$ y.

$$L_t = L_\infty(1 - e^{-Kt}) \qquad (16)$$

or

$$L_{t+1} = L_t + L_\infty(1 - e^{-K}) - L_t(1 - e^{-K}) \qquad (17)$$

leads to a linear decrease in growth rate as a function of size. L_{t+1} and L_t in Eq. 17 refer to a discrete data set whereas L_t in

Eq. 16 is a smooth, continuous function of t. Fit to the present data set, the von Bertalanffy model gives SSR = 16,515. (The time to fishery estimate from the leftmost curve in the Richards Figure 2 differs from this value owing to use of normalized Richards parameters in Figure 2 rather than von Bertalanffy parameters, done for the purpose of illustration.)

Sensitivity to Changes in the Parameters

We examined the robustness of each of the time to fishery estimates in four of the seven models by changing them ±10% then noting the behavior of the model. Results are given in the last column of Table 1. In the first model, the Richards function, ±10% variation in the parameters yields a large change in the estimate of years to fishery from 14–20 y. The Gaussian model estimate of 12.0 y to fishery changes less than 2 y with 10% changes in the parameter estimates, another point in favor of the Gaussian model. Other models gave estimated time to enter the fishery variations over the range shown. See Schnute (1981) and Ebert (1999) for discussions of parameter sensitivity.

Mortality Estimates

Method 1. Beverton & Holt (1956)

$$Z = 0.136/y$$

where $l = 115.33$ mm and

$$l_c = 5 \text{ mm}$$

where $L_\infty = 254.2$ mm, $k = 0.108$ y^{-1}.

Method 2. Ssentongo & Larkin (1973)

$$Z = 0.187/y$$

where $L_\infty = 254.2$ mm, $k = 0.108$ y^{-1}, $l_c = 5.0$ mm and, $l_m = 115.33$ mm.

Method 3. Alverson & Carney (1975)

$$Z = M = 0.113/y$$

where $k = 0.108$ y^{-1} and

$$T_{mb} = (\text{max age 50})(0.25) = 12.5$$

where $L_\infty = 254.2$ mm and $k = 0.108$ y^{-1}.

Method 4. Pauly's Empirical Equation

$$Z = M = 0.270*/\text{year}$$

where Asymptotic length = 25.4 cm and von Bertalanffy growth constant $k = 0.108$ y^{-1} and T = mean habitat temp and in this case we use 10°C.

* Note: Pauly cautions that this method may be less useful for sessile invertebrates than for fin-fish.

Method 5. Jolly Seber

$$Z = M = 0.228/y(\text{SE} = 0.017).$$

where ($L_\infty = 254.2$ mm, $k = 0.108$ y^{-1}).

DISCUSSION

Our results indicate that red abalone are slow growing animals requiring approximately 12.4 ± 1 years (mean of the four selected models) to reach the minimum legal recreational size (shell length of 178 mm) in northern California. We examine seven models, but we reject three of them outright

(reasons given in the results section). The range in estimates of time to reach the fishery from the four models is quite narrow (11.3–13.5 y) suggesting that our results are robust to model selection. Estimates from these diverse models yield remarkably similar results and the ranking of these diverse models according to goodness of fit (as measured by SSR) shows that they differ only slightly (Table 2).

We find that the Gaussian model is the most suitable of the seven models, for describing growth using our data set and perhaps other abalone data sets. The advantages of the Gaussian model include a realistic description of growth over the range of sizes examined (Fig. 1), a good fit to the data as seen by the SSR value (Table 2), and a time to fishery prediction, which is robust to 10% changes in the parameter values (Table 1). For these reasons we have selected the Gaussian model to illustrate growth for red abalone over time (Table 3).

Our results indicate that red abalone grow more slowly in northern California than in southern California. In the south, red abalone growth estimates derived from a single model, the von Bertalanffy model ranged from 5.6–11.3 y for the time necessary to grow to minimum legal size (Haaker et al. 1998). Kelps in southern California are perennials offering a more steady supply of food resources compared with annual kelps in northern California. In addition, red abalone in the south exhibited interannual and individual variation in growth (Haaker et al. 1998). Variation in individual growth is common for abalone and many marine invertebrates (Yamaguchi 1975, Troynikov & Gorfine 1998). Future work could examine spatial and temporal patterns in red abalone growth in northern California. Observation suggests that high wave energy habitats with high rock relief and or large boulder habitats with abundant drift algae and low incidences of shell infestation are conditions that promote abalone growth.

Previous estimates of red abalone growth have been made from limited growth data sets lacking juvenile growth information. In this study, we used growth data from a wide range of abalone sizes from 5–222 mm in shell length. As in some other growth studies (Urban 2002, Rogers-Bennett et al. 2003), growth information from small animals was supplemented, because growth of small size classes is important for defining the left side of the curve and is typically difficult to obtain. A common problem arising from a lack of information on juvenile growth rates has been overestimating growth of the smallest

TABLE 3.

Gaussian models predictions of red abalone shell length (mm) of ages 1–30 y. Age and length in bold type are age at minimum legal size for northern California.

Age	Length	Age	Length
1	16.1	10	166.0
2	33.9	11	173.3
3	54.3	**12**	**179.6**
4	76.2	13	185.0
5	97.8	14	189.9
6	117.1	15	194.0
7	133.3	20	209.5
8	146.5	25	220.1
9	157.2	30	228.0

individuals, a problem confounded by the use of the von Bertalanffy model (Yamaguchi 1975). This problem could lead to shorter time to fishery estimates and therefore more lenient fishing policies. Slow growth suggests that conservative fishing policies may need to be maintained for the red abalone fishery in northern California.

Ideally, results from the models presented here using tag recapture data would be compared with growth estimates derived from other methods as well as examining the impacts of tagging on growth. Growth information can be obtained from a time series of size frequency distributions from which one can track the modal progression of young abalone through the size frequency distribution over time. Unfortunately, in the case of red abalone in northern California such a time series does not exist nor are there other estimates of growth available.

Individual growth in red abalone is highly variable as has been observed in other marine invertebrates. Therefore, whereas red abalone grow to legal size in approximately 12 y, some individuals will grow faster and some slower. Our data contain dispersion in the region of the smallest size classes consistent with high individual variation in growth (K). Varying the growth constant, K, (e.g., in the Ricker model [cf. Sainsbury 1980]), produces dispersion at the smaller size classes. In addition, our abalone growth data show a wide array of large (final) sizes. We see a broad distribution in the largest size classes in our data, with animals larger and smaller than the estimated final size L_∞. It is possible that many of the animals smaller than L_∞ could be at their final size.

The biological interpretation of this broad distribution at the largest sizes remains an important unanswered question. There may be a wide array of final sizes because of independent values of K and L_∞ (cf. Sainsbury 1980) with each individual arriving at an individual final size (L_∞), or a more gradual approach to final size (cf. Beverton 1992) caused by slow continuous growth also known as indeterminate growth (cf. Sebens 1987) or a combination of the two. Given the first scenario, a certain proportion of adults may never reach the minimum legal size even at their final size, as has been suggested in other abalone fisheries (Troynikov & Gorfine 1998) and groups of small adult abalone have been coined "short beds." This implies that a minimum legal size would effectively exclude these small adults from the fishery (because they would never reach the minimum legal size). Protecting small adults could have evolutionary implications for the population and could decrease yields after many generations if fishing is intense, and refuges are eliminated (Conover & Munch 2002). Given the second scenario, these animals would not be protected from the fishery forever and as they grow very slowly, they would eventually recruit into the fishery. We are not aware of any conclusive studies that determine if one or both of these scenarios occurs for red abalone. This is an area for further research.

The von Bertalanffy model is suitable for generating mortality estimates because there were few differences in the estimates generated by the four selected growth models. The natural mortality estimates derived from the five methods used also yield similar estimates. Using the von Bertalanffy parameters we get mortality estimates ranging from 0.11–0.23 per year (because we reject Pauly's method) for the population studied. Changing the final size L_∞ parameter from 254 mm (von Bertalanffy estimate) to 303 mm (Taylor estimate [Taylor 1958]) would result in an increase in the mortality estimate. Caution must be taken however, not to overestimate natural mortality, because bias in this direction would lead to lower estimates of optimal age at first capture in fishery models biasing estimates of egg production potentially leading to overfishing (Sluczanowski 1984).

Previous studies have found comparable mortality estimates of 0.15 per year for red abalone in southern California (Tegner et al. 1989). Higher mortality rates (0.3–1.0) were found for red abalone inside the range of the predatory sea otter in central California (Hines & Pearse 1982), and inside fished sites (1.02–1.35) in northern California (Leaf et al. 2007), as might be expected. For large juveniles and adults it has been suggested that natural mortality may not vary significantly (Shepherd et al. 1982, Sainsbury 1982). In northern and southern California, mortality estimates were greater for the smallest size class (<100 mm) compared with larger size classes (Leaf et al. 2007). Moreover, mortality estimates differed across sites (with varying fishing pressure) whereas in southern California, mortality varied between years (Leaf et al. 2007).

Our results indicate that the growth and mortality estimates derived for red abalone using this data set are fairly robust to decisions regarding model selection. Results from these models suggest, red abalone life history parameters appear to be characterized by slow growth and low to intermediate natural mortality rates. Consistency in the growth estimates from these varied models lend confidence to our results of 12 y to grow (178 mm) into the fishery in the north. Similarly, mortality estimates using the same data set and multiple models resulted in a narrow range 0.11–0.23 y^{-1} of estimates. Knowledge of growth and mortality estimates, as well as how these estimates are influenced by model selection, is critical for managing abalone fisheries and guiding restoration strategies for depleted populations.

LITERATURE CITED

Akaike, H. 1979. A bayesian extension of the minimum AIC procedure of autoregressive model fitting. *Biometrika* 66:237–242.

Alverson, D. L. & M. J. Carney. 1975. A graphic review of the growth and decay of population cohorts. *J. Cons. Int. Explor. Mer.* 36:133–143.

Barrante, J. R. 1998. Applied mathematics for physical chemistry. 2nd ed. Prentice Hall, Upper Saddle River, NJ. pp. 227.

Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish Biol.* 41:137–160.

Beverton, R. J. H. & S. J. Holt. 1956. A review of methods for estimating mortality rates in fish populations, with special references to sources of bias in catch sampling. *Rapp. P-V Reun. Cons. Int. Explor. Mer.* 140:67–83.

Campbell, A. (Editors). 2000. Workshop on rebuilding abalone stocks in British Columbia. *Can. Spec. Publ. Fish. Aquat. Sci.* 130:1–150.

Carnahan, B., H. A. Luthier & J. O. Wilkes. 1969. Applied numerical methods. New York, NY:Wiley Press. pp. 604.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer, 2nd ed. USA. 722 pp.

Conover, D. O. & S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297:94–96.

Dugan, J. E. & G. E. Davis. 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* 50:2029–2042.

Day, R. W. & A. E. Fleming. 1992. The determinants and measurement of abalone growth. In: S. A. Shepherd, M. J. Tegner, & S. A. Guzmán del Próo, editors. Abalone of the world: biology, fisheries and culture. Oxford: Blackwell Scientific. 141–168.

Ebert, T. A. 1980. Estimating parameters in a flexible growth equation, the Richards function. *Can. J. Fish. Aquat. Sci.* 37:687–692.

Ebert, T. A. 1999. Plant and animal populations: methods in demography. San Diego: Academic Press. pp. 312.

Ebert, T. A. & M. P. Russell. 1993. Growth and mortality of subtidal red sea urchins *Strongylocentrotus franciscanus* at San Nicolas Island, California, USA: problems with models. *Mar. Biol.* 117:79–89.

Haaker, P. L., D. O. Parker, K. C. Barsky & C. Chun. 1998. Growth of red abalone, *Haliotis rufescens* (Swainson), at Johnson's Lee Santa Rosa Island, California. *J. Shellfish Res.* 17:747–753.

Haaker, P. L., D. O. Parker, H. Togstad. D. V. Richards, G. E. Davis & C. S. Friedman. 1992. Mass mortality and withering syndrome in black abalone, *Haliotis cracherodii*, California. In: S. A. Shepherd, M. J. Tegner, & S. A. Guzmán del Próo, editors. Abalone of the world. Oxford: Blackwell Scientific. pp. 214–224.

Hastings, A. 1997. Population biology concepts and models. New York: Springer-Verlag. pp. 227.

Hernandez-Llamas, A. & D. Ratkowsky. 2004. Growth of fishes, crustaceans and mollusks: estimation of the von Bertalanffy, Logistic, Gompertz and Richards curves and a new growth model. *Mar. Ecol. Prog. Ser.* 282:237–244.

Hines, A. H. & J. S. Pearse. 1982. Abalone, shells and sea otters: dynamics of prey populations in central California. *Ecol.* 63:1547–1560.

Hobday, A. J., M. J. Tegner & P. L. Haaker. 2001. Over-exploitation of a broadcast spawning marine invertebrate: Decline of the white abalone. *Rev. Fish Biol. Fish.* 10:493–514.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both dead and immigration-stochastic model. *Biometrika* 52:225–247.

Kalvass, P. K. & J. J. Geibel. 2007. California recreational abalone fishery catch and effort estimates for 2002 from a combined report card and telephone survey. *Calif. Fish and Game.* (In press).

Karpov, K. A., P. L. Haaker, I. K. Taniguchi & L. Rogers-Bennett. 2000. Serial depletion and the collapse of the California abalone (Haliotis spp.) fishery. *Can. Spec. Publ. Fish. Aquat. Sci.* 130:11–24.

Leaf, R. T., L. Rogers-Bennett & P. L. Haaker. 2007. Spatial, temporal and size specific variation in mortality estimates of red abalone, *Haliotis rufescens* from mark-recapture data in California. *Fish. Res.* 83:341–350.

Macias, F., Jr. 1999. All abalone are deaf. Gualala, CA: Platt and Co.

Matsuishi, T. K., S. Saito & Y. Kanno. 1995. Growth curve of abalone. *Bull. Faculty Fish Hokkaido Univ.* 46:53–62.

Moore, J. D., C. A. Finley, T. T. Robbins & C. S. Friedman. 2002. Withering syndrome and restoration of southern California abalone populations. *California Cooperative Oceanic Fisheries Investigations Reports* 43:112–117.

Nash, W. J. 1992. Growth of blacklip abalone (*Haliotis rubra*) in Tasmania. *Proc. Bur. Rural. Resour.* 12:137–141.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM studies and reviews 8. Manila, Philippines.

Richards, F. J. 1959. A flexible growth curve for empirical use. *J. Exp. Bot.* 10:290–300.

Ricker, W. E. 1954. Stock and Recruitment. *J. Fish. Res. Board Can.* 11:559–623.

Rogers, D. W. 1983. BASIC microcomputing and biostatistics. The Humana Press Inc., Totawa, NJ. pp. 274.

Rogers-Bennett, L. & J. S. Pearse. 1998. Experimental seeding of hatchery-reared juvenile red abalone in northern California. *J. Shellfish Res.* 17:877–880.

Rogers-Bennett, L. & R. T. Leaf. 2006. Elasticity analyses of size-based red and white abalone matrix models: Management and conservation. *Ecol. Apps.* 16:213–224.

Rogers-Bennett, L., D. W. Rogers, W. A. Bennett & T. A. Ebert. 2003. Modeling red sea urchin (*Strongylocentrotus franciscanus*) growth using six growth functions. *Fish. Bull. (Wash. DC.)* 101:614–626.

Sainsbury, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* 37:241–247.

Sainsbury, K. L. 1982. Populations dynamics and fishery management of the paua, *Haliotis iris* I. Population structure, growth, reproduction and mortality. *N. Z. J. Mar. Freshwater Res.* 16:147–161.

Sebens, K. P. 1987. The ecology of indeterminate growth in animals. *Ann. Rev. Ecol Syst.* 18:371–407.

Seber, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.* 38:1128–1140.

Shepherd, S. A., K. R. Rodda & K. M. Vargas. 2001. A chronicle of collapse in two abalone stocks with proposals for precautionary management. *J. Shellfish Res.* 20:843–856.

Shepherd, S. A., G. P. Kirkwood & R. L. Sandland. 1982. Studies on southern Australian abalone (genus Haliotis). Mortality of two exploited species. *Aust. J. Mar. Freshwater Res.* 33:265–272.

Sluczanowski, P. R. 1984. A management oriented model of an abalone fishery whose substocks are subject to pulse fishing. *Can. J. Fish. Aquat. Sci.* 41:1008–1014.

Ssentongo, G. W. & P. A. Larkin. 1973. Some simple methods of estimating mortality rates of exploited fish populations. *J. Fish. Res. Bd. Can.* 30:695–698.

Tanaka, M. 1982. A new growth curve which expresses infinite increase. *Publ. Amakusa Mar. Biol. Lab.* 6:167–177.

Taylor, C. C. 1958. Cod growth and temperature. *J. Cons. Int. Explor. Mer.* 23:366–370.

Tegner, M. J., J. D. DeMartini & K. Karpov. 1992. The California red abalone fishery: a case study in complexity. In: S. A. Shepherd, M. J. Tegner, & S. A. Guzmán del Próo, editors. Abalone of the world: biology, fisheries and culture. Oxford: Blackwell Scientific. pp. 370–383.

Tegner, M. J., P. A. Breen & C. E. Lennert. 1989. Population biology of red abalones, *Haliotis rufescens*, in Southern California and management of the red and pink, *H. corrugata*, abalone fisheries. *Fish. Bull. US.* 87:313–339.

Troynikov, V. S. & H. K. Gorfine. 1998. Alternative approach for establishing legal minimum lengths for abalone based on stochastic growth models for length increment data. *J. Shellfish Res.* 17:827–831.

Urban, H. J. 2002. Modeling growth of different developmental stages in bivalves. *Mar. Ecol. Prog. Ser.* 238:109–114.

Vogel, G. 2000. Migrating otters push law to the limit. *Science* 289:1271–1273.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (Inquires on growth laws II). *Hum. Biol.* 10:181–213.

White, G. C. & K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46(Suppl.):120–138.

Yamaguchi, G. 1975. Estimating growth parameters from growth rate data: Problems with marine sedentary invertebrates. *Oecologia* 20:321–332.