Incorporating temporal variation in the growth of red abalone (*Haliotis rufescens*) using hierarchical Bayesian growth models

Yan Jiao, Laura Rogers-Bennett, Ian Taniguchi, John Butler, and Paul Crone

Abstract: Many marine species exhibit temporal variation in individual growth. Yearly variation in growth has been identified for red abalone (*Haliotis rufescens*) in southern California, USA, but has not been previously incorporated into growth models. In this study, Bayesian hierarchical models were developed to describe variability in growth rates for the Johnsons Lee red abalone population. Although the Bayesian hierarchical modeling estimates are close to estimates of the nonhierarchical highly parameterized model that assigns an estimate of parameters to each data period when the sample sizes are high, the hyperparameters in the hierarchical model are more useful in incorporating the temporal variability into the stock assessment. By ignoring temporal variability, confidence intervals of the estimates of growth can be unrealistically narrow, possibly leading to bias when these models are used for developing biological reference points such as $F_{0.1}$, F_{max}, or $F_{x\%}$. The use of a Bayesian hierarchical approach is generally suggested for future growth modeling and for per-recruitment models that include growth when determining precautionary management decisions.

Résumé : Plusieurs espèces marines accusent des variations temporelles dans leur croissance individuelle. Des variations annuelles de croissance ont été signalées chez les ormeaux rouges (*Haliotis rufescens*) dans le sud de la Californie, É.-U., mais elles n'ont jamais été incorporées aux modèles de croissance. Nous avons mis au point, dans notre étude, des modèles hiérarchiques bayésiens pour décrire la variation des taux de croissance dans la population d'ormeaux rouges de Johnsons Lee. Bien que les estimations produites par la modélisation hiérarchique bayésienne soient proches des estimations d'un modèle non hiérarchique fortement paramétrisé qui assigne une estimation des paramètres à chaque période de données lorsque les tailles des échantillons sont fortes, les hyperparamètres du modèle hiérarchique sont plus commodes pour incorporer la variabilité temporelle dans l'évaluation des stocks. Lorsqu'on néglige la variabilité temporelle, les intervalles de confiance des estimations de la croissance peuvent être de façon irréaliste trop étroits, ce qui peut mener à des erreurs lorsque ces modèles servent à la détermination de points de référence biologiques, tels que $F_{0.1}$, F_{max} ou $F_{x\%}$. Nous suggérons donc d'utiliser de façon générale une méthode hiérarchique bayésienne pour la modélisation de la croissance et dans les modèles par recrutement qui incluent la croissance lorsqu'on prend des décisions préventives de gestion.

[Traduit par la Rédaction]

Introduction

The growth of marine fishes and mollusks is highly variable. Temperature, food availability, and population density are considered to be dominant factors in large growth rate differences among different populations of the same species (Krohn et al. 1997; Swain et al. 2003). Differences also exist in length at age within and among year classes of a population, with differences in invertebrates being very large (Pearse and Cameron 1991). Large variations in growth among year classes are often hypothesized to result from variability in ocean conditions such as water temperature (Hutchings and Myers 1994) and food availability (Krohn et al. 1997). Other factors that can cause variation in growth include size-selective mortality (Myers 1989; Hanson and Chouinard 1992), energy allocation (Chen and Mello 1999), population stress as a result of overexploitation (Beacham 1983; Trippel 1995), population structure (Lilly 1996), and genetics.

Red abalone (*Haliotis rufescens*) is the largest abalone and the basis for an important recreational fishery in California. Haaker et al. (1998) developed and supported the hy-

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pothesis that growth of red abalone varies significantly in different years, associated with temperature changes during El Niño ocean climate oscillations. Although Haaker et al. (1998) detected temporal variation in individual growth, no model has been developed to date to effectively incorporate this type of variation. The traditional von Bertalanffy model, which assumes constant parameters in the model, cannot accommodate temporal changes in growth even when multiyear data are included in the analysis (Clark 2003).

In this research, a multilevel prior in a hierarchical approach is used to address the problem of describing growth rates and their associated uncertainty when multiyear data are included and indicate substantial variability in growth over time. Models with multilevel priors are called hierarchical models (Gelman et al. 2004). Multilevel priors have been used to represent inter- or intra-species differences when data are hierarchical (Clark 2003; Gelman et al. 2004). Hierarchical models accommodate temporal differences but assume that these differences derive from an underlying distribution (Gelman et al. 2004).

In this study, a hierarchical growth model was used to simulate temporal variation of red abalone growth (Gelman et al. 2004). The estimated hyperparameters, the parameters that further specify the priors of the parameters in the model, capture the temporal and spatial variations and provide a more comprehensive representation of important variation in growth compared with traditional constant growth rate models. Ultimately, growth models that address such variation are likely the most useful for describing a species' overall population dynamics and providing stock status determinations in formal assessments. Per-recruit models have been widely used in fisheries stock assessment, including assessment of abalone species (Shepherd et al. 1991; Nash 1992; Shepherd et al. 1995), and to determine biological reference points (BRP), e.g., $F_{0.1}$, $F_{\%}$, $F_{\%\,SSB}$ (Caddy and Mahon 1995; Food and Agricultural Organisation of the United Nations (FAO) 1995; Quinn and Deriso 1999). Failure to incorporate or model the temporal variations of growth may result in biased BRP estimation associated with per-recruit methods.

To evaluate the potential benefits of a hierarchical modeling approach, the goodness of fit of three hierarchical models was compared with that of a nonhierarchical model. In the hierarchical models, the data sets were restructured such that (i) hierarchical growth differed each year (model M1), (ii) hierarchical growth differed every two years (model M2), and (iii) hierarchical growth was the same over all years (model M3). We also compared the above hierarchical models with the nonhierarchical models that fit to the data of all the years cumulated (model M4) and to the data of each time period (model M5). Deviance information criterion (DIC; Spiegelhalter et al. 2002) was used to compare model goodness of fit as it incorporates both model fit and model complexity. The hierarchically structured models were implemented in a Bayesian framework and analyzed using Markov chain Monte Carlo (MCMC) simulation. Bayesian methods have been shown to be effective approaches in solving hierarchical models (Gelman et al. 2004).

Materials and methods

Tag-recapture data from red abalone at Johnsons Lee (33°54′N, 120°06′W) on the south side of Santa Rosa Island, California, USA, were collected from 1978 to 1984 by California Department of Fish and Game personnel and used to measure growth (Haaker et al. 1998). SCUBA divers collected red abalone and brought them to the vessel, where they were placed in flowing-seawater tanks. Abalone were marked with numbered stainless steel tags secured with stainless steel wire through two open shell apertures (Haaker et al. 1986). Shell length (maximum shell dimension) was measured to the nearest millimetre with calipers. Abalone were marked and visited in 1978, 1979, 1980, 1981, 1982, and 1984. In each year, both tagged and additional untagged abalone were collected and measured and retagged if appropriate. Recapture information is as follows: from 1978 to 1979, 158 red abalones were recaptured; from 1979 to 1980, 86 were recaptured; from 1980 to 1981, 210 were recaptured; from 1981 to 1982, 361 were recaptured; and from 1982 to 1984, 59 were recaptured (Fig. 1). Individuals recaptured more than once were very limited. There were five individuals recaptured four times (0.2%), 24 individuals recaptured three times (1.1%), and 177 individuals recaptured twice (8.3%).

We determined growth curves from annual increments in length of tagged individuals. We used the nonlinear methodology for mark–recapture data to estimate the parameters and standard errors for the von Bertalanffy growth model (Fabens 1965; Kirkwood and Somers 1984; Quinn and Deriso 1999). The von Bertalanffy growth model can be written as

$$(1) \qquad L_t = L_\infty(1 - e^{-Kt}), \text{ or}$$
$$dL = L_{t+\Delta t} - L_t = (L_\infty - L_t)(1 - e^{-K\Delta t})$$

where L_∞ and K are parameters in the von Bertalanffy growth model, L_∞ represents the asymptotic length of red abalone, K is the Brody growth coefficient (Ricker 1975), t_0 is assumed to be 0 as used in Haaker et al. (1998), L_t is the length at time t, and $L_{t+\Delta t}$ is the length at time $t + \Delta t$. A hierarchical growth model (Gelman et al. 2004) developed in this study can be written as

$$(2) \qquad dL_s = L_{s,t+\Delta t} - L_{s,t} = (L_{s,\infty} - L_{s,t})(1 - e^{-K_s\Delta t})$$
$$L_{s,\infty} \sim N(\overline{L}_\infty, \overline{\sigma}^2_{L_\infty})$$
$$K_s \sim N(\overline{K}, \overline{\sigma}^2_K)$$

where the subscript s represents temporal-specific parameters. The hierarchical population structure is implemented in this model through a multilevel prior of temporal-specific parameters in the growth model. dL_s were assumed to follow normal distributions with mean $(L_{s,\infty} - L_{s,t})(1 - e^{-K_s\Delta t})$ and variance $\sigma^2_{dL_s}$.

The Bayesian approach uses a probability rule (Bayes' theorem) to calculate a "posterior distribution" from the observed data and a "prior distribution", which summarizes the prior knowledge of the parameters (Berger 1985; McAllister and Kirkwood 1998; Gelman et al. 2004). This approach was used to estimate the uncertainty in parameter estimates. A nonhierarchical Bayesian model describes a

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Fig. 1. Observed red abalone (*Haliotis rufescens*) length at time t versus the length at time $t + \Delta t$. Lines are the $L_t \sim L_t$ points; solid circles are the $L_t \sim L_{t+\Delta t}$ points. (*a*) 1978–1979; (*b*) 1979–1980; (*c*) 1980–1981; (*d*) 1981–1982; (*e*) 1982–1984.
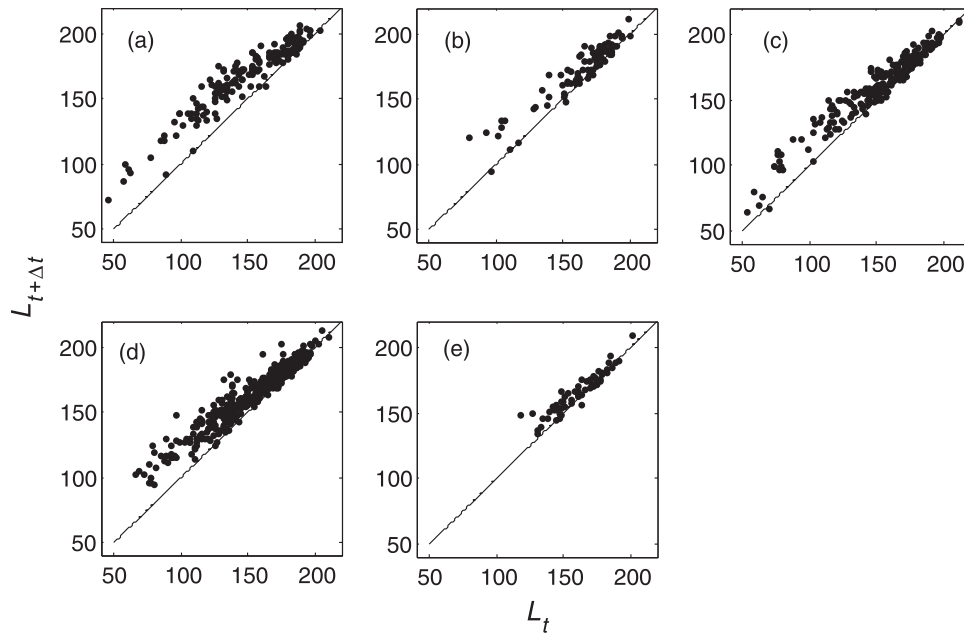
posterior density for parameters ($p(\theta|dL_s)$) using Bayes' theorem as

$$(3) \quad p(\theta = L_\infty, K | dL_s) = \frac{\prod_s f(dL_s|\theta)\,\pi(\theta)}{\int_{-\infty}^{+\infty} \prod_s f(dL_s|\theta)\,\pi(\theta)\,d\theta}$$

whereas a hierarchical Bayesian method assigns priors of hyperparameters to yield the joint posterior:

$$(4) \quad p(\theta' = L_{s,\infty}, K_s, \overline{L}_\infty, \overline{K}, \overline{\sigma}_{L_\infty}, \overline{\sigma}_K | dL)$$

$$= \frac{\prod_s f(dL_s|L_{s,\infty}, K_s)\,\pi_1(L_{\infty,s}|\overline{L}_\infty, \overline{\sigma}_{L_\infty})\,u_1(\overline{L}_\infty)\,v_1(\overline{\sigma}_{L_\infty})\,\pi_2(K_s|\overline{K}, \overline{\sigma}_K)\,u_2(\overline{K})\,v_2(\overline{\sigma}_K)}{\int_{-\infty}^{+\infty} \prod_s f(dL_s|L_{s,\infty}, K_s)\,\pi_1(L_{\infty,s}|\overline{L}_\infty, \overline{\sigma}_{L_\infty})\,u_1(\overline{L}_\infty)\,v_1(\overline{\sigma}_{L_\infty})\,\pi_2(K_s|\overline{K}, \overline{\sigma}_K)\,u_2(\overline{K})\,v_2(\overline{\sigma}_K)\,d\theta'}$$

In the above equations, $f(dL_s|\theta)$ is the probability density function of dL_s on parameter vector θ; $u_1(\overline{L}_\infty)$ and $v_1(\overline{\sigma}_{L_\infty})$ are the probability density functions of $\overline{L}_\infty$ and $\overline{\sigma}_{L_\infty}$, respectively; and $u_2(\overline{K})$ and $v_2(\overline{\sigma}_K)$ are the probability density functions of $\overline{K}$ and $\overline{\sigma}_K$, respectively.

Bayesian implementation of these models requires specification of prior distributions on all unobserved quantities. Noninformative priors (here, wide uniform distributions) were used for variances $\overline{\sigma}_{L_\infty}^2$, $\overline{\sigma}_K^2$ and $\sigma_{dL_s}^2$. Uniform prior distributions work better as noninformative priors than inverse-gamma distributions for variance parameters when dealing with hierarchical models (Gelman 2006).

A critical issue in using Markov chain Monte Carlo (MCMC) methods is how to determine when random draws have converged to the posterior distribution. Here, three methods were considered: monitoring the trace for key parameters, diagnosing the autocorrelation plot for key param-

eters, and using the Gelman and Rubin statistic (Gelman and Rubin 1992; Cowles and Carlin 1996; Spiegelhalter et al. 2004). A detailed description of the use of these methods in fisheries can be found in Su et al. (2001). In this study, three Markov chains generated using WinBugs were used (Spiegelhalter et al. 2004). The three chains converged after 50 000 iterations with a thinning interval of 5 based on the convergence criteria and were discarded. A thinning interval of 5 was then used to avoid parameter autocorrelation. Another 20 000 iterations were used to generate the posterior distributions. The posterior distributions of the key parameters were obtained through a kernel smoothing approach (Bowman and Azzalini 1997).

To compare the performance of the hierarchically structured model with the commonly used nonhierarchical von Bertalanffy growth model, another three hierarchical models were developed (Table 1). In the first hierarchical model (M1),

Table 1. Model comparison among hierarchical and nonhierarchical growth models of red abalone (*Haliotis rufes-cens*). Priors of the hierarchical models are $\overline{L}_\infty \sim U(180, 250)\ I(150, 400)$, $\overline{K} \sim U(0.15, 0.35)$. Priors for the nonhierarchical model are $L_\infty \sim U(150, 400)$, $K \sim U(0.15, 0.40)$.

		Parameter estimates	
Model	DIC	L_∞ (mean, median, SD, 95% CI)	K (mean, median, SD, 95% CI)
M1	5938.7	$\overline{L}_\infty$ (200.3, 199.9, 9.3, 183.4, 220.5)	$\overline{K}$ (0.239, 0.237, 0.039, 0.165, 0.323)
		$\overline{\sigma}^2_{L_\infty}$ (484, 452, 237, 123, 957)	$\overline{\sigma}^2_K$ (0.013, 0.007, 0.015, 0.001, 0.059)
		$L_{1,\infty}$ (223.0, 222.8, 5.5, 213.0, 234.7)	K_1 (0.285, 0.284, 0.022, 0.244, 0.329)
		$L_{2,\infty}$ (205.6, 205.1, 6.6, 194.3, 220.2)	K_2 (0.217, 0.216, 0.031, 0.161, 0.281)
		$L_{3,\infty}$ (196.8, 196.6, 4.4, 189.0, 206.2)	K_3 (0.212, 0.212, 0.018, 0.176, 0.249)
		$L_{4,\infty}$ (194.8, 194.7, 2.6, 189.9, 200.3)	K_4 (0.293, 0.293, 0.017, 0.260, 0.326)
		$L_{5,\infty}$ (177.3, 177.3, 3.5, 170.6, 184.4)	K_5 (0.172, 0.167, 0.019, 0.151, 0.221)
M2	6018.4	$\overline{L}_\infty$ (197.8, 196.6, 10.5, 181.5, 221.7)	$\overline{K}$ (0.246, 0.245, 0.049, 0.158, 0.339)
		$\overline{\sigma}^2_{L_\infty}$ (495, 468, 253, 104, 968)	$\overline{\sigma}^2_K$ (0.026, 0.017, 0.024, 0.002, 0.089)
		$L_{1,\infty}$ (211.6, 211.4, 3.6, 205.1, 219.0)	K_1 (0.297, 0.296, 0.018, 0.261, 0.333)
		$L_{2,\infty}$ (195.4, 195.4, 2.2, 191.3, 200.0)	K_2 (0.262, 0.262, 0.012, 0.238, 0.286)
		$L_{3,\infty}$ (177.4, 177.3, 3.4, 170.8, 184.2)	K_3 (0.170, 0.165, 0.017, 0.151, 0.214)
M3	6262.1	$\overline{L}_\infty$ (202.0, 199.0, 15.0, 181.3, 238.2)	$\overline{K}$ (0.255, 0.258, 0.055, 0.156, 0.344)
		$\overline{\sigma}^2_{L_\infty}$ (462, 442, 292, 20, 972)	$\overline{\sigma}^2_K$ (0.039, 0.034, 0.029, 0.001, 0.096)
		L_∞ (194.1, 194.1, 1.5, 191.2, 197.2)	K (0.282, 0.281, 0.010, 0.262, 0.301)
M4	10614.6	L_∞ (191.7, 191.7, 1.1, 189.6, 194.0)	K (0.278, 0.277, 0.008, 0.262, 0.292)
M5	1117.9	$L_{1,\infty}$ (224.2, 223.7, 6.9, 212.1, 239.4)	K_1 (0.282, 0.282, 0.026, 0.232, 0.335)
	597.4	$L_{2,\infty}$ (207.2, 206.7, 7.0, 193.7, 223.7)	K_2 (0.212, 0.208, 0.035, 0.156, 0.288)
	1421.1	$L_{3,\infty}$ (196.9, 196.6, 4.5, 188.8, 206.5)	K_3 (0.211, 0.211, 0.019, 0.175, 0.249)
	2430.7	$L_{4,\infty}$ (194.3, 194.2, 2.5, 189.6, 199.5)	K_4 (0.296, 0.296, 0.016, 0.265, 0.329)
	368.7	$L_{5,\infty}$ (177.2, 177.2, 2.8, 171.8, 182.8)	K_5 (0.163, 0.160, 0.012, 0.150, 0.195)
	Total = 5935.8		

Note: All negative growth data are included. Deviance information criterion (DIC) and posterior mean, median, standard deviation (SD), and 95% credible interval (95% CI) of the parameter estimates are provided.

each year's data, except 1983 because no tagging occurred that year, were assumed to be hierarchically structured as

(5) $\quad L_{t+\Delta t} - L_t = (L_\infty - L_t)(1 - e^{-K\Delta t})$

$\quad L_{1,\infty} \sim N(\overline{L}_\infty, \overline{\sigma}^2_{L_\infty})|_{1982-1984}I(150, 400)$

$\quad \vdots$

$\quad L_{5,\infty} \sim N(\overline{L}_\infty, \overline{\sigma}^2_{L_\infty})|_{1982-1984}I(150, 400)$

$\quad \overline{L}_\infty \sim U(180, 250)$

$\quad \overline{\sigma}^2_{L_\infty} \sim U(1, 1000)$

$\quad K_1 \sim N(\overline{K}, \overline{\sigma}^2_K)|_{1978-1979}I(0.15, 0.40)$

$\quad \vdots$

$\quad K_5 \sim N(\overline{K}, \overline{\sigma}^2_K)|_{1982-1984}I(0.15, 0.40)$

$\quad \overline{K} \sim U(0.15, 0.35)$

$\quad \overline{\sigma}^2_K \sim U(0.0001, 0.1)$

Here I represents the boundary of the distribution in Win-BUGS, i.e., $I(150, 400)$ means that the boundary of the random variable L_∞ is between 150 and 400.

In the second hierarchical model (M2), the data for every two-year period are assumed to be hierarchically structured as

(6) $\quad L_{t+\Delta t} - L_t = (L_\infty - L_t)(1 - e^{-K\Delta t})$

$\quad L_{1,\infty} \sim N(\overline{L}_\infty, \overline{\sigma}^2_{L_\infty})|_{1978-1980}I(150, 400)$

$\quad L_{2,\infty} \sim N(\overline{L}_\infty, \overline{\sigma}^2_{L_\infty})|_{1980-1982}I(150, 400)$

$\quad L_{3,\infty} \sim N(\overline{L}_\infty, \overline{\sigma}^2_{L_\infty})|_{1982-1984}I(150, 400)$

$\quad \overline{L}_\infty \sim U(180, 250)I(150, 400)$

$\quad \overline{\sigma}^2_{L_\infty} \sim U(1, 1000)$

$\quad K_1 \sim N(\overline{K}, \overline{\sigma}^2_K)|_{1978-1980}I(0.15, 0.40)$

$\quad K_2 \sim N(\overline{K}, \overline{\sigma}^2_K)|_{1980-1982}I(0.15, 0.40)$

$\quad K_3 \sim N(\overline{K}, \overline{\sigma}^2_K)|_{1982-1984}I(0.15, 0.40)$

$\quad \overline{K} \sim U(0.15, 0.35)$

$\quad \overline{\sigma}^2_K \sim U(0.0001, 0.1)$

In the third hierarchical model (M3), the model is hierarchically structured but the data were not assumed to be hierarchical:

(7) $\quad L_{t+\Delta t} - L_t = (L_\infty - L_t)(1 - e^{-K\Delta t})$

$\quad L_\infty \sim N(\overline{L}_\infty, \overline{\sigma}^2_{L_\infty})|_{1978-1984}I(150, 400)$

$\quad \overline{L}_\infty \sim U(180, 250)$

$\quad \overline{\sigma}^2_{L_\infty} \sim U(1, 1000)$

$\quad K \sim N(\overline{K}, \overline{\sigma}^2_K)|_{1978-1984}I(0.15, 0.40)$

$\quad \overline{K} \sim U(0.15, 0.35)$

$\quad \overline{\sigma}^2_K \sim U(0.0001, 0.1)$

$\overline{L}_\infty$, the hyperparameter of the mean of L_∞, was assumed to

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follow a uniform distribution between 180 mm and 250 mm. This range was based on L_∞ estimates from other studies on red abalone populations (Haaker et al. 1998; Rogers-Bennett et al. 2007). The hyperparameter of the variance of L_∞, $\overline{\sigma}^2_{L_\infty}$, was modeled as noninformative, with a wide uniform distribution between 1 and 1000. The hyperparameter of $\overline{K}$ was assumed to follow a uniform distribution between 0.15 and 0.35 based on K estimates from other studies (Haaker et al. 1998; Rogers-Bennett et al. 2007). The hyperparameter of the variance of K, $\overline{\sigma}^2_K$, was modeled as noninformative, with a wide uniform distribution between 0.0001 and 1.

The nonhierarchical von Bertalanffy growth model is

$$(8) \quad L_{t+\Delta t} - L_t = (L_\infty - L_t)(1 - e^{-K\Delta t})$$
$$L_\infty \sim U(150, 400)$$
$$K \sim U(0.15, 0.40)$$

The priors of L_∞ and K in this model are wider than the priors of their mean values in the hierarchical models. The range of L_∞ is as wide as the range of L_t in the hierarchical models to prevent the influence of the informative priors. We also added the model that assigns an estimate of parameters to each data period (M5). Sensitivities of the results to prior assumption of both parameters and hyperparameters were analyzed by changing the lower limits of $\overline{L}_\infty$ and $\overline{K}$ to 50% of the ones used above and by changing the high limit to 150% of the ones used above. Changes to both the posterior mean and variance were compared. We also analyzed the growth based on the data set with the negative growth records not incorporated.

The goodness of fit of the Bayesian hierarchical models was compared with the classical nonhierarchical model based on the estimates of the DIC (Spiegelhalter et al. 2002). DIC can be written as

$$(9) \quad \text{DIC} = 2\overline{D} - \widehat{D} \quad \text{or} \quad \overline{D} + p_D$$
$$D(y, \theta) = -2 \log\text{-likelihood}(y|\theta)$$
$$p_D = \overline{D} - \widehat{D}$$

where D is deviance, a measurement of prediction of goodness for our models, p_D is the effective number of parameters in a Bayesian model, $\overline{D}$ is the posterior mean of the deviance, and $\widehat{D}$ is the deviance of the posterior mean. The DIC is a hierarchical modeling generalization of the AIC (Akaike information criterion) and BIC (Bayesian information criterion, also known as the Schwarz criterion). It is particularly useful in Bayesian model selection problems in which the posterior distributions of the models have been obtained by MCMC simulation. Like AIC and BIC, it is an asymptotic approximation as the sample size becomes large. It is only valid when the posterior distribution is approximately multivariate normal (Spiegelhalter et al. 2002, 2004).

Results

The Gelman and Rubin statistics for all of the parameters, including all variance terms, equaled 1, which indicated convergence of the Markov chains. Further, the autocorrelation function plot indicated that a thinning interval of 5 was large enough to address potential autocorrelation in the MCMC runs (Fig. 2).

Among the 5 models, M5, the model that assigns the estimate of parameters to each data period, had the lowest DIC value (Table 1), with model M1 associated with generally similar DIC values. Among the three hierarchical models tested, M1, the model with data from each year treated as hierarchical, performed the best, resulting in the lowest DIC. Models M2 and M3, the other two models with multilevel priors of the von Bertalanffy growth parameters, also resulted in lower DIC values than the nonhierarchical model (M4). The large differences in DIC values among models used to describe population growth indicate that temporal changes in growth of red abalone can be significant and ultimately should be considered in population assessments of this species.

Using a hierarchically structured model generally resulted in parameter estimates of L_∞ and K with wider credible intervals than using a nonhierarchical model (Table 1). The credible intervals and standard deviations of L_∞ and K were considerably larger for the hierarchical von Bertalanffy models M1, M2, and M3 than the nonhierarchical model M4, which is illustrated in Table 1.

The hierarchically structured models not only describe the growth of all the individuals tagged, but also simulate the growth differences among sampling years. The hierarchical models M1 and M2 clearly indicated temporal differences in red abalone growth (Table 1). Results from the model with the best fit, M1, showed that the joint posterior distributions of L_∞ and K differed substantially between 1978–1979 (i.e., the highest growth period), 1982–1984 (i.e., the lowest growth period), and the three intermediate periods (Table 1; Fig. 3). Parameter L_∞ exhibited a decreasing trend over time (1978 to 1984). Parameter K varied also, with K_1 (0.285) and K_4 (0.293) resulting in relatively high estimates, K_2 (0.217) and K_3 (0.212) at an intermediate level, and K_5 (0.172) at the lowest value. The overall posterior von Bertalanffy growth curve showed that abalone grew faster and larger in 1978–1979, but more slowly in 1982–1984. Results from M2, when every two years of data were combined, also indicated that red abalone growth differed markedly between 1978–1980, 1982–1984, and the 1980–1982 intermediate periods (Table 1).

Residuals, estimated as the differences of the posterior mean of the length increase with the observed length increase, were plotted against the fitted growth increase (dL_s) when hierarchical model M1 was used. No obvious patterns were observed in the residual plot of model M1, with the exception of uneven sample sizes among groups of dL_s (Fig. 4). Also, residual diagnostics for model M5 revealed no visible patterns of statistical violation.

The posteriors of the hyperparameters and key parameters for most of the years in all of the hierarchical models were stable when the priors of $\overline{L}_\infty$ widened from $U(180, 250)I(150, 400)$ to $U(90, 375)I(50, 400)$ and when $\overline{K}$ widened from $U(0.15, 0.35)$ to $U(0.075, 0.525)$ (Tables 1 and 2; Fig. 5). The posteriors of the key parameters of the nonhierarchical models were also stable when L_∞ widened from $U(150, 400)$ to $U(50, 400)$, and K widened from $U(0.15, 0.40)$ to $U(0.075, 0.575)$ (Tables 1 and 2). The parameters of the period of 1982–1984 were less stable and were influenced by the boundary of K (Table 2; Fig. 3).

The percentages of negative growth data were 2%, 17%,

Fig. 2. Autocorrelation function plots of parameters when M1 is used with prior stated in Table 1 and text: (*a*) $\overline{L}_\infty$; (*b*) $\overline{\sigma}^2_{L_\infty}$; (*c*) $\overline{K}$; and (*d*) $\overline{\sigma}^2_K$.
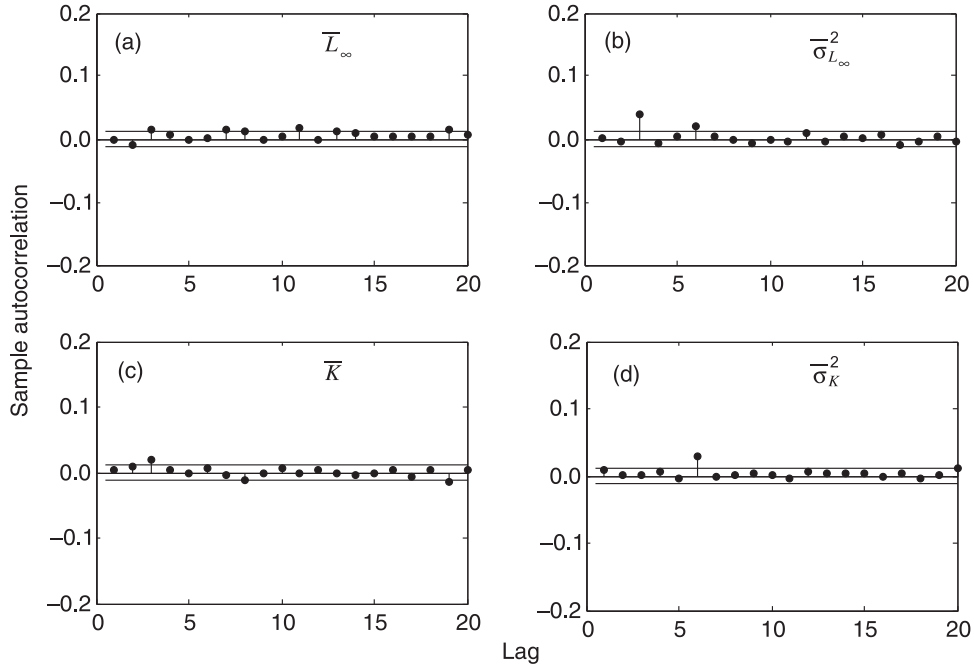
Fig. 3. Joint posterior distributions of K and L_∞ from 1978 to 1984 based on the hierarchical growth model M1 with prior stated in Table 1: red, 1978–1979; magenta, 1979–1980; yellow, 1980–1981; green, 1981–1982; blue, 1982–1984.
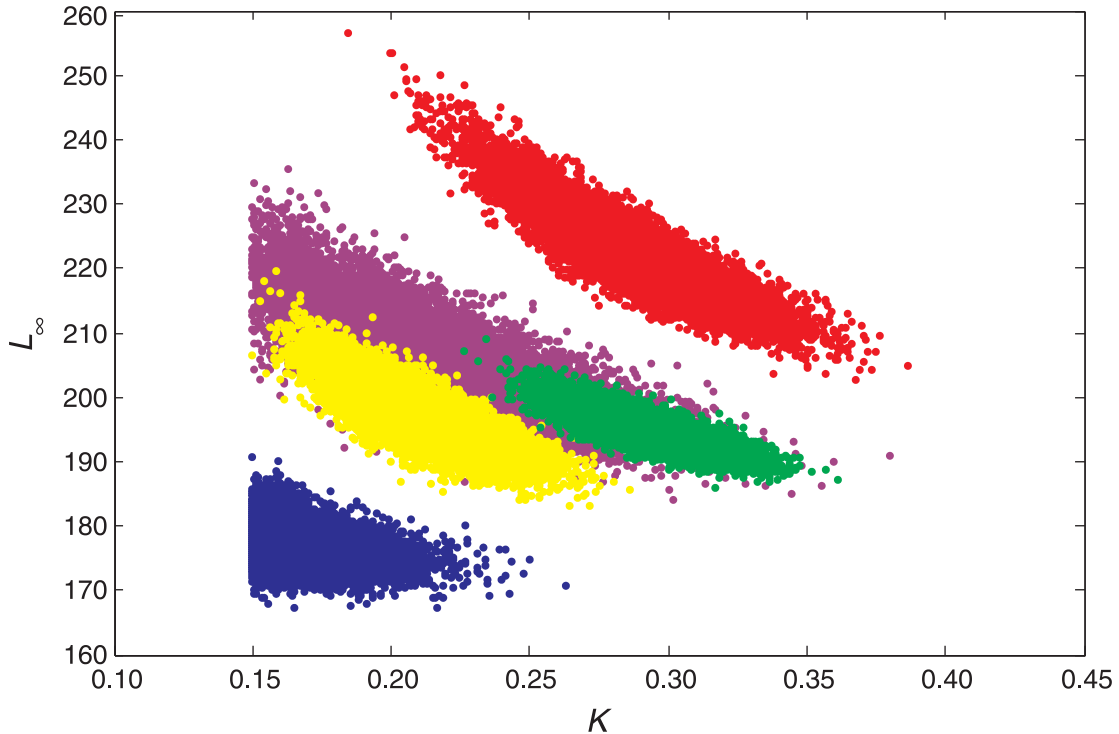

18%, 12%, and 23% during the 5-year tagging periods. In all of the models, omission of the negative data resulted in changes to the estimated growth parameters, depending on the amount of negative values in the total data set for each tag–recapture period, e.g., period 1982–1984 had highest percentage of negative values and resulted in the largest differences (Table 3). Finally, inclusion or omission of the negative growth information in the modeling analyses con-

ducted here indicated that temporal variation in the growth of red abalone is likely a significant attribute in this species' biology off the southern California coast (San Miguel Island).

Discussion

Although the Bayesian hierarchical modeling estimates are close to estimates of the nonhierarchical model that as-

Fig. 4. Residuals plots when model M1 is used with prior stated in Table 1 and the text: (*a*) 1978–1979; (*b*) 1979–1980; (*c*) 1980–1981; (*d*) 1981–1982; and (*e*) 1982–1984.
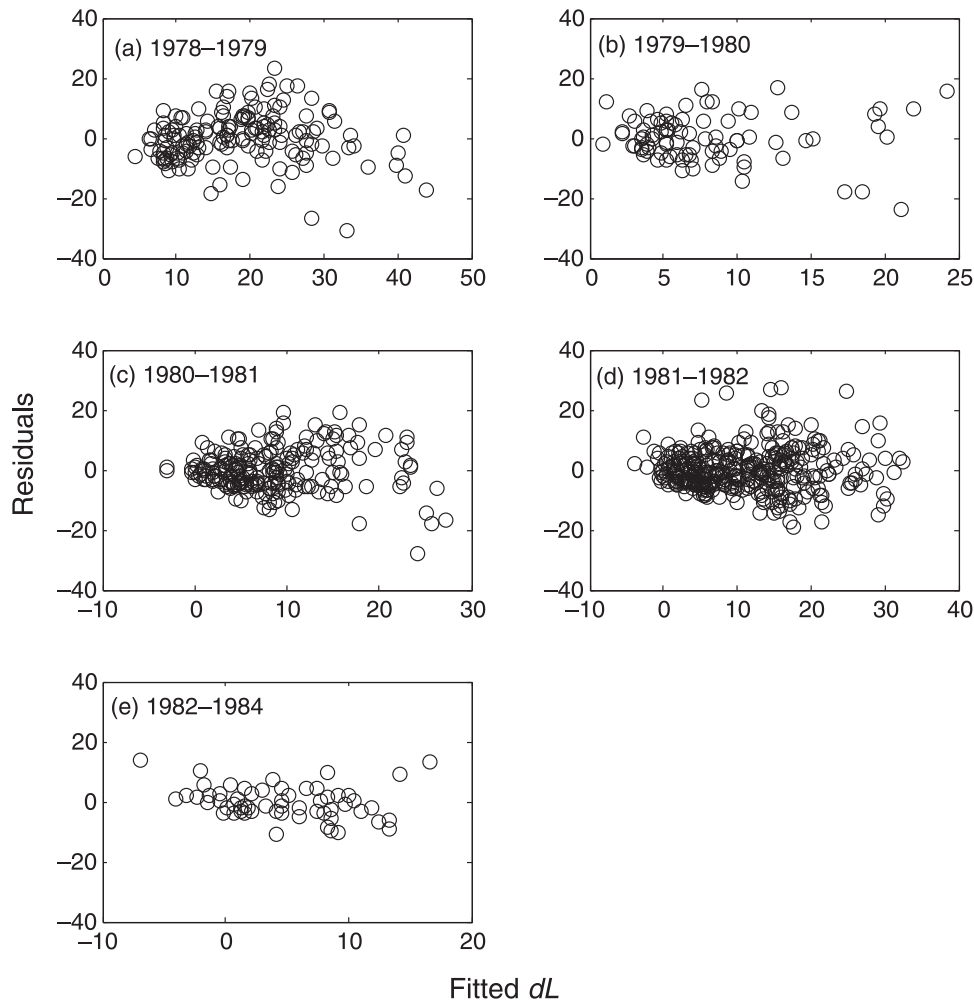
signs an estimate of parameters to each data period in this study, the hyperparameters in the hierarchical model are often very useful in incorporating the temporal variability into the stock assessment (Gelman et al. 2004). The goodness of fit of the hierarchical models can be worse than that of the highly parameterized model when the number of data groups is small. The fits for each data group are not as good because the hierarchical model assumes that the differences among the data groups are from the same underlying distribution; at the same time, the number of parameters in the hierarchical models is not much less than in the highly parameterized model because the number of groups is low. In this study, there were five years of recaptures; the fits using M1 and M5 were close, with M5 being slightly better. When the number of years of recaptures increases, say to 10 years or more, the goodness of fit using hierarchical models will be much better because of better parsimony. In spite of the goodness of fit, the hierarchical models always estimate the parameters of all data groups simultaneously, and the hyperparameters can be used in future stock assessment when the specific temporal change is less predictable.

The hierarchical growth model captured the dramatic temporal variation in growth including years of warm and normal sea surface temperatures (SST) in southern California.

Slow growth rates from 1982 to 1984 occurred during a major El Niño event (Figs. 6 and 7). We found that L_∞ had a significant negative relationship with average SST anomalies ($p = 0.0081$; Fig. 7). More work is needed to investigate the impacts of cold sea surface conditions on the growth of red abalone. We suggest that this relationship between SST and red abalone growth could be factored into future management algorithms and decisions. Currently, few fishery management plans explicitly incorporate SST (or other measures of ocean productivity) into fishery models. One exception is the management of Pacific sardines in which it is widely hypothesized that ocean warming greatly influences sardine productivity and abundance and, therefore, SST is used formally when setting harvest guidelines for this species (Conser et al. 2002). For red abalone, we see that few individuals will grow into the legal size (197 mm for commercial fisheries and 178 mm for recreational fishery) during warm-water years. As a result, if fishing effort remains unchanged and population dynamics models ignore this growth variation, then exploitation rate, the percent taken, will be higher in these years than anticipated (Parma 2002).

Warm water also impacts food availability, having a negative effect on kelp growth (Leighton 1974; Tegner and Dayton 1987; Tegner et al. 1992). In laboratory experiments,

Table 2. Model comparison among hierarchical and nonhierarchical growth models of red abalone (*Haliotis rufescens*). Priors of the hierarchical models are $\overline{L}_\infty \sim U(90, 375)\ I(50, 400)$, $\overline{K} \sim U(0.075, 0.525)$. Priors for the nonhierarchical model are $L_\infty \sim U(50, 400)$, $K \sim U(0.075, 0.525)$.

Model	DIC	Parameter estimates	
		L_∞ (mean, median, SD, 95% CI)	K (mean, median, SD, 95% CI)
M1	5936.2	$\overline{L}_\infty$ (200.8, 200.8, 9.9, 181.3, 220.9)	$\overline{K}$ (0.230, 0.229, 0.058, 0.116, 0.361)
		$\overline{\sigma}^2_{L_\infty}$ (447, 404, 247, 88, 953)	$\overline{\sigma}^2_K$ (0.020, 0.013, 0.019, 0.002, 0.077)
		$L_{1,\infty}$ (222.6, 222.3, 5.6, 212.5, 234.6)	K_1 (0.286, 0.286, 0.022, 0.243, 0.331)
		$L_{2,\infty}$ (206.5, 205.7, 7.3, 194.4, 223.1)	K_2 (0.213, 0.212, 0.033, 0.150, 0.279)
		$L_{3,\infty}$ (197.0, 196.7, 4.4, 189.0, 206.4)	K_3 (0.211, 0.210, 0.019, 0.176, 0.248)
		$L_{4,\infty}$ (194.7, 194.6, 2.6, 189.9, 200.1)	K_4 (0.294, 0.294, 0.017, 0.261, 0.327)
		$L_{5,\infty}$ (183.6, 182.7, 6.7, 172.7, 198.4)	K_5 (0.126, 0.122, 0.031, 0.079, 0.194)
M2	6016.7	$\overline{L}_\infty$ (196.8, 196.9, 12.7, 170.2, 222.6)	$\overline{K}$ (0.243, 0.234, 0.088, 0.095, 0.449)
		$\overline{\sigma}^2_{L_\infty}$ (465, 431, 265, 69, 965)	$\overline{\sigma}^2_K$ (0.036, 0.029, 0.026, 0.004, 0.094)
		$L_{1,\infty}$ (211.4, 211.2, 3.6, 204.8, 219.0)	K_1 (0.297, 0.297, 0.019, 0.261, 0.335)
		$L_{2,\infty}$ (195.5, 195.4, 2.2, 191.3, 200.1)	K_2 (0.261, 0.261, 0.012, 0.238, 0.286)
		$L_{3,\infty}$ (183.7, 183.0, 6.6, 172.9, 198.1)	K_3 (0.122, 0.119, 0.029, 0.078, 0.188)
M:	6261.7	$\overline{L}_\infty$ (194.0, 193.9, 22.6, 147.4, 241.0)	$\overline{K}$ (0.292, 0.289, 0.113, 0.093, 0.504)
		$\overline{\sigma}^2_{L_\infty}$ (502, 503, 287, 26, 977)	$\overline{\sigma}^2_K$ (0.044, 0.041, 0.029, 0.002, 0.097)
		L_∞ (194.0, 194.0, 1.5, 191.2, 197.1)	K (0.282, 0.282, 0.010, 0.262, 0.302)
M4	10614.5	L_∞ (191.7, 191.7, 1.1, 189.6, 193.9)	K (0.278, 0.278, 0.008, 0.263, 0.293)
M5	1117.9	$L_{1,\infty}$ (224.1, 223.6, 6.9, 212.0, 239.0)	K_1 (0.282, 0.282, 0.027, 0.232, 0.335)
	597.9	$L_{2,\infty}$ (209.2, 207.6, 10.4, 194.0, 234.3)	K_2 (0.204, 0.204, 0.040, 0.126, 0.284)
	1421.2	$L_{3,\infty}$ (196.9, 196.6, 4.5, 188.8, 206.6)	K_3 (0.211, 0.211, 0.019, 0.175, 0.249)
	2430.64	$L_{4,\infty}$ (194.3, 194.2, 2.5, 189.6, 199.5)	K_4 (0.297, 0.296, 0.016, 0.265, 0.329)
	367.2	$L_{5,\infty}$ (182.9, 182.3, 5.2, 174.3, 194.5)	K_5 (0.120, 0.119, 0.023, 0.081, 0.170)
	Total = 5934.8		

Note: All the negative growth data are included. Deviance information criterion (DIC) and posterior mean, median, standard deviation (SD), and 95% credible interval (95% CI) of the parameter estimates are provided.

Fig. 5. Posterior probability density functions of hyperparameters when model M1 is used under three situations corresponding to Tables 1–3 (S1, S2, and S3): (*a*) $\overline{L}_\infty$; (*b*) $\overline{\sigma}^2_{L_\infty}$; (*c*) $\overline{K}$; and (*d*) $\overline{\sigma}^2_K$. S1, continuous line; S2, dotted line; S3, dotted–dashed line.

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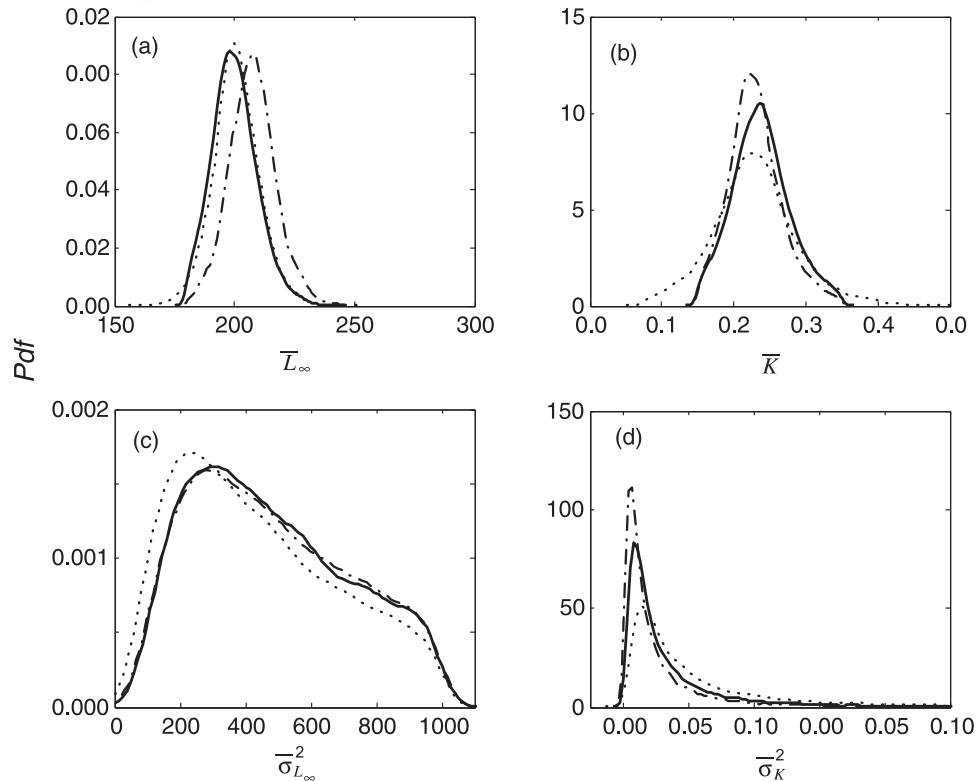
Table 3. Model comparison among hierarchical and nonhierarchical growth models of red abalone (*Haliotis rufescens*). Priors of the hierarchical models are $\overline{L}_\infty \sim U(180, 250)\, I(150, 400)$, $\overline{K} \sim U(0.15, 0.35)$. Priors for the nonhierarchical model are $L_\infty \sim U(150, 400)$, $K \sim U(0.15, 0.40)$.

Model	DIC	Parameter estimates	
		L_∞ (mean, median, SD, 95% CI)	K (mean, median, SD, 95% CI)
M1	4935.1	$\overline{L}_\infty$ (207.4, 207.2, 9.9, 187.9, 228.0)	$\overline{K}$ (0.231, 0.229, 0.036, 0.164, 0.313)
		$\overline{\sigma}^2_{L_\infty}$ (486, 453, 239, 118, 958)	$\overline{\sigma}^2_K$ (0.010, 0.005, 0.014, 0.001, 0.054)
		$L_{1,\infty}$ (228.4, 228.0, 6.2, 217.3, 241.9)	K_1 (0.269, 0.269, 0.021, 0.228, 0.312)
		$L_{2,\infty}$ (212.3, 211.6, 7.3, 200.0, 228.4)	K_2 (0.239, 0.237, 0.034, 0.176, 0.308)
		$L_{3,\infty}$ (208.4, 208.0, 6.2, 197.4, 221.8)	K_3 (0.201, 0.200, 0.019, 0.164, 0.240)
		$L_{4,\infty}$ (204.7, 204.5, 3.9, 197.8, 212.7)	K_4 (0.259, 0.259, 0.017, 0.225, 0.293)
		$L_{5,\infty}$ (182.6, 182.6, 4.5, 174.0, 191.6)	K_5 (0.171, 0.166, 0.019, 0.151, 0.221)
M2	4973.1	$\overline{L}_\infty$ (203.8, 203.2, 11.9, 183.0, 229.5)	$\overline{K}$ (0.240, 0.237, 0.048, 0.158, 0.337)
		$\overline{\sigma}^2_{L_\infty}$ (520, 501, 251, 112, 970)	$\overline{\sigma}^2_K$ (0.025, 0.015, 0.024, 0.002, 0.089)
		$L_{1,\infty}$ (218.3, 218.2, 4.4, 210.4, 227.6)	K_1 (0.285, 0.285, 0.019, 0.249, 0.324)
		$L_{2,\infty}$ (205.8, 205.7, 3.4, 199.7, 212.8)	K_2 (0.237, 0.237, 0.013, 0.211, 0.264)
		$L_{3,\infty}$ (182.7, 182.7, 4.4, 174.2, 191.5)	K_3 (0.169, 0.164, 0.018, 0.151, 0.216)
M3	5193.7	$\overline{L}_\infty$ (207.4, 205.5, 15.4, 182.5, 241.7)	$\overline{K}$ (0.252, 0.252, 0.055, 0.156, 0.345)
		$\overline{\sigma}^2_{L_\infty}$ (466, 447, 288, 22, 970)	$\overline{\sigma}^2_K$ (0.039, 0.033, 0.029, 0.001, 0.096)
		L_∞ (203.4, 203.4, 2.2, 199.2, 208.0)	K (0.258, 0.258, 0.011, 0.237, 0.280)
M4	8707.5	L_∞ (200.6, 200.6, 1.7, 197.5, 204.0)	K (0.255, 0.255, 0.008, 0.239, 0.272)
M5	1076.2	$L_{1,\infty}$ (229.4, 228.8, 7.7, 215.9, 246.1)	K_1 (0.268, 0.267, 0.026, 0.218, 0.320)
	458.3	$L_{2,\infty}$ (212.9, 212.0, 8.4, 199.0, 232.0)	K_2 (0.238, 0.237, 0.038, 0.168, 0.316)
	1099.6	$L_{3,\infty}$ (209.4, 209.0, 6.4, 197.9, 223.0)	K_3 (0.197, 0.197, 0.019, 0.161, 0.237)
	2047.8	$L_{4,\infty}$ (204.1, 203.9, 3.9, 197.0, 212.5)	K_4 (0.262, 0.262, 0.018, 0.227, 0.297)
	251.1	$L_{5,\infty}$ (182.5, 182.5, 3.6, 175.3, 189.7)	K_5 (0.164, 0.160, 0.013, 0.150, 0.198)
	Total = 4932.9		

Note: All the negative growth data are deleted. Deviance information criterion (DIC) and posterior mean, median, standard deviation (SD), and 95% credible interval (95% CI) of the parameter estimates are provided.

warm water temperatures halted growth, reduced reproduction, and increased the onset of a lethal abalone disease, withering syndrome (WS) (Vilchis et al. 2005). To distinguish the impacts of warm water from other factors, laboratory experiments with abundant kelp in WS disease free conditions were conducted that resulted in the cessation of abalone growth (Rogers-Bennett et al. 2010). These laboratory-based growth results correspond to results for red abalone in the field, which further supports their incorporation into the growth modeling work.

Negative growth data were recorded in this study. Reasons for this negative growth can be both measurement error and real negative growth caused by conditions of poor food and physiological stress. L. Rogers-Bennett (personal observation) has seen this negative growth in the lab in warm water and poor food conditions. Haaker et al. (1998) concluded that there was no significant effect caused by the tagging performance. We suggest considering the negative growth values in the modeling analysis in this situation. A possible supplementary approach is to use a measurement error model, which does not assume that the length measurements are perfect but with measurement errors (Jiao et al. 2006; Cope and Punt 2007).

Potential effects from both sampling selectivity and fishery selectivity can be a problem (Myers 1989; Sinclair et al. 2002). If the fastest-growing individuals reached the legal size sooner, they would be differentially removed, and growth estimation would become negatively biased over time. Conversely, if larger abalone are easier to locate

(size-selective sampling), then the fastest-growing small abalone would have a higher probability of recapture during subsequent sampling, and growth rates for small (but fast-growing) individuals could be overestimated. Although the study site was open to extraction, with commercial minimum catchable size of 197 mm and recreational minimum catchable size of 178 mm, Haaker et al. (1998) and Tegner et al. (1989) concluded that there was no obvious effect caused by the sampling selectivity and fishing selectivity based on length sampling during this time period on this population.

Individual-level hierarchical models may be used when the percentage of multiple recaptures is high, because if a single abalone contributes to more than one data point in the analysis, then each point is not strictly independent and the potential correlation among replicate observations from each individual needs to be accounted for (Gelman et al. 2004; Zhang et al. 2009). However, in this study, the percentage of recaptures, including abalone captured more than once, in the 6 years of the recapture study was very low, and therefore, we did not consider this effect. It may be explored in a future study.

Some other modeling approaches may be considered in the future based on the characteristics of this red abalone population. Growth parameters L_∞ and K are strongly correlated, so models with explicit treatments of the known strong correlations among growth parameters may be used for red abalone growth in this population (Helser and Lai 2004; He and Bence 2007). A "random-walk" approach

Fig. 6. Sea surface temperature anomalies of ENSO (Joint Institute for the Study of the Atmosphere and Ocean 2007). Global ENSO SST (tropics minus extratropics) (C) 1950 – July 2007. The rectangle indicates the period when the red abalone (*Haliotis rufescens*) were tagged at Johnsons Lee.
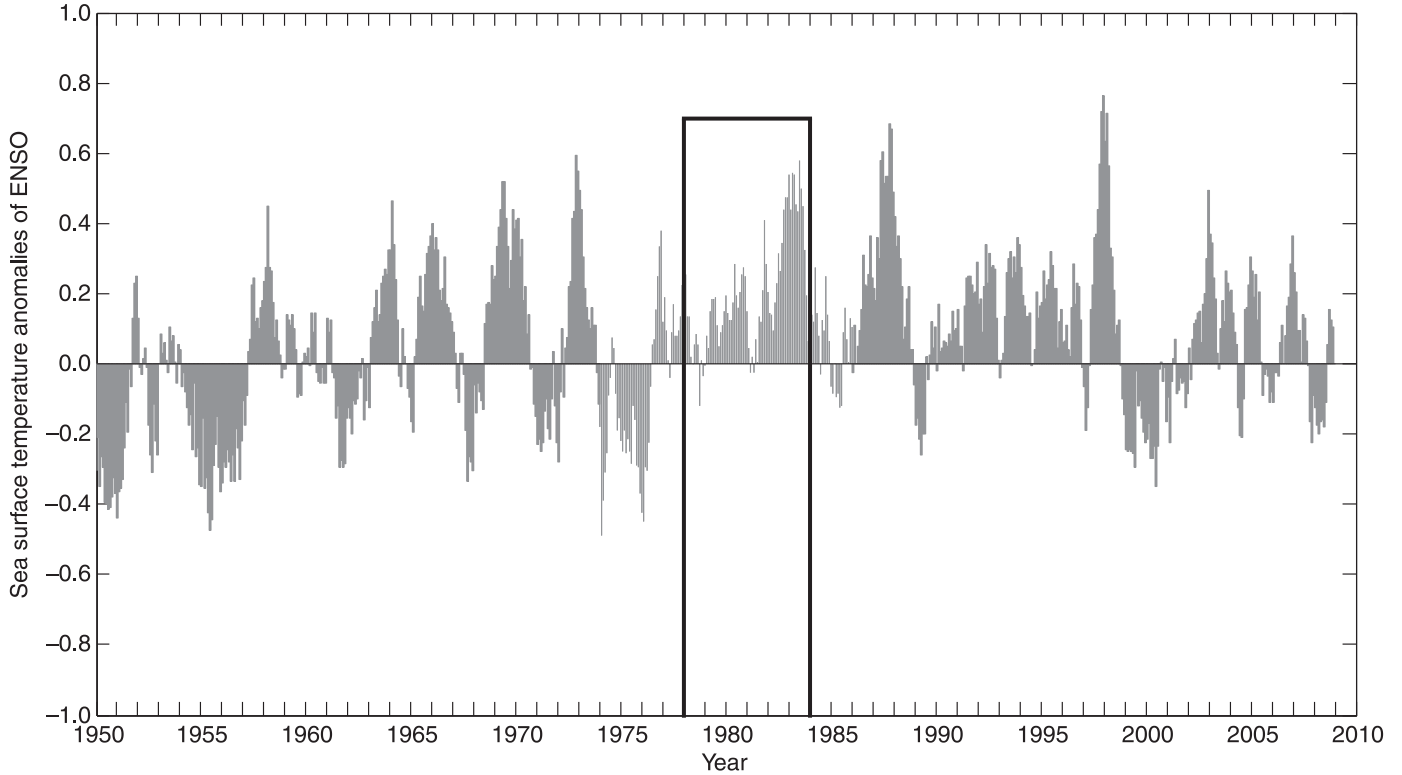
Fig. 7. Analysis between sea surface temperature (SST) anomalies and growth parameters (posterior means from model M1). Average anomalies of SST are calculated as the mean SST anomalies over years. For example, for individuals tagged in 1978 and recaptured at 1979, the corresponding average SST anomaly equals the mean SST anomalies of 1978 and 1979. (*a*) $L_{s,\infty} \sim$ averaged SST anomaly; (*b*) $K_s \sim$ averaged SST anomaly.
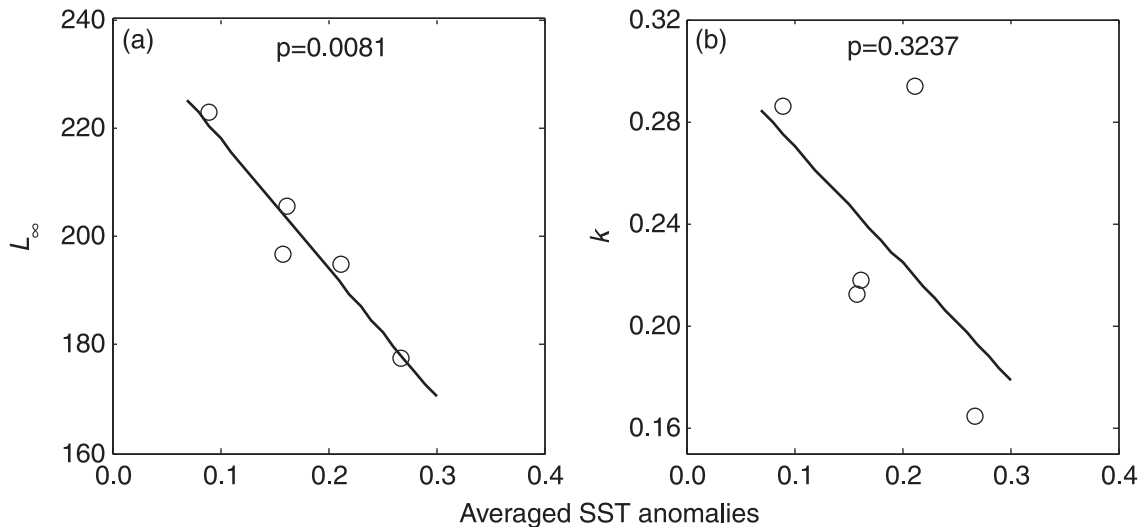
(Szalai et al. 2003; Jiao et al. 2009) might be better suited to time-varying parameters that can describe trends of the parameters. Also the very strong relationship between L_∞, K, and SST anomaly suggests that it might be effectively used as a direct covariate in the hierarchical analysis. Introducing categorical or continuous covariates into this type of analysis is relatively straightforward and may be much more parsimonious than allowing additional parameters for variable growth over years or arbitrary groupings of years (Helser et al. 2007). We need to select the type of models to explore according to the data characteristics and our preliminary knowledge of the effects of the possible covariates. In situations when either the data for each time period were not balanced, with some years having small sample size or narrow

length range, or the relationship between growth parameters and covariate is possibly nonlinear, which is usually true, the use of hierarchical models is suggested. The hierarchical model would allow the years with low sample size or narrow length range to borrow strength from other years with large sample size in the first situation. It would estimate the time-changing parameters and then look into the relationship between parameters and the covariates.

In this study, the base growth curve considered is the von Bertalanffy curve, but other growth curves can perform better or are worthwhile to be explored in the future (Katsanevakis 2006; Rogers-Bennett et al. 2007; Haddon et al. 2008). Uncertainty in model selection can be high when different growth curves are used. Model averaging and Bayesian model averaging can be alternative approaches to incorporate this model selection uncertainty (Burnham and Anderson 2002; Jiao et al. 2008).

Temporal variation of red abalone growth has been determined to be an important biological feature of these long-lived marine invertebrates (Haaker et al. 1998; Hobday and Tegner 2002). A model that can incorporate these temporal variations is needed to better capture abalone growth dynamics. For long-term management purposes, these variations need to be included in the stock assessment of abalone. When yield-per-recruit (YPR) and egg-per-recruit (EPR) models are used for stock assessment purposes, a hierarchical growth model as developed in this study may be used instead of nonhierarchical models that are more generally employed. YPR and EPR models are sensitive to growth variation and are certainly not safe to be used for abalone stock assessment (Tegner et al. 1989). A nonhierarchical model can underestimate the uncertainty caused by growth variation over time, which could contribute to overfishing during periods of low ocean productivity.

Growth during 1982 to 1984 was reduced to such a level that most abalone would not grow to the minimum legal size at that rate. This result is a challenge for stock assessment modeling and management because growth is widely used in developing biological reference points from per-recruitment analyses. Lower growth rates in the population than used in the modeling work could result in high $F_{0.1}$ and $F_{x\%}$ estimates from YPR and EPR models given the same minimum catchable size limit because most would be smaller than the size limit. However, the availability of abalone of catchable sizes would be low. A comprehensive modeling system that is capable of recognizing and incorporating important variability in growth rates and its relation with ocean climate if possible is needed for abalone and other species that exhibit highly variable growth rates. Hierarchical growth modeling may be a component of an ecosystem-based fishery management approach that can incorporate important changes in vital rates as they respond to fluctuations in oceanographic conditions.

Acknowledgements

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