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A hierarchical Bayesian approach for estimating freshwater mussel growth based on tag-recapture data

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ABSTRACT

In fisheries stock assessment and management, the von Bertalanffy growth model is commonly used to describe individual growth of many species by fitting age-at-length data. However, it is difficult or impossible to determine accurate individual ages in some cases. Mark-recapture survey becomes an alternative choice to collect individual growth information. In mark-recapture studies, some tagged animals can be recaptured more than one time and ignorance of the autocorrelations for each individual may result in substantial biases in estimations of growth parameters. To investigate the existence of individual and sex variability in growth, we designed an experiment to collect mark-recapture data for one endangered freshwater mussel species (*Epioblasma capsaeformis*) and one common, non-imperiled species (*Actinonaias pectorosa*) by using a passive integrated transponder (PIT) technique. Models with individual and sex variability (M1), sex-related differences (M2), individual variability (M3) and nonhierarchy (M4) were developed to estimate growth of *E. capsaeformis* and *A. pectorosa*. Deviance information criterion (DIC) was used to measure the performance of these models. For *E. capsaeformis*, female mussels tended to have higher means of asymptotic length (44.96 mm) and growth rate coefficient (0.283/year) than males (42.18 mm and 0.213/year). The model M3 yielded the lowest DIC value for both species, indicating individual differences should be considered in parameter estimation. Thus, we suggest that a hierarchical approach be used to consider individual variability for modeling growth of mussels with mark-recapture data, especially when there is a high percentage of multiple recaptures.

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1. Introduction

Freshwater mussels are major components of freshwater biodiversity in North America. However, they have experienced severe declines during the last several decades (Williams et al., 1993; Neves et al., 1997; Neves, 1999; Lydeard et al., 2004). To successfully implement conservation actions for freshwater mussels, managers must understand and estimate their life history parameters, such as individual growth rates (Dennis et al., 1991). Knowledge of growth is a critical consideration in assessing population dynamics and population sustainability (Alo's et al., 2010). The von Bertalanffy growth model is commonly used in fisheries science and management to describe individual growth of many species and populations (Hilborn and Walters, 1992; Quinn and Deriso, 1999; Haddon, 2010). Generally, non-linear regression is used to estimate key parameters: L_∞ (asymptotic length), K (growth rate coefficient), and t_0 (the age when length was zero) (von Bertalanffy, 1938). In

most cases, the parameters in the von Bertalanffy model are considered as parameters of a population, and they are assumed to represent all individuals from the same population. However, this assumption can be unrealistic, as growth rate from that population can be influenced by many factors, such as temperature, food availability, latitude, and population density (Krohn et al., 1997; Swain et al., 2003; Kimura, 2008; Jiao et al., 2010). Individual growth can differ due to different responses to these factors among individuals. It is more biologically realistic to assume each individual has its unique growth pattern even in a population (Sainsbury, 1980; James, 1991; Smith et al., 1997).

In growth estimation, von Bertalanffy models are usually fit to age-at-length data. However, for some species, it is difficult or impossible to determine accurate individual ages. For example, there are two commonly used methods to determine the age of freshwater mussels, growth ring counts on the outside of the shell and thin section counts of the internal shell growth annuli, with detailed descriptions of each method provided by Clark (1980) and Neves and Moyer (1988). However, these methods may lack accuracy or are inappropriate for a large number of mussels due to cost and time (Neves and Moyer, 1988). In these cases, a tag-recapture

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survey may be a better alternative for collecting individual growth information for freshwater mussels. To conduct such a survey, a number of mussels must be collected, tagged and then released to a site. The tagged mussels can be recaptured and measured for lengths after a period of time. The von Bertalanffy model can be reformulated to fit tag-recapture data to include the lengths and times at initial tagging and each recapture (Fabens, 1965; Quinn and Deriso, 1999).

The main problem in implementing a mark-recapture survey is that of monitoring tagged individuals effectively so that continuous data can be used in growth analyses. In this study, we used a passive integrated transponder (PIT) technology to monitor *Epioblasma capsaeformis* and *Actinonaias pectorosa* in the Clinch River in southwestern Virginia. The PIT tag is a small-sized tag, virtually eliminating negative impacts on animals and has little or no influence on growth-rate, behavior, health, or predator susceptibility (Elbin and Burger, 1994). The PIT tag has no battery and therefore its longevity appears indefinite (Gibbons and Andrews, 2004; Kurth et al., 2007). The PIT tag is activated by a fixed or portable reader, which transmits its unique code to the reader to identify the individual animal. While PIT technology was first used to monitoring fish movement, its use has expanded to include mammals, reptiles, amphibians, birds, and invertebrates (Prentice et al., 1990; Gibbons and Andrews, 2004). In recent years, PIT tags have been increasingly applied to freshwater mussels. Compared with traditional mussel mark-recapture methods, which largely depend on glue-on shellfish tags and visual encounters to locate mussels, PIT tags enhance the recapture rate, especially in muddy water conditions (Kurth et al., 2007).

In a conventional approach, individual growth is ignored when fitting the von Bertalanffy growth model, as it does not incorporate individual growth characteristics when modeling growth, which can introduce bias in stock assessment (Watson and Pauly, 2001; Lewin et al., 2006). Furthermore, in mark-recapture studies, some tagged animals can be recaptured more than one time. Individual lengths, which are measured at every recapture, provide growth data over the period. However, the mark-recapture length data contain autocorrelations for each individual and ignoring the autocorrelations may result in substantial biases in estimations of growth parameters (Maller and deBoer, 1988; Wang et al., 1995; Eveson et al., 2007; Zhang et al., 2009).

Two species were selected as example freshwater mussel species for this study. The oyster mussel (*E. capsaeformis*) is one of the few remaining extant species of the genus *Epioblasma*, which represents the most endangered group of freshwater mussels in North America (Jones et al., 2006), and it was selected as a representative endangered mussel species. It was historically distributed throughout the Tennessee and Cumberland River systems in Virginia, North Carolina, Georgia, Tennessee, Kentucky and Northern Alabama (Johnson, 1978). However, it has suffered great declines during the last 100 years and was listed as an endangered species in 1996 (Cummings and Cordeiro, 2012). On the other hand, the pheasantshell (*A. pectorosa*) was selected to represent a non-imperiled species. It is distributed throughout the Tennessee and Cumberland River systems. The species exhibits a different life history than *E. capsaeformis* in that it is typically longer-lived and more abundant (Scott, 1994). Both species have been selected as augmentation species for restoration of freshwater mussels in the Upper Tennessee River Basin by the Virginia Department of Game and Inland Fisheries (VDGIF, 2010). In previous studies, the von Bertalanffy model was used to estimate the "average" growth parameters of *E. capsaeformis* and *A. pectorosa* (Scott, 1994; Jones and Neves, 2011). However, neither study considered variation in growth among individuals.

In recent years, hierarchical Bayesian methods have been widely used in fisheries science because they provide a reliable tool to estimate vital parameters and quantify uncertainty by incorporating stochastic factors in modeling population dynamics (Punt and Hilborn, 1997; Helser and Lai, 2004; Forrest et al., 2010). These statistical methods are ideally suited for analyses of fish growth using the von Bertalanffy growth model (Pilling et al., 2002; Zhang et al., 2009). In acknowledging the existence of individual variance in a population, a hierarchical approach can effectively address the question of describing variation in growth of individuals. Individual growth rate is connected to population growth due to various biological and environmental factors, which can be represented by multilevel priors in a hierarchical model (Zhang et al., 2009). The multilevel priors are assumed to follow underlying distributions in a hierarchical growth model (Gelman et al., 2004; Jiao et al., 2009, 2010). Thus, the hierarchical Bayesian approach enables us to conveniently integrate uncertainty at both the individual and population level.

The aim of this paper is to investigate the existence of individual and sex variability in growth of mussels. Specifically, we first designed a field study to collect mark-recapture data for *E. capsaeformis* and *A. pectorosa* using PIT tag technology and then secondly, we developed Bayesian hierarchical models to incorporate individual growth variability to fit our mark-recapture data. We further extended the study to estimate growth variability between males and females, as *E. capsaeformis* exhibits pronounced sexual dimorphism (male and female shells differ in form). Analyses of individual and sex variability in growth rate estimation will be useful in evaluating population restoration activities and provide insights for conservation and management of mussels.

2. Materials and methods

2.1. Study sites

Cleveland Islands is located near the town of Cleveland in Russell Co., Virginia at Clinch River Mile (CRM) 270.8 (Fig. 1). A Norfolk Southern Railroad runs parallel to the stream along the right ascending bank and the site contains three mature islands that create four braided channels (Eckert et al., 2008). This site has been selected as an augmentation reach to implement components of the Virginia Freshwater Mussel Restoration Plan (Eckert et al., 2008). Cleveland Islands represents a biologically significant section in the upper Clinch River, has stable habitat for mussels to survive and grow, and has been regularly surveyed since 2002 to monitor freshwater mussel abundance and diversity (Eckert et al., 2008). However, growth of mussel species has not been estimated quantitatively and will be useful in evaluating population restoration activities at the site.

2.2. Mark-recapture experiment and data collection

A Bio-mark PIT tag kit, which include the FS2001F-ISO reader, portable BP antenna and bulk PIT tags (TX1411SST), was used for monitoring released *E. capsaeformis* and *A. pectorosa*. We placed external PIT tags on 30 male (length: 22–40 mm) and 30 female (length: 28–44 mm) *E. capsaeformis* and 60 *A. pectorosa* (length: 51–109 mm) collected from Kyles Ford (CRM 189) in the Clinch River in July, 2011. We affixed the PIT tag to the mussel's right shell using super glue and encapsulated it in dental cement to increase tag retention, a technique developed by D. Hua at the Freshwater Mollusk Conservation Center, Blacksburg, VA (Hua, D., personal communication). During the tagging process, mussels were kept in water at all times except when tagging them to minimize handling stress. The shell length of each mussel was measured to the nearest millimeter using a caliper. After tagging, the mussels were placed at Cleveland Islands. A Global Positioning System (GPS) was used to
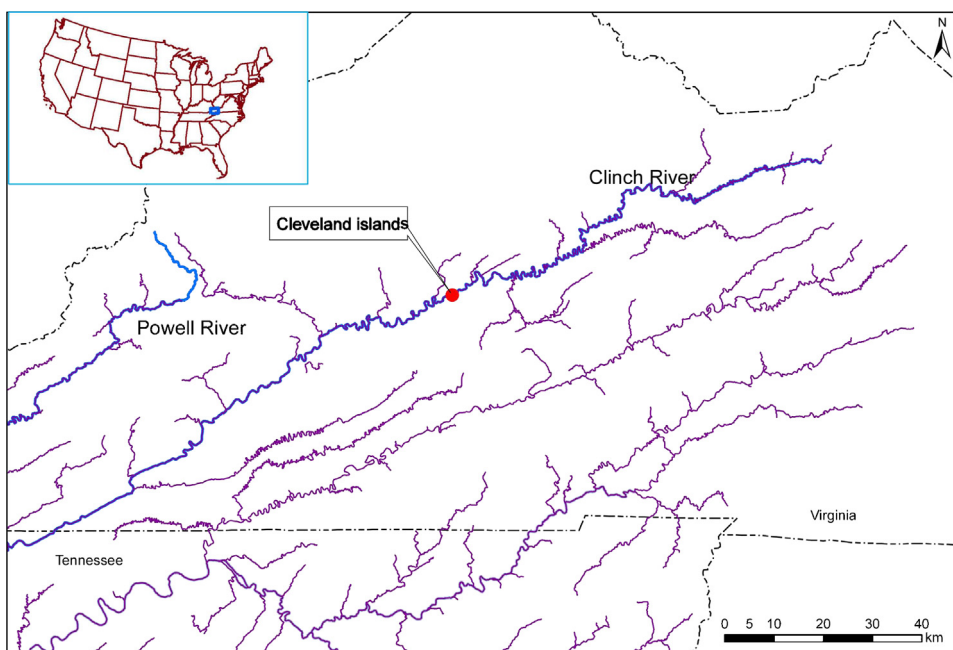
Fig. 1. The location of Cleveland Islands (Clinch River Mile 270.8) in the Clinch River.

record the location where mussels were placed. We recaptured the tagged mussels in August and September 2011 and July 2012 with the mobile PIT detection unit (Table 1) and the measured length changes were shown in Fig. 2. The shell length of each recaptured mussel was measured in situ and released to its point of collection after recording the tag code. Because mussels can move by themselves or be moved by water flow or animals, it is likely that they may change their original locations by moving slightly upstream, laterally or downstream. During recapture events, the area to be scanned was expanded by 20 percent down stream based on the collection location of mussels. If tagged mussels were found in the expanded area, the area scanned would be expanded again by 20 percent and so forth. If not, we would stop scanning and assumed there were no more tagged mussels beyond the surveyed area.

2.3. Growth models

To determine the growth curve from time-based length increases of tagged individuals, the von Bertalanffy model was fitted to mark-recapture data to estimate the parameters of interest

(Fabens, 1965; Haaker et al., 1998; Jiao et al., 2010). It can be written as:

$$E(\Delta L) = L_{t+\Delta t} - L_t = (L_\infty - L_t)\left(1 - e^{-K\Delta t}\right) \tag{1}$$

where L_t is the length at time t, $L_{t+\Delta t}$ is the length at time $t + \Delta t$, and t_0 is assumed to be 0 in this case (Haaker et al., 1998). Some mussels exhibited negative growth in this study period because of measurement errors or shell shrinkage (Downing and Downing, 1993). To include the negative growths, ΔL was assumed to follow a normal distribution with mean $(L_\infty - L_t)(1 - e^{-K\Delta t})$ and variance $\sigma^2_{\Delta L}$.

We assumed that each individual could grow following its own von Bertalanffy growth curve. Therefore, L_∞ and K should vary among individuals. We constructed four models to explore the growth rate of translocated freshwater mussels.

Table 1
Number of released and recaptured mussels collected during the mark-recapture survey at Cleveland Islands in the upper Clinch River, VA.

| Species	Survey	Number of mussels	Shell length (mm)		
			Mean	Min.	Max.
E. capsaeformis (male)	July 6th, 2011	30	31	22	40
	August 8th, 2011	28	32.1	22.7	41.3
	September 30th, 2011	28	32.2	23.7	41.4
	July 12th, 2012	29	33.7	27.0	41.1
E. capsaeformis (female)	July 6th, 2011	30	35	28	44
	August 8th, 2011	30	36.0	28.5	43.4
	September 30th, 2011	29	36.7	29.7	43.5
	July 12th, 2012	21	37.3	31.5	43.8
A. pectorosa	July 6th, 2011	60	79	51	109
	August 8th, 2011	59	80.5	50.0	108.2
	September 30th, 2011	58	81.0	51.0	108.0
	July 12th, 2012	56	81.5	52.7	108.1
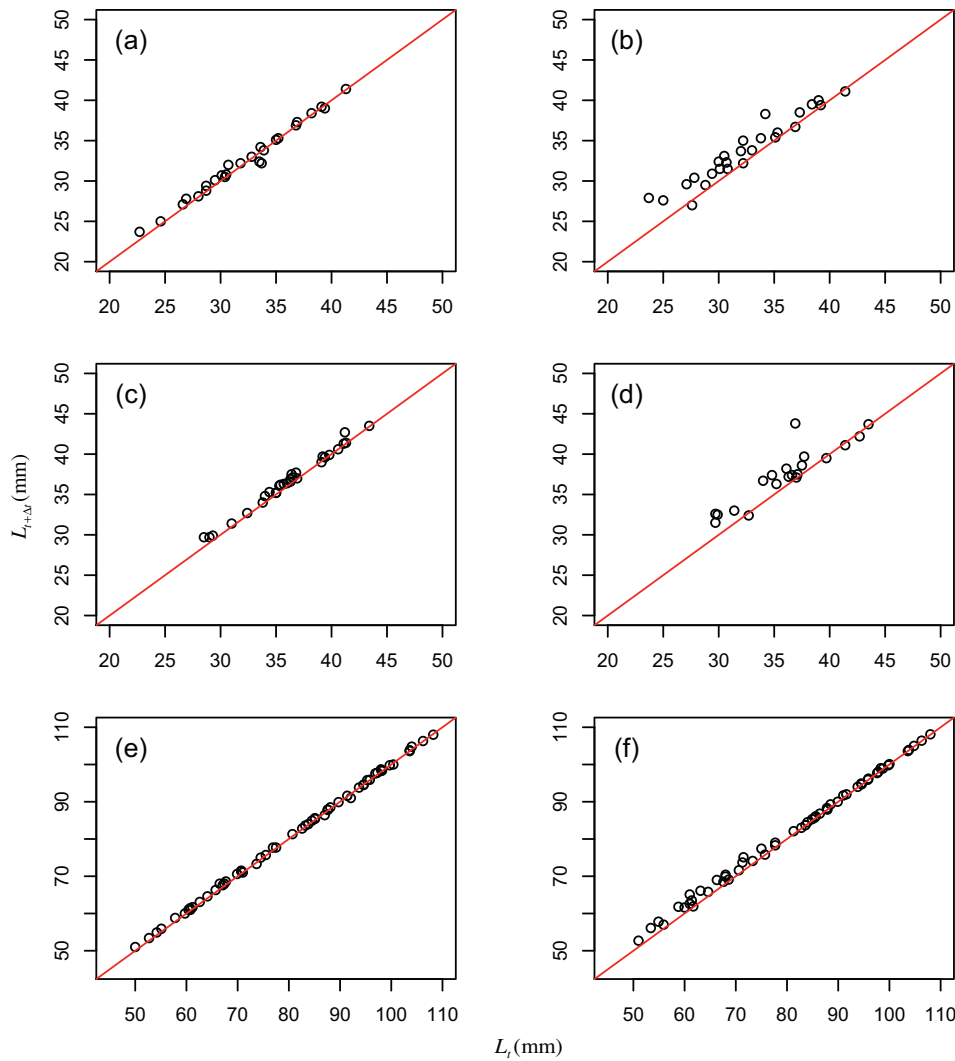
Fig. 2. Comparison of observed length at time t and the length at time $t + \Delta t$ for *Epioblasma capsaeformis* and *Actinonaias pectorosa* at Cleveland Islands. Red lines represent the $L_t \sim L_t$, circles represent the $L_t \sim L_{t+\Delta t}$ points. (a) Male *E. capsaeformis* at August 2011–September 2011; (b) Male *E. capsaeformis* at September 2011–July 2012; (c) female *E. capsaeformis* at August 2011–September 2011; (d) female *E. capsaeformis* at September 2011–July 2012; (e) *A. pectorosa* at August 2011–September 2011; (f) *A. pectorosa* at September 2011–July 2012.

In the first model (M1), both individual variability and sex-related differences were considered and the data were assumed to be hierarchically structured as:

$$L_{i,j,s} - L_{i,j-1,s} = (L_{\infty,j,s} - L_{i,j-1,s})(1 - e^{-K_{i,s}\Delta t_{j-1}})$$

$$L_{\infty,i,s} \sim N(\bar{L}_{\infty,s}, \sigma^2_{L_{\infty,s}})I(30, 70)$$

$$\bar{L}_{\infty,s} \sim N(\bar{L}_\infty, \sigma^2_{L_\infty})I(30, 70)$$

$$\bar{L}_\infty \sim U(30, 60)$$

$$\sigma^2_{L_{\infty,s}} \sim U(0, 100)$$

$$\sigma^2_{L_\infty} \sim U(0, 100)$$

$$K_{i,s} \sim N(\bar{K}_s, \sigma^2_{K_s})I(0, 1)$$

$$\bar{K}_s \sim N(\bar{K}, \sigma^2_K)I(0, 1)$$

$$\bar{K} \sim U(0, 0.8)$$

$$\sigma^2_{K_s} \sim U(0, 0.2)$$

$$\sigma^2_K \sim U(0, 0.2)$$

(2)

where i represent the ith individual, j represent the jth recapture ($j = 2$ and 3) and s represents sex of *E. capsaeformis* (males, $s = 1$; females, $s = 2$). The $L_{i,j,s}$ is the shell length of individual i during the jth recapture. The Δt_{j-1} is the time interval between the jth and $j - 1$th recapture. By considering the individual variation, the corresponding individual parameters were assumed to come randomly from a population distribution. $L_{\infty,i,s}$ and $K_{i,s}$ were assumed to be from normal distributions $N(\bar{L}_{\infty,s}, \sigma^2_{L_{\infty,s}})$ and $N(\bar{K}_s, \sigma^2_{K_\infty})$, respectively. The $\bar{L}_{\infty,s}$ and $\bar{K}_s$ represent population characteristics of male or female *E. capsaeformis* and were assumed to follow normal distributions $N(\bar{L}_\infty, \sigma^2_{L_\infty})$ and $N(\bar{K}, \sigma^2_K)$. The $\bar{L}_\infty$ and $\bar{K}$ exhibit population characteristics of *E. capsaeformis*, and were assumed to be from uniform distributions. Here I is used to limit the boundary of the distribution in WinBUGS. For example, $I(30, 70)$ means length should lie between 30–70 mm. We assumed the asymptotic length of each individual lay in the range of 30–70 mm because in previous research the predicted asymptotic length for male and female *E. capsaeformis* were 33.8–42.6 mm and 47.0–52.2 mm (Jones and Neves, 2011).

In the second model (M2), we developed a von Bertalanffy model considering sex-related differences, which was written as:

$$L_{j,s} - L_{j-1,s} = (L_{\infty,s} - L_{j-1,s})(1 - e^{-K_s \Delta t_{j-1}})$$

$$L_{\infty,s} \sim N(\bar{L}_\infty, \sigma^2_{L_\infty})I(30, 70)$$

$$\bar{L}_\infty \sim U(30, 60)$$

$$\sigma^2_{L_\infty} \sim U(0, 100) \tag{3}$$

$$K_s \sim N(\bar{K}, \sigma^2_K)I(0, 1)$$

$$\bar{K} \sim U(0, 0.8)$$

$$\sigma^2_K \sim U(0, 0.2)$$

The individual differences were ignored in this model, i.e. there was no individual dependence during multiple recaptures. $L_{\infty,s}$ and K_s represent population characteristics of male or female *E. capsaeformis* and were assumed to follow normal distributions. The $\bar{L}_\infty$ and $\bar{K}$ show population characteristics of *E. capsaeformis* and were assumed to follow uniform distributions.

In the third model (M3), the growth model was developed and written as:

$$L_{i,j} - L_{i,j-1} = (L_{\infty,i} - L_{i,j-1})(1 - e^{-K_i \Delta t_{j-1}})$$

$$L_{\infty,i} \sim N(\bar{L}_\infty, \sigma^2_{L_\infty})I(30, 70)$$

$$\bar{L}_\infty \sim U(30, 60)$$

$$\sigma^2_{L_\infty} \sim U(0, 100) \tag{4}$$

$$K_i \sim N(\bar{K}, \sigma^2_K)I(0, 1)$$

$$\bar{K} \sim U(0, 0.8)$$

$$\sigma^2_K \sim U(0, 0.2)$$

Here, only individual variability was incorporated. The different performances between models M1 and M3 reflected the importance of sex-related differences in parameter estimations. This comparison was just applied for *E. capsaeformis*.

The nonhierarchical von Bertalanffy growth model (M4) was written as:

$$L_{i,j} - L_{i,j-1} = (L_\infty - L_{i,j-1})(1 - e^{-K \Delta t_{j-1}})$$

$$L_\infty \sim U(30, 70) \tag{5}$$

$$K \sim U(0, 1)$$

Both individual variability and sex-related differences were ignored in this model. The ranges of L_∞ and K were wider than the mean of priors in the hierarchical model because a narrow range of priors may provide more information and further influence the estimates.

Male and female *A. pectorosa* are similar in appearance and hard to distinguish. Thus, models M3 and M4 that did not consider sex-related difference were applied to fit tag-recapture data of *A. pectorosa*. As *A. pectorosa* and *E. capsaeformis* exhibit quite different length and longevity expectations, different boundaries for the distributions were used in their estimation. The priors in model M3 were $\bar{L}_\infty \sim U(80, 130)$, $\bar{K} \sim U(0, 0.8)$, $\sigma^2_{L_\infty} \sim U(0, 200)$ and $\sigma^2_K \sim U(0, 0.2)$. The boundaries of the asymptotic length and growth rate coefficient for *A. pectorosa* were $I(70, 140)$ and $I(0, 1)$, respectively. The ranges of L_∞ and K were wider in model M4, which were $L_\infty \sim U(70, 140)$ and $K \sim U(0, 1)$.

To test the sensitivity of estimates to prior assumptions, we changed the lower bounds of $\bar{L}_\infty$ and L_∞ to 50% of those used above and changed the upper bounds of $\bar{L}_\infty$ and L_∞ to 150% of those used above. We also extended the upper limit of K to 1. Sensitivity analyses were conducted for both *A. pectorosa* and *E. capsaeformis*.

Table 2
Model comparison by the deviance information criterion (DIC) values among the model with individual and sex variability (M1), the model with sex-related differences (M2), the model with individual variability (M3) and the non-hierarchical model (M4) for *Epioblasma capsaeformis* and *Actionaias pectorosa*. DIC values from sensitivity analyses are shown in brackets. See priors used from the text.

Model	Species	
	E. capsaeformis	*A. pectorosa*
M1	173.711 (164.966)	–
M2	296.211 (295.808)	–
M3	171.584 (164.941)	125.392 (124.849)
M4	302.808 (302.992)	229.172 (229.280)

2.4. Bayesian method and priors

WinBUGS (Spiegelhalter et al., 2004) is a Bayesian analysis software that uses Markov Chain Monte Carlo (MCMC) to fit statistical models. Any Bayesian analysis requires specification of prior distributions on all unknown parameters. Uniform distributions usually work better than inverse-gamma distributions for variance parameters in hierarchical models (Gelman, 2006). Thus, uniform priors were used for variances $\sigma^2_{L_{\infty,s}}$, $\sigma^2_{L_\infty}$, $\sigma^2_{K_s}$, and σ^2_K.

The deviance information criterion (DIC) was used to select the "best" model in this study. It is a composite measure of the goodness of fit and model complexity (Spiegelhalter et al., 2002; Jiao et al., 2010). The DIC is calculated by:

$$DIC = 2\bar{D}(\theta) - \hat{D}(\theta) \text{ or } \bar{D}(\theta) + P_D$$

$$\bar{D}(\theta) = E_{\theta|y}(-2\log \text{Likelihood}(y|\theta))$$

$$\hat{D}(\theta) = -2\log \text{Likelihood}(y|\bar{\theta}) \tag{6}$$

$$p_D = \bar{D}(\theta) - \hat{D}(\theta)$$

where D is deviance; p_D denotes the effective number of parameters in the model, which counts the differences between $\bar{D}(\theta)$ and $\hat{D}(\theta)$ and is a measurement of model complexity; $\bar{D}(\theta)$ is the posterior mean of the deviance, a Bayesian measurement of model fit; $\hat{D}(\theta)$ is defined as the deviance evaluated at the posterior mean of the parameters. The DIC is intended as a hierarchical modeling generalization of the AIC (Akaike information criterion) and BIC (Bayesian information criterion, also known as the Schwarz criterion). Like AIC and BIC, the preferred model is the one with the minimum DIC value.

The first 100,000 iterations with a thinning interval of 100 were treated as a burn-in period and the other 100,000 iterations were saved in the Bayesian analysis to estimate the growth rates for each species. Three chains were generated with different initial values to allow the Gelman–Rubin convergence statistic (Spiegelhalter et al., 2004; Jiao et al., 2008, 2009) to be applied.

3. Results

For all of the parameters, the ratios from the Gelman–Rubin statistics, which assesses the within-chain variability as compared to between-chain variability, were equal to 1, indicating convergence of chains. The thinning interval of 100 for growth rate estimations was sufficient to reduce autocorrelations of parameters and to help generate independent samples among Markov chains.

Among the developed models, model M3, which incorporated individual variability, yielded the lowest DIC value for both species (Table 2). For *E. capsaeformis*, the model M1, which assumed that individual variability and sex-related differences in growth, had a slightly higher DIC value compared with model M3. The difference of DIC between models M1 and M3 was 2.127, indicating

Table 3
Estimates of parameters of the model with individual and sex variability (M1) and the model with individual variability (M3) for *Epioblasma capsaeformis*, and the best model (M3) for *Actinonaias pectorosa*. Estimates of parameters from sensitivity analyses are shown in brackets.

Species	Model	Parameter	Mean	Standard deviation	95% Credible interval	
E. capsaeformis	M1	$\bar{L}_\infty$	43.73 (43.49)	4.79 (5.20)	34.38 (32.80)	53.99 (54.58)
		$\sigma^2_{L_\infty}$	42.47 (43.33)	28.65 (28.74)	1.79 (1.56)	96.37 (96.31)
		$\bar{L}_{\infty,s=1}$	42.18 (42.05)	2.49 (2.63)	38.48 (37.99)	48.14 (48.27)
		$\sigma^2_{L_{\infty,s=1}}$	17.51 (26.00)	14.64 (20.74)	2.30 (2.93)	60.29 (81.01)
		$\bar{L}_{\infty,s=2}$	44.96 (45.20)	2.48 (2.86)	40.94 (41.05)	50.61 (52.23)
		$\sigma^2_{L_{\infty,s=2}}$	29.26 (32.25)	17.39 (19.99)	7.13 (7.46)	74.43 (85.48)
		$\bar{K}$	0.28 (0.28)	0.15 (0.17)	0.03 (0.03)	0.64 (0.70)
		σ^2_K	0.07 (0.07)	0.057 (0.057)	<0.01 (<0.01)	0.19 (0.19)
		$\bar{K}_{s=1}$	0.21 (0.22)	0.08 (0.06)	0.12 (0.11)	0.34 (0.35)
		$\sigma^2_{K_{s=1}}$	0.01 (0.01)	0.01 (0.01)	<0.01 (<0.01)	0.03 (0.03)
		$\bar{K}_{s=2}$	0.28 (0.28)	0.08 (0.08)	0.16 (0.14)	0.47 (0.46)
		$\sigma^2_{K_{s=2}}$	0.02 (0.02)	0.01 (0.01)	<0.01 (<0.01)	0.05 (0.05)
	M3	$\bar{L}_\infty$	45.34 (46.00)	2.34 (2.97)	41.36 (41.34)	50.46 (52.93)
		$\sigma^2_{L_\infty}$	32.67 (45.65)	15.18 (22.25)	11.01 (13.28)	68.62 (94.04)
		$\bar{K}$	0.19 (0.18)	0.04 (0.05)	0.13 (0.11)	0.30 (0.29)
		σ^2_K	0.01 (0.01)	0.01 (0.01)	<0.01 (<0.01)	0.02 (0.02)
A. pectorosa	M3	$\bar{L}_\infty$	104.20 (104.30)	2.95 (3.13)	99.02 (98.83)	110.60 (111.20)
		$\sigma^2_{L_\infty}$	73.56 (76.00)	38.01 (40.34)	12.32 (13.23)	164.00 (171.20)
		$\bar{K}$	0.06 (0.06)	0.01 (0.01)	0.05 (0.05)	0.08 (0.08)
		σ^2_K	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)

that sex-related differences were also considerable in growth estimation for *E. capsaeformis* (Table 2). The difference (124.627) in DIC values between models M2 and M3 and the larger difference (131.224) in DIC values between models M4 and M3 demonstrated that individual variability was an important factor and should be considered in the growth analyses of *E. capsaeformis*. From the results in model M1, the 95% credible interval for L_∞ for male *E. capsaeformis* varied between 38.48 and 48.14 mm, with a mean of 42.18 mm (Table 3). Females ranged from 40.94 and 50.61 mm, with a mean of 44.96 mm. Thus, the estimated asymptotic length for males was smaller than females (Table 3). The 95% credible interval for K for male *E. capsaeformis* varied between 0.12 and 0.34 with a mean of 0.21 and ranged from 0.16 to 0.47 with a mean of 0.28 for female *E. capsaeformis*, indicating that the estimated growth rate coefficient for males was smaller than females (Table 3). There was some overlap in the joint posteriors of L_∞ and K between females and males but overall the differences were quite observable (Fig. 3), which also demonstrated considerable sex difference was shown for this species in the von Bertalanffy growth model.

For *A. pectorosa*, model M3, the model that incorporated individual variability, had the lowest DIC value (Table 2). The difference in DIC values between models M3 and M4 was 103.936, which is larger than 10, indicating that individual variability was important and should be considered in the growth analyses of mark-recapture data for *A. pectorosa*. The 95% credible interval for estimated asymptotic length by model M3 varied between 99.02 and 110.6 mm with a mean of 104.2 mm, and the growth rate varied from 0.05–0.08 with a mean of 0.06 (Table 3).

We conducted a set of sensitivity analyses to test the influence of the priors of $\bar{L}_\infty$ and $\bar{K}$ on both the model selection and the key parameters in the growth model. The model with individual variability (M3) still yielded the lowest DIC value for both species (Table 2). The results also showed that the posteriors of parameters of interest in the growth models for both species were not sensitive to the choice of priors in both the hierarchical and nonhierarchical models (Table 3; Fig. 4).

4. Discussion

The conservation of freshwater mussel species requires knowledge of their biology and accurate and efficient assessment of mussel population dynamics. The mark-recapture method is commonly used for individual monitoring and risk assessment in many biological populations (Anthony et al., 2001; Hart et al., 2001; Rogers et al., 2001; Villella et al., 2004). However, most investigators have relied on visual searches, which are largely influenced by location, time, flow, gender, species, etc. In previous studies, the average recapture rates of tagged mussels through visual searches were less than 47% (Cope and Waller, 1995; Kurth et al., 2007). Here, we used the PIT tag technique to monitor the growth of *E. capsaeformis* and *A. pectorosa* and obtained a high percentage of multiple recaptures at this site (Table 1). The unique codes from PIT tags enabled us to record the length of each individual mussel. Thus, the PIT tag technique provided a very useful tool to monitor individual mussels, especially when there were a limited number of available mussels for conducting a mark-recapture study.
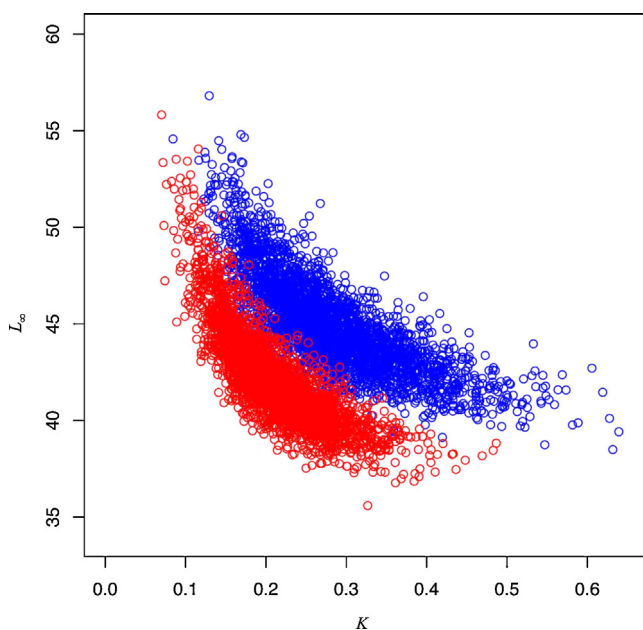

Fig. 3. Joint posterior distributions of asymptotic lengths (L_∞) and growth rates (K) for *Epioblasma capsaeformis* at Cleveland Islands when model M1 is used with narrow priors. Red, male *E. capsaeformis*; blue, female *E. capsaeformis*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
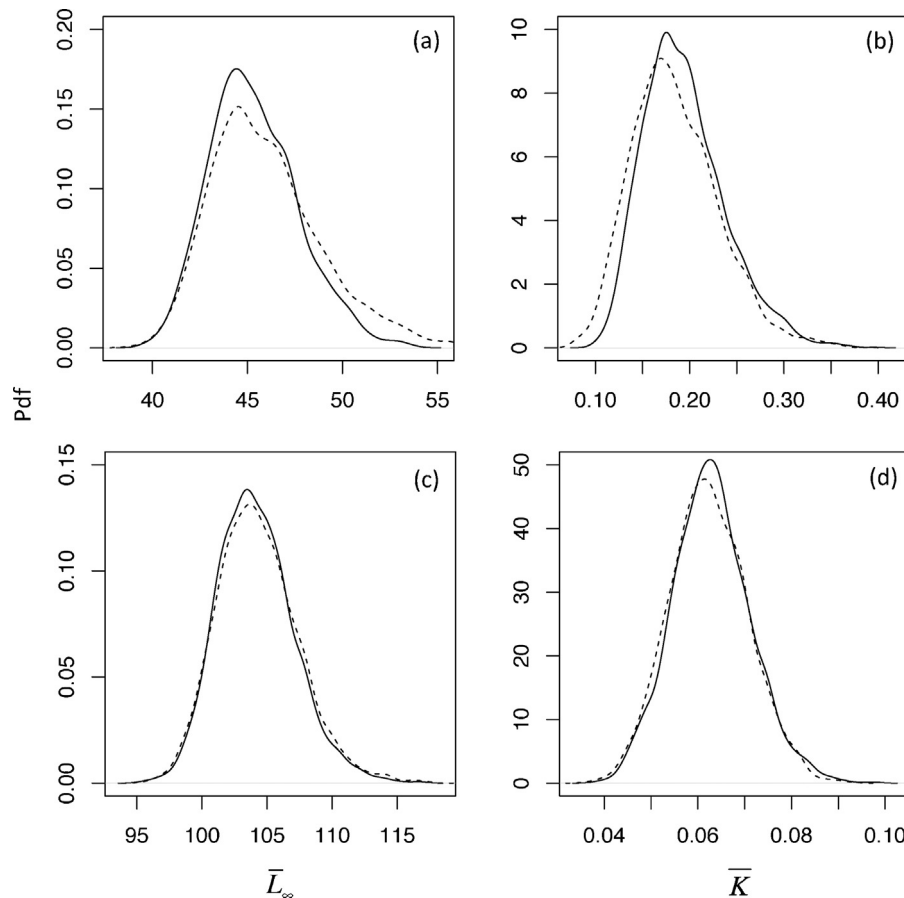
Fig. 4. Posterior probability density functions (pdf) of $\bar{L}_\infty$ and $\bar{K}$ for *Epioblasma capsaeformis* and *Actinonaias pectorosa* when model M3 was used. (a) $\bar{L}_\infty$ for *E. capsaeformis*; (b) $\bar{K}$ for *E. capsaeformis*; (c) $\bar{L}_\infty$ for *A. pectorosa*; (d) $\bar{K}$ for *A. pectorosa*. Continuous line: estimates with narrow priors; dotted line: estimates with wide priors.

Recently, more and more researchers in fishery science emphasize the importance of fitting individual variability in growth curves (Pilling et al., 2002; Helser and Lai, 2004; Zhang et al., 2009). The Bayesian hierarchical approach is very useful for analyzing tag-recapture data (Jiao et al., 2010). When incorporating individual variability in models, the growth parameters of individuals were assumed to follow a normal distribution related to the population average. This relationship can be conveniently described by a Bayesian hierarchical approach by using multilevel priors estimated through joint posterior distributions. In addition, the Bayesian approach can provide good prediction accuracy even in cases involving small sample sizes (Kontkanen et al., 1997; Jiao et al., 2010).

To estimate the individual growth of *E. capsaeformis* and *A. pectorosa* at Cleveland Islands, hierarchical and nonhierarchical models were proposed and compared by DIC values. The hierarchical model with individual variability (M3) gave the best fit for growth of these two species using DIC. The Bayesian hierarchical model is very flexible and easy to update if more tag-recapture data are available from a future survey. Besides its goodness of fit, we suggest that the hierarchical model be used to fit tag-recapture data with a high percent of multiple recaptures to incorporate potential correlation among replicate observations. Furthermore, in the conventional approach, the variability of L_∞ and K for the entire population only covered the measurement errors, but the variability in L_∞ and K among individuals that reflect the processes inherent to each species was ignored. It is appropriate to use the hierarchical model to accurately reflect the individual growth in a population and the estimates can also be applied to individual simulation analyses. In addition, the accurate and precise estimates

of the growth of mussels could help decrease errors in the analyses of population dynamics and ecological questions and improve management of freshwater mussels.

In a previous study, female *E. capsaeformis* were found to grow larger than males but have a lower individual grow rate coefficient (K) than males (Jones and Neves, 2011). The results obtained here agree with the statement about asymptotic length. However, according to the results in this study, the mean growth rate coefficient for females was larger than that for males. The somatic growth of mussels is likely influenced by temperature, flow discharge, food availability, site substrate characteristics, etc. (Krohn et al., 1997; Jiao et al., 2010; Jones and Neves, 2011). Because the survey lasted only for one year, it is possible that the habitat at Cleveland Islands or some special environmental condition during the survey duration may have caused the female growth rate to increase or that for males to decrease. More recapture surveys would be better, such as involving multiple years of data or incorporating spatial factors, to increase the validity of qualitative descriptions of mussel growth at the individual level.

Regardless of species difference, the high detection rates of PIT tagged mussels suggest that PIT provides a valid approach to monitor individual mussels in the field and further enhances the accuracy of growth estimates. In this study, a Bayesian hierarchical model demonstrated its advantages in incorporating variations among individuals. By considering individual variation, the growth of the two example species has been estimated more accurately and precisely, which will help improve understanding of the biological characteristics of these two species. Furthermore, the PIT tag technique and hierarchical Bayesian approach could be applied to other freshwater mussel species to explore their demographic

characteristics and guide the conservation of endangered freshwater mussels. In future studies, sexes, sites and temporal variations could also be considered through a Bayesian hierarchical model to analyze survey data of other species. We suggest that long-term surveys for mussels be conducted because additional data will help increase the accuracy of parameters on life history and population estimation using the Bayesian hierarchical approach.

References

Aloˊs, J., Palmer, M., Balle, S., Grau, A.M., Morales-Nin, B., 2010. Individual growth pattern and variability in *Serranus scriba*: a Bayesian analysis. ICES J. Mar. Sci. 67, 502–512.

Anthony, J.L., Kesler, D.H., Downing, W.L., Downing, J.A., 2001. Length specific growth rates in freshwater mussels (Bivalvia: Unionidae): extreme longevity or generalized growth cessation? Freshwater Biol. 46, 1349–1359.

Cummings, K., Cordeiro, J., 2012. *Epioblasma capsaeformis*. In: IUCN 2012. IUCN Red List of Threatened Species, http://www.iucnredlist.org/details/7866/0

Clark, G.R., 1980. Study of molluscan shell structure and growth lines using thin sections. In: Rhoads, D.C., Lutz, R.A. (Eds.), Skeletal Growth in Aquatic Organisms. Plenum Press, New York, pp. 603–606.

Cope, W.G., Waller, D.L., 1995. Evaluation of freshwater mussel relocation as a conservation and management strategy. Regul. Rivers Res. Manag. 11, 147–155.

Dennis, B., Munholland, P.L., Scott, J.M., 1991. Estimation of growth and extinction parameters for endangered species. Ecol. Monogr. 61, 115–143.

Downing, W.L., Downing, J.A., 1993. Molluscan shell growth and loss. Nature 362, 506.

Eckert, N.L., Ferraro, J.J., Pinder, M.J., Watson, B.T., 2008. Freshwater Mussel and Spiny Riversnail Survey of Slant, Clinch River, Virginia: Augmentation Monitoring Site–2005. VDGIF, Richmond, Final Report http://www.dgif.virginia.gov/awcc/freshwater-mussel-restoration/mussel-survey-report-2005.pdf

Elbin, S.B., Burger, J., 1994. In my experience: implantable microchips for individual identification in wild and captive populations. Wildl. Soc. Bull. 22, 677–683.

Eveson, J.P., Polacheck, T., Laslett, G.M., 2007. Consequences of assuming an incorrect error structure in von Bertalanffy growth models: a simulation study. Can. J. Fish. Aquat. Sci. 64, 602–617.

Fabens, A.J., 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29, 265–289.

Forrest, R.E., McAllister, M.K., Dorn, M.W., Martell, S.J.D., Stanley, R.D., 2010. Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock–recruit function. Can. J. Fish. Aquat. Sci. 67, 1611–1634.

Gelman, A., 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Anal. 1, 515–533.

Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis. Chapman & Hall/CRC, London.

Gibbons, J.W., Andrews, K.M., 2004. PIT tagging: simple technology at its best. Bioscience 54, 447–454.

Haaker, P.L., Parker, D.O., Barsky, K.C., Chun, C.S.Y., 1998. Biology-growth of red abalone, *Haliotis rufescens* (Swainson), at Johnsons Lee, Santa Rosa Island, California. J. Shellfish Res. 17, 747–754.

Haddon, M., 2010. Modelling and Quantitative Methods in Fisheries. Chapman & Hall/CRC, London.

Hart, R.A., Grier, J.W., Miller, A.C., Davis, M., 2001. Empirically derived survival rates of a native mussel, *Amblema plicata*, in the Mississippi and Otter Tail Rivers. Minnesota. Am. Midl. Nat. 146, 254–263.

Helser, T.E., Lai, H.L., 2004. A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, *Micropterus salmoides*. Ecol. Model. 178, 399–416.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty. Chapman & Hall, New York.

James, I.R., 1991. Estimation of von Bertalanffy growth curve parameters from recapture data. Biometrics 47, 1519–1530.

Jiao, Y., Neves, R., Jones, J., 2008. Models and model selection uncertainty in estimating growth rates of endangered freshwater mussel populations. Can. J. Fish. Aquat. Sci. 65, 2389–2398.

Jiao, Y., Reid, K., Smith, E., 2009. Model selection uncertainty and Bayesian model averaging in fisheries recruitment modeling. In: Beamish, R.J., Rothschild, B.J. (Eds.), The Future of Fisheries Science in North America. Springer, Berlin, pp. 505–524.

Jiao, Y., Rogers-Bennett, L., Taniguchi, I., Butler, J., Crone, P., 2010. Incorporating temporal variation in the growth of red abalone (*Haliotis rufescens*) using hierarchical Bayesian growth models. Can. J. Fish. Aquat. Sci. 67, 730–742.

Johnson, R.I., 1978. Systematics and zoogeography of *Plagiola* (= *Dysnomia* = *Epioblasma*), an almost extinct genus of freshwater mussels (Bivalvia: Unionidae) from middle North America. Bull. Mus. Comp. Zool. 148, 239–320.

Jones, J.W., Neves, R.J., 2011. Influence of life history variation on demographic responses of three freshwater mussel species (Bivalvia: Unionidae) in the Clinch River, USA. Aquat. Conserv. Mar. Freshwater Ecosyst. 21, 57–73.

Jones, J.W., Neves, R.J., Ahlstedt, S.A., Hallerman, E.M., 2006. A holistic approach to taxonomic evaluation of two closely related endangered freshwater mussel species, the oyster mussel *Epioblasma capsaeformis* and tan riffleshell *Epioblasma florentina walkeri* (Bivalvia: Unionidae). J. Mollus. Stud. 72, 267.

Kimura, D.K., 2008. Extending the von Bertalanffy growth model using explanatory variables. Can. J. Fish. Aquat. Sci. 65, 1879–1891.

Kontkanen, P., Myllymäki, P., Silander, T., Tirri, H., Grunwald, P., 1997. Comparing predictive inference methods for discrete domain. In: Proceedings of the Sixth International on Artificial Intelligence and Statistics, Ft. Lauderdale, USA, pp. 311–318.

Krohn, M.M., Reidy, S.P., Kerr, S.R., 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54, 113–121.

Kurth, J., Loftin, C., Zydlewski, J., Rhymer, J., 2007. PIT tags increase effectiveness of freshwater mussel recaptures. J. N. Am. Benthol. Soc. 26, 253–260.

Lewin, W.C., Arlinghaus, R., Mehner, T., 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev. Fish. Sci. 14, 305–367.

Lydeard, C., Cowie, R.H., Ponder, W.F., Bogan, A.E., Bouchet, P., Clark, S.A., Cummings, K.S., Frest, T.J., Gargominy, O., Herbert, D.G., 2004. The global decline of nonmarine mollusks. Bioscience 54, 321–330.

Maller, R.A., deBoer, E.S., 1988. An analysis of two methods of fitting the von Bertalanffy curve to capture-recapture data. Aust. J. Mar. Freshw. Res. 39, 459–466.

Neves, R., 1999. Conservation and commerce: management of freshwater mussel (Bivalvia: Unionoidea) resources in the United States. Malacologia 41, 461–474.

Neves, R.J., Bogan, A.E., Williams, J.D., Ahlstedt, S.A., Hartfield, P.W., 1997. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity. In: Benz, G.W., Collins, D.E. (Eds.), Aquatic Fauna in Peril: The Southeastern Perspective. Southeast Aquatic Research Institute, Decatur, Georgia, pp. 43–85, Special Publication No. 1.

Neves, R.J., Moyer, S.N., 1988. Evaluation of techniques for age determination of freshwater mussels (Unionidae). Am. Malacol. Bull. 6, 179–188.

Pilling, G.M., Kirkwood, G.P., Walker, S.G., 2002. An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. Can. J. Fish. Aquat. Sci. 59, 424–432.

Punt, A.E., Hilborn, R., 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. 7, 3563.

Prentice, E.F., Flagg, T.A., McCutcheon, C.S., Brastow, D.F., 1990. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Am. Fish. Soc. Symp. 7, 323–324.

Quinn, T.J., Deriso, R.B., 1999. Quantitative Fish Dynamics. Oxford University Press, USA.

Rogers, S.O., Watson, B.T., Neves, R.J., 2001. Life history and population biology of the endangered tan riffleshell (*Epioblasma florentina walkeri*) (Bivalvia: Unionidae). J. N. Am. Benthol. Soc. 20, 582–594.

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

Scott, J.C., 1994. Population Demographics of Six Freshwater Mussel Species (Bivalvia: Unionidae) in the Upper Clinch River, Virginia and Tennessee. Virginia Polytechnic Institute and State University, Blacksburg (MS thesis).

Smith, E.B., Williams, F.M., Fisher, C.R., 1997. Effects of intrapopulation variability on von Bertalanffy growth parameter estimates from equal mark-recapture intervals. Can. J. Fish. Aquat. Sci. 54, 2025–2032.

Spiegelhalter, D., Best, N.G., Carlin, B.P., van der Linde, A., 2002. Bayesian measures of model complexity and fit (with discussion). J. Roy. Stat. Soc. Ser. B 64, 583–639.

Spiegelhalter, D., Thomas, A., Best, N., Lunn, D., 2004. WinBUGS User Manual. Mdeical Research Council Biostatistics Unit, Cambridge, UK.

Swain, D.P., Sinclair, A.F., Castonguay, M., Chouinard, G., Drinkwater, K.F., Fanning, L., Clark, D.S., 2003. Density-versus temperature-dependent growth of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence and on the Scotian Shelf. Fish. Res. 59, 327–341.

Villella, R., Smith, D., Lemarie, D., 2004. Estimating survival and recruitment in a freshwater mussel population using mark-recapture techniques. Am. Midl. Nat. 151, 114–133.

Virginia Department of Game Inland Fisheries (VDGIF), 2010. Virginia Freshwater Mussel Restoration Strategy: Upper Tennessee River Basin. Virginia Department of Game and Inland Fisheries, Bureau of Wildlife Resources, Wildlife Diversity Division, Nongame and Endangered Wildlife Program, Richmond, VA http://www.dgif.virginia.gov/awcc/freshwater-mussel-restoration/virginia-freshwater-mussel-restoration-strategy-UTRB.pdf

von Bertalanffy, L., 1938. A quantitative theory of organic growth. Human Biol. 10, 181–213.

Wang, Y.G., Thomas, M.R., Somers, I.F., 1995. A maximum likelihood approach for estimating growth from tag-recapture data. Can. J. Fish. Aquat. Sci. 52, 252–259.

Watson, R., Pauly, D., 2001. Systematic distortions in world fisheries catch trends. Nature 414, 534–536.

Williams, J.D., Warren, M.L., Cummings, K.S., Harris, J.L., Neves, R.J., 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18, 6–22.

Zhang, Z., Lessard, J., Campbell, A., 2009. Use of Bayesian hierarchical models to estimate northern abalone, *Haliotis kamtschatkana*, growth parameters from tag-recapture data. Fish. Res. 95, 289–295.