Bayesian population dynamics modeling to guide population restoration and recovery of endangered mussels in the Clinch River, Tennessee and Virginia

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ABSTRACT

Freshwater mussels have played an important role in the history of human culture and also in ecosystem functioning. But during the past several decades, the abundance and diversity of mussel species has declined all over the world. To address the urgent need to maintain and restore populations of endangered freshwater mussels, quantitative population dynamics modeling is needed to evaluate population status and guide the management of endangered freshwater mussels. One endangered mussel species, the oyster mussel (*Epioblasma capsaeformis),* was selected to study its population dynamics for my research. The analysis was based on two datasets, length frequency data from annual surveys conducted at three sites in Clinch River: Wallen Bend (Clinch River Mile 192) from 2004-2010, Frost Ford (CRM 182) from 2005 to 2010 and Swan Island (CRM 172) from 2005 to 2010, and age-length data based on shell thin-sections. Three hypothetical scenarios were assumed in model estimations: (1) constant natural mortality; (2) one constant natural mortality rate for young mussels and another one for adult mussels; (3) age-specific natural mortality. A Bayesian approach was used to analyze the age-structured models and a Bayesian model averaging approach was applied to average the results by weighting each model using the deviance information criterion (DIC). A risk assessment was conducted to evaluate alternative restoration strategies for *E. capsaeformis*. The results indicated that releasing adult mussels was the quickest way to increase mussel population size and increasing survival and fertility of young mussels was a suitable way to restore mussel populations in the long term. The population of *E. capsaeformis* at Frost Ford had a lower risk of decline compared with the populations at Wallen Bend and Swan Island.

Passive integrated transponder (PIT) tags were applied in my fieldwork to monitor the translocation efficiency of *E. capsaeformis* and *Actinonaias pectorosa* at Cleveland Islands (CRM 270.8). Hierarchical Bayesian models were developed to address the individual variability and sex-related differences in growth. In model selection, the model considering individual variability and sex-related differences (if a species has sexual dimorphism) yielded the lowest DIC value. The results from the best model showed that the mean asymptotic length and mean growth rate of female *E. capsaeformis* were 45.34 mm and 0.279, which were higher than values estimated for males (42.09 mm and 0.216). The mean asymptotic length and mean growth rate for *A. pectorosa* were 104.2 mm and 0.063, respectively.

To test for the existence of individual and sex-related variability in survival and recapture rates, Bayesian models were developed to address the variability in the analysis of the mark-recapture data of *E. capsaeformis* and *A. pectorosa*. DIC was used to compare different models. The median survival rates of male *E. capsaeformis,* female *E. capsaeformis* and *A. pectorosa* were high (>87%, >74% and >91%), indicating that the habitat at Cleveland Islands was suitable for these two mussel species within this survey duration. In addition, the median recapture rates for *E. capsaeformis* and *A. pectorosa* were >93% and >96%, indicating that the PIT tag technique provided an efficient monitoring approach. According to model comparison results, the non-hierarchical model or the model with sex–related differences (if a species is sexually dimorphic) in survival rate was suggested for analyzing mark-recapture data when sample sizes are small.

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General Introduction

1.1   Biological and ecological characteristics of freshwater mussels

Freshwater mussels possess a soft body that is protected by two hard calcareous outer coverings called shells. The shells come in a variety of colors, shapes, sizes, and textures, and the variety of bumps and ridges among species helps identify and determine species relationships and their phylogenetic relationships among different groups of mussels (Parmalee and Bogan, 1998).

Typically mussels are adapted to life in rivers and streams. It is believed that mussels do better in flowing water conditions because of a more abundant and continuing food supply provided by river current (Parmalee and Bogan, 1998). Freshwater mussels spend their entire juvenile and adult lives in the benthos of aquatic ecosystems. With only a small portion of their bodies exposed, they bury themselves in the substrate, typically in a mixture of sand, silt, mud and gravel. The substrate helps to support and secure their heavy shells. Although mussels are able to move and change their position using their large foot, an individual will rarely move more than a few hundred yards during its life span unless it is carried elsewhere by the current or an animal (Parmalee and Bogan, 1998). However, the burying behavior of mussels makes them vulnerable to environmental changes (Strayer 2008). For instance, other aquatic organisms are able to actively move away from deteriorating environments, but for freshwater mussels, substrates hamper their movement and leave them vulnerable to drought, predation, and other environmental changes, which may be one of the reasons why the population sizes of some freshwater mussel species have decreased sharply in recent years.

1.2   The stock recruitment of freshwater mussels

The life cycle of a freshwater mussel is unique (Coker et al. 1921). The sexes in most freshwater mussel species are usually separate (Parmalee and Bogan. 1998). A female mussel carries eggs inside her gills, which are fertilized by sperm drawn inside

her gill cavity while filtering water. The fertilized embryos then develop into a larval stage called a glochidium. Mussels release thousands of glochidia into the water column that must attach to the gills, fins, or scales of a suitable host fish to transform or metamorphose into a juvenile mussel. Some mussel species use only a few fishes as hosts and many mussel-host relationships are still unknown. Generally, the glochidia stage lasts a few days to several weeks. Once the larvae transform into juvenile mussels, they drop off the fish and fall into suitable habitat to begin a life in the stream bottom (Murray and Leonard 1962). Unlike other animals that can actively search for a mate, the female mussels depend heavily on the river current to deliver sperm released by males. Thus, measuring the recruitment of freshwater mussels is often difficult and complex, which varies not only with individual characteristics, such as age and species, but also with biotic and abiotic environmental variables (Strayer 2008).

Due to the complexity of reproduction, the recruitment of freshwater mussels is affected by many biotic and abiotic factors. Among these environmental factors, the most important are water temperature and flow (Hastie et al., 2003). Changes in temperature potentially affect individual growth, longevity, and reproductive success (Hastie et al., 2003). The increase and decrease of temperature can change the timing of spawning, causing females to release glochidia into the water column earlier or later, which might disrupt the timing of mussel and fish reproduction cycles. Also, the availability of host fish might decline due to climate change or other factors. Some host fish are sensitive to temperature rise, and changes in water temperature also have an influence on dissolved oxygen level, which can affect the growth and survival of host fish (Strayer 2008).

Mussel populations may also be detrimentally affected by river discharge. Effects of increased discharge on the recruitment of mussels will vary due to the size and hydraulic characteristics of each river (Hastie et al., 2003). Sometimes mussels appear to recruit well during wet years, because mussels require clean well-aerated substrate, higher river flows associated with wet years may be able to increase habitat (Hastie et al., 2003). However, heavy rainfall may also have a negative effect on mussel habitat availability by increasing high flow and runoff thereby changing patterns of eroding underlying gravel and cobble in the mussel bed, which disturbs the stability of the mussel

bed and further affects the recruitment of freshwater mussels (Payne and Miller, 2000). Sometimes mussels appear to have recruited more successfully in drier conditions because low water velocity associated with low discharge might enhance fertilization success (Yokely 1972). In addition, changes in seasonal flow patterns may be harmful to mussel populations, especially in a hot and dry summer. For example, mussel beds may be in danger of drying out and silt deposits, algal growth, and organic debris could increase, possibly causing mortality (Payne and Miller, 2000).

1.3   Status of freshwater mussels in North America

North American freshwater mussels are major components of freshwater biodiversity, playing an important role in both ecology and economy. They have been used as a supplemental food source to peoples for centuries (Parmalee and Bogan, 1998). With the appearance of freshwater pearls, many mussel species were harvested for the production of jewelry and pearl buttons. Freshwater mussels feed by using their gills to filter the water for microorganisms, such as protozoans, bacteria, and organic particles suspended in the water (Parmalee and Bogan, 1998). Mussels are also economically important (Anthony et al., 2001), as these organisms can influence phytoplankton ecology (Daukas et al., 1981), water quality, and nutrient cycling (Nalepa et al., 1991). Mussels may also constitute a significant component of the biomass of freshwater macrobenthios (Negus, 1966) and their obligate parasitic larvae can affect fish mortality (Matteson, 1948).

Mussels in North America are experiencing severe declines with nearly 70% of species considered extinct, endangered, threatened, or of special concern (Williams et al., 1993), the decline is now considered a biodiversity crisis by many experts. The rapid loss of many unionid mussel species has been attributed to commercial exploitation, water quality degradation, impoundment, habitat destruction, spread of exotic species, and watershed alteration (Williams et al., 1993). These declines in unionid mussels will likely have serious implications for freshwater ecology and biodiversity in North America.

1.4   Research and conservation of endangered freshwater mussels

To address the urgent need to maintain and restore populations of endangered mussels in North America, protection and recovery activities have been initiated in recent decades to prevent further extinctions. The Endangered Species Act (1973) provides a legal statute to recognize, protect, and recover rare freshwater molluscs in the United States. Further, the National Native Mussel Conservation Committee (NNMCC, 1998) prepared a national strategy to conserve all native freshwater mussels in the United States. In addition, several states have taken actions, including population surveys and mussel propagation, to recover and conserve mussels and ensure that their economic, ecological and biological values are maintained.

Management and conservation programs will need a thorough knowledge of species life history and population biology (NNMCC, 1998). Vital rates such as age, growth, mortality and recruitment are especially critical in assessing the risk of extinction of rare and endangered mussels (Dennis et al., 1991). However, such rates are poorly understood for most species. Dynamics, including species longevity, somatic growth, and host fish usage fluctuate greatly over space and time. Previous studies found that population dynamics of even the same species can differ widely under various ecological conditions (Negus, 1966; Neves and Widlak, 1987; Hastie et al., 2000; Payne and Miller, 2000; Howard and Cuffey, 2009).

The lack of quantitative population dynamics data has hampered efforts to conserve freshwater mussels (Neves et al., 1997). Quantification of population characteristics, such as age class structure and recruitment, will help determine the effects of changes in stream discharge, water temperature, habitat quality, host fish availability and other environmental variables in mussel populations.

1.5   Risk assessment and restoration strategies

Risk assessment is the process that evaluates possible outcomes or consequences and estimates their probability of occurrence. It is an efficient means of screening out low risk activities and focusing increasing attention on those activities assessed as having an adverse impact on population survival. Noticing the decline of freshwater mussel

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resources, biologists from the U.S. Fish and Wildlife Service (USFWS) and the U.S. Geological Survey (USGS) along with other Federal, State, and private agencies have developed a National Strategy for the Conservation of Freshwater Mussels, which serves as a blueprint for native mussel restoration (NNMCC 1998). This National Strategy has presented several suggested strategies, such as habitat reconstruction and mussel population restoration. The implementation of these strategies needs the assessment of how various perturbations impact mussel populations and the evaluation of the technology necessary to reintroduce juvenile mussels and to hold and translocate adult mussels. Based on the available data, different hypothetical restoration strategies were considered in my study (Jiao et al., 2009). I conducted a simulation study to assess the efficiency of each restoration strategy to quantitatively evaluate the outcome of releasing mussels at different ages.

1.6   Characteristics of example species

As a group, freshwater mussels are often portrayed as long-lived and slow-growing (Strayer et al., 2004). Although some mussel species are known to grow slowly and reach advanced ages (e.g. >100 years old *Margaritifera margaritifera*) (Bauer, 1992; Ziuganov et al., 2000), many appear to grow more rapidly and have more modest life spans (e.g., 10 years for *Alasmidonta heterodon*) (Michaelson and Neves, 1995). Consequently, the general description of freshwater mussels as either long-lived or short-lived may be misleading in our understanding of their demographic characteristics and applicable management strategies.

The Clinch and Powell rivers, which are part of the Upper Tennessee River system, contain more federally threatened and endangered mussel species than any other rivers in the United States (Diamond et al. 2002). The mussel assemblage has been monitored for more than 30 years (1979-2010) (Ahlstedt et al., 2005); however, demographic rates of these populations have rarely been assessed, and only a few studies have used age-class structure to study population dynamics (Scott 1994; Jones and Neves 2002; Jones and Neves 2011).

Two species were selected to study individual growth and demographic rates, including one endangered species *Epioblasma capsaeformis* and one special concern species *Actinonaias pectorosa*. Species belonging to the genus *Epioblasma* have suffered the most severe declines over the past 100 years and represents the most endangered genus of freshwater mussels in North America, perhaps due to the specialized life history characteristics of the species in this group (Jones et al., 2006). Thus, *E. capsaeformis* was selected as a representative of the genus to investigate endangered mussel population dynamics and management strategies. In contrast, *A. pectorosa,* is a non-listed and commonly collected species in the Clinch River and was selected as a representative of a non-imperil species. It was also selected because it exhibits a very different life history. Specifically, in comparison with *E. capsaeformis*, *A. pectorosa* has a much longer longevity, uses different fish species as a host and typically shows a higher abundance in the Clinch River and other rivers (Layzer and Khym 2005; Scott 1994; Yeager and Saylor, 1995).

The oyster mussel (*Epioblasma capsaeformis)* is endemic to the Tennessee and Cumberland River system. It historically occurred in Virginia, North Carolina, Georgia, Tennessee, Kentucky and Northern Alabama (Johnson, 1978). This species is now only extant in a handful of stream and river reaches in four States in the Tennessee and Cumberland River system (USFWS 2004). The shell is elliptical or irregular obovate in outline and of medium size with a maximum length of about 70 mm (Parmalee and Bogan, 1998). This length information states significant prior information when using Bayesian estimation. Valves are sub-solid and somewhat inequilateral. The posterior end of males is slightly protruded while females are more broadly rounded (Parmalee and Bogan, 1998). This species has been found to be bradytictic (a long-term brooder): gravid individuals have been observed from fall into spring. When releasing glochidia, female mussels move up onto the surface with the ventral margin uppermost. The oyster mussel has a short longevity (10-12 years) and presumably low larval dispersal capabilities because of the fish hosts it utilizes (Jones and Neves 2011). Fish species identified as hosts for the glochidia include the spotted darter (*Etheostoma maculatum*), redline darter (*E. rufilineatum*), wounded darter (*E. vulneratum*), dusky darter (*Percina sciera*), and banded sculpin (*Cottus carolinae*) (Yeager and Saylor, 1995). The population of oyster

mussels in the upper Clinch River in Tennessee and Virginia declined from being a dominant species in 1973-1976 to a very scarce species in 1986 (Dennis, 1987). Because of population declines in the Clinch River and throughout its range, the oyster mussel was listed as an endangered mussel in 1996 (Bogan 2000).

The pheasantshell (*Actinonaias pectorosa*) is endemic to the Tennessee and Cumberland River system (Parmalee and Bogan, 1998). The shell of this species is large, elongate, and moderately solid to thick in older individuals. Mature individuals may attain a length of 140-150 mm. The pheasantshell lives in sand-gravel substrates in riffles with fast to moderate current, typically in water less than three feet deep. Females become gravid in September with eggs and then have glochidia by late fall to early winter, so this species is also bradytictic (Ortmann, 1921). The rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), spotted bass (*M. punctulatus*), banded sculpin (*Cottus carolinae*), and sauger (*Sander canadensis*) are recorded as host fish for the glochidia of pheasantshell (Layzer and Khym 2005).

1.7 Bayesian analysis

Traditionally, numerical methods and algorithms have been applied to stock assessments to estimate population parameters of interest. Such analyses provide managers with information to regulate fish and mussels stocks (Goulletquer et al., 1994; Walters and Maguire, 1996; Ramachandran et al., 1998; Jiao et al., 2008). There are now a variety of estimation methods that incorporate uncertainty in both data and model parameters, such as least square, maximum likelihood, jackknife, bootstrap, and Bayesian estimation (Deriso and Quinn, 1985; Fournier and Archibald, 1982; Richards and Schnute, 1998; McAllister and Ianelli, 1997).

The Bayesian approach is increasingly being used as a new framework for arriving at solutions to complex statistical models (Rannala and Yang, 1996; Larget and Simon, 1999; Newton et al., 1999; Huelsenbeck et al., 2004). Bayesian methods can be used to estimate parameters through a procedure that derives the posterior probabilities for models or parameters based on the available data and prior information. It always

requires prior distributions for the parameters, which may be based on various types of input data, including an assessment of the relative likelihoods of parameters or the results of non-Bayesian observations. Posterior distribution, the distribution of unknown parameters conditional on available data, combines the knowledge of the prior distributions with the probability of data given parameters to present updated beliefs.

The main reason for using a Bayesian approach for stock assessment is that it facilitates incorporating the full range of uncertainties related to models and parameter values. In contrast, most decision analyses based on conditional maximum likelihood (or least squares) estimation involve fixing (conditioning on) the values of parameters that may, in actuality, have an important bearing on the final outcome of the analysis and for which there is considerable uncertainty (Punt and Hilborn, 1997). In the past, the effects of uncertainty have been evaluated through sensitivity analysis. In general, this involved changing the value of a single parameter only and rerunning the entire stock assessment. This limitation of accessing only a single parameter was due to time constraints and was needed to avoid large amounts of model output. There is clearly a need for sensitivity analysis for any stock assessment. However, current practice cannot guarantee that some combination of parameter values does not give rise to behavior that would not be expected from the results of sensitivity tests which involve changing the value of a single parameter only. In addition, they can also integrate across uncertainties and alternative hypotheses to simplify the presentation of results (Givens et al. 1994).

Bayesian modeling techniques have several features that make them useful in many real-life data analysis and management questions. They provide a way to handle missing data, they allow for combining data with domain knowledge, they facilitate learning about causal relationships between variables, they can show good prediction accuracy even with rather small sample sizes (Kontkanen et al., 1997), and they can be easily combined with decision analytical tools to aid management (Kuikka et al., 1999; Marcot et al., 2001; Jensen and Nielsen, 2007). Bayesian methods associated with Bayesian networks provide an efficient and principled approach for avoiding over-fitting of data (Heckerman, 2008).

In my study, to guide the recovery of endangered freshwater mussel populations, an age-structured model was developed and a Bayesian framework was applied to analyze the models given different hypothetical scenarios. The results from the Bayesian stock assessment were applied directly to risk analyses of alternative management strategies to restore populations of endangered freshwater mussels. To evaluate the efficiency of another restoration strategy, mussel translocation, a field survey was conducted to detect *E. capsaeformis* and *A. pectorosa* using a passive integrated transponder (PIT) technique to investigate the individual growth, recapture and survival rates of these two mussel species.

1.8   Goals and objectives

The goal of this study was to develop quantitative statistical models to improve our understanding of population dynamics and management of endangered mussels in the upper Tennessee River watershed. The main objectives were as follows: (1) to develop statistical age-structured models to represent the population dynamics of *E. capsaeformis* and investigate its population dynamics using a Bayesian approach; (2) to perform a risk assessment to analyze the impact of possible restoration strategies on population abundance over time; and (3) to estimate individual growth, recapture and survival rates of *E. capsaeformis* and *A. pectorosa* based on collected mark-recapture data.

More specifically, in Chapter 2, I constructed an age-length transition to transit age frequency data to length frequency data, and developed statistical age-structured models to estimate the population dynamics of *E. capsaeformis* at Wallen Bend, Frost Ford, and Swan Island in Clinch River. Then I explored the influences of different restoration strategies on the population of *E. capsaeformis* through risk analyses and recommended applicable alternatives for natural resource agencies to help conserve and restore this endangered mussel species. In Chapter 3, I conducted field research, releasing and recapturing *E. capsaeformis* and one non-listed species *A. pectorosa,* with PIT tags at Cleveland Islands, and Bayesian hierarchical models incorporating individual variation were developed to investigate the growth of *E. capsaeformis* and *A. pectorosa.* In Chapter 4, I analyzed the mark-recapture data to determine the recapture and survival

rates of translocated *E. capsaeformis* and *A. pectorosa* to evaluate the efficiency of PIT tag technique.

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Table 1.1. Biological characteristics of *Epioblasma capsaeformis* and *Actinonaias pectorosa* (data are from Scott 1994; Yeager and Saylor, 1995; Parmalee and Bogan, 1998; Layzer and Khym 2005; Jones and Neves, 2011) .

Species	Oyster mussel (*E. capsaeformis*)	Pheasantshell (*A. pectorosa)*
Distribution	Cumberland and Tennessee River system	Cumberland and Tennessee River system
Maximum shell length	~70 mm	140-150 mm
Life history	Bradytictic	Bradytictic
Host fish	Spotted darter, redline darter, dusky darter, banded sculpin, wounded darter	Rock bass, smallmouth bass, largemouth bass, spotted bass, banded sculpin
Individual growth rate	0.27-0.42	0.08-0.18
Longevity	10-12 years	Possibly >30 years (Jess Jones, USFWS, personal communication)
Status	Endangered	Non-imperiled

Chapter 2

Population dynamics modeling and risk assessment to restore populations of endangered freshwater mussels: a case study with the oyster mussel (*Epioblasma capsaeformis*)

2.1 Abstract

The abundance and diversity of freshwater mussel species has declined greatly over the past 100 years and mussels are now considered one of the most imperiled faunal groups in North America. Restoration of populations is now urgently needed to begin species recovery and conservation programs will need a thorough understanding of their life history and population biology to make effective management decisions. In this study, I constructed an age-length transition matrix to transit age frequency to length frequency based on a stochastic von Bertalanffy growth model for the oyster mussel (*Epioblasma capsaeformis*), a federally endangered freshwater mussel species occurring in the southeastern United States. Statistical age-structured models were developed given alternative scenarios to investigate the population dynamics of *E. capsaeformis* in the Clinch River, Tennessee, at Wallen Bend, Frost Ford and Swan Island. A Bayesian modeling approach was used to estimate parameters and a Bayesian model averaging approach was used to average the results by weighting each model based on the deviance information criterion. My results showed that natural mortality rates of adult mussel (age $\geq$ 5 yrs) were much higher than those of young mussels at these sites. A risk assessment was conducted using a Leslie matrix model to evaluate alternative restoration strategies for *E. capsaeformis*. I found that restoration strategies that released adult mussels could increase population size the quickest. Elasticity analysis indicated that the population growth rate was more sensitive to the fertility of age 5 individuals and survival of age 1-4 individuals at Wallen Bend and Frost Ford and was more sensitive to fertility of age 5 and 10^+ individuals and survival of age 1-4 and 10^+ individuals at Swan Island. This study provides a modeling method for biologists and managers to explore population dynamics and assess a range of possible restoration strategies for endangered mussel species.

2.2 Introduction

Freshwater mussels (Bivalvia: Unionoidea) have been on the decline for decades and are considered one of the most endangered groups of animals, which should be protected and conserved urgently (Downing et al., 2010). During the past 100 years, the abundance and species diversity of freshwater mussels has declined greatly, making them one of the most imperiled faunal groups in NA, of the 297 recognized species in North America, 70% are considered extinct, endangered, or of special concern (Williams et al., 1993; Neves et al., 1997; Neves, 1999; Lydeard et al., 2004). The decline of freshwater mussels is primarily due to habitat destruction and water quality degradation associated with adverse anthropogenic activities, such as dam construction and operation, mining, pollution from factories and farming, introducing exotic species (e.g. zebra mussel), and other human impacts (Bogan, 1993; Neves et al., 1997; Ricciardi et al., 1998). To minimize species losses and initiate recovery of endangered mussel species, biologists from the U.S. Fish and Wildlife Service (USFWS), U.S. Geological Survey (USGS), and many other Federal, State, and non-governmental organizations have participated in the development of a National Strategy for the Conservation of Freshwater Mussels, which serves as a blueprint for native mussel conservation and protection (NNMCC, 1998). Many actions have been implemented during the last 14 years, including releasing laboratory propagated juvenile mussels and translocating adult mussels to augment and re-establish populations. However, conservation management programs will need a thorough understanding of species life history and population biology to be effective at restoring and monitoring populations.

Age-structured models are widely used in population dynamic analysis in fisheries. Models range from simple deterministic methods, such as virtual population analysis (Megrey 1989), to more complex statistical methods (Deriso and Quinn, 1985). Statistical age-structured models are superior to deterministic models (Haddon 2001), because they can estimate statistical uncertainty and confidence intervals for various parameters of interest. The estimated uncertainty can then be incorporated into stock and risk assessment models to help manage populations. In this study, I developed statistical age-structured models to analyze the population dynamics of oyster mussel (*Epioblasma*

capsaeformis) and demonstrated how to conduct a risk assessment by utilizing the results from developed models.

E. capsaeformis was selected as representative endangered freshwater mussel species for my study. It is one of the few extant species belonging to the genus *Epioblasma,* which represents the most endangered group of freshwater mussels in North America (Jones et al., 2006). *E. capsaeformis* is a short-lived (10-12 years old) and small sized (35-50 mm long) freshwater mussel species, which has undergone an estimated >90% decline from its historical abundance and distribution throughout the Tennessee and Cumberland River system (Johnson, 1978; USFWS, 2004). Because of such severe declines in its distribution and abundance, *E. capsaeformis* was listed as a federally endangered species in 1996 (USFWS, 2004). Studies have been undertaken to investigate the species sensitivity to contaminants and characterize population genetic and demographic structure (Buhay et al., 2002; Jones et al., 2004; Jones et al., 2006; Valenti et al., 2006; Wang et al., 2007; Jones and Neves, 2011). However, additional demographic analyses and data are now needed to help implement freshwater mussels conservation, such as predicting how population changes over time are influenced by biotic and abiotic factors and assessing alternative population management strategies. Estimation of vital rates such as growth, mortality and recruitment are especially critical in assessing risk of extinction of rare and endangered species (Dennis et al., 1991). Thus, to more effectively conduct the restoration of *E. capsaeformis* populations, demographic analysis and risk assessment is needed to help guide management actions.

The goal of my study was to assess the current status of *E. capsaeformis* populations in Clinch River and predict population trends based on the efficacy of alternative population restoration strategies. The specific objectives were the following: (1) construct an age-length transition matrix for *E. capsaeformis* based on the von Bertalanffy growth model to connect length frequency data with age-structured models; (2) build age-structured models given three different mortality scenarios to explore the population dynamics of *E. capsaeformis* at three sites in the Clinch River and use deviance information criteria (DIC) to compare alternative models; (3) evaluate the

effectiveness of hypothetical restoration strategies with respect to their influence on population abundance.

2.3 Material and methods

2.3.1 Data sources

Annual surveys conducted from 2004 to 2010 at Wallen Bend (CRM 192), and from 2005 to 2010 at Frost Ford (CRM 182) and Swan Island (CRM 172) in late summer to early autumn. These three sites were selected because they represent the upper, middle, and lower boundaries of the study area, respectively. Furthermore, the habitat characteristics of these three sites are appropriate for long-term monitoring of freshwater mussels. During the annual surveys, quadrats (area 0.25 m^2) were evenly placed along transect lines and spaced equally over the entire shoal area. The sampled numbers of mussels per quadrat at these locations were recorded (J. W. Jones et al. unpublished data). The length of each sampled mussel was measured (nearest 0.1mm) using a digital caliper and then returned to its collection location (J. W. Jones et al. unpublished data). Age-at-length data based on shell thin-sections were obtained from mussel surveys at various sites in the Clinch River from 2004 to 2006, in which thin sections were cut from shells to examine internal shell annuli (Jones and Neves, 2011).

2.3.2 Statistical age-structured model to estimate natural mortality rate and recruitment

I developed statistical age-structured models and estimated parameters of interest through a Bayesian approach, which has been used recently as an method to solve complex statistical models (Rannala and Yang, 1996; Larget and Simon, 1999; Newton et al., 1999; Huelsenbeck et al., 2004; Jiao et al., 2012). The dynamic behavior of the *E. capsaeformis* population was described by a statistical age-structured model and was written as:

$$N_{a,y,s} = \begin{cases} R_{y,s} & a = 1 \\ N_{a-1,y-1,s}e^{-f(M_s)} & 2 \le a \le 9 \\ N_{a-1,y-1,s}e^{-f(M_s)} + N_{a,y-1,s}e^{-f(M_s)} & a = 10^+ \end{cases}$$

(1)

where a is age; y is year; s is the sth site (Wallen Bend, Frost Ford and Swan Island; s=1, 2 or 3); $R_{y,s}$ represents the recruitment in year y at site s; $N_{a,y,s}$ represents the population size at age a in year y at site s and $f(M_s)$ represents the instantaneous natural mortality rate at site s which is described in section 2.3.3. Since the recruitment of a mussel population is highly influenced by both biotic or abiotic factors, such as host fish availability and river discharge, the recruitment in year y, R_y , is regarded as an unknown parameter with a prior distribution instead of being modeled as regulated curves, such as in the Beverton-Holt or Ricker models (Beverton and Holt, 1957; Ricker, 1954). The observed maximum age of *E. capsaeformis* in the Clinch River is 12 years. However, few mussels live that long based on the research of Jones and Neves (2011), and the typical longevity of *E. capsaeformis* is about 8-10 years. Therefore, mussels greater than or equal to 10 years were considered to belong to the age group 10^+. Mussels in age group 10^+ were assumed to survive partially instead of die entirely in this model.

The total population abundance in each year was

$$N_{y,s} = \sum_a N_{a,y,s} .$$

(2)

The expected abundance index was calculated as

$$E(I_{y,s}) = q_s N_{y,s} ,$$

(3)

where $I_{y,s}$ is the observed abundance index of mussels in year y at site s and q_s is the catchability coefficient at site s. The $log(I_{y,s})$ was assumed to follow a normal distribution with mean $log(q_s N_{y,s})$ and variance $\sigma^2_{I_{y,s}}$.

Based on the survey data, the age frequency of mussels in year y was calculated and transformed into length frequency using an age-length transition,

$$P_{a,y,s} = \frac{N_{a,y,s}}{N_{y,s}},$$

(4)

and

(5)

$$E(P_{l,y,s}) = P_{a,y,s}P_{l|a},$$

where $P_{a,y,s}$ is the probability of mussels belonging to age group a in year y at site s,

$P_{l,y,s}$ is the probability of mussels belonging to length group l in year y at site s and $P_{l|a}$ is

an age-length transition taken from the von Bertalanffy growth equation (see below).

Based on the available data and developed models, I estimated the age frequency ($P_{a,y,s}$)

instead of the absolute $N_{a,y,s}$, natural mortality rate and relative $R_{y,s}$. I assumed

multinomial error structure for the measurement errors of length frequency.

The estimation of age is essential to study the population statistics of freshwater

bivalves. The most commonly used methods to age freshwater bivalves are the external

growth ring method and thin section technique, with detailed descriptions of each method

provided by Clark (1980) and Neves and Moyer (1988). However, the growth ring

method is often inaccurate and imprecise as it may be hampered by the erosion of shell

surface and can be subjective when counts of growth rings near the valve margin of older

specimens are examined. The thin section technique can determine the age of a mussel

much more precisely but requires sacrificing the mussel's life, which cannot be applied to

age determination of endangered mussels.

Because of the short-comings of these two methods, I constructed an age-length

transition based on accurate age-length data collected from the thin section technique by

Jones and Neves (2011) and then applied the data to a von Bertalanffy model to create the

transition. This transition can be used to transit age frequency to length frequency so that

length frequency data can be fitted to an age-structured model, which decreases the

uncertainty by directly fitting the age-structured data. Individual growth was assumed to

follow the von Bertalanffy model:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}),$$

(6)

where L_t is the length at age t, L_∞ represents the asymptotic maximum length of *E. capsaeformis*, K is the growth rate coefficient, and t_0 is the hypothetical age at which the length equals zero. A Bayesian method was used to estimate the posterior distribution for parameters of interest. Based on the joint posterior distribution, the length probability of falling into each length group was estimated as follows: (1) for each age, compute the corresponding length; (2) for each length interval, sum the number of estimated lengths falling within the interval; (3) the length probability at age *a* in length group *l* is then the number of mussels within length group *l* divided by the total number of estimated lengths at age *a*.

2.3.3   Alternative scenarios for natural mortality rate

Fish mortality is a very important parameter in fish stock assessment. It can be divided into two types: fishing mortality and natural mortality. Fishing mortality counts the death of fish due to fishing activities; natural mortality is the death of fish due to any reason other than fishing, such as disease, competition, cannibalism, old age, predation, pollution, etc. Because *E. capsaeformis* is an endangered species and there is no harvest from its populations, I just considered the natural mortality rate in this study. Natural mortality rate is one of the most important parameters in fish stock assessment models because it determines the productivity of the stock and relates to biological reference points and stock sustainability (Hewitt et al., 2007). In freshwater mussel conservation, natural mortality rate is also critical to access the extinction risk. Thus, I provided three scenarios to investigate the change of natural mortality rate for *E. capsaeformis* in the following paragraphs.

The traditional exponential growth model demonstrates the relationship among population abundance, time and population growth rate, which assumes population growth rate is constant (Jiao et al., 2008). However, this model is not adequate as the population growth rate varies depending on life history of the species and weekly, monthly or yearly environmental changes (Jiao et al., 2012). Based on the commonly used exponential growth model, three hypothetical scenarios were developed to model natural mortality rate: (1) assuming the natural mortality rate was constant; (2) assuming

the natural mortality rate of young mussels differed from that of adults (Jones and Neves, 2011); (3) assuming the natural mortality rates differed in different age groups.

For the first hypothetical scenario (H1), the statistical age-structured model was developed with a stationary natural mortality rate:

$$f(M_s) = M_s$$
$$M_s \sim U(b_1, b_2)$$ (7)

where M_s is the natural mortality rate at site s and follows a uniform distribution. In this model, I assumed that M was constant and would not change with age or year.

For the second hypothetical scenario (H2), $f(M_s)$ was written as:

$$f(M_s) = \begin{cases} M_{1,s} \sim U(b_1, b_2) & 1 \le a \le 4 \\ M_{2,s} \sim U(b_1, b_3) & 5 \le a \le 10^+ \end{cases}$$ (8)

$f(M_s)$ was developed based on the life history of *E. capsaeformis*, according to which, individuals becomes sexually mature at age 5 (Jones and Neves, 2011). Thus, I considered age 5 as a division point where the mortality rate was constant from age 1 to 4 at site s, referred as $M_{1,s}$ and the mortality rate from age 5 to 10^+ was a constant, referred as $M_{2,s}$.

The third hypothetical scenario (H3) was expressed by a random walk process to model the changes of natural mortality rate over age (Peterman et al., 2003; Jiao et al., 2009b, 2012):

$$f(M_s) = M_{a,s}$$
$$M_{a=1,s} \sim U(b_1, b_2)$$ (9)
$$M_{a,s} = M_{a-1,s} + \varepsilon_s$$

where $M_{a,s}$ is the natural mortality rate at age a site s and modeled as a random walk process. The $M_{a,s}$ follows a normal distribution with mean $M_{a-1,s}$ and variance $\sigma^2_{M_s}$ and $M_{a=1,s}$ further follows a uniform distribution between b_1 and b_2.

2.3.4 Bayesian approach and priors

Because the Bayesian method shows good prediction accuracy even with rather small sample sizes (Kontkanen et al., 1997), it is a good choice to derive the posterior distribution of the parameters of interest based on the annul survey data and priors, since sample sizes of endangered mussels typically are not very large. In this study, the Bayesian approach was used to fit models to the data. To implement the Bayesian approach, prior distributions for unknown variables were specified. The uniform distributions were used for the priors of L_∞, K and t_0, the lower and upper bounds were based on data from available literature (Jones and Neves, 2011) and field observations. In the statistical age-structured model, I cared about the natural mortality rate, fertility rate and age structure of the mussel population instead of the actual number of mussels in each age group. Thus, the initial population size at age 1 in year 2004 was fixed at 1000 individuals and the uniform priors of the initial population sizes at other age groups and recruitment levels were $U(1,10000)$. Besides the above priors, other non-informative priors were used for variance parameters. A summary of the priors is shown in Table 1.1.

WinBUGS computer software, was used to implement the Bayesian statistical analysis using the Markov chain Monte Carlo (MCMC) method to estimate the model parameters (Gilks, 1995; Spiegelhalter et al., 2004). In this study, three chains with 30 thinning intervals were used, the first 40,000 iterations were discarded and parameters were evaluated based on another 40,000 to 100,000 iterations from MCMC simulation of the joint posterior distributions. Three Bayesian diagnostic procedures were performed to evaluate convergence of the posterior distribution: monitoring the trace plot, diagnosing the autocorrelation and Gelman and Rubin statistics (Spiegelhalter et al., 2004; Jiao et al., 2008, 2009b).

2.3.5 Bayesian model averaging (BMA)

The deviance information criterion (DIC) was employed to assess the model complexity and compare different models to select the most plausible one. The DIC is calculated by:

$$DIC = 2\overline{D}(\theta) - \hat{D}(\theta) \ or \ \overline{D}(\theta) + p_D$$
$$\overline{D}(\theta) = E_{\theta|y}(-2\log Likelihood(y \mid \theta))$$
$$\hat{D}(\theta) = -2\log Likelihood(y \mid \overline{\theta})$$
$$p_D = \overline{D}(\theta) - \hat{D}(\theta)$$

(10)

where D is deviance; p_D denotes the effective number of parameters in the model, a
measurement of model complexity; $\overline{D}(\theta)$ is the posterior mean of the deviance, a
Bayesian measurement of model fit; $\hat{D}(\overline{\theta})$ 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 best model is the
one with the smallest DIC value.

In many cases, model averaging has proved to be more effective in prediction
than a single model since estimates from a single model ignore the model selection
uncertainty (Hoeting et al., 1999; Burnham and Anderson, 2002; Jiao et al., 2008, 2009b).
Therefore, for each site, I calculated model averaged estimates of natural mortality rate,
fertility rate and age structure, weighting the posterior distributions for estimated
parameters from different models based on weights from their DIC differences:

$$\Delta_{DIC_i} = DIC_i - \min(DIC)$$

(11)

$$weight_i = \frac{e^{-2\Delta_{DIC_i}}}{\sum_i e^{-2\Delta_{DIC_i}}}$$

where Δ_{DIC_i} is the difference between model i and the best model and $weight_i$ is the
weight of model i. Usually, it is hard to tell what constitutes an important DIC difference.
According to Spiegelhalter et al. (2004), $\Delta DIC > 10$ should definitely rule out the model
with a higher DIC value because of the extremely small weight.

2.3.6 Demographic model and risk assessment

2.3.6.1 A demographic model

The Leslie matrix is commonly used for demographic analysis to evaluate management actions for endangered species (Schemske et al., 1994; Heppell, 1998; Zambrano et al., 2007; Jiao et al., 2009a), which was written as:

$$A_s N_{y,s} = N_{y+1,s}$$

$$A_s = \begin{bmatrix} f_{1,s} & f_{2,s} & \cdots & f_{a-1,s} & f_{a,s} \\ S_{1,s} & 0 & \cdots & 0 & 0 \\ 0 & S_{2,s} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & S_{a-1,s} & S_{a,s} \end{bmatrix} \qquad (12)$$

where a is the age of an individual, s is the sth site, $f_{a,s}$ is the age-specific fertility at site s, and $S_{a,s}$ is the survival rate from age a to age $a+1$ in year y at site s (Wallen Bend, Frost Ford and Swan Island; $s=1$, 2 or 3).

$$S_{a,s} = e^{-M_{a,s}} \qquad (13)$$

where $M_{a,s}$ is the natural mortality at age a site s. The range of $S_{a,s}$ is between 0 and 1 and the range of $f_{a,s}$ is positive.

The data on survivals, fertilities and initial population vectors all came from the posterior distributions of the averaged model at each site. Recruitment-per-spawner (recruitment of age-1 mussels per spawner) was calculated based on the survival of mussels age 5 and older as *E. capsaeformis* is usually mature at age 5:

$$\begin{cases} f_{a,s} = 0 & \text{if } a < 5 \\ f_{a,s} = \dfrac{R_s}{spawner_s} = \dfrac{N_{a=1,s}}{\sum\limits_{a=5}^{10^+} N_{a,s}} & \text{if } 5 \le a \le 10^+ \end{cases} \qquad (14)$$

This is not the best way to estimate the fertility rate because it assumed that the fertility rate was not age-specific. However, this seems to be a reasonable choice to estimate the fertility rate because there are no data available on the survival rate from the larval stage to juveniles and to an age-1 mussel in the wild.

The initial population vector at each site is based on the product of population age structure in the most recent year (2010) and the population size.

$$N_{0,s} = \begin{bmatrix} P_{a=1,s} \\ P_{a=2,s} \\ \vdots \\ P_{a=10^+,s} \end{bmatrix} \times I_s \times Area_s \tag{15}$$

where $N_{0,s}$ is the population vector at site s, $P_{a,s}$ is the probability that one belongs to age group 1, I_s is the abundance index in 2010 with unit of m^{-2} and $Area_s$ represents the site dimensions at Wallen Bend, Frost Ford and Swan Island with unit of m^2.

2.3.6.2 Population growth rate from projection matrix and elasticity analysis

The matrix model has a dominant eigenvalue λ, which represents the intrinsic long-term growth rate of the population and a corresponding right eigenvector w that represents the stable age distribution of the population (Caswell, 2001; Jiao et al., 2009). Furthermore, the dominant eigenvalue λ of the matrix equals to e^r, representing the rate of population growth, where r is the intrinsic rate of increase of the population in the exponential growth population equation. If λ is larger than 1, the population size will increase; if λ is equal to1, the population size will not change; if λ is lower than 1, the population size will decrease and has a risk of extinction or local extirpation.

Elasticity is the measure of proportional sensitivity, which represents the proportional sensitivity of model results to proportional changes of model parameters. In order to compare the contributions of the matrix elements (survival and fertility) to λ, I calculated the elasticity of λ (Caswell, 2001; Jiao et al. 2009a), which is defined as:

$$e = \frac{x\partial\lambda}{\lambda\partial x} = \frac{x\Delta\lambda}{\lambda\Delta x}$$
(16)

2.3.6.3 Evaluation of population restoration strategies

Risk assessment is used to quantitatively or qualitatively estimate the probability that a particular event will occur related to specified strategies. Until now, the assessments of some strategies, such as relocation, host fish infection and water quality, were based on analyzing data from lab experiments or fieldwork survey (Haag and Warren, 2005; Peredo et al., 2005; Ward et al., 2007), which did not clearly provide future population trends for different restoration strategies. Based on research needs identified in the federal recovery plan to restore populations and available data, I assessed the effectiveness of releasing mussels at different ages on population growth (USFWS 2004). Simulations were conducted using Leslie matrix models to determine the efficacy of different restoration strategies at three sites, respectively.

The simulation began with the initial population vector ($N_{0,s}$) and the population projection matrix (A_s). For each simulation year, the total number of mussels ($N_{y,s}$) was examined and the risk was defined as the probability that $N_{y,s}$ was less than $N_{0,s}$. The probability of releasing no mussels during the first five years was used as the baseline. The alternative strategies were releasing a number of mussels every year per age class during the first five years, first at age 1only (S1), second at age 2 only (S2), third at age 3 (S3); and on up to age 10^{+} (S10). The strategies that released 500, 1000, and 1500 mussels were evaluated, respectively. The simulation went on for 50 years.

Uncertainties in natural mortality, fertility and initial population structure were analyzed through Bayesian joint posterior distributions and a nonparametric bootstrap approach. I sampled 10,000 times from the joint posterior distributions of the models given the four hypothetical scenarios based on model weights. To apply the Monte Carlo technique, I also resampled the 2010 quadrats data 1000 times to obtain a distribution for the abundance index. The parameter distributions were applied to the Leslie matrix to assess population changes over 50 year period based on alternative restoration strategies to examine the risk probability.

2.4   Results

The data analysis showed that hypothetical scenario H2, which assumed different natural mortality rates of young mussels versus sexually mature mussels, yielded the smallest DIC value at Wallen Bend and Frost Ford, while hypothetical scenario H1 yielded the smallest DIC value at Swan Island (Table 2.2). At Wallen Bend, scenario H1 with a constant natural mortality rate resulted in the largest DIC value (270.795), indicating H1 yielded the worst model fit among the three scenarios. The ΔDIC value between scenarios H2 and H3 was 2.929, which was less than 5 (Table 2.2). At Frost Ford, scenario H2 gave the lowest DIC value while H1 yielded the highest DIC value (Table 2.2). The ΔDIC between scenarios H2 and H1 was 46.397, which was larger than 10. Thus, DIC weight for H1 at Frost Ford was not considered when averaging models. At Swan Island, hypothetical scenario H1 yielded the smallest DIC value and the ΔDIC values between scenarios H1 and H2 and H3 were 0.943 and 4.159 (Table 2.2), indicating the H1 resulted in the best model fit among the three scenarios but the results from H2 also contributed to Bayesian model averaging significantly.

The DIC weights were used to average models by weighting the posterior distributions of different models. The fits of length frequency data at the three sites based on results of the BMA approach are shown in Figure 2.1. The estimated posterior means of the length frequency by the BMA approach fit the observed length frequency data better at Wallen Bend and Frost Ford than at Swan Island (Figure 2.1).

Based on the results of the BMA analysis, natural mortality rate appeared to change with age at the three sites (Figure 2.2). Generally, the natural mortality rates of adult mussels (age $\geq$ 5 yrs) were higher than those of young mussels. The mean natural mortality rates of young and adult mussels at Wallen Bend were higher than that at Swan Island and Frost Ford (Figure 2.2). Additionally, the mean natural mortality rates of young mussels at Swan Island were larger than those at Frost Ford but the mean natural mortality rates of adult mussels at Swan Island were less than those at Frost Ford (Figure 2.2b and c).

The age structures of *E. capsaeformis* at Wallen Bend and Frost Ford differ from the age structure at Swan Island (Figure 2.3). At Wallen Bend and Frost Ford, the age structure appears similar, where age 1 to age 4 individuals dominated the age structure and abundance of the population. After age 4, the abundance of older individuals decreased quickly (Figure 2.3a and b). In 2010, mussels ages 1-6 nearly dominated the entire population while mussels ages 7-10$^+$ comprised a much smaller proportion of the population at Wallen Bend and Frost Ford. At Swan Island, mussels at age 1 took up the largest proportion of the total mussel population at 2010. Ages 1-5 and 10$^+$ individuals dominated the age structure and abundance of the population (Figure 2.3c). In general, the population age structure in 2010 was distributed more evenly at Swan Island than at Wallen Bend and Frost Ford (Figure 2.3).

The mean stock recruitment relationships show different patterns at these three sites (Figure 2.4). Recruitment in 2007, 2008 and 2009 was much higher compared with other years at Wallen Bend and Frost Ford (Figure 2.4a and b). Recruitment in 2009 and 2010 varied greatly though the spawning population sizes were similar in these two years. Moreover, quite different spawning population sizes produced a similar amount of recruitment in 2006 and 2010. At Swan Island, mean recruitment in 2007 was the highest whereas mean recruitment in 2009 the lowest (Figure 2.4c). Though the spawning population sizes in 2006, 2008, and 2010 were different, recruitment in these years were similar.

Both median and the upper and lower bounds of the 95% confidence interval for the population growth rate estimates at Wallen Bend and Swan Island were much lower than those at Frost Ford. In this study, the median predicted population growth rate of *E. capsaeformis* at Wallen Bend was 1.002 and the corresponding 95% confidence intervals were 0.807-1.166 according to the demographic model (Figure 2.5a). At Frost Ford, the median predicted population growth rate was 1.184 with a 95% confidence interval from 0.987 to 1.304 (Figure 2.5b). At Swan Island, the median predicted population growth rate was 0.983 (95% confidence interval, 0.748-1.238) (Figure 2.5c). Population growth rate (λ) was more sensitive to fertility of age 5 individuals and survival rate of age 1-4 individuals at Wallen bend and Frost Ford, and λ was more sensitive to fertility of age 5

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and 10^+ and survival rate of age 1-4 and 10^+ individuals at Swan Island (Figure 2.6). In addition, survival affected population growth rate more than fertility.

The probability that population size was less than the initial population size during a 50-year simulation period is shown in Figure 2.7. Probabilities under scenarios 5-10 were very similar, and plus (+) was used to represent the probabilities of the population being less than N_0 over a 50 year period under these various scenarios. The probability values for S0-10 at Frost Ford were very small, resulting in convergence of the lines (Figure 2.7d, e and f). However, it is obvious that the more mussels released during the first five years, the less probability that the population size would be less than N_0. And strategies 5-10 always led to lower probabilities compared to the other restoration strategies, especially during the initial few decades, indicating that these strategies were more efficient at increasing population size in a short period (Figure 2.7a, b, c, g, h and i). From Figure 2.7, it can be seen that releasing mussels could help to decrease the probabilities of population size being less than N_0 and efficacy increased from S1 to S5-10. The same trend can be seen from the computed probabilities at Frost Ford.

2.5 Discussion

Estimation algorithms for population dynamic analysis and stock assessment, such as virtual population analysis (VPA) (Murphy, 1965), cohort analysis (Pope 1972) and catch at age analysis (Fournier and Archibald, 1982; Deriso et al., 1985; Shepherd, 1999), rely heavily on age-structure information. The age determination methods in use for mussels are hampered by inaccuracy, imprecision (e.g. growth ring method) or a lack of feasibility (e.g. thin-section method). Based on the age-at-length data I have for *E. capsaeformis*, the age-length transition was calculated via the von Bertalanffy growth equation using a Bayesian method. Instead of using the best estimates of the parameters of interest, the joint posterior distributions were applied to compute the length frequency at each age, which effectively minimized the estimation bias and helped reduce bias in the demographic analysis. This approach can be applied to a population for which aging methods are impractical (e.g. a lack of application for endangered species, etc.).

However, caution must be exercised in cases where the collected age-length data may not represent all of the life stages in the population.

The DIC was used to evaluate the plausibility of each model. It suggests that models with ΔDIC >10 from the best model should be ruled out; models with ΔDIC between 5 and 10 from the best model are substantial; models with ΔDIC <5 from the best model should be considered acceptable (Spiegelhalter et al., 2002; Jiao et al., 2008; Jiao et al., 2009b; Jiao et al., 2011). However, just reporting the best model is misleading and may ignore other models suitable for population estimation and prediction. In this study, the model that assumed different natural mortality rates for young mussels versus adult mussels had the lowest DIC value at Wallen Bend and Frost Ford, suggesting scenario H2 was the "best" model. However, at Swan Island, the model assuming constant natural mortality rate (H1) had the smallest DIC value. DIC measures the fit of the data to the model as well as model complexity (Spiegelhalter 2002). The sample sizes of individual mussels collected from quadrats during the annual surveys at Swan Island were much less than those at Wallen Bend and Frost Ford. Thus, the advantage of model scenario H2 is not obvious at Swan Island due to the much small number of mussels collected from quadrat samples. However, the difference of DIC values between H1 and H2 are very limited, results from H1 apparently contributed in model averaging at Swan Island. However, it is still possible that the natural mortality difference between adult and young mussels is too small to be detected by the alternative models and thus the model with the constant natural mortality assumption (H1) led to the best-estimated results. Based on the results, I averaged estimated results through the BMA approach because using only the "best" model may lead to overconfident inferences compared to the BMA model, potentially increasing risk during decision analysis (Draper, 1995; Jiao et al., 2008), and the averaged model results showed good fits of observed length frequency data at the three sites.

A good understanding of the mortality rates of endangered mussel populations is critical for effective management. The results of the BMA model demonstrated that natural mortality rates can differ at different life stages. Traditionally, the natural mortality rate of fishes is assumed to be high during the larval stage and declines as age

increases until eventually becoming stable (Jennings et al., 2001). However, in this study, the general pattern of natural mortality curves is that natural mortality rates for ages 1-4 are much lower when compared to mortality rates for ages 5-10$^+$. The estimated pattern agreed with the findings of Jones and Neves (2011). These different mortality rates may be related to the life history of this species. Typically, young mussels are completely buried in the stream bottom substrate for several years until becoming mature, which allows them to feed and grow and be protected from predators, such as raccoons, otters, muskrats and fishes. Whereas, adult mussels will expose themselves at the river bed surface to release and collect sperm and for female mussels to release glochidia utilizing a variety of mantle lure structures or conglutinates to attract host fishes (Grabarkiewicz and Davis 2008). In addition, freshwater mussels will burrow deeper into the substrata to prevent dislodgement during flood events (Di Maio and Corkum, 1995). For example, Hastie et al. (2001) observed higher mortality of adult freshwater pearl mussels (*Margaritifera margaritifera L.*) in several European populations due to flood events. Thus, it is likely that buried young *E. capsaeformis* are at less risk of being washed away or preyed on, while larger adults are generally more exposed, therefore increasing their natural mortality rates.

Low river discharge occurred in spring-summer (i.e. the glochidia, larval mussel, release season of *E. capsaeformis*) of 2006, 2007 and 2008 (Figure 2.8), which may have led to the high recruitment observed from 2007 to 2009 (Figure 2.4a and c). It is possible that low river discharge improves water clarity, which is beneficial to female mussels while attracting host fish when displaying their mantle-lure, thereby increasing the infection rate of glochidia (Jones and Neves, 2011). Moreover, the low river discharge may be favorable to the settlement, filter feeding and growth of juvenile mussels, which further increases survival and recruitment (Jones and Neves, 2011). However, at Swan Island, recruitment in 2009 was much lower than in other years, which may be related to low detection due to small population size and the specific habitat and population structure of *E. capsaeformis* at that site, where the proportion of adults was less than those at other two sites.

The current population of *E. capsaeformis* at these three sites showed different population growth rates. At Wallen Bend, Swan Island and Frost, the median population growth rates (λ) based on the BMA approach were 1.002, 0.983 and 1.184, respectively. Although the 95% confidence intervals of the λs overlap with 1, I still cannot rule out the possibility that the population at each site could decline over time. The risk analysis of *E. capsaeformis* indicated that releasing mussels ages 5-10$^+$ are the preferred restoration strategies to increase population size over a short time period. Although these adult age classes have high natural mortality rates, their higher fertility contributed to greater increases in population growth. In addition, releasing a large number of mussels is a reasonable strategy to stop population decline. However, in the long run, the probability that population size will decline will approach the probability under the default strategy of no released mussels. Hence, releasing mussels is a method that could increase population size of mussels but some additional method, such as protecting and restoring quality mussel habitat, should also be applied to change the population characteristics to recover this endangered species. In the simulation study, the probabilities that population size decreased at Frost Ford were less than 5% after two-years of reproduction and therefore releasing additional mussels would not change these probabilities too much, indicating that the population of *E. capsaeformis* at this site likely occurs in better natural habitat and is able to maintain itself without anthropogenic intervention. However, the populations of *E. capsaeformis* at Wallen Bend and Swan Island had a relatively high risk of decrease. Conducting annual surveys is recommended in order to monitor the population trend of *E. capsaeformis* and make sure the populations at these two sites are sustainable. Furthermore, releasing mussels could help decrease the risk of population decline based on the results of this study.

In the elasticity analysis, the high elasticity to f_{10} and s_{10} at Swan Island was due to the low mortality rate, which increased the accumulative contribution of the 10$^+$ group. According to the results of the elasticity analysis, increasing f_5, s_1, s_2, s_3 and s_4 (with f_{10} and s_{10} at Swan Island) had a greater impact on the population growth rate than the same proportional change in any other rate and the impact of survival on the population growth rate was higher than that of fertility. Thus, strategies that could increase the

survival rate of *E. capsaeformis* should be implemented first when releasing mussels. I also recognize that the costs and risks associated with rearing mussels to larger sizes at a hatchery must also be considered. However, from a purely demographic point of view, releasing mussels of *E. capsaeformis* at a size or age when first mature will have the greatest effect on the population growth rate.

I investigated the population dynamics of *E. capsaeformis* at three sites in Clinch River, where each local population exhibited different dynamics. The various ecological processes, such as flow, temperature, habitat quality, etc., may influence the population at each site. I suggest that restoration strategies of *E. capsaeformis* should be evaluated site by site.

Importantly, this study provides a method for biologists and managers to explore population dynamics and assess a range of possible restoration strategies for endangered mussel species. The method I used to construct the age-length transition can be used to guide population dynamic analysis of other species that may also lack precise age determination data. Moreover, incorporating the Bayesian decision making framework helped avoid the potential biases associated with using only one model to estimate population parameters of the *E. capsaeformis* population at three sites in the Clinch River. I recommend continued monitoring of *E. capsaeformis* to advance understanding of its population dynamics and the environmental factors that influence it.

2.6   Acknowledgements

2.7   References

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Table 2.1. Parameter values and priors used in the statistical age-structured models developed for the *Epioblasma capsaeformis* (Jones and Neves, 2011).

Parameter	Value
$N_{1,1,s}\left(s=1,2,3\right)$	1000
$N_{a,y,s}\left(a\neq1,\ y=1,\ s=1,2,3\right)$	$U\left(1,10000\right)$
$R_{y,s}\left(y\neq1,\ s=1,2,3\right)$	$U\left(1,10000\right)$
b_1	0
b_2	1
b_3	2
q_1	$U\left(0.001,1\right)\times10^{-4}$
q_2	$U\left(0.001,5\right)\times10^{-5}$
q_3	$U\left(0.0001,1\right)\times10^{-3}$
L_∞	$U\left(30,65\right)$
K	$U\left(0.01,0.8\right)$
t_0	$U\left(-2,-0.01\right)$

Table 2.2. The deviance information criterion (DIC) values of age-structured models for *Epioblasma capsaeformis* with three hypothetical scenarios (H1; H2; H3) at Wallen Bend, Frost Ford and Swan Island.

Site	Scenario	DIC	Weight
	H1	270.795	0
Wallen Bend	H2	262.328	0.0028
	H3	265.257	0.9972
	H1	642.699	0
Frost Ford	H2	596.302	0.9996
	H3	600.225	0.0004
	H1	125.383	0.8681
Swan Island	H2	126.326	0.1317
	H3	129.542	0.0002

Figure 2.1. The fits of length-frequency data for *Epioblasma capsaeformis* at three sites: (a) Wallen Bend from 2004-2010, (b) Frost Ford from 2005-2010, and (c) Swan Island from 2005-2010 in the Clinch River, TN. Bars represent the observed length frequencies. Lines with dots represent the estimated posterior means of the length frequency by Bayesian model averaging.

(a)

(b)

(c)

Frequency

Length (mm)
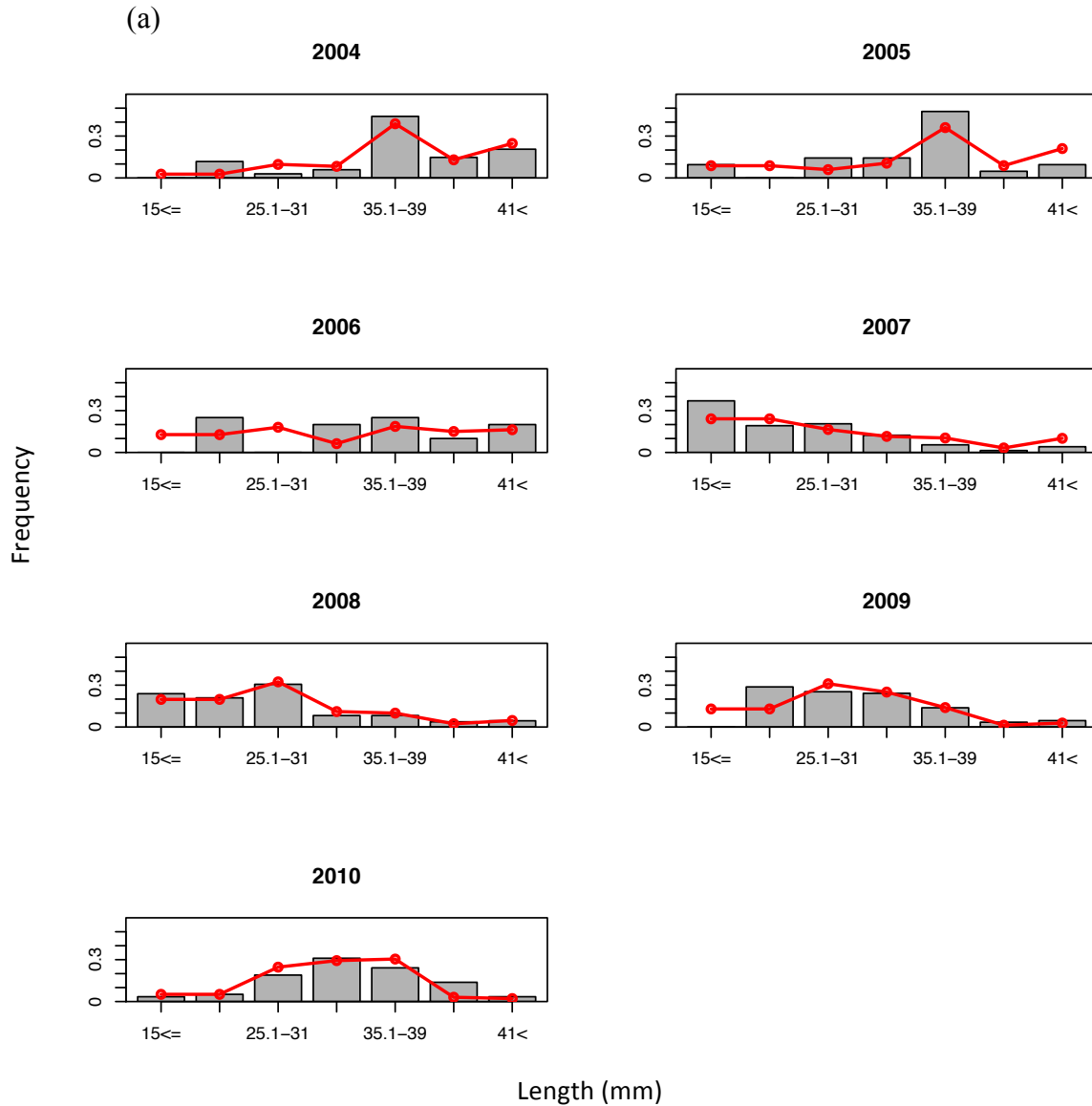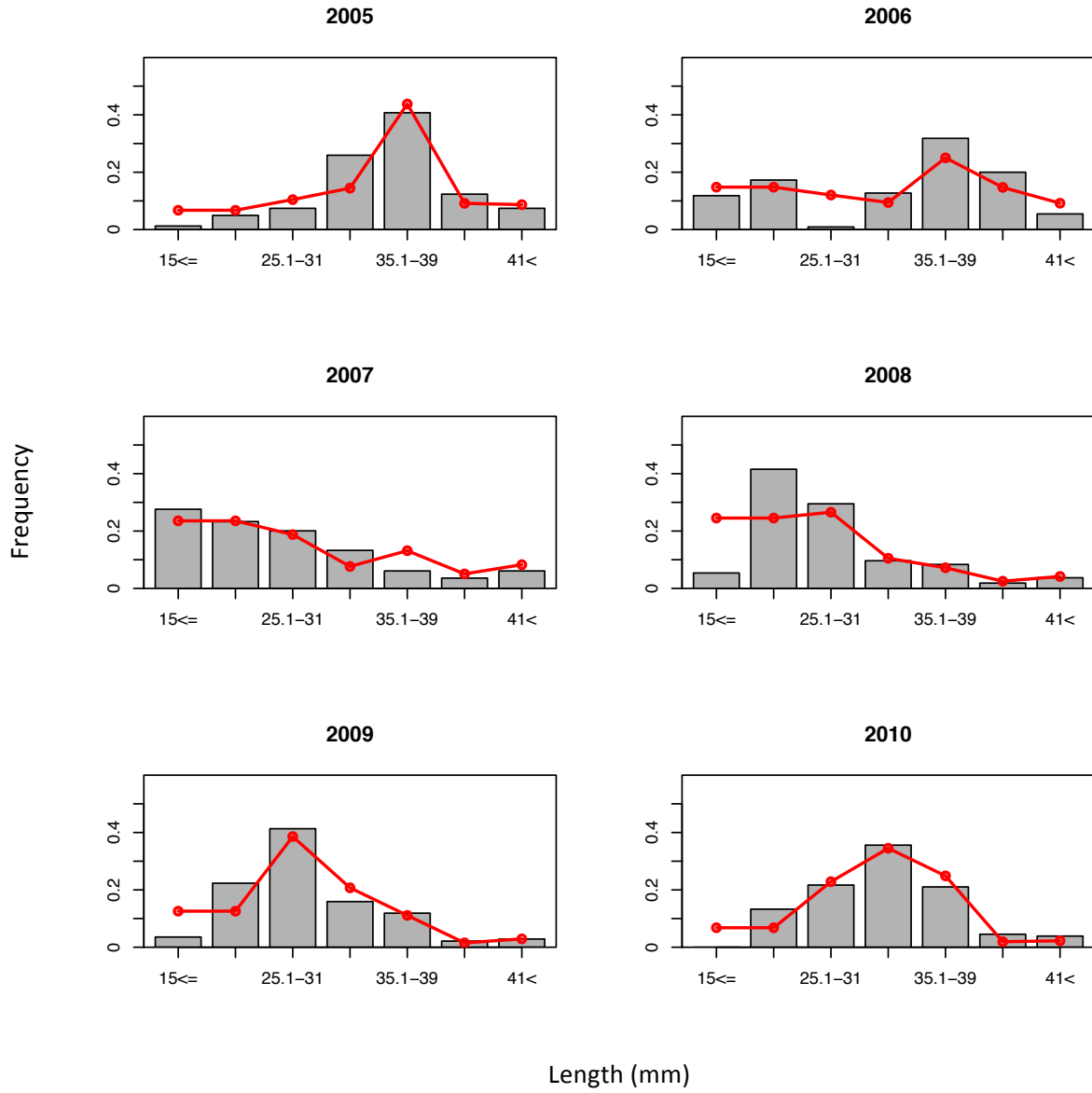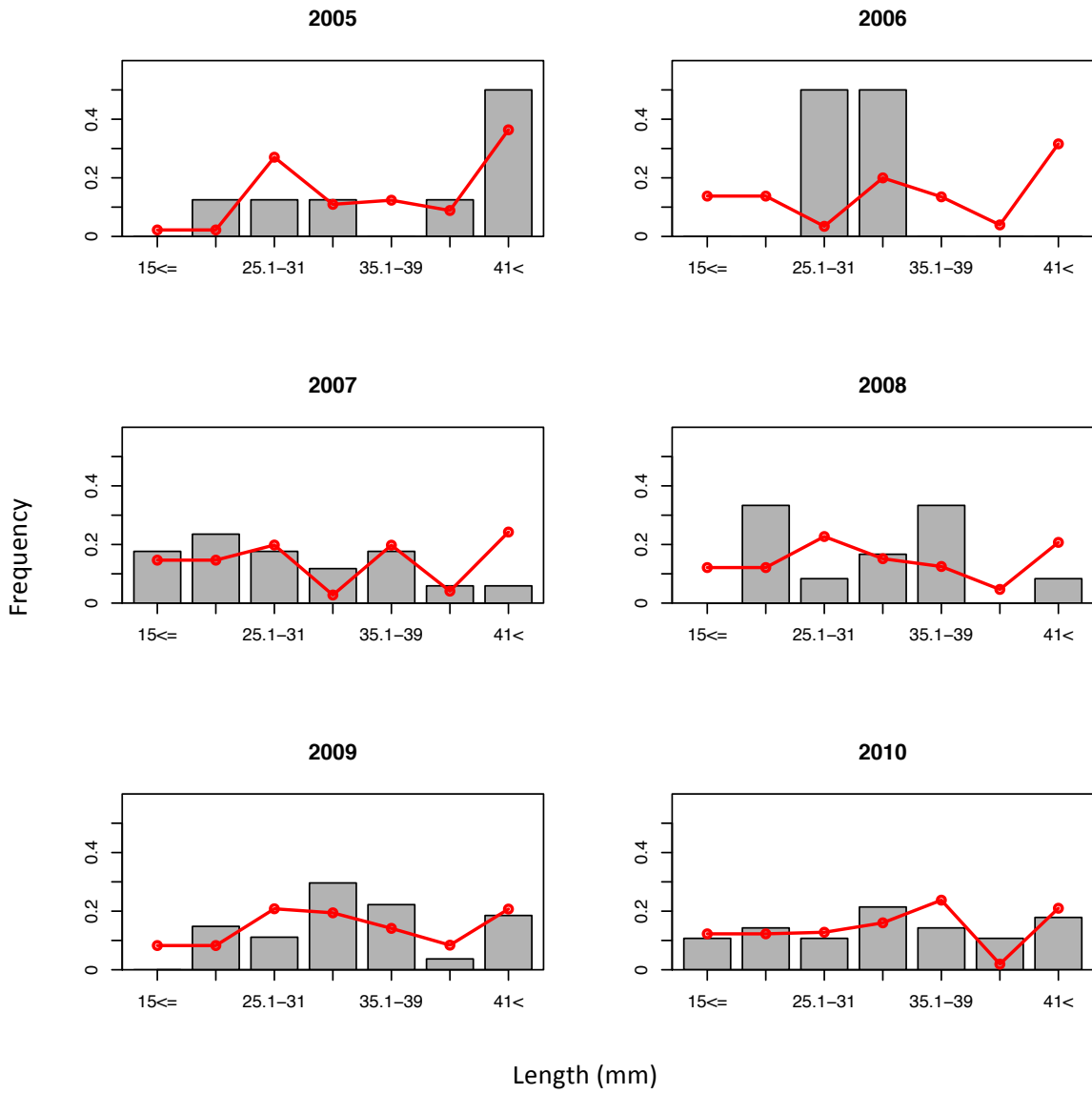
Figure 2.2. Estimates of natural mortality rate over age for *Epioblasma capsaeformis* at (a) Wallen Bend, (b) Frost Ford and (c) Swan Island based on Bayesian model averaging. Solid lines represent median estimates and dotted lines represent 95% credible interval.
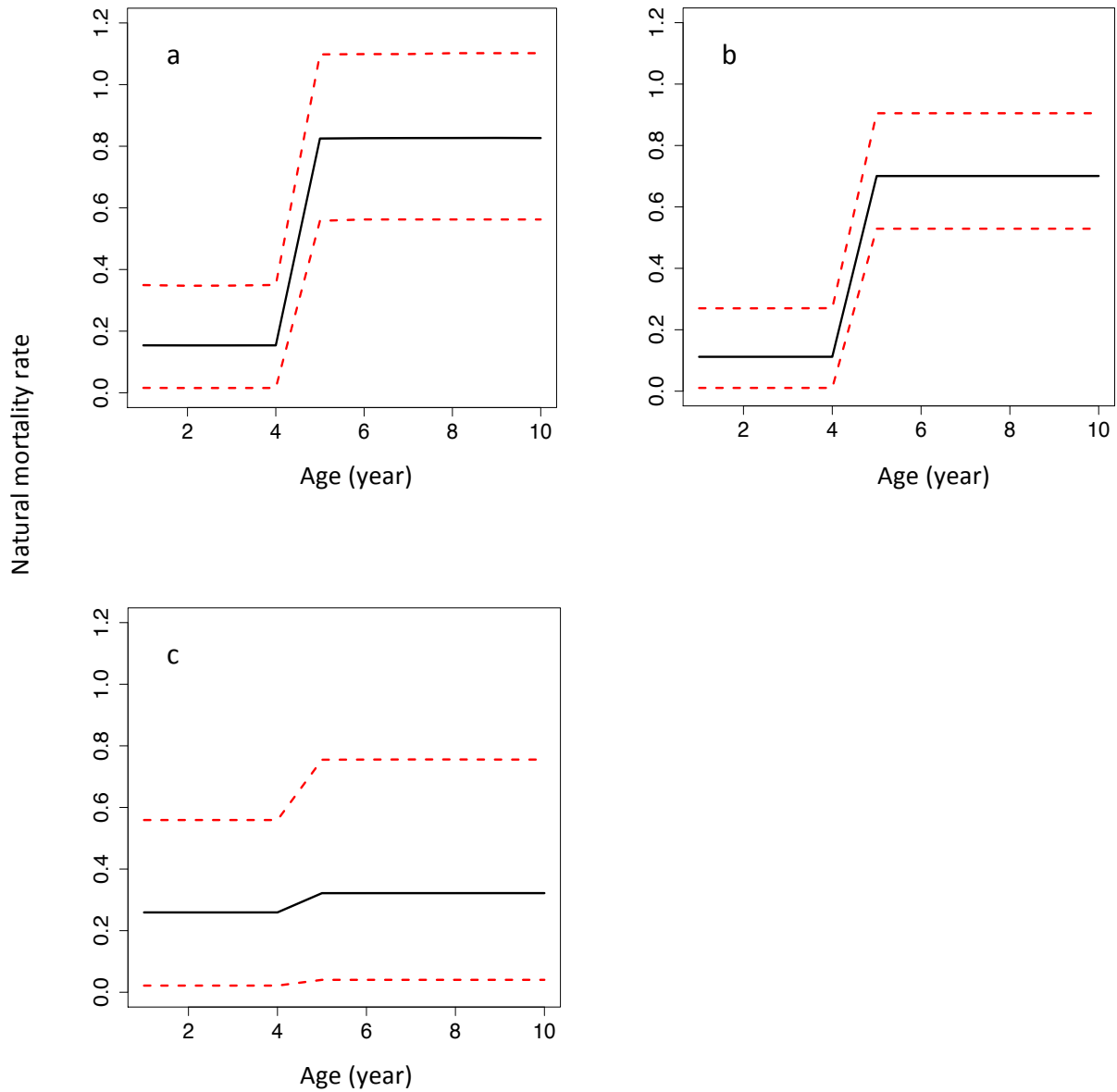
Figure 2.3. Estimates of age structures for *Epioblasma capsaeformis* at (a) Wallen Bend, (b) Frost Ford and (c) Swan Island based on Bayesian model averaging.
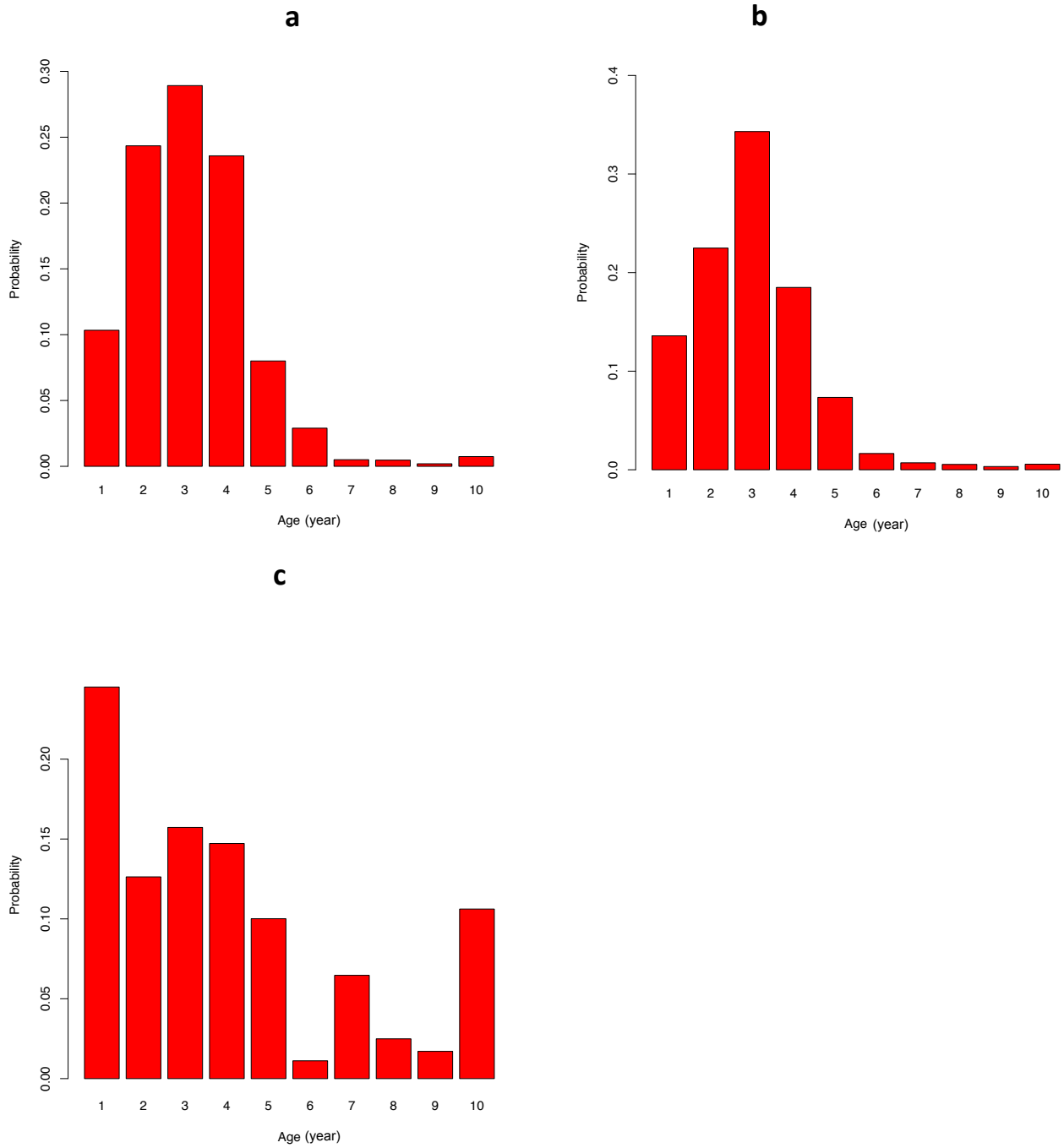
Figure 2.4. Posterior means of spawners and recruits for *Epioblasma capsaeformis* at (a) Wallen Bend, (b) Frost Ford and (c) Swan Island from Bayesian model averaging.
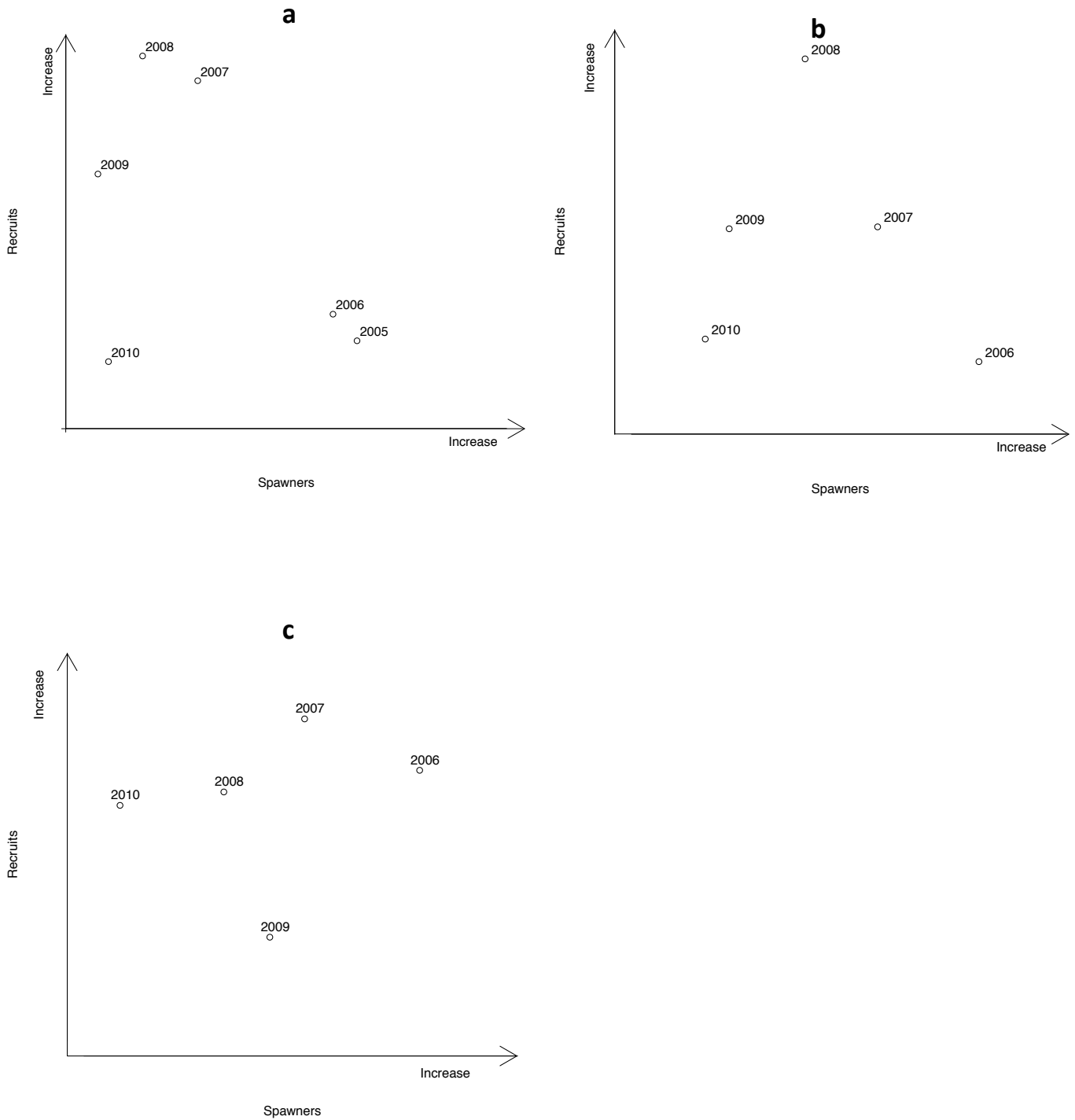
Figure 2.5. Population growth rate (λ) for *Epioblasma capsaeformis* at (a) Wallen Bend,
(b) Frost Ford and (c) Swan Island. Three red lines represent 2.5%, 50% and 97.5%
quantiles of λ.
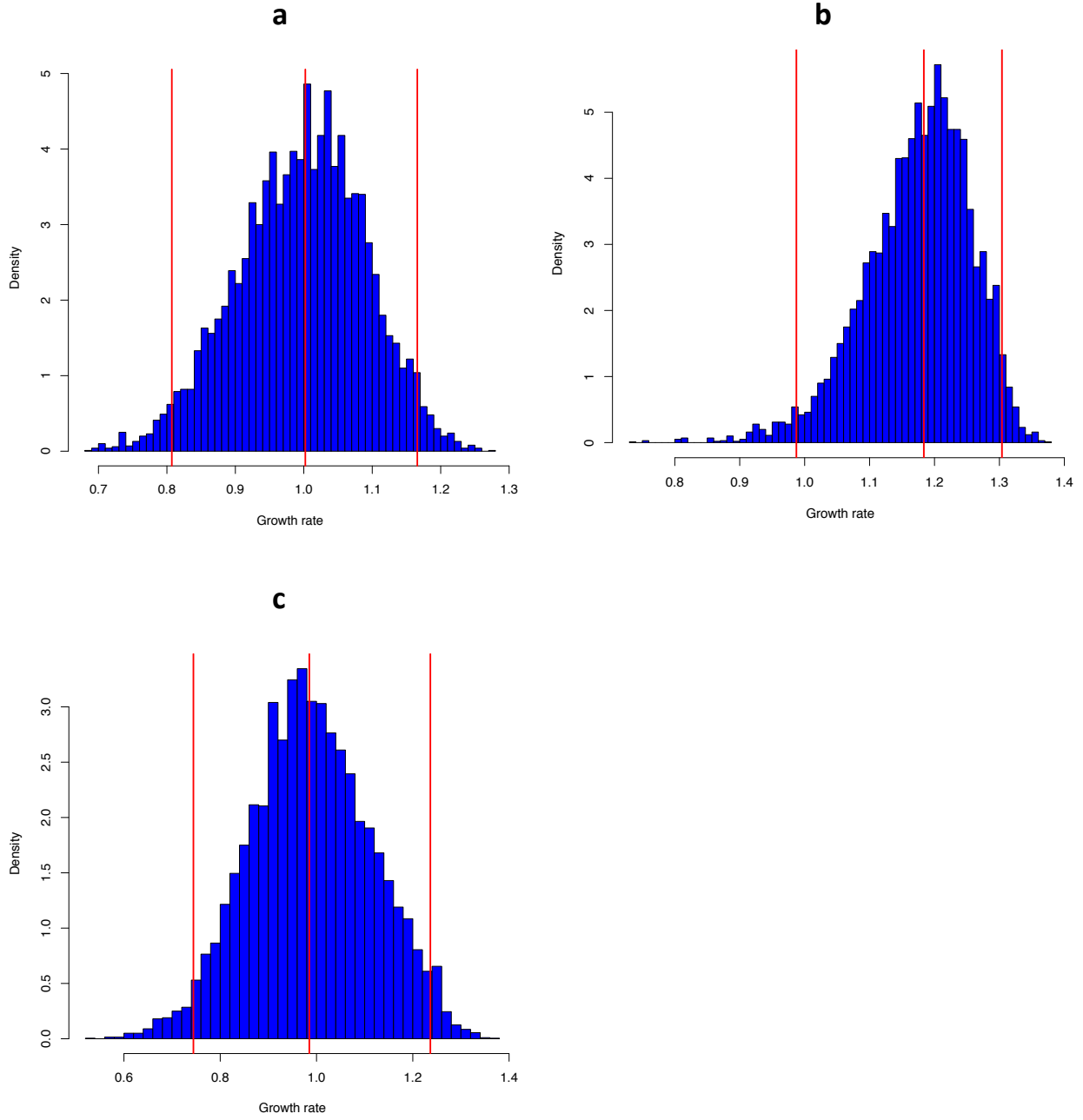
Figure 2.6. Elasticity of population growth rate to age-specific survival and fertility for *Epioblasma capsaeformis* at (a and b) Wallen Bend, (c and d) Frost Ford and (e and f) Swan Island. Solid line represents median estimation and broken line represents 95% confidence intervals.
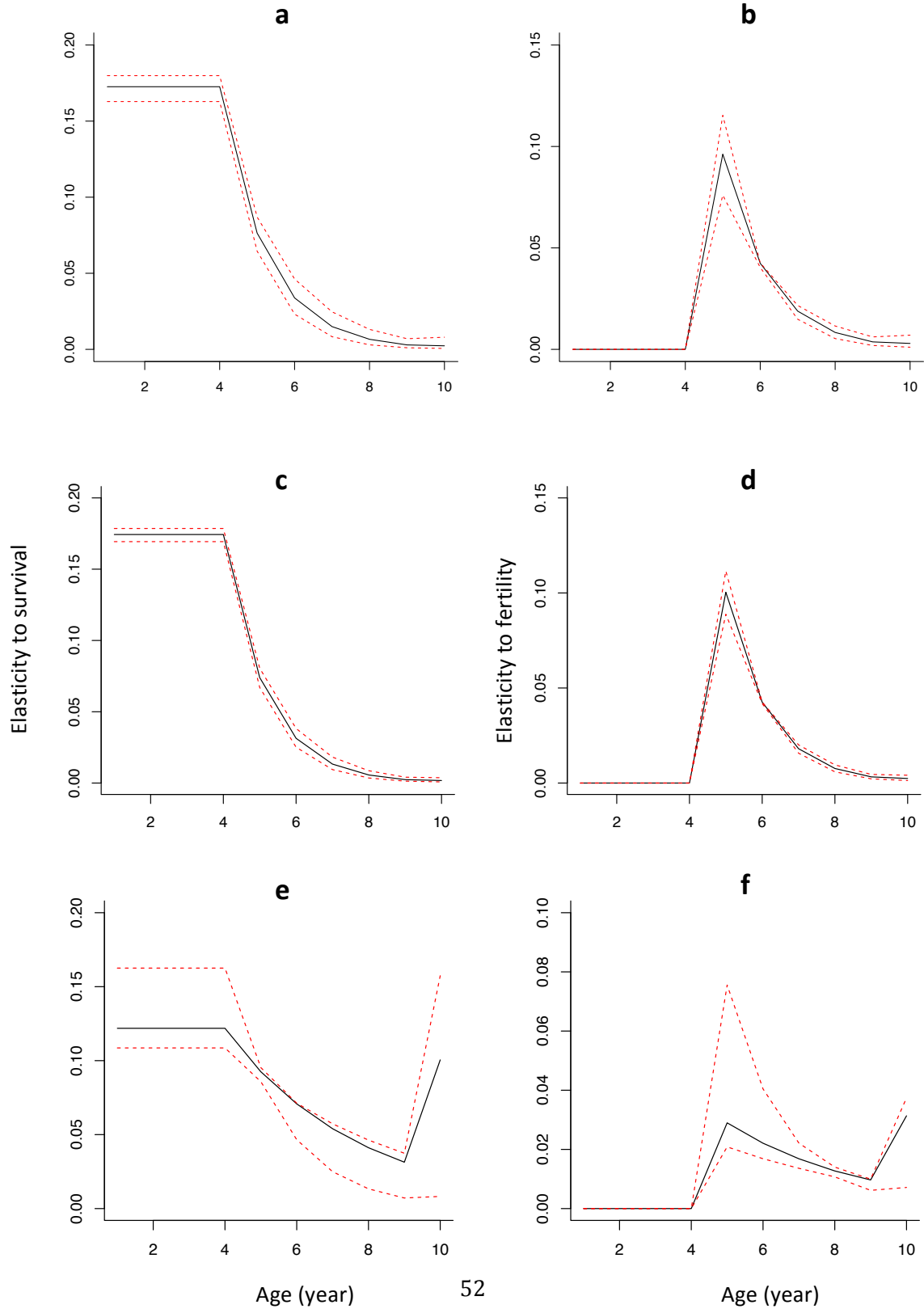
Figure 2.7. Probability of population size less than the initial population size under alternative restoration scenarios (S0-10) with 500, 1000, and 1500 released mussels at (a, b and c) Wallen Bend, (d, e and f) Frost Ford and (g, h and i) Swan Island, respectively.
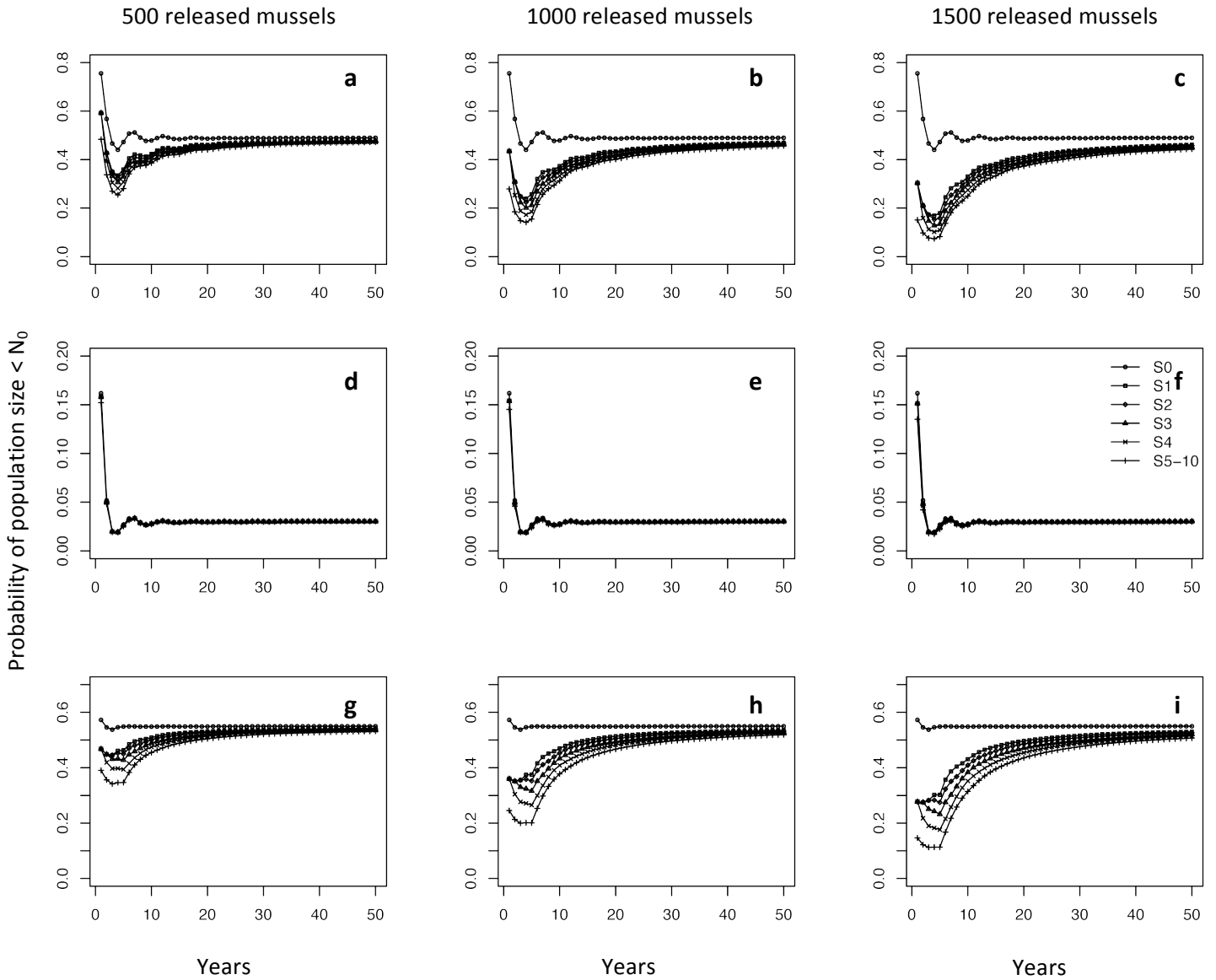
Figure 2.8. Stream discharge per month in the Clinch River taken at gauge #0352800 located upstream of Tazewell, Claiborne Co., TN (USGS, 2012).
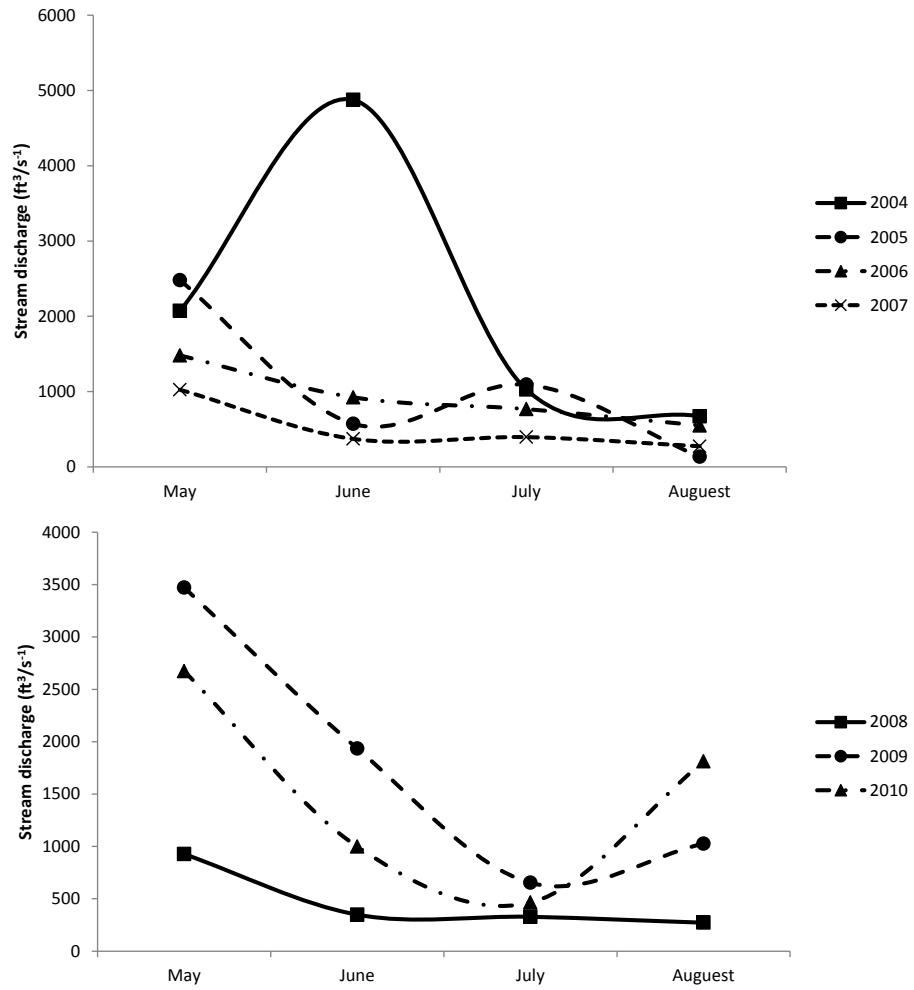
Chapter 3

A hierarchical Bayesian approach for estimating *Epioblasma capsaeformis* and *Actinonaias pectorosa* growth based on tag-recapture data

3.1 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 results in substantial biases in estimations of growth parameters. To investigate the existence of individual and sex variability in growth, I designed an experiment to collect mark-recapture data for one endangered freshwater species (*Epioblasma capsaeformis*) and one common, non-imperil species (*Actinonaias pectorosa*) by using a passive integrated transponder (PIT) technique. Models with individual and sex variability (M1), sex-related differences (M2), and individual variability (M3) were developed to estimate the 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 asymptotic length (45.34 mm) and growth rate (0.279) than males (42.09 mm and 0.216). The model incorporating individual and sex variability (M1) yield the lowest DIC value, indicating sex and individual differences should be considered in parameter estimation. For *A. pectorosa*, M1 also gave the lowest DIC value. Thus, I suggest that a hierarchical approach be used to consider individual variability and sex-related differences (if a species has sexual dimorphism) for modeling growth of mussels with mark-recapture data, especially with a high percentage of multiple recaptures.

3.2   Introduction

To successfully implement conservation actions for freshwater mussels, managers must understand and estimate their vital rates, such as the individual growth (Dennis et al., 1991). Knowledge of growth is a critical consideration in assessing population dynamics and population sustainability (Alós 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 life history parameters: L_∞ (asymptotic length), K (growth rate), 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, which are assumed to have the same life history for all individuals from the same group, and mean growth parameters are used to describe growth for all the individuals in the population. However, this assumption can be unrealistic and questionable, as growth rate 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 differs due to different responses to these factors among individuals. It is more appropriate 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 of the shell to count internal 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; Commons, 2010). In these cases, tag-recapture survey may be a better alternative to collect individual growth information for freshwater mussels. To conduct such a survey, a number of mussels should be collected, tagged and then released to a site. The tagged mussels can be recaptured and measured for lengths after various periods.

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 to monitor tagged individuals effectively so that continuous data can be utilized in growth analyses. Here, I used a passive integrated transponder (PIT) technology to monitor *Epioblasma capsaeformis* and *Actinonaias pectorosa*. The PIT tag is a small-sized tag, virtually eliminating negative impacts on animals with 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 many other animals and objects (Prentice et al., 1990; Gibbon 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, the von Bertalanffy growth model overlooks individual variability, 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 results in substantial biases in estimations of growth parameters (Maller and de Boer, 1988; Wang and Tomas, 1995; Eveson et al., 2007; Zhang et al., 2009).

In this study, I developed several growth models, taking into account individual growth and sex-related variability to estimate growth of two freshwater mussel species, *Epioblasma capsaeformis* and *Actinonaias pectorosa*. *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). Thus, *E. capsaeformis* was selected as a representative endangered mussel species. It was historically distributed throughout the Tennessee and Cumberland River system 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 mussel species in 1996 (Bogan, 2000; USFWS, 2004). On the other hand, *A. pectorosa* was selected to represent a non-imperiled species. It is distributed in the Tennessee and Cumberland River system. It exhibits a different life history (e.g. the observed maximum longevity of *A. pectorosa* is 21 yrs.) and is typically more abundant in comparison with *E. capsaeformis* (Scott, 1994). These two species have been selected as augmentation species for restoration of freshwater mussels in the Upper Tennessee River Basin (VDGIF, 2010). In previous studies, the von Bertalanffy model has been used to estimate the "average" growth parameters of *E. capsaeformis* and *A. pectorosa* (Scott, 1994; Jones and Neves, 2011), However, both of them did not considered the variation in growth among individuals.

In this research, a hierarchical approach was used to address the question of describing individual variation in growth. Individual growth rate connects to the population growth due to biological and environmental characteristics, 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).

To investigate the growth of these two freshwater species, I designed an experiment to collect mark-recapture data using PIT tag technology. Bayesian hierarchical models were developed to incorporate individual growth variability to fit mark-recapture data for *E. capsaeformis* and *A. pectorosa*. I further extended the study to growth variability between males and females, as *E. capsaeformis* exhibits pronounced sexual dimorphism (male and female shells differ in form). Deviance information criterion (DIC), which incorporates both model fit and model complexity, was used to

compare different hierarchical models (Jiao et al., 2008, 2009, 2010; Spiegelhalter et al., 2004).

3.3 Materials and methods

3.3.1 Study sites

Cleveland Islands is located near the town of Cleveland in Russell Co., Virginia at Clinch River Mile (CRM) 270.8. 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) (Figure 3.1). Cleveland Islands represents a biologically significant section in the upper Clinch River, has stable habitat for mussels to survive and grow, and has been surveyed to monitor freshwater mussels there since 2002 (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.

3.3.2 Mark-recapture data

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*. I 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. I 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 et al., 2011). 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 as a treatment group. Global Positioning System (GPS) was used to record the location where mussels were placed. I recaptured the PIT-tagged mussels in August and September, 2011 and July, 2012 with a mobile PIT detection unit (Figure 3.1, Table 3.1). 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 the stream based on the recorded latitude and longitude. If tagged mussels were found in the expanded area, the scan area would be expanded again by 20 percent and so forth. If not, I would stop scanning and assumed there were no more tagged mussels beyond this area.

3.3.3 Growth models

To determine the growth curve from time-based length increases of tagged individuals, the von Bertalanffy model was used for mark-recapture data to estimate the parameters of interest (Fabens, 1965; Haaker et al., 1998; Jiao et al., 2010). It can be written as:

$$E(\Delta L) = L_{t+\Delta t} - L_t = (L_\infty - L_t)(1 - e^{-K\Delta t})$$
(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). *dL* was assumed to follow a normal distribution with mean $(L_\infty - L_t)(1 - e^{-K\Delta t})$ and variance $\sigma_{\Delta L}^2$.

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

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

$$L_{i,j,s} - L_{i,j-1,s} = \left(L_{\infty,i,s} - L_{i,j-1,s}\right)\left(1 - e^{-K_{i,s}\Delta t_{j-1}}\right)$$
$$L_{\infty,i,s} \sim N\left(\overline{L}_{\infty,s}, \sigma^2_{L_{\infty,s}}\right)I(30,70)$$
$$\overline{L}_{\infty,s} \sim U(30,60)$$
$$\sigma^2_{L_{\infty,s}} \sim U(0,100) \tag{2}$$
$$K_{i,s} \sim N\left(\overline{K}_s, \sigma^2_{K_s}\right)I(0,1)$$
$$\overline{K}_s \sim U(0,0.8)$$
$$\sigma^2_{K_s} \sim U(0,0.2)$$

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 between the jth and j-1th recapture. By considering the individual variation, the corresponding individual parameters were assumed to come randomly from some population distributions. $L_{\infty,i,s}$ and $K_{i,s}$ were assumed to be from normal distributions $N\left(\overline{L}_{\infty,s}, \sigma^2_{L_{\infty,s}}\right)$ and $N\left(\overline{K}_{s,g}, \sigma^2_{K_{s,g}}\right)$, respectively. The $\overline{L}_{\infty,s}$ and $\overline{K}_s$, represent population characteristics of male or female *E. capsaeformis* and were assumed to follow 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 mm and 70 mm.

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

$$L_{j,s} - L_{j-1,s} = \left(L_{\infty,s} - L_{j-1,s}\right)\left(1 - e^{-K_s\Delta t_{j-1}}\right) \tag{3}$$
$$L_{\infty,s} \sim U(30,60)$$
$$K_s \sim U(0,0.8)$$

The individual differences were ignored in this model, e.g. 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 uniform distributions (Table 3.2). This model was also applied to data of *A. pectorosa* but using different prior distributions for parameter estimation (Table 3.2).

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

$$L_{i,j} - L_{i,j-1} = \left(L_{\infty,i} - L_{i,j-1}\right)\left(1 - e^{-K_i \Delta t_{j-1}}\right)$$
$$L_{\infty,i} \sim N\left(\overline{L}_\infty, \sigma_{L_\infty}^2\right)I(30,70)$$
$$\overline{L}_\infty \sim U(30,60)$$
$$\sigma_{L_\infty}^2 \sim U(0,100)$$
$$K_i \sim N\left(\overline{K}, \sigma_K^2\right)I(0,1) \tag{4}$$
$$\overline{K} \sim U(0,0.8)$$
$$\sigma_K^2 \sim U(0,0.2)$$

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

The same models were applied to fit tag-recapture data of *A. pectorosa* except that the sex-related factor was excluded because male and female *A. pectorosa* are similar in appearance and hard to distinguish. In this case, the M1 would become the same as M3, thus I just used M1 and M2 to analyze the mark-recapture data for *A. pectorosa*. The boundaries of the asymptotic length and growth rate for *A. pectorosa* were $I(70,140)$ and $I(0,1)$, respectively. As *A. pectorosa* and *E. capsaeformis* exhibit quite different length and longevity expectations, different boundaries for the distributions were used in their estimation, which are shown in Table 3.2.

3.3.4 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 priors were used for variances $\sigma_{L_\infty,s}^2$, $\sigma_{L_\infty}^2$, $\sigma_{K_s}^2$, and σ_K^2. Uniform distributions usually work better than inverse-gamma distributions for variance parameters in hierarchical models (Gelman, 2006). The summary of all prior distributions is shown in Table 3.2.

In my study, 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. The DIC was used to select the "best" model in this study. It is a composite measure of the goodness of fit and model complexity. The preferred model is the one with the minimum DIC value. To diagnose the convergence by Gelman-Rubin diagnostics (Spiegelhalter et al., 2004; Jiao et al., 2008, 2009), three chains were generated with different initial values.

3.4 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, M1which incorporated individual variability and sex-related differences yielded the lowest DIC value for both species (Table 3.3). For *E. capsaeformis*, M3 which assumed that there were no sex-related differences in growth had a slightly higher DIC value compared with M1. The difference of DIC between M1 and M3 was 5.18, which is larger than 5, indicating that the sex-related differences were more likely to exist in growth estimation for *E. capsaeformis* (Table 3.3). The larger differences (128.635) in DIC values between M2 and M1 demonstrated that individual viability was an important factor and should also be considered in the growth analyses of *E. capsaeformis*. The results from the best fit model, M1, showed the joint posteriors of L_∞ and *K* differed over sexes for *E. capsaeformis*, although there was some overlap which is understandable since they are produced from the same species (Figure 3.3a). For *A. pectorosa*, M1, the model that incorporated individual variability, had the lower DIC value (Table 3.4). The parameters L_∞ and *K* at the individual level were negatively correlated (Figure 3.3b).

From the results in M1, the 95% credible interval for L_∞ for male *E. capsaeformis* varied between 38.24 and 49.17 mm, with a mean of 42.09 mm at Cleveland Islands (Table 3.3). Females ranged from 40.88 and 51.88 mm, with a mean of 45.34 mm. Thus, the estimated asymptotic length for males was smaller than females at

this site (Figure 3.4, Table 3.3). The 95% credible interval for K for male $E.$ $capsaeformis$ varied between 0.112 and 0.351 with a mean of 0.216 and ranged from 0.143 and 0.473 with a mean of 0.279 for female $E.$ $capsaeformis$, indicating that the estimated growth rate for males was smaller than females (Figure 3.4). However, by using M2, the 95% credible interval of K for females was wider than for males and the estimated mean growth rate for males was larger than for females (Table 3.3).

For $A.$ $pectorosa$, the 95% credible interval for estimated asymptotic length by M1 varied between 99.02 and 110.6 mm with a mean of 104.2 mm at Cleveland Islands and the growth rate was from 0.047-0.081 with a mean of 0.063 (Table 3.4). The estimated asymptotic length by M2 varied from 98.24-108.3 mm with a mean of 102.8 mm at Cleveland Islands and the growth rate was from 0.056-0.081 with a mean of 0.069 (Table 3.4). The hierarchical model incorporating individual variability resulted in wider credible intervals in the estimates of asymptotic length and growth rate than using the non-hierarchical model, which are also shown in the estimated von Bertalanffy model for $A.$ $pectorosa$ (Figure 3.5).

3.5   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, mostly 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, I 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 sites (Table 3.4). The unique codes from PIT tags enabled me to record the length of each individual mussel. Thus, PIT tag technique provided a very useful tool to monitor individual mussels, especially when there was a limited number of available mussels for such a mark- recapture study.

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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 attractive 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 rates of *E. capsaeformis* and *A. pectorosa* at this site, three models were proposed and compared by DIC values. The hierarchical model with individual variability (M1) gave the best fit for growth of these two species. 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, I 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. Thus, 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* tend to grow larger than males but have a lower individual grow rate (*K*) than males (Jones and Neves, 2011). The results obtained here agree with the statement about asymptotic length. However, when incorporating individual variability, the mean growth rate for females was larger than that for males in this study. The somatic growth of mussels is likely influenced by

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temperature, flow discharge, food availability, site substrate characteristics, etc. (Krohn et al., 1997; Jiao et al., 2010; Jones and Neves, 2011). The estimated lengths of young *A. pectorosa* in this study were less than those found by Scott (1994) at other sites, in the Clinch River, Virginia, which is due to the lower estimated growth rate. The lower growth rate may have been related to PIT tagged *A. pectorosa*, in which only a few young *A. pectorosa* were collected and marked. In addition, the habitat at Cleveland Islands or some special environmental condition during the survey duration may also have caused the lower observed growth rate of *A. pectorosa*. The estimated growth rate with individual variability reflected mussel growth at an individual level. As this survey lasted only for one year, more recapture surveys would be better, such as involving multiple years data or incorporating spatial factors, to increase the validity of qualitative descriptions of mussel growth at the individual level.

In addition to individual differences, the relationship between asymptotic length and growth rate at the individual level was negative. This kind of relationship has been found and confirmed by many researchers (Pilling et al., 2002; Helser et al., 2007; Jiao et al., 2010). The negative correlation reflected a trade off between somatic growth and reproduction (Alós et al., 2010).

The high detection rates of PIT tagged mussels suggest that this tool 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 indicates its advantages in incorporating variations among individuals. In future studies, sexes, sites and temporal variations could also be considered through a Bayesian hierarchical model to analyze survey data of other species. I suggest long-term surveys for mussels be conducted because additional data will help increase the accuracy of population estimation using the Bayesian hierarchical approach.

3.6   Acknowledgements

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3.7 References

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Table 3.1 Number of released and recaptured mussels during the mark-recapture survey at Cleveland Islands in the upper Clinch River, VA. The dates for release and each recapture are: July 6th, 2011, August 8th, 2011, September 30th, 2011 and July 12th, 2012.

Species	Survey	Number of mussels	Shell length (mm)		
			Mean	Min.	Max.
E. capsaeformis (male)	Mussel release	30	31	22	40
	1st recapture	28	32.1	22.7	41.3
	2nd recapture	28	32.2	23.7	41.4
	3rd recapture	29	33.7	27.0	41.1
E. capsaeformis (female)	Mussel release	30	35	28	44
	1st recapture	30	36.0	28.5	43.4
	2nd recapture	29	36.7	29.7	43.5
	3rd recapture	21	37.3	31.5	43.8
A. pectorosa	Mussel release	60	79	51	109
	1st recapture	59	80.5	50.0	108.2
	2nd recapture	58	81.0	51.0	108.0
	3rd recapture	56	81.5	52.7	108.1

Table 3.2. Prior information for male and female *Epioblasma capsaeformis* and *Actinonaias pectorosa* in the model with individual and sex variability (M1), the model with sex-related differences (M2), and the model with individual variability (M3).

Species	M1	M2	M3
E. capsaeformis	$\bar{L}_{\infty,s} \sim U(30,60)$ $\bar{K}_s \sim U(0,0.8)$ $\sigma^2_{L_{\infty,s}} \sim U(0,100)$ $\sigma^2_{K_s} \sim U(0,0.2)$	$L_{\infty,s} \sim U(30,60)$ $K_s \sim U(0,0.8)$	$\bar{L}_\infty \sim U(30,60)$ $\bar{K} \sim U(0,0.8)$ $\sigma^2_{L_\infty} \sim U(0,100)$ $\sigma^2_K \sim U(0,0.2)$
A. pectorosa	$\bar{L}_\infty \sim U(80,130)$ $\bar{K} \sim U(0,0.8)$ $\sigma^2_{L_\infty} \sim U(0,200)$ $\sigma^2_K \sim U(0,0.2)$	$L_\infty \sim U(80,130)$ $K \sim U(0,0.8)$	–

As male and female *A. pectorosa* are similar in appearance, models without sex-related differences were applied to *A. pectorosa*. In this case, the M1 would become the same as M3, thus I just used M1 and M2 to analyze the mark-recapture data for *A. pectorosa*.

Table 3.3. Model comparison by the deviance information criterion values among the model with individual and sex variability (M1), the model with sex-related differences (M2) and the model with individual variability (M3) for *Epioblasma capsaeformis*.

Model	DIC	Parameter	Mean	Standard deviation	95% Credible interval	
M1	166.404	$\overline{L}_{\infty,s=1}$	42.090	2.720	38.240	49.170
		$\sigma^2_{L_{\infty,s=1}}$	17.680	14.430	2.511	56.910
		$\overline{L}_{\infty,s=2}$	45.340	2.834	40.880	51.880
		$\sigma^2_{L_{\infty,s=2}}$	30.680	18.260	7.371	77.360
		$\overline{K}_{s=1}$	0.216	0.060	0.112	0.351
		$\sigma^2_{K_{s=1}}$	0.012	0.009	0.002	0.035
		$\overline{K}_{s=2}$	0.279	0.087	0.143	0.473
		$\sigma^2_{K_{s=2}}$	0.016	0.014	0.002	0.054
M2	295.039	$L_{\infty,s=1}$	41.830	2.902	37.990	49.170
		$L_{\infty,s=2}$	47.520	3.792	42.080	57.010
		$K_{s=1}$	0.225	0.057	0.115	0.339
		$K_{s=2}$	0.223	0.069	0.111	0.374
M3	171.584	$\overline{L}_{\infty}$	45.340	2.345	41.360	50.460
		$\overline{K}$	32.670	15.180	11.010	68.620
		$\sigma^2_{L_{\infty}}$	0.194	0.043	0.126	0.296
		σ^2_{K}	0.008	0.005	0.003	0.022

Table 3.4. Model comparison by the deviance information criterion values between the model with individual variability (M1) and the nonhierarchical model (M2) for *Actinonaias pectorosa*.

Model	DIC	Parameter	Mean	Standard deviation	95% Credible interval	
M1	125.392	$\overline{L}_\infty$	104.200	2.946	99.020	110.600
		$\sigma^2_{L_\infty}$	73.560	38.010	12.320	164.000
		$\overline{K}$	0.063	0.008	0.047	0.081
		σ^2_K	0.001	0.000	0.000	0.001
M2	229.328	L_∞	102.800	2.536	98.240	108.300
		K	0.069	0.006	0.056	0.081

Figure 3.1. The location of Cleveland Islands (Clinch River Mile 270.8) in the Clinch River (adapted from Brett Ostby, Virginia Tech).
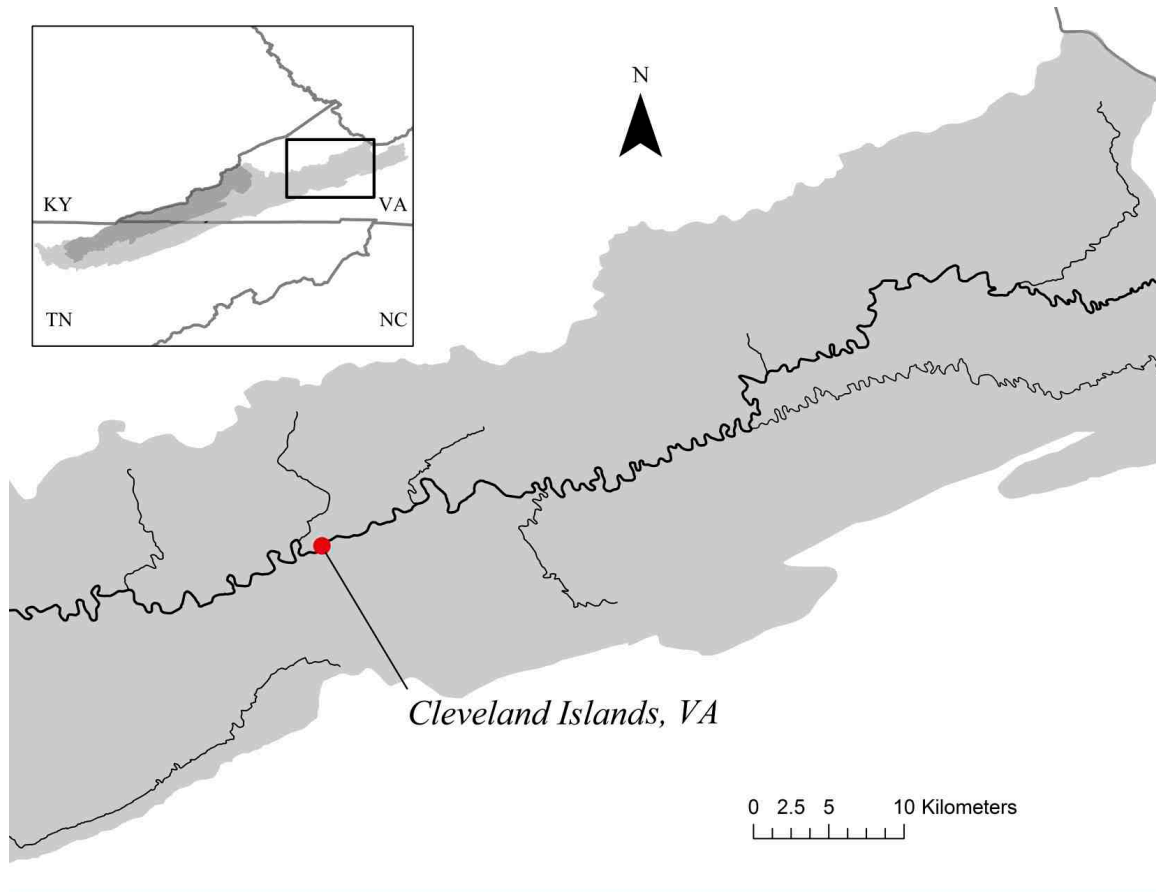
Figure 3.2. Comparison of observed length at time t and the length at time $t + \Delta t$ for *Epioblasma capsaeformis* and *Actinonaias pectorosa* at Cleveland Islands. Red lines represent the $L_t \sim L_t$, circles represent the $L_t \sim L_{t+\Delta t}$ points. (a) Male *Epioblasma capsaeformis*; (b) female *Epioblasma capsaeformis*; (c) *Actinonaias pectorosa*.
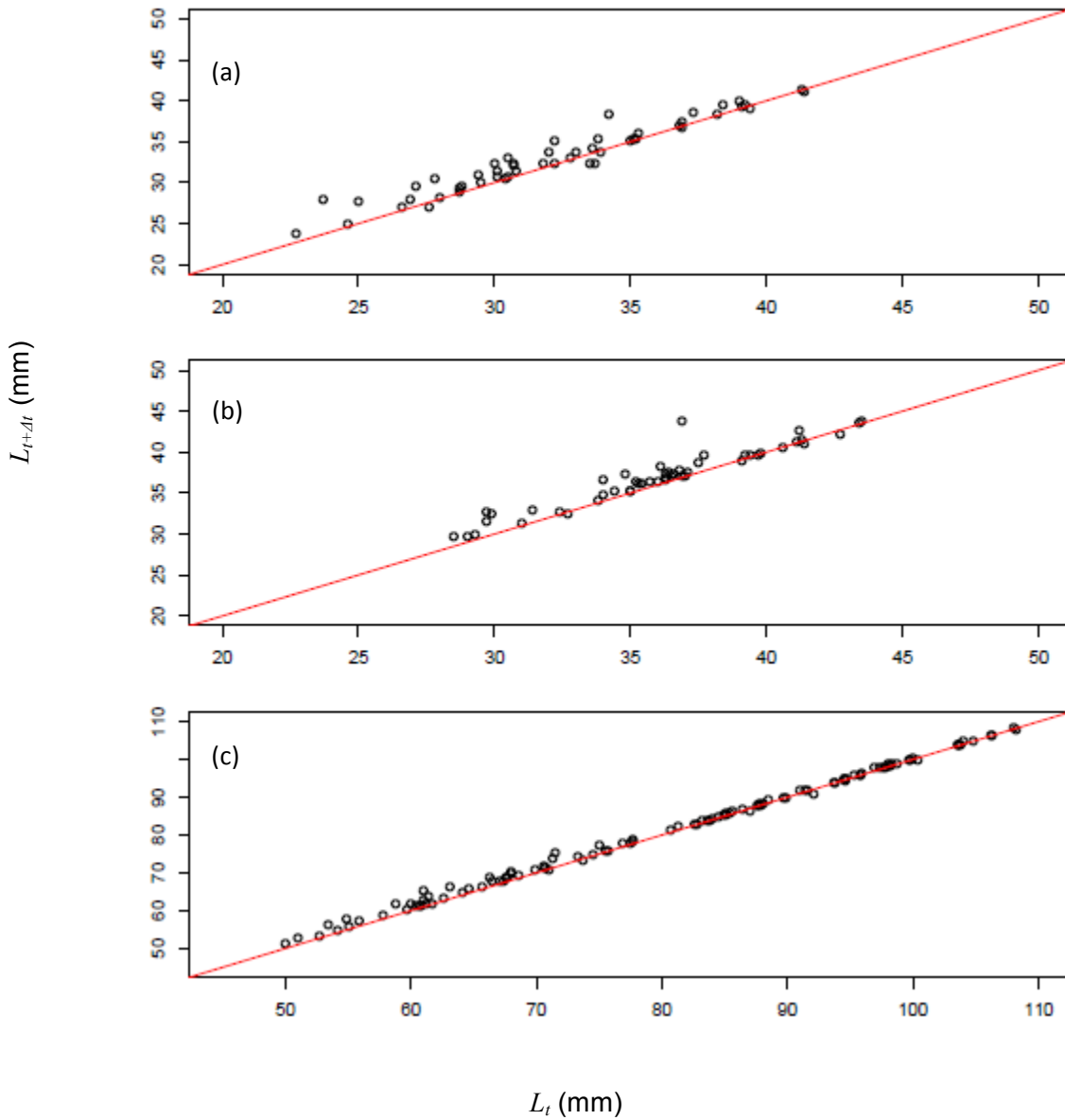
Figure 3.3. Joint posterior distributions of asymptotic lengths (L_∞) and growth rates (K) for *Epioblasma capsaeformis* and *Actinonaias pectorosa* at Cleveland Islands when M1 is used. (a) Red, male *Epioblasma capsaeformis*; black, female *Epioblasma capsaeformis*. (b) *Actinonaias pectorosa*.
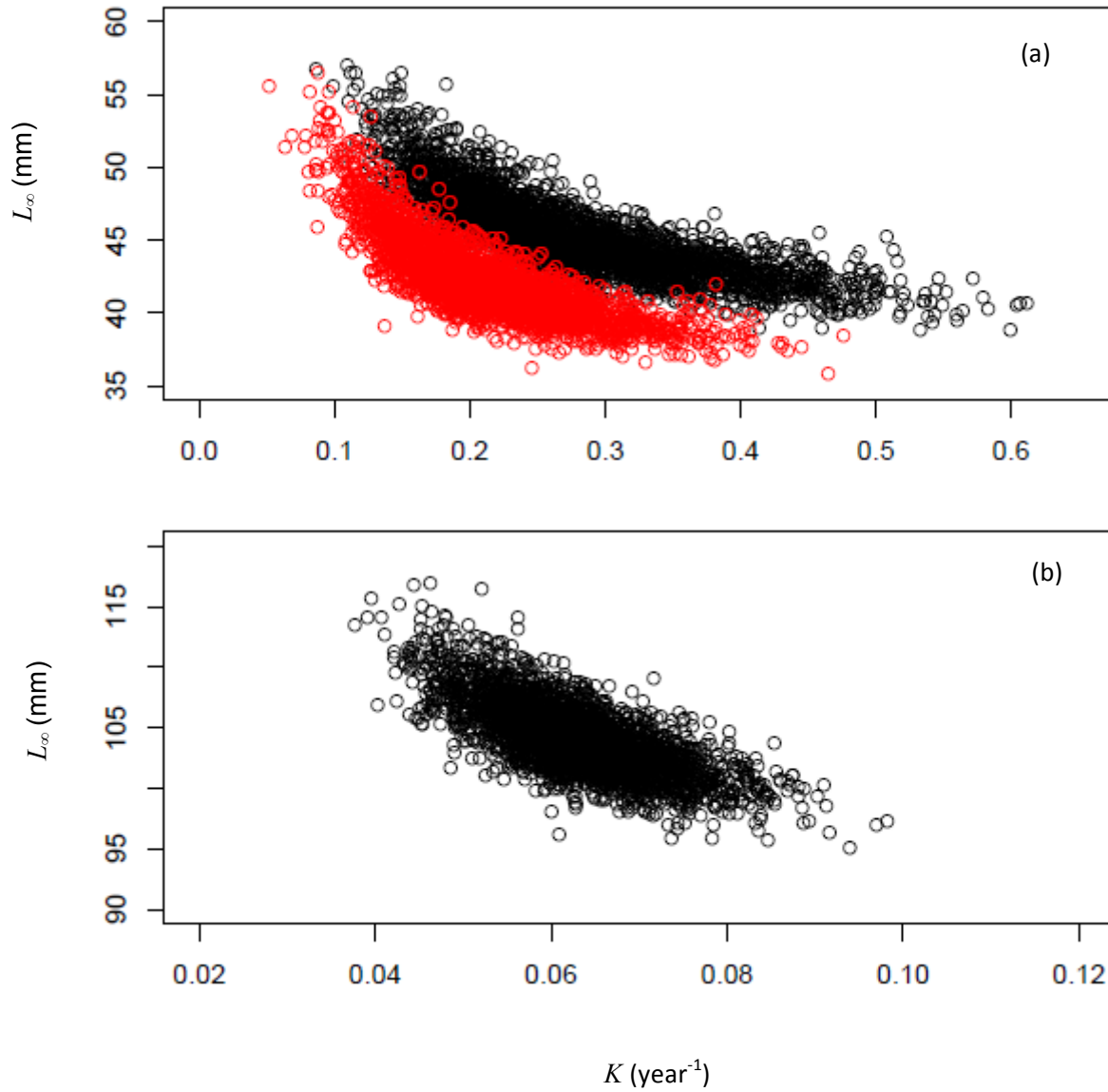
Figure 3.4. Von Bertalanffy growth curves for *Epioblasma capsaeformis* from four models. Solid lines represent the means of estimated von Bertalanffy growth curves from posterior distributions and dotted lines represent the 95% credible interval of estimated von Bertalanffy growth curves from posterior distributions. Black represents male and red represents female. (a) Curves from the model with individual and sex variability (M1); (b) curves from the model with sex-related differences (M2); (c) curves from the model with individual variability (M3).

Figure 3.5. Von Bertalanffy growth curves for *Actinonaias pectorosa* at Cleveland Islands. Solid lines represent the means of estimated von Bertalanffy growth curves from posterior distributions and dotted lines represent the 95% credible interval of estimated von Bertalanffy growth curves from posterior distributions. (a) Curves from the model with individual variability model (M1); (b) curves from the non-hierarchical model (M2).

Chapter 4

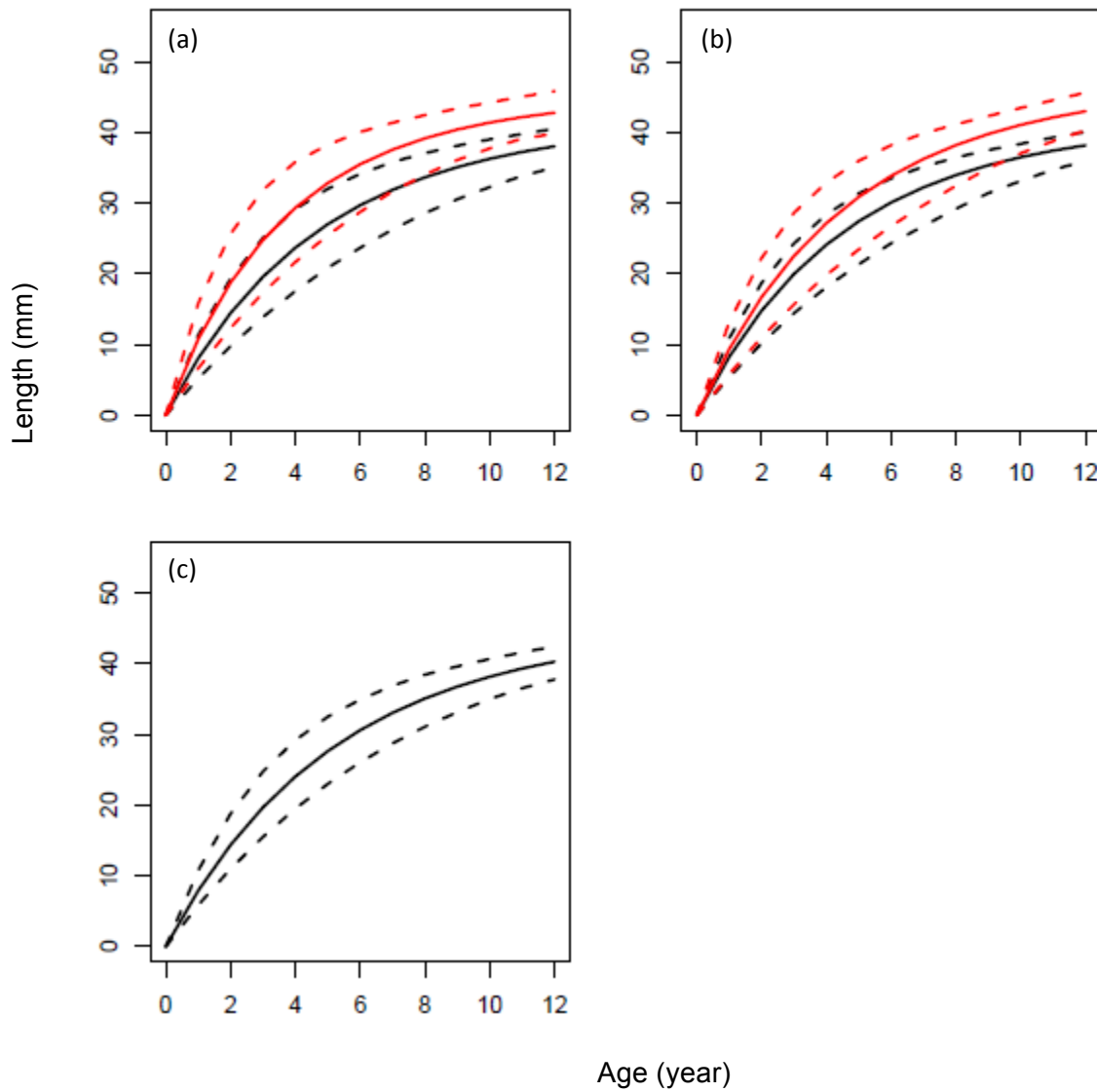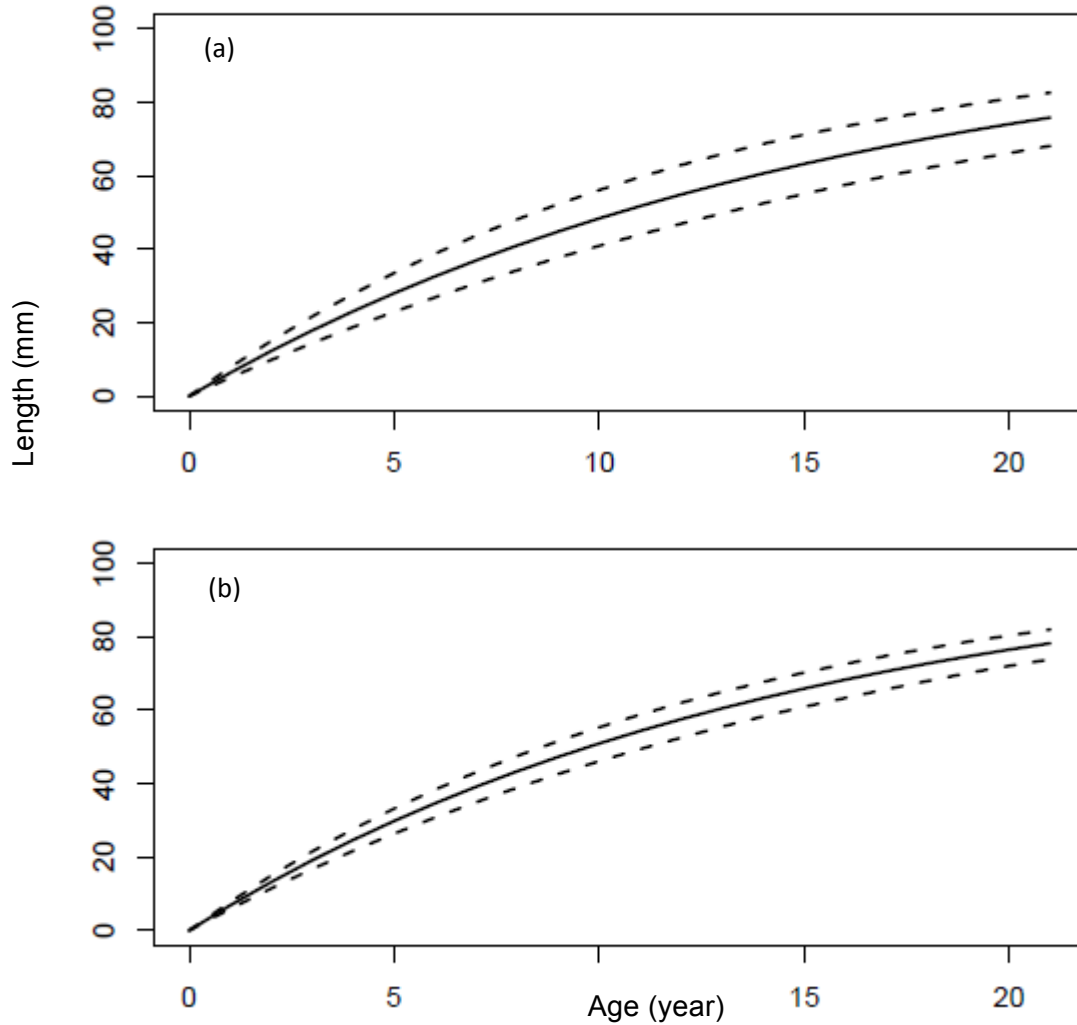# Hierarchical Bayesian models for estimating survival and recapture rates of *Epioblasma capsaeformis* and *Actinonaias pectorosa* based on mark-recapture data

4.1 Abstract

Translocation has been used as a conservation technique to recover mussel populations due to dramatic declines of this faunal group during the last several decades. An effective monitoring method for translocated mussels is essential because accurate assessment of survival and growth of individuals can help managers access how effective translocation efforts are for species recovery. In this study, a mark-recapture experiment was designed to estimate the recapture and survival rates of translocated mussels marked by passive integrated transponder (PIT) tags. Bayesian models were developed to estimate the survival and recapture rates of one endangered species (*Epioblasma capsaeformis*) and one common species (*Actinonaias pectorosa*), using mark-recapture data. The existence of individual and sex-related variability in survival and recapture were tested in this study. The deviance information criterion (DIC) was used to compare different models. The median survival rates of male *E. capsaeformis,* female *E. capsaeformis* and *A. pectorosa* were very high (>87%, >74% and >91%), indicating the habitat at Cleveland Islands is suitable for these two mussel species within the survey duration. In addition, the median recapture rates for *E. capsaeformis* and *A. pectorosa* were > 93% and >96%, indicating that the PIT tag technique provided an efficient monitoring approach and the high detectability of the approach helped improve accuracy of survival estimates. According to model comparison results, I recommend applying the non-hierarchical model or the model with sex–related difference (if a species is sexually dimorphic) in survival rate to analyze mark-recapture data when sample sizes are small.

4.2 Introduction

Freshwater mussels have experienced dramatic declines in the U.S. during the last several decades. About 70% of freshwater mussel species are listed as endangered, threatened, of special concern or extinct (Williams et al. 1993; NNMCC, 1998). The National Native Mussel Conservation Committee has prepared a National Strategy for the Conservation of Native Freshwater Mussels to conserve the nation's freshwater mussel fauna (NNMCC, 1998). One of the goals of the strategy is to "develop, evaluate, and use the techniques necessary to hold and translocate large numbers of adult mussels" (NNMCC, 1998).

Translocation of animals has been used as a conservation management tool to establish and augment populations (Griffith et al., 1989). However, the success rate of translocation has varied considerably due to abiotic and biotic factors, such as the number of animals released, habitat quality, predation, competition, etc. (Griffith et al., 1989; Wolf et al., 1996). Previous studies of mussel translocations are largely based on visual searches (Bolden and Brown, 2002; Cope et al., 2003). A review of mussel translocation studies by Cope and Waller (1995) found that the average recapture rate was 43% (range: 1-97%). Kurth (2007) found that the recapture rate using visual searches was 30-47% at all sites studied. Lack of effective monitoring methods has hampered freshwater mussel conservation efforts (Kurth et al., 2007). Research is now needed to develop appropriate monitoring methods and population and individual based dynamics models to evaluate the effectiveness of translocation efforts to establish viable populations.

Accurate estimation of survival rate is essential in fisheries science and management, and mark-recapture methods are widely used in demographic analysis of natural organisms and to conduct population risk assessments (Pollock et al., 1990; Schwarz and Seber, 1999; Zheng et al., 2007). Typically, mark-recapture methods require marking a number of individuals in a population, then returning them to their collection site and then conducting repeated sampling to estimate demographic parameters. In addition, the recognition of uniquely marked individuals can allow biologists to identify the specific life history or movement of each individual (Villella et al., 2004). Recently, the use of passive integrated transponder (PIT) tagging technique has expanded from monitoring mammals, reptiles, amphibians and birds to freshwater mussels (Gibbons and Andrews, 2004; Kurth et al., 2007). PIT tag kits are composed of a reader, portable

antenna and PIT tags. The PIT tag is small (8-10 mm long) and has an indefinite longevity (Kurth et al., 2007; Gibbons and Andrews, 2004). Its unique code, which can be detected by the transponder (reader and antenna), make it easy to identify individual organisms. Compared with traditional mussel mark-recapture methods, which largely depend on glue-on shellfish tags and visual encounters to locate mussels, PIT tags exhibit much higher recapture rates in marking and tracking individual freshwater mussels (Kurth et al., 2007). Thus, the PIT tag technique is ideally suited to freshwater mussel tranlocation studies with small population sizes.

In analyses of mark-recapture data, a commonly used model is the Cormack-Jolly-Seber (CJS) model, which focus on the estimation of survival parameters in a population (Cormack, 1964; Jolly, 1965; Seber, 1965). Important assumptions in the original model are that all individuals have the same capture probability and survival rate during each survey and that there is no emigration or immigration by individuals. However, the limitations of these assumptions are more apparent today. For example, an organism is very likely to have its own unique life history though it belongs to a population. Responses to environmental changes can differ among individuals. In addition, the sex variability may also influence the survival and recapture rate of mussels.

In this study, multilevel priors were used to model variability among individuals and between sexes in the probability of recapture and survival. Bayesian methods are very appropriate to mark–recapture studies because it conveniently allows multilevel priors in the model (Pollock et al., 1990; Gelman et al., 2004; Jiao et al., 2008, 2010). Prior information can be obtained from a previous study and it is easy to update the posterior distributions with additional data. The variability among individuals and between sexes in the probability of recapture and survival was assumed to follow underlying population distributions, which could be modeled as multilevel priors.

In this study, to test whether individual variability and sex variability should be considered in mark-recapture analysis, I developed five hierarchical models to account for heterogeneity among individuals and between sexes in the estimation of recapture and survival rates for *Epioblasma capsaeformis*. As *Actinonaias pectorosa* is not obviously sexual dimorphic, I only applied the last two models that did not incorporate sex variability for this species. The description of these two species was given in Chapter 3. These hierarchical models were

analyzed using Bayesian methods via Markov Chain Monte Carlo (MCMC) sampling for parameter estimation and inference. Deviance information criterion (DIC), which incorporates both model fit and model complexity (Spiegelhalter et al., 2004), was used to compare the different models.

4.3 Materials and methods

4.3.1 Data sources

Detailed descriptions of the mark-recapture data sources are available in Chapter 3. The recapture of each mussel is a sequence of independent Bernoulli events. Here, I defined 1 as the event that the mussel was captured alive; otherwise, the event equaled 0. For example, given an individual who was not captured during the 1st recapture but survived and was captured during the 2nd recapture, its recapture history would be recorded as {0 1}.

4.3.2 Recapture tree

To represent the capture histories, I present a recapture tree which indicates the relationship between survival/ death and captured/ not captured (Figure 4.1). The survival of tagged mussels during the tth recapture was conditional on the survival or death of mussels in the t-1th recapture. Capture or sighting of tagged mussels during the tth recapture was conditional on the survival or death of mussels in that recapture. The dead mussels would be removed. Thus, there was no capture or sighting happening on dead mussels during the following recapture. If there were more occasions of recapture, the recapture tree would replicate this process at each recapture.

4.3.3 Models and estimation

In the following models, several assumptions were made:

1) capture and PIT tagging of a mussel did not impact its expectation of life, such as predation and movements.

2) recapture and annual survival rates were constant throughout the survey duration and were independent of the ages of mussels.

*3) individual and sex-related differences influenced the recapture and survival rates of tagged mussels.

Assumption *3 would be violated later in each model to assess the impact of individual variations and sex-related differences on the estimation of recapture and survival rates of tagged mussels.

Under assumptions 1 and 2 and considering sex-related variability, the mark-recapture model (M1) was written as:

$$surviving_{i,t,g} = Ps_g{}^y \times Data\_surviving_{i,t-1,g}$$
$$Data\_surviving_{i,t,g} \sim Bern(surviving_{i,t,g})$$
$$capture_{i,t,g} = Pc_g \times Data\_surviving_{i,t,g}$$
$$Data\_capture_{i,t,g} \sim Bern(capture_{i,t,g})$$
$$Ps_g \sim N(Ps, \sigma_s^2)I(0,1)$$
$$Pc_g \sim N(Pc, \sigma_c^2)I(0,1)$$
$$Ps \sim Beta(1,1)$$
$$Pc \sim Beta(1,1)$$

(1)

where i represents the ith individual, y represents time interval between two recaptures, g represents the gender of *E. capsaeformis* (g=1 referred as male; g=2 referred as female) and t represents the tth recapture (t = 0, 1, 2 and 3). The tagging time was denoted by 0th recapture. Ps_g is the annual survival rate of male or female *E. capsaeformis*. Pc_g is the recapture rate of male or female *E. capsaeformis*. As the survival of mussels from one recapture depends on the last one and the capture of mussels depends on the survival or death during the occasion of recapture, I used two multiplicative equations to represent the dependence. By considering the sex-related variation, the corresponding parameters were assumed to follow certain random distributions. Variability in Ps_g and Pc_g among individuals were reflected in estimates of σ_s^2 and σ_c^2, respectively. Ps and Pc represent population characteristics and were assumed to follow beta distributions.

In the second model (M2), I ignored the impact of sexual dimorphism for *E. capsaeformis* on recapture rate:

$$surviving_{i,t,g} = Ps_g{}^y \times Data\_surviving_{i,t-1,g}$$
$$Data\_surviving_{i,t,g} \sim Bern(surviving_{i,t,g})$$
$$capture_{i,t,g} = Pc \times Data\_surviving_{i,t,g}$$
$$Data\_capture_{i,t,g} \sim Bern(capture_{i,t,g})$$
$$Ps_g \sim N(Ps,\sigma_s^2)I(0,1)$$
$$Ps \sim Beta(1,1)$$
$$Pc \sim Beta(1,1)$$

(2)

In the third model (M3), I ignored the impact of sexual dimorphism for *E. capsaeformis* on survival rate:

$$surviving_{i,t,g} = Ps^y \times Data\_surviving_{i,t-1,g}$$
$$Data\_surviving_{i,t,g} \sim Bern(surviving_{i,t,g})$$
$$capture_{i,t,g} = Pc_g \times Data\_surviving_{i,t,g}$$
$$Data\_capture_{i,t,g} \sim Bern(capture_{i,t,g})$$
$$Pc_g \sim N(Pc,\sigma_c^2)I(0,1)$$
$$Ps \sim Beta(1,1)$$
$$Pc \sim Beta(1,1)$$

(3)

In the fourth model (M4), I ignored the impact of sexual dimorphism for *E. capsaeformis* on both recapture and survival rates and the non-hierarchical model was structured as:

$$surviving_{i,t,g} = Ps^y \times Data\_surviving_{i,t-1,g}$$
$$Data\_surviving_{i,t,g} \sim Bern(surviving_{i,t,g})$$
$$capture_{i,t,g} = Pc \times Data\_surviving_{i,t,g}$$
$$Data\_capture_{i,t,g} \sim Bern(capture_{i,t,g})$$
$$Ps \sim Beta(1,1)$$
$$Pc \sim Beta(1,1)$$

(4)

According to the estimated results from the above three models, M2 yielded the lowest DIC value which indicated M2 gave the best fit of mark-recapture data of *E. capsaeformis*. Thus, the fifth model (M5) was developed to incorporate individual variability based on M2. M5 was written as:

$$surviving_{i,t,g} = Ps_{i,g}{}^{y} \times Data\_surviving_{i,t-1,g}$$

$$Data\_surviving_{i,t,g} \sim Bern(surviving_{i,t,g})$$

$$capture_{i,t,g} = Pc_{i} \times Data\_surviving_{i,t,g}$$

$$Data\_capture_{i,t,g} \sim Bern(capture_{i,t,g})$$

$$Ps_{i,g} \sim N(Ps_{g}, \sigma_{s,g}^{2})I(0,1)$$

$$Ps_{g} \sim N(Ps, \sigma_{s}^{2})I(0,1) \tag{5}$$

$$Pc_{i} \sim N(Pc, \sigma_{c}^{2})I(0,1)$$

$$Ps \sim Beta(1,1)$$

$$Pc \sim Beta(1,1)$$

Here, Ps_i is the survival rate of individual i. Pc_i is the recapture rate of individual i. By considering the individual variation, the corresponding parameters were assumed to come from some population distributions. Variability in $Ps_{i,g}$ and Pc_i among individuals were reflected in estimates of $\sigma_{s,g}^{2}$ and σ_{c}^{2}, respectively.

As *A. pectorosa* does not have obvious sexual dimorphism, sex-related variance was not considered for this species. Only M4 and M5 without sex differences were applied to estimate the demographic rates of *A. pectorosa* to test for the existence of individual variability.

As I described above, multilevel priors were used to address the problem of estimating survival and recapture rates and their associated uncertainty when incorporated with individual variations and sex differences. Bayesian approach is based on Bayes' theorem to combine the observed data with the information of prior distribution to produce the posterior distribution. Compared with the non-hierarchical model, Bayesian hierarchical model assigns priors of hyperparameters to yield the joint posterior distribution, which was written as (the posterior function of M1 was shown as an example):

$$p(\theta \mid Data\_capture)$$

$$= \frac{(\prod_{g}(\prod_{t}\prod_{i} f(Data\_capture_{i,t,g} \mid Ps_{g}, Pc_{g}))\pi(Ps_{g} \mid Ps, \sigma_{s})\pi(Pc_{g} \mid Pc, \sigma_{c}))\mu(Ps)\mu(Pc)\upsilon(\sigma_{s})\upsilon(\sigma_{c})}{\int (\prod_{g}(\prod_{t}\prod_{i} f(Data\_capture_{i,t,g} \mid Ps_{g}, Pc_{g}))\pi(Ps_{g} \mid Ps, \sigma_{s})\pi(Pc_{g} \mid Pc, \sigma_{c}))\mu(Ps)\mu(Pc)\upsilon(\sigma_{s})\upsilon(\sigma_{c})d\theta}$$

where θ represents parameters of interest. The $f(Data\_capture_{i,t,g} | Ps_g, Pc_g)$ is the probability density function of recapture data on the parameter vector Ps_g and Pc_g. The probability densities of Ps_g and Pc_g are conditional on Ps and σ_S and Pc and σ_C, respectively. The $\mu(Ps)$ and $\mu(Pc)$ are the probability density functions of Ps and Pc, respectively, and the $\upsilon(\sigma_S)$ and $\upsilon(\sigma_C)$ are the probability density function of σ_S and σ_C, respectively. As uniform prior distributions work better than inverse-gamma priors for variance when dealing with hierarchical models (Gelman, 2006), σ_S and σ_C were assumed to follow uniform distributions.

WinBUGS is a statistical software for conducting Bayesian analysis using Markov chain Monte Carlo (MCMC) methods (Spiegelhalter et al., 2004), and it was used in parameter estimation in this study. Three chains with different starting points were run to assess the convergence of the Markov chains. A burn-in of 100,000 iterations was used, and the next 900,000 iterations were thinned by taking every 250 iteration. Combining the three chains resulted in a sample of draws from the posterior distribution, which was used to make an inference. Deviance information criterion (DIC) was employed to select the most plausible model.

4.4 Results

The mark-recapture data analysis showed that M2 gave the lowest DIC (38.37) values for *E. capsaeformis*, and M4, the non-hierarchical model, had a slightly higher DIC value (55.72) than the best model (M2) (Table 4.1). In addition, M1, incorporating sex-related variability in both survival and recapture rates estimations, and M3 with sex-related variability in recapture rate estimations, yielded much higher DIC values (Table 4.1). The large difference in DIC values between the best model (M2) and the above three models (M1, M3 and M4) indicated sex-related variability in recapture rate was less significant than that in survival rate. The DIC value estimated by M5 (65.45) was higher than by M2, indicating that there is little individual variability in recapture and survival rates in this mark-recapture data analyses. For *A. pectorosa*, the non-hierarchical model (M4) had the lower DIC value (22.46) (Table 4.1), indicating this model performed better in fitting mark-recapture data for *A. pectorosa*. The difference between DIC values of the non-hierarchical model (M4) and hierarchical model (M5) was larger than 10,

which indicated that little individual variability was shown in recapture and survival rates in this mark-recapture data analyses.

The posterior medians of the survival rate by these five models for *E. capsaeformis* were higher than 74% and males showed much larger survival rate than females (Figure 4.2). From the results in M1, M2 and M5, the median survival rates for male *E. capsaeformis* were 94.4%, 93.9% and 87.5%, respectively, which were higher than the rates for females (74.4%, 75.3% and 75.0%) (Figure 4.2 a, b and d). The posterior medians of survival rate for *A. pectorosa* were higher than 91% in M4 and M5, which were 94.4% and 91.4%, respectively (Figure 4.3).

The median recapture rates for both male and female *E. capsaeformis* were higher than 93% (Figure 4.4). The median recapture rate for male *E. capsaeformis* in M1 was 93.1%, which was higher than for female *E. capsaeformis* (96.0%). In M3, the median recapture rate for male *E. capsaeformis* was similar to that for females, which was 93.6% (Figure 4.4 a and b). The posterior medians of the recapture rate for *A. pectorosa* were higher than 96%, which was larger than for *E. capsaeformis* (Figure 4.5). The median recapture rate estimated by the non-hierarchical model (M4) (97.8%) was larger than the hierarchical model considering individual variability (M5) (96.7%) (Figure 4.5). The credible intervals of the recapture rate in M4 were narrower than those by hierarchical model (M5) (Figure 4.5).

4.5 Discussion

Usually, the detectability of freshwater mussels is determined by species, substrate, water transparency, and time of year, etc. Villella et al. (2004) detected only 7–19% of *Elliptio complanata*, *E. fisheriana* and *Lampsilis cariosa* during the warmer periods of spring and summer and about 3% in the fall and winter. A previous study of PIT tags effectiveness with freshwater mussel recaptures showed the recapture rate of tagged mussels was 72-80% (Kurth et al., 2007). Higher recapture rates for *E. capsaeformis* and *A. pectorosa* (>93 % and >96%, respectively) were found in this study. The different recapture rates between these two PIT tag studies may be due to the choice of example species, habitat differences, or survey methods. Even considering these factors, the recapture rates using the PIT tag technique are higher than visual searches, suggesting that this technique can improve recapture efficiency greatly. Even in muddy rivers, PIT tagged mussels can be found with the reader and antenna. In addition, the

external PIT tags also provide a visual cue for surveyors to see tagged mussels in clear water. Several mussels could not be captured during the surveys, which may be due to tag loss or tag break down from severe abrasion, deep burial or emigration out of the original translocation area due to high stream flow discharges.

The efficiency and application of the PIT tag technique can be influenced by site locations and stream characteristics (Hill et al., 2006). The maximum effective depth of the antenna is limited and differs among sites (Kurth et al., 2007). Thus, some deeply buried mussels may not be detected due to limitation of the equipment. Further study should be taken to investigate the effective range of the antenna and help distinguish non-detected mussels due to equipment limitation from immigration. In addition, the initial cost for PIT tag kits should be considered in the experimental design. The PIT tags we used cost $6 each, but they work for a long period and reduce the requirement for mark-recapture studies. So despite its limitations, the PIT tag approach exhibits high recapture rate and provides a useful tool to monitor individual mussels, especially where visual searches are not practical for long-term monitoring.

The annual survival rates of tranlocated mussels were high in this study, especially for male *E. capsaeformis* and *A. pectorosa*. The survival rate for female *E. capsaeformis* was slightly lower than that for males, which may be due to the factor that female mussels spend a lot of energy to reproduce during spawning season and their mantle lures attracting host fishes increase the risk of being preyed on. The high survival rates of translocated *E. capsaeformis* and *A. pectorosa* at Cleveland Islands indicated that the habitat and water quality at this site are suitable for the two species to survive and grow. A previous study that calculated survival rate of *E. capsaeformis* in the Clinch River in Tennessee based on a catch-curve analysis of annual survey data showed the annual survival rate of this species was 0.32 ± 0.189 (Jones and Neves, 2011), which is much lower than the estimated survival rates in this mark-recapture study. One reason for this difference in survival rates may be that many of the mussels tranlocated in this mark-recapture survey were younger than those collected in the annual survey, which increased the annual survival rate of mussels since young mussels (1-5 years old) tend to have higher survival rate than adults (6-10 years old) (Jones and Neves, 2011). Hart et al. (2001) showed *Amblema plicata* has a high mean annual survival (>97%) in natural habitats based on mark-recapture methods, and *Elliptio complanata*, *E. fisheriana* and *Lampsilis cariosa* also have very

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high annual adult survival rates (>90%) estimated by mark-recapture analysis (Villella et al., 2004). Future studies should emphasize combining mark-recapture data with historical annual survey data to investigate how the collection or analyses method influences survival rate estimates for young and adult mussels.

As the mark-recapture survey was only performed for one year, the estimated survival rate is only for one year. The results may be biased due to some particular hydrological and biological conditions at Cleveland Islands. The survey duration is too short to be confident that both species would keep high recapture and survival rates in the future. I suggest continuing mark-recapture surveys at the site to monitor the tagged mussels to assess translocation success and improve survival estimates. The developed models and Bayesian approach could also be applied to other freshwater species or future mark-recapture analysis.

The non-hierarchical model (M4) had the lowest DIC value for *A. pectorosa* and M2 incorporating sex-related variability in survival provided the lowest DIC value for *E. capsaeformis*. However, the DIC values from M5 that considered individual variability were higher than those from the best models, respectively. The higher DIC values may be due to more parameters in the hierarchical models compared with non-hierarchical models with regard to small sample sizes (Jiao et al., 2010, 2011). With more mark-recapture data, the goodness of fit using the hierarchical model may be preferred because of parsimony in assessing model fit (Mulaik et al., 1989; Hu and Bentler, 1995; Jiao et al., 2010). Due to the small sample sizes in this study, the advantage of hierarchical models is not obvious. On the other hand, it is possible that there is little variability among these individuals in recapture and survival rates, which results in selecting the model without individual variability. According to the results, I recommend that the model with sex–related difference (if a species is obviously sexually dimorphic) in survival rate be applied to analyze mark- recapture data when sample sizes are small.

In conclusion, the high recapture rate in this mark-recapture study demonstrated that the PIT tag technique can provide an efficient monitoring approach in this one-year survey, which could improve the accuracy of survival estimation. The technique can be used to track the characteristics of individuals to improve the understanding of freshwater mussel life history, especially for endangered species, such as purple bean (*Villosa perpurpurea*), Cumberlandian

Combshell (*Epioblasma brevidens*), Rough rabbitsfoot (*Quadrula cylindrica strigillata*) and other species. Furthermore, it can be used to track survival of translocated mussels and assess the overall success of translocation strategies in mussel conservation to provide managers with an idea of how effective translocation is at different selected sites. One of the advantages of the Bayesian approach is that it allows for prior distributions of parameters and the flexibility to deal with many assumptions. Other assumptions, such as whether the recapture and survival rates were influenced by season, temperature, flow, shell length, etc., can also be tested as more mark-recapture data become available for mussels.

4.6 Acknowledgements

4.7 References

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Table 4.1. Model comparison values derived from the deviance information criterion for *Epioblasma capsaeformis* and *Actinonaias pectorosa* estimated by M1 incorporating sex-related variability in recapture and survival rates, M2 incorporating sex-related variability in survival rate, M3 incorporating sex-related variability in recapture rate, M4 non-hierarchical model and M5 incorporating individual variability based on M2.

Model	Species	
	E. capsaeformis	A. pectorosa
M1	67.95	-
M2	38.37	-
M3	61.25	-
M4	55.72	22.46
M5	65.45	40.09

Only M4 and M5 that just considered individual variability were applied to *A. pectorosa* because this species does not have obvious sexual dimorphism.

Figure 4.1. Recapture tree of possibilities for two recaptures of an imaginary individual. It indicates the survival of tagged mussels was conditional on the survival or death of mussels in the last recapture and the capture or sighting for tagged mussels was conditional on the survival or death of mussels.

Released individual mussel after tagging

Individual

Survival   Death

1st recapture

Captured   Not captured   Captured   Not captured

Survival   Death   Survival   Death   Death

2nd recapture
⋮

Captured Not captured Captured Not captured Captured Not captured Captured Not captured Captured Not captured
⋮   ⋮   ⋮   ⋮   ⋮   ⋮   ⋮
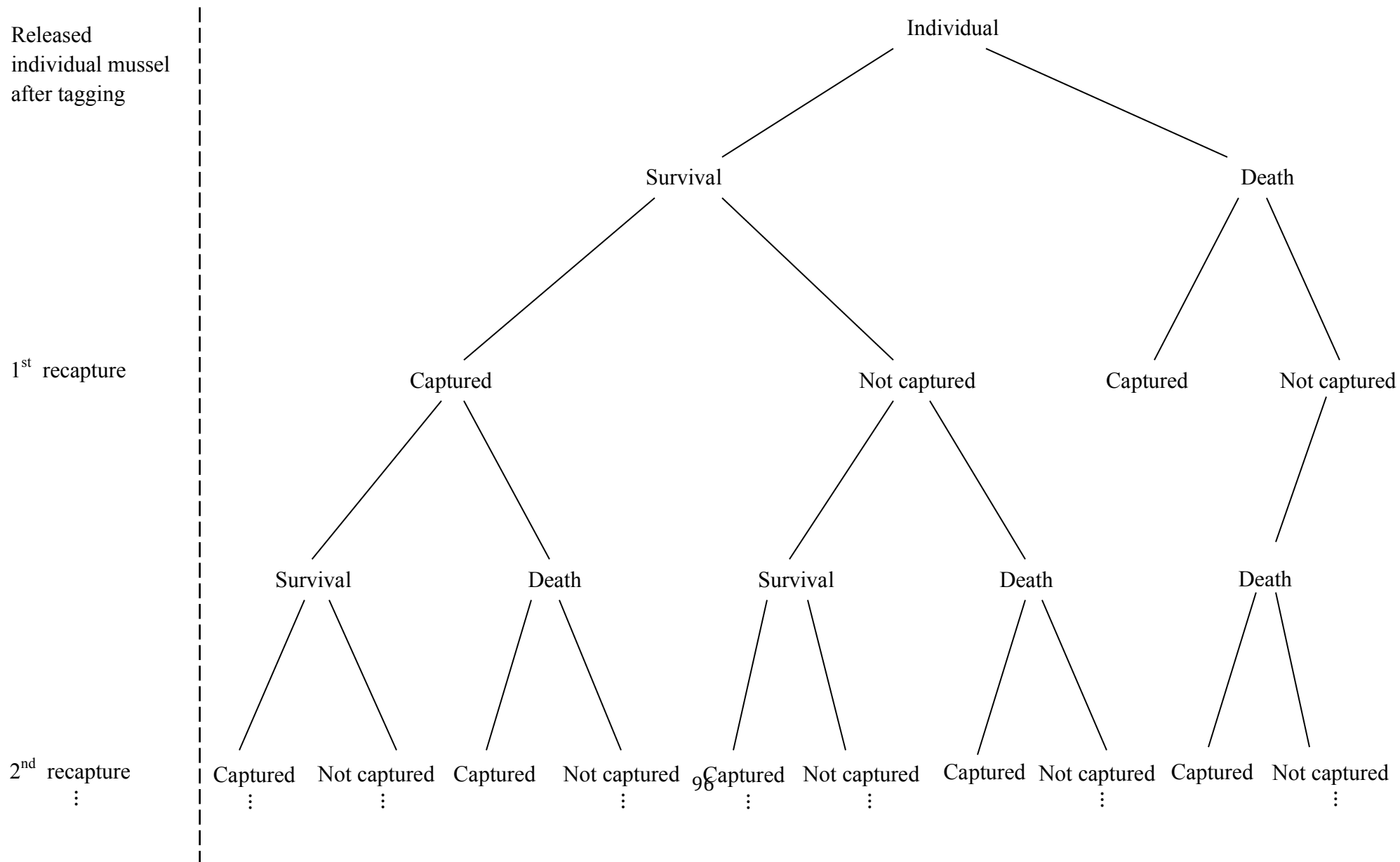
96

Figure 4.2. Estimated survival rate of *Epioblasma capsaeformis*. The survival rate is referred to as the possibility of the survival of mussels: (a) survival rates for males and females estimated by a model considering sex-related differences in both survival and recapture (M1); (b) survival rates for males and females estimated by a model considering sex-related differences in survival (M2); (c) survival rate of *E. capsaeformis* estimated by a non-hierarchical model (M4); (d) survival rate of *E. capsaeformis* estimated by a model considering individual differences (M5).
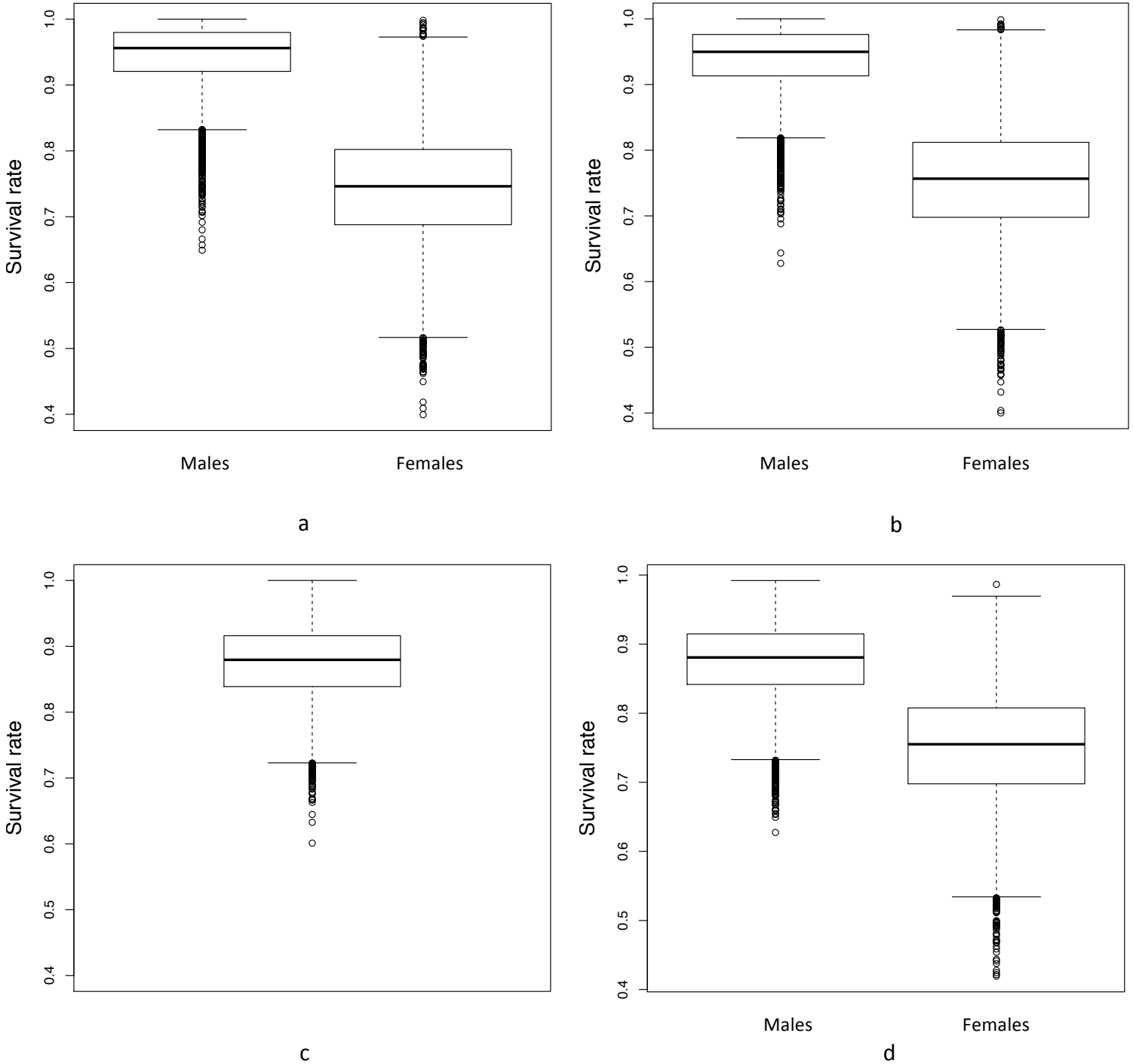

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Figure 4.3. Estimated survival rate of *Actinonaias pectorosa*: (a) survival rates for *A. pectorosa* estimated by a non-hierarchical model (M4); (b) survival rate of *A. pectorosa* estimated by a model considering individual differences (M5).
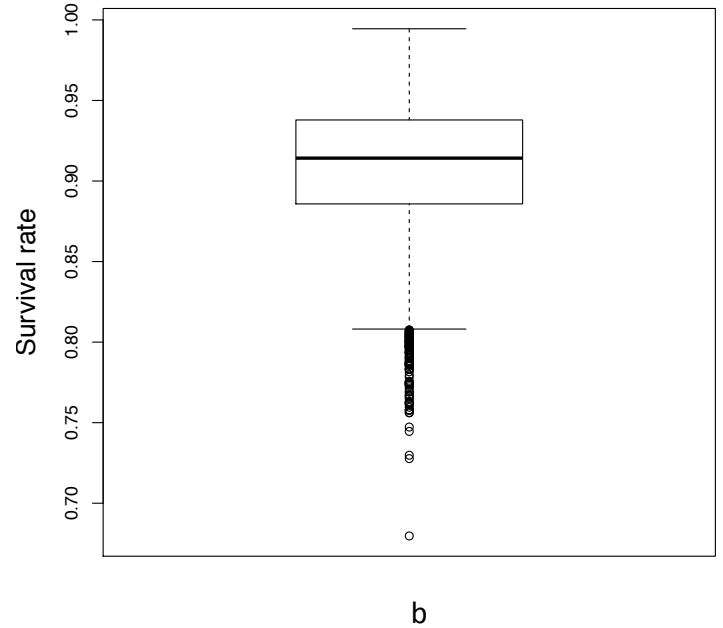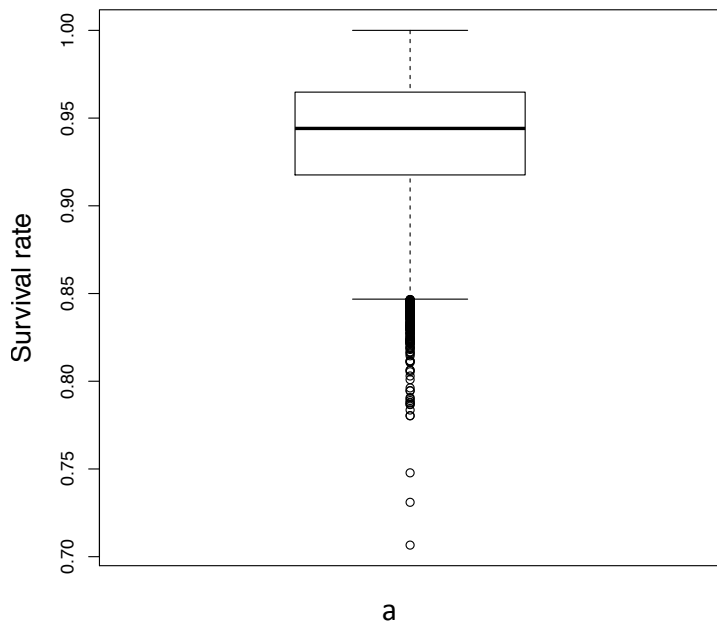
Figure 4.4. Estimated recapture rate of *Epioblasma capsaeformis*. The recapture rate is referred to as the possibility of the recapture of mussels: (a) recapture rates for males and females estimated by a model considering sex-related differences in both survival and recapture (M1); (b) recapture rates for males and females estimated by a model considering sex-related differences in recapture (M3); (c) recapture rate of *E. capsaeformis* estimated by a non-hierarchical model (M4); (d) recapture rate of *E. capsaeformis* estimated by a model considering individual differences (M5).
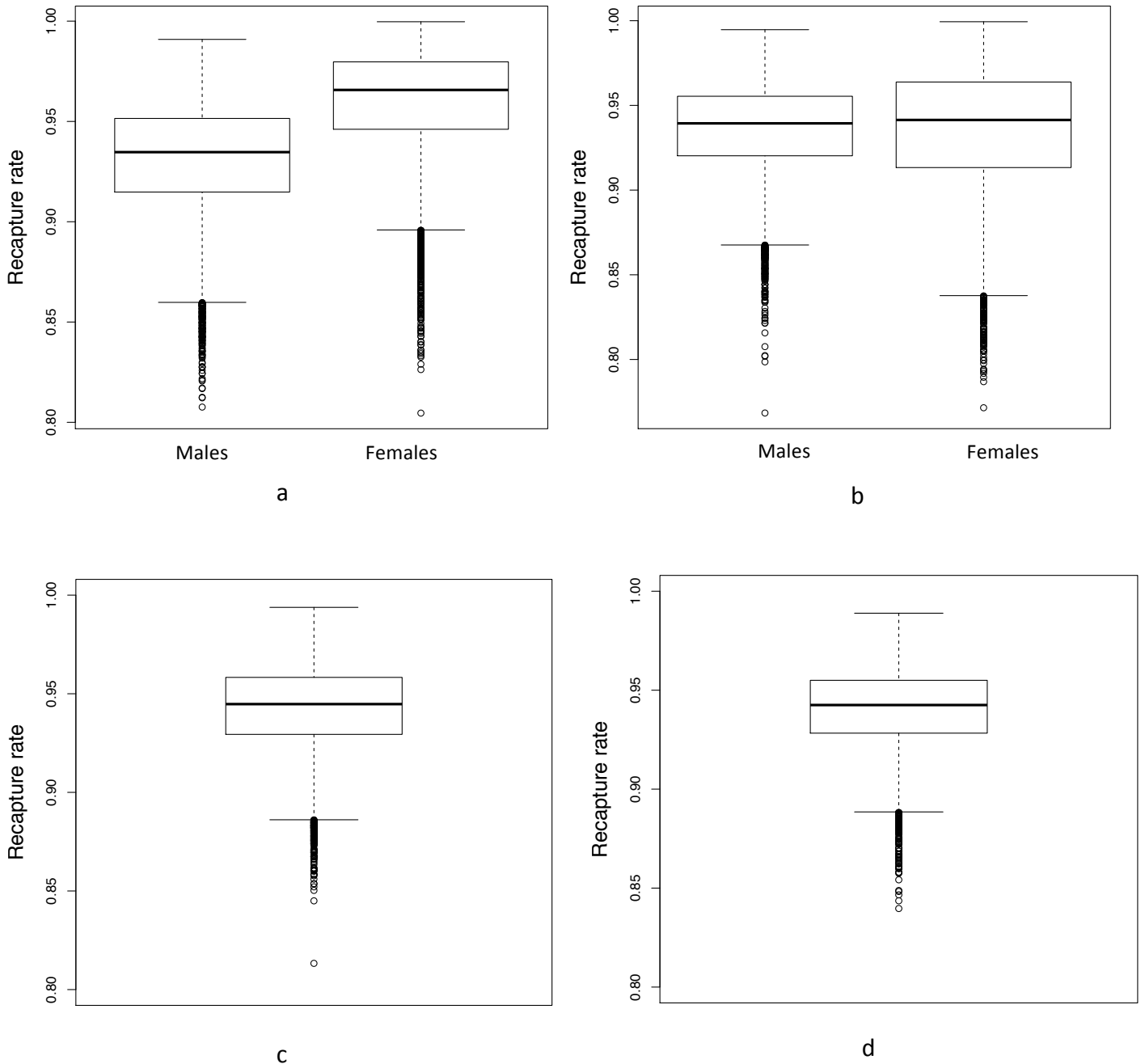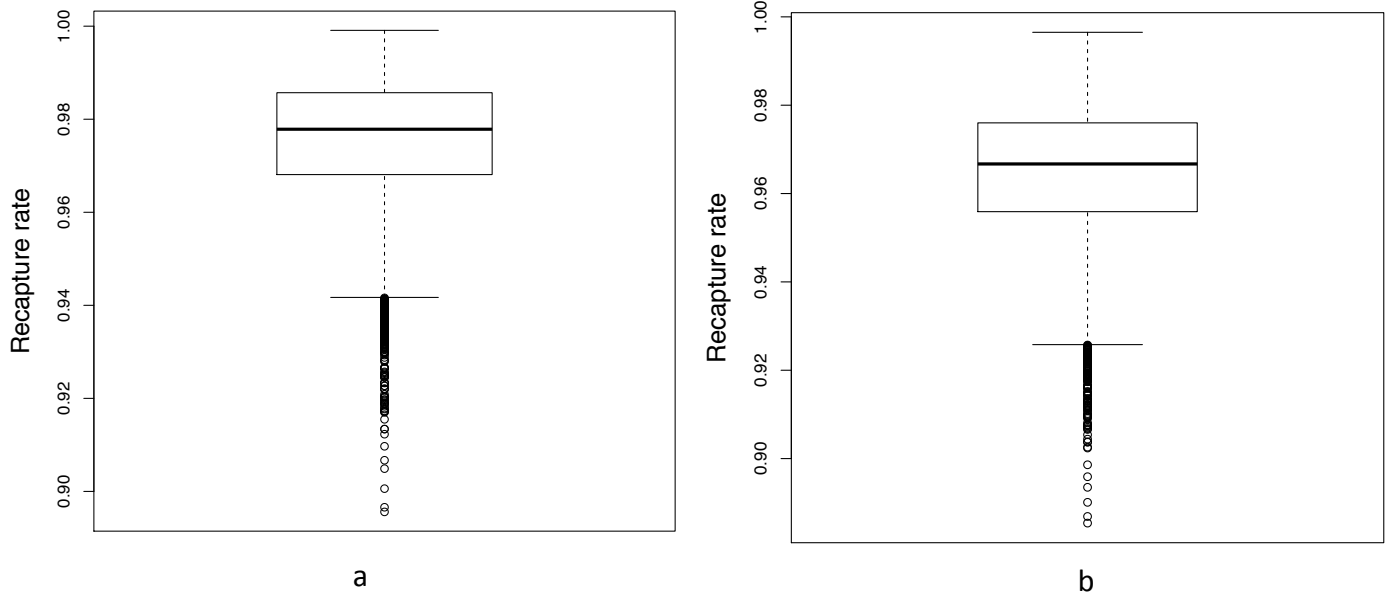
Figure 4.5. Estimated reapture rate of *Actinonaias pectorosa*: (a) recapture rates for *A. pectorosa* estimated by a non-hierarchical model (M4); (b) recapture rate of *A. pectorosa* estimated by a model considering individual differences (M5).

Chapter 5

General conclusions

In this study, I explored the population dynamics of *Epioblasma capsaeformis* (endangered species) and performed risk assessment to evaluate alternative restoration strategies. I also conducted a mark-recapture study for *E. capsaeformis* and *Actinonaias pectorosa* (species of special concern) by using passive integrated transponder (PIT) technique. Hierarchical models were developed to estimate the growth and recapture and survival rates of these two species. The results from population dynamics modeling showed the natural mortality rate of young mussels for *E. capsaeformis* were less than that of adults among theses investigated three sites. The populations of *E. capsaeformis* at Wallen Bend and Swan Island were at greater risk of decrease compared with that at Frost Ford. In the mark-recapture study, incorporation of individual and sex-related variability is recommend in the estimation of individual growth of freshwater mussels, especially when the percentage of multiple recaptures is high. The high survival rates for both species indicated the habitat at Cleveland Islands is suitable for these two mussel species within the survey duration. The high recapture rates (>93% for *E. capsaeformis* and >96% for *A. pectorosa*) proved that the PIT tag technique provided an efficient monitoring approach in mark-recapture survey.

This study helps improve our understanding of the life history and management of freshwater mussels. The higher natural mortality of adult of *E. capsaeformis* suggests that adult mussels are more sensitive to abiotic and biotic factors, such as river discharges and predators. The estimated growth rates show the different characteristics of each species and between sexes, which is very important in species conservation because it shows adaptation to the environment, evolutionary optimization and constraints in organisms. The risk assessment indicated that the restoration strategies that released adult mussels could increase population size the quickest. In future studies, the costs and risks associated with rearing mussels to larger sizes at a hatchery should also be considered. In the evaluation of translocation strategies, the PIT tag technique has been shown to have a high recapture for freshwater mussels, which can help improve the accuracy of survival estimates, which suggests using these mark-recapture studies in the future. Continuing mark-recapture surveys should be conducted to monitor tagged mussels to assess

translocation success and improve survival estimates at Cleveland Islands and other sites in the river.

Bayesian statistics offers a framework to analyze complex models and in risk analysis in this study. This method provides a useful approach for biologists and managers to explore population dynamics and assess a range of possible restoration strategies for endangered mussel species. The hierarchical Bayesian modeling approach is suggested for future mark-recapture data analysis or mark-recapture study for other species to explore the growth, recapture and survival. Continued monitoring of theses two species is suggested to advance the understanding of population dynamics. Additional data will help update the results of population dynamics analysis through a Bayesian approach and strengthen the risk assessment of recommended restoration strategies.