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Estimating Survival and Recruitment in a Freshwater Mussel Population Using Mark-recapture Techniques

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Abstract.—We used a mark-recapture method and model averaging to estimate apparent survival, recruitment and rate of population growth in a native freshwater mussel population at a site on the Cacapon River, which is a tributary to the Potomac River. Over 2200 *Elliptio complanata, E. fisheriana* and *Lampsilis cariosa* were uniquely tagged over a period of 4 y. Recapture probabilities were higher in spring and summer than in winter except for *L. cariosa* which had a low probability of recapture regardless of time of year. All three species had high annual adult survival rates (>90%) with lower estimated survival of small (≤55 mm) mussels (43%–69%). The variation in apparent survival over time was similar for all three species. This suggests that whatever environmental variables affect survival of mussels in this site affected all three species the same. Recruitment rates were low (1–4%) for both *E. complanata* and *L. cariosa,* with *E. fisheriana* having several periods of high (15–23%) recruitment. Distribution within the site was affected by both downstream and upstream movement, though movement rates were generally <1%. Average population growth rates for *E. complanata* ($\lambda = 0.996$, SE = 0.053), *L. cariosa* ($\lambda = 0.993$, SE = 0.076) and *E. fisheriana* ($\lambda = 1.084$, SE = 0.276) indicated static populations. Population growth rate approximating 1.0 suggests this site supports a stable freshwater mussel population through a life history strategy of low but constant recruitment and high annual adult survival.

Introduction

Unionid mussels are one of the most imperiled fauna in the world (Williams *et al.*, 199 Ricciardi and Rasmussen, 1999) with populations continuing to decline accompanied a growing concern for the loss of species. The decline in many populations can be linked development associated with expanding human populations which often leads to extensi habitat alteration and destruction that continue to impact North America's freshwat fauna. Attempts to address the cause of these declines is often limited by insufficie knowledge of the ecology of unionid populations. Consequently, monitoring freshwat mussel populations has begun to receive increasing emphasis. The objective of monitori is often to detect differences in the life history traits between species within a population, differences between populations over space and time, with the assumption that the differences may indicate a change in overall fitness as reflected in changes in recruitme and survival (Manly, 1985). The important dynamics in populations, such as recruitme and survival, are usually dependent on natural processes that vary across time. Therefor monitoring of unionid populations is a long-term commitment to detect real changes population parameters. While basic life history of unionid mussels has been studied sin the early 1900s, rates of recruitment, survival and movement have not been we documented. Because these factors influence the rate of population change, our ability evaluate population viability is limited.

Measuring survival rates in populations is often difficult and complex, with the probabili of survival varying not only with individual characteristics, such as age, but with biotic ar abiotic environmental variables as well. Estimating survival rates and testing hypothes pertaining to survival are vital not only to understanding population dynamics but developing effective management and conservation efforts. These population paramete

can often only be determined in the field from the study of uniquely marked individu followed over time. Use of marked individuals and mark-recapture models are commo used for population monitoring and risk assessment in many biological populatic (Pollock *et al.*, 1990; Lebreton *et al.*, 1992; Anderson *et al.*, 1995; Schwarz and Seber, 199 but have rarely been used to assess mussel populations (*see* Anthony *et al.*, 2001; Hart *et* 2001; Rogers *et al.*, 2001). Mark-recapture studies typically involve repeated sampling a target population allowing for recognition of uniquely marked individuals previou sampled. A variety of marking techniques exist for uniquely identifying animals (Seb 1992) that allow us to analyze the specific capture history and movements of each individ animal. Each animal is marked when sampled for the first time, released back into th habitat and then has a chance of being recaptured on subsequent sampling occasions. (each sampling occasion the numbers of marked and unmarked animals are recorded. T marked animals are followed over time to estimate survival and capture probabilit (Cormack, 1964) and the ratio of marked to unmarked animals is used to estimate numb of new recruits to the population (Burnham *et al.*, 1987). The unifying characteristic multiple release mark-recapture data is there are known releases in separate independe cohorts. Animals in these cohorts are then subject to a survival process about whi biologists wish to make inferences. The released cohorts are the samples and the resulti multiple counts of live animals provide the basis for inferences about the survival proce

Parameters in mark-recapture models (*e.g.*, recapture rate, survival rate) are estimated finding the rate that minimizes the difference between the observed recapture values a the recaptures as predicted by the models. There are a number of assumptions for prop application of mark-recapture models. Some of the assumptions depend on the stu design, such as the tagging, capture and recapture procedures. For example, it is import that tags are not lost or become illegible, recaptures must be recorded accurately, taggi and handling must not affect the survival or capture of animals and tagged animals must representative of the target population. Other assumptions depend on the behavio characteristics of the animals. For example, the fate of one tagged animal must not linked to the fate of others. Violations of these assumptions can bias estimates to varyi degrees (Carothers 1973, 1979; Pollock *et al.*, 1990). For example, because unionids a long-lived, it is important the marking method that is used is durable and is not susceptil to high tag loss which can negatively bias parameter estimates. Our objective was to descri the dynamics of a freshwater mussel population under natural conditions. We used ma recapture models for populations open to recruitment, mortality and migration determine apparent survival rates, recapture probabilities, recruitment, movement a rates of population change. We believed these methods would be useful not only evaluating population dynamics, but in risk assessment, specifically where there is a need evaluate the effects of a site specific disturbance on changes in mussel populations.

METHODS

Study site.—We chose a long-term monitoring site on the Cacapon River, a 5th order tribut in the upper Potomac River drainage in eastern West Virginia. The river is approximately 1 km in length and lies within the Ridge and Valley physiographic province. Approximately 7 of the basin is forested, but disturbance from agriculture and increasing development in t watershed is a primary concern. The study reach was located at Davis Ford (River Kilomet RKM 94) and was 240 m long with an average width of 35 m. We marked the reach into 12 2 long bands that extended bank to bank. The upper bands were mostly pool habitat with ar of run, the middle bands were a long riffle and the lower bands were primarily run habit

Bands were labeled A through L, with A being the uppermost band and L designating t downstream band at the bottom of the study area.

Field methods.—Prior to initiating the study we evaluated various types of tags a adhesives. Long-term tag retention, legibility and short drying times were the main factors deciding which tags and adhesives we would use. The combination of shellfish tag (Hallpr Inc., Holden Hill, New South Wales, Australia) and cyanoacrylate (Krazy Glue, Borden, Ir Columbus, OH) was found to provide a good long-term marking method (Lemarie *et* 2000). Based on the tag evaluation study, animals were kept out of the water a minimum c min after tagging to allow time for the glue to dry. Survey and tagging was initiated in J 1996 with seasonal sampling and tagging occurring in January, April, June and Octol 1997. Beginning in July 1998 we sampled and tagged mussels annually during the sumn when most animals are likely to be available at the substrate surface. For each sampli occasion all untagged animals were tagged and tag numbers were recorded for previou tagged animals.

We conducted timed searches within each of the 12 bands by snorkeling to cover t entire area. We attempted to equalize sampling effort among bands by limiting the sear time within bands to one person hour. All animals seen at the substrate surface w collected and a uniquely coded tag applied to both valves to minimize losing informati due to tag loss. Double tagging can be used to estimate tag loss for adjusting model estima (Seber, 1982:94). We recorded species, length in mm, left and right valve tag numbers, ba number in which the animals were collected and time spent sampling. All animals were th returned to the bands where they were collected.

We used an enclosure study to evaluate potential tag induced mortality. A total of animals (30 tagged and 30 untagged) was randomly assigned to four enclosures plac immediately downstream of the study site. The enclosures were checked several tin during years one and two of the study. The number of live and dead animals, species and numbers were recorded.

Data analysis.—Analysis involved choosing a set of candidate models testing the fit of t models to the data and model averaging to estimate population parameters. We used t software program MARK (White and Burnham, 1999) which provides parameter estima and associated standard errors for models developed from data on the encounter historie marked animals. To estimate apparent survival and recapture probabilities, we used t Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965; Brownie, 19 Pollock *et al.*, 1990) for open populations, selecting models on the basis of the parsimo criteria and biological significance (Lebreton *et al.*, 1992). Apparent survival (S) is definec the probability of surviving between successive sampling occasions given that the animal l not permanently emigrated from the site. The recapture rate (p) is the probability of an anir being seen on a sampling occasion given that it is alive. Since we expected apparent surviva vary by species and over time, we included models with both a group (species) and time eff to evaluate the importance of these variables on survival (g and t, respectively). To evalu survival rates for small vs. large animals we used the design matrix to construct models wh apparent survival is estimated conditioned on size (length) of individual animals as a covaria

The multi-strata model (based on Brownie *et al.*, 1993 and Hestbeck *et al.*, 1991) was us to estimate the rate of upstream and downstream movement of animals between ban Evaluating movement of animals required combining the 20 m bands into 40 m wide ban due to several bands having insufficient recaptures. We did not expect adult freshwa mussels to have an unlimited ability to move great distances in an upstream directi therefore, we constructed models where we fixed the distance animals could move in upstream direction.

We used models developed by Pradel (1996) to estimate recruitment (f) and the finii rate of population change (λ), where λ is the population size at time $i+1$ divided by th population size at the initial time i. Recruitment is the number of new animals (from bot reproduction and immigration) of a minimum detectable size in the population at time per animal in the population at time $t-1$. Our data indicated the minimum detectable siz at the substrate surface is 20 mm. We were interested in whether the population wa increasing ($\lambda > 1$), stationary ($\lambda = 1$), or decreasing ($\lambda < 1$). The additional assumption tha the size of the study site remains unchanged must be met for estimating rate of populatio change. Having unequal time intervals between sampling occasions (seasonal versu annual), we annualized the time intervals prior to running the models to make the rates c survival, movement, recruitment and population change for each of the interva comparable.

To evaluate the fit of our set of models to the data we used a parametric bootstra Goodness-of-Fit (GOF) test on the most general model, *i.e.*, the model with the mo parameters. If the structure of the general model adequately fit the data, then subsequer models that are constraints of the general model can be derived. These bootstra simulations also provide an estimate of the over-dispersion parameter ($\hat{c}$) calculated as th observed deviance divided by the average of the simulated deviances ($\hat{c} = 1$ if the model fi perfectly). The Akaike Information Criteria (AIC_c) for small sample sizes was used to ran the candidate models relative to each other (Burnham and Anderson, 1998:46) and th ΔAIC_c, or difference between the model AIC_c values, was used for calculating the AIC weights. The better the model fit relative to the number of model parameters, the smalle the AIC_c and the larger the value of the AIC_c weight (w_i). Burnham and Anderson (199E provide a framework for using the ΔAIC_c values to rank models from best to worst. Mode with ΔAIC_c between seven and 10 should be considered plausible with models havin $\Delta AIC_c \leq 2$ given the greatest support. There often is not one best model for describin the variation in the data. Instead, several similar models may be essentially equal fc describing the data, resulting in parameter estimates having an additional component c uncertainty, *i.e.*, uncertainty associated with sampling plus uncertainty due to mode selection. Model averaging as presented in Burnham and Anderson (1998) was used t arrive at our estimates, where parameter estimates were weighted across a set of the be ranked models, allowing model selection uncertainty to be incorporated as a component c variance. Model averaging also reduces bias in the parameter estimates, especially whe there are a number of models with similar AIC_c values.

RESULTS

The mussel assemblage consisted of seven species, including *Elliptio complanata* (Ligh foot), *E. fisheriana* (Lea), *Strophitus undulatus* (Say), *Alasmidonta varicosa* (Lamarck), *A undulata* (Say), *Lasmigona subviridis* (Conrad) and *Lampsilis cariosa*. *Elliptio complanata* was th dominant species. We identified all *Lampsilis* as *L. cariosa* though there is some question as t which species is found in the upper Potomac River basin. It is uncertain whether *L. cardiu* (Rafinesque), a species introduced into the upper Potomac River, has supplanted *L. carios* (Say) or whether they have hybridized. Similarity in coloration and morphology has led t taxonomic questions that necessitate a more accurate means of identification.

Data were collected from July 1996 through June 2000 representing eight samplin occasions. Number of animals sufficient to model survival rates were collected for three c the seven species; *Elliptio complanata*, *E. fisheriana* and *Lampsilis cariosa*. Of these three specie a total of 2251 animals were tagged with the majority (85%) being *E. complanata*. We tagge 1909 *E. complanata*, of which 504 were seen again, with 158 of those being multipl

TABLE 1.—Data array of observed recaptures for three species, where i = time of release, j = t period of recapture, $R(i)$ = the number of individuals captured in time i and released with tags back the population (referred to as a cohort), $m(i,j)$ = the number of tagged individuals captured for the time during interval j from the cohort released at time i, $r(i)$ = the total number of the $R(i)$ ind uals released that are captured again, $m(j)$ = the total number of marked individuals capture the jth sample, and $z(j)$ = the total number of captures at intervals $j+1, \ldots, k$ from releases in coh $R_1, \ldots, R_{j-1}$

		Observed recaptures for *Elliptio complanta* $m(i,j)$						
Time i	$R(i)$	j = 1/97	4/97	6/97	10/97	7/98	7/99	6/00
7/96	515	10	24	54	8	26	37	34
1/97	48		8	8	1	2	2	1
4/97	254			50	10	24	22	16
6/97	451				11	50	59	34
10/97	75					7	8	8
7/98	299						52	35
7/99	436							61
$m(j)$		10	32	112	30	109	180	189
$z(j)$		183	173	183	307	221	128	0

		Observed recaptures for *Elliptio fisheriana* $m(i,j)$						
Time i	$R(i)$	j = 1/97	4/97	6/97	10/97	7/98	7/99	6/00
7/96	47	1	0	6	1	1	4	1
1/97	4		0	0	1	1	1	0
4/97	14			4	1	1	2	1
6/97	43				2	3	4	5
10/97	14					0	5	0
7/98	30						5	2
7/99	75							7
$m(j)$		1	0	10	5	6	21	16
$z(j)$		13	16	15	24	23	9	0

		Observed recaptures for *Lampsilis cariosa* $m(i,j)$						
Time i	$R(i)$	j = 1/97	4/97	6/97	10/97	7/98	7/99	6/00
7/96	30	1	0	0	0	0	3	4
1/97	4		0	0	0	0	1	0
4/97	11			2	0	0	2	0
6/97	26				0	1	3	4
10/97	11					1	1	1
7/98	18						0	4
7/99	27							4
$m(j)$		1	0	2	0	2	10	17
$z(j)$		7	8	10	18	19	13	0

recaptures. A total of 206 *E. fisheriana* and 136 *L. cariosa* were tagged with 50 and 30 be recaptured, respectively. *Lampsilis cariosa* had the lowest number of multiple recaptures. complete data array of observed recaptures is presented in Table 1. Using the data fo *complanata* to demonstrate, 515 marked animals were released July 1996 with 10 mar animals recaptured for the first time in January 1997, 24 in April, 54 in June and October, 26 in July 1998, 37 in July 1999 and 34 in June 2000 for a total of 193 recaptu from that cohort. The 48 animals in R_2 (Time 1/97) represent animals released that v

TABLE 2.—Statistics for the candidate set of live-recapture models

Model[a]	ΔAIC_c	np	AIC Weight
S(g + t) *p*(t)	0.00	11	0.36867
S(t) *p*(g + t)	1.33	11	0.18941
S(t)*p*(t)	1.71	11	0.15703
S(g*t)*p*(t)	3.02	13	0.08144
S(g + t)*p*(g + t)	3.81	13	0.05478
S(g + t)*p*(g*t)	4.78	17	0.03387
S(t)*p*(g*t)	4.90	17	0.03177
S(·)*p*(t)	5.55	8	0.02294
S(g*t)*p*(g*t)	5.56	18	0.02284
S(·)*p*(g + t)	6.96	9	0.01136
S(g)*p*(t)	7.21	9	0.01001
S(·)*p*(g*t)	8.35	14	0.00567
S(g)*p*(g + t)	8.98	10	0.00415
S(g*t)*p*(g + t)	9.06	16	0.00397

[a] *S*() and *p*() indicate survival and recapture parameters are functions of the factors in parenthe The letters g and t represent species and time effects. If group or time effects are not specified (·), tl the parameters are assumed to be constant. When the parameters are a function of group and ti simultaneously, these factors can then interact fully (g*t) or the effects can be additive (g + t). np is number of parameters estimated

a mix of 38 individuals initially tagged in January 1997, plus 10 previously tagged anim that were recaptured on this sampling occasion. The highest numbers of animals releas and/or captured occurred during the summer sampling occasions, with greater inciden of recaptures coinciding with increasing number of sampling occasions. Although the low number of individuals captured and tagged was during the second (winter) sampli occasion, almost 50% of those animals were seen again.

Apparent survival estimates.—One thousand bootstrap simulations indicated no obvious la of fit of the general model ($P > 0.10$) with only minor over-dispersion ($\hat{c} = 1.35$). A total of live recapture models were fit to the data; of these, 14 had a $\Delta AIC_c < 10$ (Table 2) indicati several of the models were nearly equal in describing the data. We averaged model paramet across the 14 best fitting models and found that 72% of the weighting came from the top thı models. Apparent survival varied over time (94% of the weight came from models witl varying with time) as did recapture probabilities. Survival varied less by species (24% of t weight came from models with species-specific *S*), though the top model did indicate spec was important in evaluating differences in apparent survival rates. This species effect v evident in the apparent survival estimate for the interval between the first and second sampli occasion (July to January) (Table 3). *Elliptio fisheriana* had lower estimated survival (0.50, s 0.22) than *E. complanata* (0.58, SE=0.20) and *L. cariosa* (0.62, SE=0.24). Estimated annual ad survival over the 4 y ranged between 0.50 and 0.99. The highest standard errors of the appar survival estimates were associated with the January sampling occasion, indicating a lack precision in the survival estimate due to the low recapture probabilities. Apparent survival all three species increased between the second and third sampling interval (81% survival both *Elliptio* species and 77% for *L. cariosa*) then remained high and fairly constant (99%), w a slight decrease (86–89%) between the fifth and sixth sampling occasion. The overall patte in apparent survival was the same for all three species with a constant and parallel difference the apparent survival estimates among species.

TABLE 3.—Model-averaged estimates of apparent survival (*S*) and recapture probability (*p*). Appare survival pertains to the interval between sampling occasions and recapture probability pertains a single sampling occasion

	E. complanata			*E. fisheriana*			*Lampsilis cariosa*		
Time	*S*	SE	95% CI	*S*	SE	95% CI	*S*	SE	95% CI
7/96–1/97	0.58	0.204	(0.19, 0.97)	0.50	0.221	(0.07, 0.93)	0.62	0.236	(0.16, 1.08)
1/97–4/97	0.81	0.342	(0.14, 1.48)	0.81	0.394	(0.04, 1.58)	0.77	0.329	(0.13, 1.41)
4/97–7/97	0.99	0.037	(0.92, 1.06)	0.99	0.039	(0.91, 1.07)	0.99	0.018	(0.96, 1.03)
7/97–10/97	0.99	0.027	(0.94, 1.04)	0.99	0.039	(0.91, 1.07)	0.99	0.046	(0.90, 1.08)
10/97–7/98	0.86	0.099	(0.67, 1.05)	0.86	0.131	(0.60, 1.11)	0.89	0.115	(0.67, 1.12)
7/98–7/99	0.99	0.056	(0.88, 1.09)	0.99	0.018	(0.96, 1.02)	0.99	0.018	(0.96, 1.02)
	E. complanata			*E. fisheriana*			*Lampsilis cariosa*		
Time	*p*	SE	95% CI	*p*	SE	95% CI	*p*	SE	95% CI
1/97	0.03	0.021	(0.01, 0.07)	0.03	0.015	(0.00, 0.06)	0.02	0.026	(0.00, 0.07)
4/97	0.07	0.016	(0.04, 0.10)	0.06	0.027	(0.01, 0.11)	0.03	0.020	(0.00, 0.07)
7/97	0.18	0.020	(0.14, 0.22)	0.19	0.036	(0.12, 0.26)	0.08	0.041	(0.00, 0.16)
10/97	0.03	0.007	(0.02, 0.04)	0.04	0.015	(0.01, 0.07)	0.01	0.001	(0.008, 0.01
7/98	0.12	0.016	(0.09, 0.15)	0.11	0.025	(0.07, 0.16)	0.05	0.026	(0.01, 0.10)
7/99	0.17	0.020	(0.13, 0.21)	0.18	0.030	(0.12, 0.24)	0.10	0.039	(0.02, 0.18)

The enclosure data indicated the lower survival rate between the first and second sampli occasion was not due to higher mortality from tagging nor did tagging affect mortali Mortality in tagged and untagged individuals was the same (2%) after 1 y. Mortality increas to 12% after 2 y, with 4% mortality in tagged animals vs. 8% in untagged animals.

Recapture probabilities varied with time and species. Recapture probabilities show seasonal variability with highest recapture rates (7–19%) occurring during the warm periods of spring and summer and averaging about 3% in the fall and winter. *Lamps cariosa* had the lowest estimated recapture rates regardless of time of year.

We looked at annual and monthly stream flow from 1996 through 2000. The mean annu stream flow for the year 1996 was approximately 10% above the 74 year mean stream flow 581 ft^3/s, 1997 was below the long-term annual mean, 1998 was a high water year and strea flow for 1999 and 2000 was below normal (Table 4), with mean annual flow for 19 approximately half of the long-term mean. Of note were the extreme high flows during the f and winter of 1996 and the first half of 1998, corresponding with the low survival and recaptu estimates over the fall-winter 1996 and the lower survival estimate over late winter to spri 1998. These high flows could have influenced the recapture rate estimate in the summer 19 sampling occasion, which was lower than the summer 1997 and 1999 recapture estimates.

Apparent survival with size as a covariate.—We averaged model parameters over the five b models to estimate apparent survival based on size of individual animals. Small animals of three species had lower estimated apparent survival with survival rate increasing with s (Fig. 1). A species effect was evident (67% of the weight came from models with *S* havi a species effect), with *Elliptio fisheriana* having the lowest estimated rate of survival for sm individuals, 43% for animals 20 mm in size versus 69% for *E. complanata* and 57% *Lampsilis cariosa* of the same size. Difference in apparent survival among species was evide for animals between 20 and 55 mm in length with survival estimates becoming more simi with increasing size. *Elliptio complanata* $\geq$ 55 mm and *E. fisheriana* $\geq$ 75 mm in length h apparent survival rates >90%. *Lampsilis cariosa* $\geq$ 65 mm had apparent survival rate $\geq$90

TABLE 4.—Monthly streamflow statistics for the Cacapon River. The gage is located at Great Cacap downstream of Davis Ford near the mouth to the Potomac River. The 74 year annual mean streamflo 581 ft^3/s, and the mean of monthly flows is based on data collected from 1923 through 2000

	Mean monthly streamflow in ft^3/s												Mean ann
Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	stream fl
1996	1166	381	497	358	725	386	351	198	61.7	851	1252	1486	643
1997	478	709	1452	462	307	521	118	94.5	91.1	99.2	1026	272	469
1998	1751	3234	2113	1406	1261	516	162	117	73.9		88.3	90.5	983
1999	300	169	791	550	209	72.5	53.8	56.7	198	343	179	430	279
2000	157	661	852	633	304	242	105	444	281				409
Mean	643	894	1286	1110	855	427	192	232	176	333	369	516	

Pradel's models.—We fit 59 candidate models for estimating recruitment rate (f); of the: 13 had a $\Delta AIC_c < 10$. We model averaged to arrive at our parameter estimate and fou that 82% of the weighting came from the top four models. The most likely models i estimating the rate of recruitment indicated a strong species effect (98% of the weight ca from models with f varying with species). Recruitment also varied over time (85% of t weight came from models with f having a time effect) with the top two models indicating additive effect of group and time [71% weight for the f(g + t) model parameter] i evaluating differences in recruitment rates. The species effect reflects the recruitme estimates for *Elliptio fisheriana* (Fig. 2), which had higher estimates and higher variability the estimates. All three species showed the same general pattern of recruitment (*i.e.*, high recruitment estimates for the same times of year). However, recruitment rate varied lit over time for both *Elliptio complanata*, the dominant species in this assemblage, and *Lamps cariosa*, which is far less common. Highest estimated recruitment occurred for the fi sampling occasion (summer-winter 1996) for *E. complanata* ($f = 0.037$, SE = 0.058) and *cariosa* ($f = 0.041$, SE = 0.091), with the remaining estimates slightly lower and consta Highest estimated recruitment for *E. fisheriana* occurred over summer-winter 1996 (f 0.155, SE = 0.043) and the summer 1998 to summer 1999 time period ($f = 0.225$, SE = 0.2 Lowest estimates were seen for the period of spring-early summer 1997 and again for t year July 1999 to June 2000 ($f = 0.001$, SE = 0.005), the same intervals of low no recruitment for *E. complanata* and *L. cariosa*. While all three species had a higher annu recruitment rate for July 1998 through early summer of 1999, a decline in annu recruitment was seen for all three species for the following year.

Population growth rate (λ) increased after the first sampling occasion for all three speci with a leveling off at a fairly constant rate for the remaining intervals (Fig. 3). Populati growth rate was slightly negative for *Elliptio complanata* ($\lambda = 0.98$, SE = 0.03) and *Lamps cariosa* ($\lambda = 0.97$, SE = 0.02) for the interval of October 1997 to July 1998, with a sligh positive growth rate for *E. fisheriana* ($\lambda = 1.03$, SE = 0.09) for the same time period. *Ellip fisheriana* had a static rate of population growth ($\lambda = 1.00$, SE = 0.002) between April and Ju 1997, with a positive growth rate estimated for winter-spring ($\lambda = 1.08$, SE = 0.32), summ fall ($\lambda = 1.09$, SE = 0.14), fall-summer ($\lambda = 1.03$, SE = 0.09) with highest positive growth ra for the summer 1998 to summer 1999 period ($\lambda = 1.22$, SE = 0.19). There was little change population growth (average $\lambda \approx 1$) from January 1997 through July 1999 for *E. complan* and *L. cariosa*, with positive population growth (average $\lambda = 1.1$) for *E. fisheriana*. However, the first interval is included then population growth rate over the four years was negative f

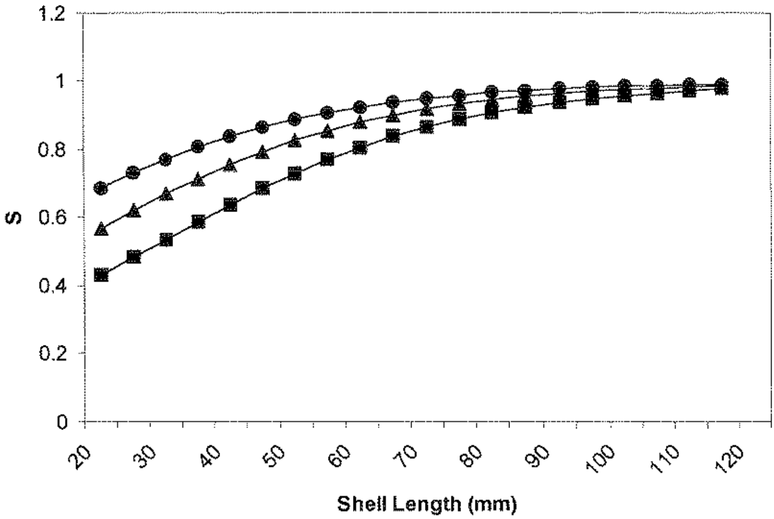

FIG. 1.—Apparent survival (S) modeled with length as a covariate for *Elliptio complanata* (circles *fisheriana* (squares) and *Lampsilis cariosa* (triangles)

E. complanata and *L. cariosa* (average $\lambda = 0.96$) with slight positive population growth fo *fisheriana* (average $\lambda = 1.02$) over the same four year period. Because the low recap probabilities from the winter sampling occasion led to estimates of survival with la variances, we did not use the λ estimates (average 0.76, SE = 0.33) for the first interval.

Movement.—The estimated probability of moving between bands (*psi*) was model avera over four competing models. There was both downstream and upstream movemen animals within the site. Overall downstream movement for all species was less than (average *psi*=0.008, SE=0.003) (Fig. 4a). Most of the movement occurred within a distanc 40 m or less (*psi*=0.009, SE=0.014) with some movement detected between 40 and 80 m in downstream direction (*psi*= 0.007, SE = 0.052). The majority of movement in the 0 to 4 distance occurred from band A to band B (*psi*=0.016, SE=0.031) in pool habitat at the to the site (Fig. 4b) with lower but nearly equal estimates of movement throughout remaining bands (average *psi*=0.007, SE=0.014). Though we detected little movement in 40 to 80 m distance, it did occur in all bands and was consistent among bands (Fig. Upstream movement occurred throughout the study site (*psi*=0.04, SE=0.031) (Fig. 4a) the majority of upstream movement occurring at the top of the site from band B to band A =0.13, SE=0.001) (Fig. 4d). The substrate in bands A and B where the animals were found predominantly sand and silt, with mainly gravel and cobble substrates and higher flows in remaining bands downstream. Eighty-nine percent of the weight came from the top mo which fixed movement downstream at a constant rate but allowed movement to and f bands A and B to occur at a different rate (Table 5). The model structure reflected the hab differences of bands A and B compared to the remainder of the site. The model that fixe movement at a constant rate regardless of band had no support for describing the data.

DISCUSSION

Long-term studies of marked animals are essential to answering many of the quest fundamental to our understanding the population dynamics of freshwater mussels. Effe

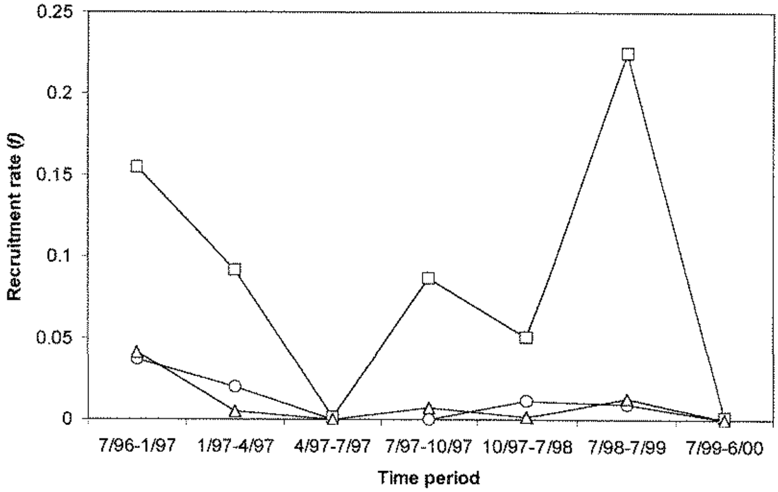

FIG. 2.—Recruitment rate estimates for *Elliptio complanata* (circles), *E. fisheriana* (squares) a *Lampsilis cariosa* (triangles). Recruitment rate (f) is the number of new animals of a minim detectable size in the population at time t per animal in the population at time $t - 1$

management decisions rely on knowing something about the vital rates (survival, recruitm and movement) governing the population of interest. Survival is often difficult to estim precisely because survival must be distinguished from the probability of seeing the anir again (Nichols, 1992). Mark-recapture studies require at a minimum 3 y to estimate t probability of recapture with a longer time frame required to arrive at more precise estima if the recapture probabilities are low. The advantage of mark-recapture modeling is tha allows us to make separate inferences about survival and capture rates (Lebreton *et al.*, 19 resulting in accurate estimates of survival on large samples of marked animals.

One of the study objectives was to estimate the survival rates of the species in the mus assemblage at our study site. We developed the model structure on how we expect t parameter to vary; *e.g.*, is the probability of survival time, size and/or species-specific or i constant over time? The various combinations of these variables led to a number of mod identified as nearly equally useful for making inferences about the population. Though t top model was almost twice as well supported as the next best model, this was not suffici evidence to be designated as the best model. We had three models that were feasible as a b model and a total of five models with sufficient evidence to also be considered as a possi best model. With this amount of model selection uncertainty it made sense to model aver to arrive at our estimates. Since we followed one population and did not tag at multiple si we did exploratory analysis and did not focus on hypothesis testing. Our goal was to arrive the best estimates of the population parameters based on our candidate set of models a not on finding the best model.

We expected the apparent survival rate for *Elliptio complanata*, *E. fisheriana* and *Lamps cariosa* would vary over time, but we did not expect a nearly identical pattern of survival ra *Elliptio complanata* is the overwhelmingly dominant species not only in this site b throughout the river and is considered to be a habitat generalist (Clarke, 1981), so expected higher survival rate estimates than the two rarer species *E. fisheriana* and *L. cari Elliptio fisheriana* was found only in areas of slow current and small particle size near t

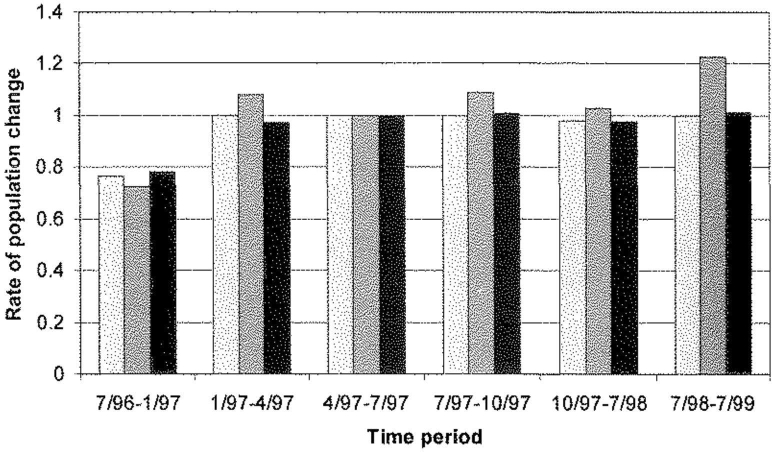

FIG. 3.—Rate of population growth (λ) for *Elliptio complanata* (light gray bar), *Elliptio fisheriana* (c gray), and *Lampsilis cariosa* (black)

stream bank. These areas are often prone to drying during periods of drought, a comm occurrence in this river, but the fine substrate may allow these animals to compensate moving more readily to areas nearby that are still watered. It is also feasible these ar provide some protection during periods of high flow and scour events, enhancing surv rates and allowing animals to avoid being displaced (Downing *et al.*, 2000). *Lampsilis car* is also found in low numbers but with a spatial distribution within the site similar tc *complanata.* Though found in all substrate types and flows, *L. cariosa* was most often fou almost completely buried within the substrate, possibly enhancing its survival.

Based on Akaike weights, time was the important predictor of apparent survival (94 with very little species effect (24%) though the change in survival over time was sm Apparent survival approximated 1.0 (100%) for the intervals of late spring and summer a the last interval which represents an annual survival rate from July 1998 to July 1999 (Ta 3). The winter through spring intervals had lower survival estimates with lowest estima survival rate for the first sampling interval (fall to early winter). This presumed mortality not induced by tagging, similar to results reported in other tagging studies (Kesler a Downing, 1997), nor was the estimate negatively biased due to tag loss since tag loss r after 2 y was minimal (Lemarie *et al.*, 2000). We expected temporal variation in the recapt probabilities and our model estimates reflect this variation. Since the apparent surv estimate is dependent on the probability of being seen (captured) at a subsequent sampl occasion (Burnham *et al.*, 1987), the lack of precision of the survival estimates associa with winter sampling reflects both the low recapture probability (2–3%) in the Janu sampling occasion and, being early in the study, few capture occasions.

Factors influencing whether animals are at or below the substrate surface inch temperature and day length, high flows and reproductive condition (Balfour and Smc 1995; Amyot and Downing, 1991, 1997). *Elliptio complanata* begin moving to the surface spring (often by late April at our latitude) with most animals at the surface in sumr (June–July), they reburrow in fall and often remain there until the following spring (Am and Downing, 1998; Watters and O'Dee, 2001). For species that are short-term breed spawning in spring and releasing glochidia by fall, as well as some that are conside

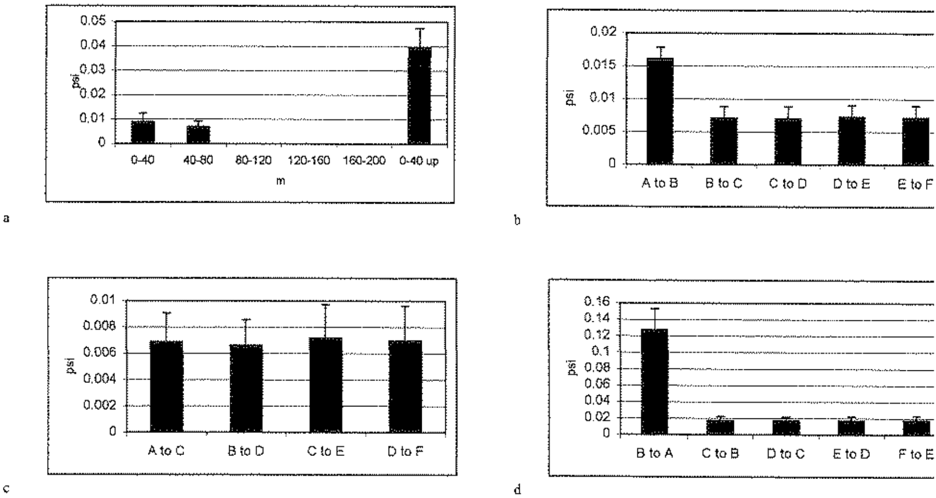

FIG. 4.—Estimates of rate of movement of *Elliptio complanata, E. fisheriana* and *Lampsilis cariosa*: distance moved in meters downstream and upstream within the site, b) within band downstre: movement of 0–40 meters and c) 40–80 meters, and d) within band upstream movement, plus 1 Letters A through F represent 40 meter wide bands with A being the band at the top of the site. represents the probability that an animal moves from one strata (band) to another during interva Estimates of *psi* are model averaged over 4 models

long-term breeders such as *Lampsilis cariosa,* this pattern of vertical movement to the surfa is associated with spawning (Watters and O'Dee, 2001). Though we have found glochic collected in drift samples in almost every month (R. Villella, pers. obs.), the peak periods release were found from June to September. The two periods of low recapture were January and October when temperatures (especially January 1997) were cold, flows we higher than normal and animals were less active. Although it appeared the over-wint survival was lower, what is more important is the probability of being observed and captur was greatly reduced. With so few animals at the surface in winter, sampling occasions f mark-recapture studies should be restricted to those times of the year when the majority adult mussels are available at the surface. To arrive at better estimates and a bett understanding of over-winter survival of freshwater mussels would require a large sampli effort with a considerable amount of excavation which may not be desirable.

Our models also indicated that apparent survival was size dependent. Adults had high survival estimates than small animals, especially mussels over 55 mm in length (Fig. 1). *Ellip complanata* >55 mm had a higher rate of survival (>91%) than smaller individuals, with : estimated survival rate of 69% for individuals 20 mm in length. We saw the same pattern f both *E. fisheriana* where animals >55 mm had >77% survival rate vs. 43% for animals 20 m in length and *Lampsilis cariosa* where large mussels survived at a rate of >85% vs. 57% f small individuals. Survival rate approached 100% for all species for animals ≥100 mm in si: High survival estimates of adults compared to juveniles have been seen in other long-liv species where the annual survival rate is normally high (Brownie *et al.*, 1985). However, v suspect the apparent survival estimates, though lower than adults, may be higher for anim: <55 mm in size than predicted by the models. Insufficient sample size of small anim: resulted in the apparent survival rate estimates for these individuals having large varianc

TABLE 5.—Statistics for the candidate models for estimating movement of *Elliptio complanta*, *fisheriana* and *Lampsilis cariosa* between bands. The model likelihood is the ΔAICc weight for the mo of interest divided by the ΔAICc weight of the best model. This value is the strength of evidence of model relative to other models in the set of models considered. np is the number of parame estimated

Model	ΔAIC_c	AIC Weight	Model Likelihood	r
S(t) *p*(t) *psi*(bands constant, A&B differ, fix far upstream to 0)	0.00	0.89294	1.0000	[illegible]
S(t) *p*(t) *psi*(bands constant, A to and from differ, fix far upstream to 0)	5.74	0.05058	0.0566	[illegible]
S(t) *p*(t) *psi*(bands constant, B to and from differ, fix far upstream to 0)	6.36	0.03704	0.0415	[illegible]
S(t) *p*(t) *psi*(fix far upstream to 0)	7.65	0.01944	0.0218	[illegible]
S(t) *p*(*t*) *psi*(bands constant, fix far upstream to 0)	26.56	0.00000	0.0000	1

Most of the *E. complanata* (94%) were ≥55 mm, one *L. cariosa* was smaller than 55 mm a 60% of *E. fisheriana* that were tagged were ≥55 mm in length (Fig. 5). We accounted for so of the variation in survival and recapture by incorporating into the models our assumpti about these parameters, allowing survival and recapture to vary over time, by species or size. Though our models indicated that time and animal size were important predictors recapture probability, the assumption of equal catchability may have been violated despite indication of any violation from the goodness of fit tests.

The assumption of equal catchability is violated when some individuals temporarily leave sampling area (*i.e.*, in the case of mussels those that move below the surface and not availa for detection in a given sampling period) and return during subsequent sampling occasic This temporary emigration results in those animals below the surface temporarily having a z capture probability while those available at the surface have a capture probability greater th zero. However, the buried mussels could return to the surface and be available for capture the next sampling occasion and mussels that were available for capture the previous sampl occasion are now buried. There are two types of temporary emigration: completely rand and Markovian (Kendall *et al.*, 1997). Temporary emigration is considered completely rand when the probability that a mussel is buried is unrelated to whether it was buried in a previ sampling occasion. In Markovian temporary emigration whether a mussel is buried depe on its vertical position at the previous sampling occasion. We can realistically assu temporary emigration of adult mussels is a random event and therefore there would be littl no bias in the survival estimate (Carothers, 1973; Burnham, 1993; Hestbeck, 1995) thou precision of the estimate may be reduced. We cannot assume completely random tempor emigration of small mussels since a small mussel buried at a previous sampling occasio likely to remain buried until it reaches a larger size. Several studies have shown that sn mussels remain buried beneath the substrate even during warmer periods of the year (Am and Downing, 1991; Balfour and Smock, 1995) when larger animals move to the surfa Balfour and Smock (1995) studied the vertical movement of *Elliptio complanata* and found t small animals remained below the surface until they reached about 50 mm in size. The la variances in the apparent survival estimates for small mussels and the low capture probabili reflect a higher incidence of temporary emigration for this size group (Kendall *et al.*, 19 than we had expected. The parameter values are, therefore, more difficult to interpre

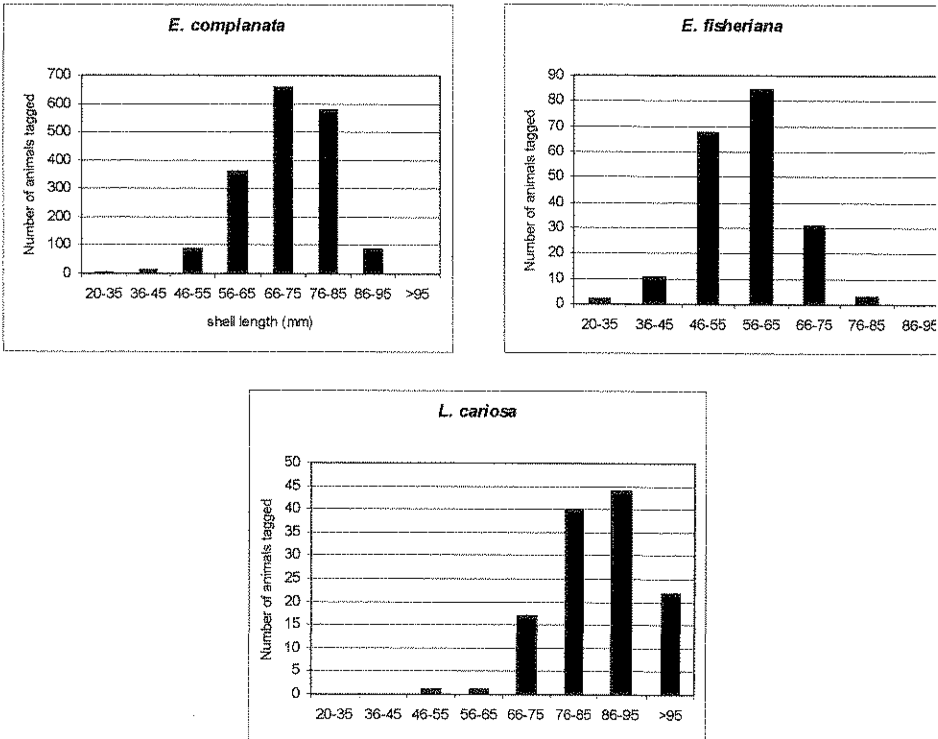

FIG. 5.—Size distribution of species based on total shell length measurements in mm

actual terms for this small size class which is more prone to emigration and mo heterogeneous in their recapture rates. We concluded that temporary emigration was a important determinant of the seasonal pattern of recapture probabilities in this populatio Unequal catchability is likely to exist in all capture-recapture studies to some degree due imperfect detectability. Smith *et al.* (1999) found detectability of mussels varied by habitat ar mussel size with differences in detection among substrate types greatest for smaller musse Though there is no study design to completely eliminate it, there are ways to reduce it. When is suspected recapture probability may depend on some measurable characteristic such as s or size that variable should be recorded so the sample can be stratified for analysis. In our ca we had insufficient number of small animals to stratify our sample. Applying the robust desig to estimate temporary emigration rate can be applied (Kendall *et al.*, 1997; Kendall ar Bjorkland, 2001). The robust design involves sampling several times over a brief period (*e.g* sampling and tagging mussels each day for 3 d) to estimate capture probabilities using close population models and then repeating this sampling annually so that vital rates can l estimated using open population models. This approach can be time consuming and ofte resources aren't available to implement this design. A preferred approach would be to incluc some amount of excavation to sample both buried mussels and mussels at the surface (Stray and Smith 2003). The vertical position of individual mussels can be recorded on each samplir occasion. Multi-state models that allow for transition between locations (surface vs. buriec could then be used to estimate survival of those at the surface and survival of those below surface (Brownie *et al.*, 1993).

The high apparent survival estimates of adult mussels are similar to the survival estim (>97%) in a mark-recapture study of adult *Amblema plicata* (Say) (Hart *et al.*, 2001a) Minnesota and the mean annual survival estimate (94 ± 3%) of adult *Elliptio dila* (Rafinesque) in Lake Pepin, Wisconsin, that were cleaned of zebra mussels (Hart *et* 2001b). High survival (average survival >97%) was also reported in a comparison relocation studies involving multiple species of adult freshwater mussels after 2 y (Dunn *et* 1999). Once these animals successfully pass the early vulnerable glochidia and juvenile stages, the hard shell of the adult valves would provide some protection against adv environmental conditions.

It is important to recognize the survival parameter (*S*) we were estimating is appar survival which includes both mortality and permanent emigration. Therefore, estimate apparent survival are almost certainly underestimates of true survival because some anin will also have emigrated from the study site. However, we believe there was little perman emigration of animals at this site. Our model estimates indicated there was very li movement. Longitudinal movement of unionid mussels has been reported (Negus, 19 Kat, 1982; Amyot and Downing, 1991, 1997; Balfour and Smock, 1995), but similar to findings, most of this movement is infrequent (downstream movement rate of <1%) a similar to the findings of Balfour and Smock (1995), mussels can move both upstream a downstream. While most of the downstream movement occurred within the 0 to 4(distance, most of this movement probably was less than 40 m. Mussels moving over 1(downstream have been documented in small streams (Kat, 1982; Balfour and Smock, 19 but was shown to be rare. Some of this movement may be due to displacement by high flo animals located near the top or bottom of one band and moving short distances into adjoining band or misplacement of animals after tagging. While the rate of upstre movement was slightly greater than the rate of downstream movement (Fig. 4a), almost of this movement occurred at the top of the site where there was very low current a substrate particle size was predominantly sand and silt. The upstream movement in remaining bands was probably due to animals being located in close proximity to ba boundaries. Mussels may move greater distances than previously thought and our res indicate that studies designed to monitor population trends or response of a mu population to some perturbation need to ensure the size of the study site is large enough detect movement. Continued tagging and capture occasions may help determine how mussels move and by modeling movement rate with environmental and biological covari such as sex, age or size, we may be able to determine why they move.

While several studies suggest considerable year to year variability in recruitment (Neg 1966; Strayer *et al.*, 1981) both *Elliptio complanata* and *Lampsilis cariosa* had a low (≤4%) a fairly constant rate of recruitment including an interval with no evident recruitment. Onl *fisheriana* showed much variability in recruitment, which may reflect the variability in habitat where changes in flow have greater effect on temperature, dissolved oxygen and a of available wetted habitat. Our models indicate that recruitment did occur for all specie 1996 through 1998 with virtually no annual recruitment for all three species for the inte of July 1999 to June 2000, suggesting that very few new animals were added to population in June 2000 since the previous sampling in July 1999. Mean annual stream f in 1999 and the first 6 mo of 2000 was approximately half the long-term mean stream f for the same time period. Whether a year of no recruitment was an unusual occurrence was due to adverse environmental conditions has yet to be determined. Additional capt occasions are needed to determine whether these species have occasional periods successful higher recruitment with longer intervals of low and possibly no recruitment whether we happened to miss a large year class.

The recruitment parameter for open populations includes recruitment from bo reproduction and immigration. Complicating our interpretation of these recruitme estimates for freshwater mussels is their need for a host to complete their life cycle. cannot distinguish whether some of this recruitment was from reproduction in t population or was it from reproduction in another mussel bed upstream or downstre with new animals deposited by the fish host.

A second objective of this study was to evaluate how the survival and recruitment estima influenced population trends over time. Though the structure of the top four mod indicated both recruitment and rate of population growth vary over time the changes growth between years was small. The average population growth rate (λ) approximated for *Elliptio complanata* and *Lampsilis cariosa*, with both species experiencing slightly negat population growth between the fifth and sixth sampling interval. While the population v virtually static both within and between years for *E. complanata* and *L. cariosa*, avera population growth over the same three year interval for *E. fisheriana* was slightly positive (λ 1.084) with the intervals of higher positive growth corresponding to the intervals of high recruitment. Whatever environmental cues trigger recruitment elicited basically the sa response for all three species. Even though *E. fisheriana* had the lowest apparent survival ra for small individuals, the occasional intervals of higher recruitment and high annual ad survival enables the species to sustain some positive population growth. Sites with estimates $\lambda \approx 1$ could reflect self-sustaining stationary populations, populations requiring hi immigration to maintain stability or a combination of both. The λ estimates approximati 1.0 suggest the mussel population at this site on the Cacapon River supports a self-sustaini static population through a life history strategy of low, but constant recruitment and hi annual adult survival to maintain stability. In variable environments, such as those inhabit by freshwater mussels, high adult survival rates probably allow individuals and populations persist through potentially extended periods of less favorable reproductive conditio Estimates of λ for this 4 y period should not be used to predict future population trends th can only be addressed by longer-term studies. However, with many native freshwater mus populations experiencing declines, the trend in population growth rate does warrant som concern. Though low recruitment rates and low mortality of adults may be sufficient maintain a population of these species at this location, it may not be sufficient to mainta a population at this site should a catastrophic event occur. The low recruitment rate of adu emphasizes the importance of ensuring the continued longevity of adult mussels and t importance of determining whether there are limiting factors to increasing recruitment this population. While our models suggest recruitment may potentially be what is limiti population growth we do not know the factor or factors limiting recruitment.

Adult survival in long-lived vertebrate species is the sensitive demographic paramet affecting population change, whereas species with shorter life spans, fecundity is often mo important in affecting change in the population (Boyce, 1992). High adult survival is a l history characteristic that is common to large mammals and vertebrates in general but is n found among other freshwater invertebrates. Unionids are unique among freshwat invertebrates both in their longevity and their high and constant adult survival. This l history strategy is instead similar to large mammals and some freshwater vertebrates such hellbenders and some fish species. Their life history strategy can be considered a hybr between an r and K-strategist. Unionids share some qualities of K-strategists (longevity a high adult survival) and they also share some of the qualities of r-strategists (high output glochidia, lower survival of young, no parental care). It is possible that continuous (thou low) reproduction during a long adult life span can be beneficial for unionids and may an evolutionary strategy in response to uncertain larval and juvenile survival. The surv estimates from this and other similar studies are an important contribution to comparative data on freshwater mussels for several reasons. First, few estimates are availa for freshwater species with such potential longevity. With environmental conditions vary between sites we would expect different rates of adult survival among populations, e those in close proximity. Therefore, a one size fits all management strategy may not ens protection of a mussel population. To ensure the management plan will be effective i important to develop estimates of survival and recruitment for additional populations. T may be difficult to achieve for some endangered species that are present in such numbers making recapture probabilities too low to arrive at precise estimates of survi Substituting information from other species or populations may not be appropriate un the range of variability in survival and recruitment are known (Beissinger and Westp 1998). To arrive at better estimates of the variance in rates of survival, recruitment movement requires measurements of these rates be made over a sufficient number of ye to sample the range of environmental conditions. Secondly, the high survival rates of ac mussels in this and other populations suggests individuals may reach advanced ages previously thought attainable in freshwater mussels inhabiting lotic systems. A m recapture study of freshwater mussels in lacustrine environments revealed high annual ac survival with mean age estimates for *Elliptio complanata* as high as 75 ± 29 y and 73 ± 50 y *Lampsilis siliquoidea* (Barnes) (Anthony *et al.*, 2001). These estimates are not unlike sc marine mollusks such as the hard clam, *Mercenaria mercenaria* (Linnaeus) which can longer than 40 y (Eversole *et al.*, 2000) and the ocean quahog *Arctica islandica* (Linnae which can live 100 y or more (Thompson *et al.*, 1980).

Pollock *et al.* (1990) and Burnham *et al.* (1987) have sections on the design of m recapture experiments. We offer a few guidelines for designing mark-recapture studies freshwater mussel populations: (1) make sufficient effort to sample the entire study are the sample population is representative of your target population and to ensure capt probabilities are high; (2) use either the robust design or include a sufficient leve excavation to address the issue of temporary emigration of mussels, especially for small classes; (3) sample at a time of year when most mussels are likely to be available at the sur for capture; (4) use a tagging/marking method, such as double tagging, that does influence survival rate and has a high tag retention rate to prevent losing information can negatively bias the survival estimates; (5) tagged mussels should be returned to the a where they were collected; and (6) mark and release a large number of animals on e sampling occasion. Brownie *et al.* (1985) recommend marking a minimum of 300 animals year and more for animals that are expected to have low recapture rates. In our study marked and released from 299 to over 500 animals during the summer sampling occasi Finally, mark-recapture studies of freshwater mussels should be long-term. For long-li species studies >10 y would be recommended as a minimum goal. Long-term mark-recapt studies can also be used to address the questions about senescence in freshwater muss which might be indicated by a decline in the survival probabilities with increasing age, a model in which survival varied as a function of relative age of adults since they were marked. Though exact age of individuals would not be known, one could test for a declin survival with successive recaptures (and therefore aging) of individuals.

To date we have sampled and tagged on eight separate occasions over 4 y, a relatively sh time frame for the study of a long-lived fauna. However, this study has provided so important insights into the ecology of freshwater mussels with additional tagging capture occasions improving the precision of these population estimates. The study res illustrate that tagging can be used to obtain estimates of important life history parameter: freshwater mussels and make inferences about the ecological relationships affect population dynamics from the capture history of uniquely marked individuals. Additio replicated, long-term tagging studies are needed to place these findings into a broa ecological perspective. Long-term mark-recapture data sets can be an important source information to test hypotheses about factors affecting not only survival but also recruitme movement patterns and other aspects of population dynamics.

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LITERATURE CITED

AMYOT, J. P. AND J. A. DOWNING. 1991. Endo-and epibenthic distribution of the unionid mollusc *Ell complanata. J. N. Am. Benthol. Soc.,* **10**(3):280–285.

——— AND ———. 1997. Seasonal variation in vertical and horizontal movement of the freshw bivalve *Elliptio complanata* (Mollusca: Unionidae). *Freshwater Biol.,* **37**:345–354.

——— AND ———. 1998. Locomotion in *Elliptio complanata* (Mollusca: Unionidae): a reproduc function? *Freshwater Biol.,* **39**:315–358.

ANDERSON, D. R., G. C. WHITE AND K. P. BURNHAM. 1995. Some specialized risk assessment methodolo for vertebrate populations. *Environ. and Ecol. Stat.,* **2**:91–115.

ANTHONY, J. L., D. H. KESLER, W. L. DOWNING AND J. A. DOWNING. 2001. Length-specific growth rate freshwater mussels (Bivalvia: Unionidae): extreme longevity or generalized growth cessati *Freshwater Biol.,* **46**:1349–1359.

BALFOUR, D. L. AND L. A. SMOCK. 1995. Distribution, age, and movements of the freshwater mussel *Ell complanata* (Mollusca: Unionidae) in a headwater stream. *J. Freshwater Ecol.,* **10**(3):255–268

BEISSINGER, S. R. AND M. I. WESTPHAL. 1998. On the use of demographic models of population viabilit endangered species management. *J. Wildl. Manage.,* **62**(3):821–841.

BOYCE, M. S. 1992. Population viability analysis. *Annu. Rev. Ecol. Syst.,* **23**:481–506.

BROWNIE, C. 1987. Recent models for mark-recapture and mark-resighting data. *Biometrics,* **43**:1017–1(

———, D. R. ANDERSON, K. P. BURNHAM AND D. S. ROBSON. 1985. Statistical inference from band reco data—a handbook, 2nd ed. U. S. Fish Wild. Serv. Resour. Publ. No. 156, Washington, D.C. 30

———, J. E. HINES, J. D. NICHOLS, K. H. POLLOCK AND J. B. HESTBECK. 1993. Capture-recapture studies multiple strata including non-markovian transitions. *Biometrics,* **49**:1173–1187.

BURNHAM, K. P. 1993. A theory for combined analysis of ring recovery and recapture data, p. 199–214. J. D. Lebreton and P. M. North (eds.). Marked individuals in the study of bird populati Birkhäuser-Verlag, Basel, Switzerland.

———, D. R. ANDERSON, G. C. WHITE, C. BROWNIE AND K. H. POLLOCK. 1987. Design and analysis meth for fish survival experiments based on release-recapture. *Am. Fish. Soc. Monogr. No. 5,* Bethes Maryland. 437 p.

——— AND ———. 1998. Model selection and inference: a practical information theoretical approa Springer-Verlag, New York. 353 p.

CAROTHERS, A. D. 1973. The effects of unequal catchability on Jolly-Seber estimates. *Biometrics,* **29**:79–1

———. 1979. Quantifying unequal catchability and its effect on survival estimates in an ac population. *J. Anim. Ecol.,* **48**:863–869.

CLARKE, A. H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, Natio Museums of Canada, Ottawa, Canada.

CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika,* **51**:429–4

DOWNING, J. A., H. V. LEEUWEN AND L. A. DIPAOLO. 2000. Substratum patch selection in the lacustr mussels *Elliptio complanata* and *Pyganadon grandis grandis. Freshwater Biol.,* **44**:641–648.

DUNN, H. L., B. E. SIETMAN AND D. E. KELNER. 1999. Evaluation of recent unionid (Bivalvia) relocati and suggestions for future relocations and reintroductions, p. 169–183. *In:* R. Tankersley, D

Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson and R. S. Butler (eds.). Freshwa mollusk symposia proceedings. Ohio Biological Survey, Columbus, Ohio.

EVERSOLE, A. G., N. DEVILLERS AND W. D. ANDERSON. 2000. Age and size of *Mercenaria mercenaria* in sisters creek, South Carolina. *J. Shellfish Res.*, **19**(1):51–56.

HART, R. A., J. W. GRIER, A. C. MILLER AND M. DAVIS. 2001a. Empirically derived survival rates of a na mussel, *Amblema plicata*, in the Mississippi and Otter Tail Rivers, Minnesota. *Am. Midl. N* **146**(2):254–263.

———, M. DAVIS, J. W. GRIER AND A. C. MILLER. 2001b. Survival of unionids following removal of attacl zebra mussels. *J. Freshwater Ecol.*, **16**(1):29–33.

HESTBECK, J. B. 1995. Bias in transition-specific survival and movement probabilities estimated us capture-recapture data. *J. Appl. Stat.*, **22**:737–750.

———, J. D. NICHOLS AND R. A. MALECKI. 1991. Estimates of movement and site fidelity using ma resight data of wintering Canada geese. *Ecology*, **72**(2):523–533.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigrat stochastic models. *Biometrika*, **52**:225–247.

KAT, P. W. 1982. Effects of population density and substratum type on growth and migration of *Elli complanata* (Bivalvia: Unionidae). *Malacolog. Rev.*, **15**:119–127.

KENDALL, W. L. AND R. BJORKLAND. 2001. Using open robust design models to estimate tempor emigration from capture-recapture data. *Biometrics*, **57**:1113–1122.

———, J. D. NICHOLS AND J. E. HINES. 1997. Estimating temporary emigration using capture-recapt data with Pollock's robust design. *Ecology*, **78**(2):563–578.

KESLER, D. H. AND J. A. DOWNING. 1997. Internal shell annuli yield inaccurate growth estimates in freshwater mussels *Elliptio complanata* and *Lampsilis radiata*. *Freshwater Biol.*, **37**:325–332.

LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT AND D. R. ANDERSON. 1992. Modeling survival and test biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Mon* **62**(1):67–118.

LEMARIÉ, D. P., D. R. SMITH, R. F. VILLELLA AND D. A. WELLER. 2000. Evaluation of tag types and adhes for marking freshwater mussels (Mollusca: Unionidae). *J. Shellfish Res.*, **19**(1):247–250.

MANLY, B. F. J. 1985. The statistics of natural selection on animal populations. Chapman and H London, England.

NEGUS, C. L. 1966. A quantitative study of growth and production of unionid mussels in the r Thames at Reading. *J. Anim. Ecol.*, **35**(3):513–532.

NICHOLS, J. D. 1992. Capture-recapture models. *BioScience*, **42**:94–102.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE AND J. E. HINES. 1990. Statistical inference for captu recapture experiments. *Wildl. Monogr.*, **107.** 97 p.

PRADEL, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and populat growth rate. *Biometrics*, **52**:703–709.

RICCIARDI, A. AND J. B. RASMUSSEN. 1999. Extinction rates of North American freshwater fauna. *Cons Bio.*, **13**(5):1220–1222.

ROGERS, S. O., B. T. WATSON AND R. J. NEVES. 2001. Life history and population biology of the endange tan riffleshell (*Epioblasma florentina walkeri*) (Bivalvia: Unionidae). *J. N. Am. Benthol. S* **20**(4):582–594.

SCHWARZ, C. J. AND G. A. F. SEBER. 1999. Estimating animal abundance: review III. *Statistical Scie* **14**:427–456.

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

———. 1982. The estimation of animal abundance and related parameters, 2nd ed. Charles Griffin Co., Ltd., London. 506 p.

———. 1992. A review of estimating animal abundance II. *International Statistical Review*, **60**:129–16

SMITH, D. R., R. F. VILLELLA, D. P. LEMARIÉ AND S. OETTINGEN. 1999. How much excavation is neede monitor freshwater mussels? p. 203–218. *In:* R. Tankersley, D. I. Warmolts, G. T. Watters, I Armitage, P. D. Johnson and R. S. Butler (eds.). Freshwater mollusk symposia proceedi Ohio Biological Survey, Columbus, Ohio.

STRAYER, D. L., J. J. COLE AND G. E. LIKENS. 1981. Biomass and annual production of the freshwater r *Elliptio complanata* in an oligotrophic softwater lake. *Freshwater Biol.*, **11**:435–440.
——— AND D. R. SMITH. 2003. A guide to sampling freshwater mussel populations. American Fis Society Monograph No. 8, Bethesda, Maryland.
THOMPSON, I., D. S. JONES AND J. W. ROPES. 1980. Advanced age for sexual maturity in the ocean q *Arctica islandica* (Mollusca:Bivalvia). *Mar. Biol.*, **57**:35–39.
WATTERS, G. T. AND S. H. O'DEE. 2001. Patterns of vertical migration in freshwater mussels (Bi Unionoida). *J. Freshwater Ecol.*, **16**(4):541–549.
WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK—survival estimation from populations of m animals. *Bird Study*, **46**:120–138.
WILLIAMS, J. D., M. L. WARREN, JR., K. S. CUMMINGS, J. L. HARRIS AND R. J. NEVES. 1993. Conservation of freshwater mussels of the United States and Canada. *Fisheries*, **18**:6–22.

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