mussels that were not recovered. This conditioning implies that θ may be estimated by maximizing $l(\theta)$ and that generalized linear models of binomial responses (McCullagh and Nelder, 1989) can be used to examine differences in θ between treatments. Therefore, for each species the treatment effects (i.e. the effects of relocation) were tested by comparing the maximized log–likelihood function without treatment effects against the maximized log–likelihood function with treatment effects. A log–likelihood ratio statistic denoted by G^2 was used to compare the two models and to test whether the estimates of survival were significantly different between treatments.

In large samples log–likelihood ratios have chi-squared distributions, and hypothesis testing is accomplished by comparing G^2 with chi-squared critical values. However, the small sample sizes of our replicates (four mussels per enclosure) invalidate the chi-squared approximation for the sampling distribution of G^2. Therefore, randomization tests (Edgington, 1987) were used to approximate the sampling distribution of G^2 and to test whether the estimated differences in survival among treatment groups were statistically significant. In these tests the responses (number of mussels recovered alive and number of mussels recovered dead) were randomly assigned to each treatment group, and G^2 was computed to evaluate the improvement in fit of a model that included treatment effects against a model that lacked these effects. Random assignments were repeated 5000 times to approximate the sampling distribution of G^2 under the null hypothesis of no treatment effects. The significance probability associated with the test of no treatment effect was computed as the proportion of the 5000 G^2 values that equaled or exceeded the log–likelihood ratio statistic observed in the experiment.

RESULTS AND DISCUSSION

A total of 192 mussels were relocated to three sites in the Apalachicola River mainstem in July 1993. In May 1994 when the relocated mussels were retrieved, their conditional survival (θ) was 0.89. Species-specific estimates of the survival of mussels relocated to three destination sites ranged from 1.0 (complete survival) to 0 (no survival) (Tables I and II).

The two largest mussels, *Elliptoideus sloatianus* and *Megalonaias boykiniana*, had the highest overall recovery rates as well as the highest survival rates. The type of substrate at the relocation sites had a significant effect on the survival of these relocated mussel species. Survival of *E. sloatianus* relocated to cobble or limestone substrates was 1.0 and was significantly greater ($p = 0.035$) than the survival of *E. sloatianus* transplanted to the stable sand substrate (0.69). For *M. boykiniana*, survival was highest in the

Table I. Cross-classification of the number of mussels that were found alive (A), dead (D) or unrecovered (U) in enclosures in the Apalachicola River 10 months after relocation. Treatments correspond to substrate composition at the relocation site

Treatment	Enclosure	*Elliptio crassidens*			*Elliptoideus sloatianus*			*Lampsila teres*			*Megalonaias boykiniana*		
		A	D	U	A	D	U	A	D	U	A	D	U
Cobble	1	2	2	0	4	0	0	0	0	4	4	0	0
	2	1	0	3	4	0	0	1	0	3	4	0	0
	3	1	0	3	4	0	0	0	0	4	3	1	0
	4	3	0	1	4	0	0	0	1	3	3	1	0
Limestone/sand	1	2	0	2	4	0	0	0	0	4	4	0	0
	2	2	0	2	4	0	0	0	0	4	4	0	0
	3	4	0	0	4	0	0	0	0	4	4	0	0
	4	2	0	2	4	0	0	0	0	4	4	0	0
Stable sand	1	3	0	1	4	0	0	1	0	3	4	0	0
	2	2	0	2	2	2	0	1	0	3	4	0	0
	3	3	1	0	2	2	0	0	3	1	4	0	0
	4	4	0	0	0	3	1	0	0	4	4	0	0

Table II. Estimates of the conditional probability of survival of mussels relocated to different substrates in the Apalachicola River, Florida. G^2 is the log–likelihood ratio statistic realized in the experiment. p is the significance probability for the effects of relocation estimated in randomization tests

Species	Cobble	Limestone/sand	Stable sand	G^2	p
Elliptio crassidens	0.78	1.00	0.92	3.33	0.391
Elliptoideus sloatianus	1.00	1.00	0.69	12.20	0.035
Lampsilis teres	0.50	0.00	0.40	1.08	0.829
Megalonaias boykiniana	0.88	1.00	1.00	4.57	0.014

limestone and stable sand substrates (1.0), and survival (0.88) was significantly lower in the cobble substrate ($p = 0.014$).

The specific habitat requirements of *Megalonaias boykiniana* and *Elliptoideus sloatianus* are not known, and, in general, information from the Apalachicola River Basin suggested that both species occurred in a wide range of habitats. *Megalonaias boykiniana* was reported from muddy sand, sand and rocky substrated (Heard, 1979) and those descriptive observations are consistent with this study, where *M. boykiniana* had significantly higher survival rates in both the limestone and stable sand substrates than in the cobble substrate. In the Apalachicola River Basin, *Elliptoideus sloatianus* was reported from sand in moderate current (Heard, 1979) to sand, fine gravel and muddy sand (Heard, 1975). In this study the survival of *E. sloatianus* was significantly higher in the coarse substrates than in the stable sand substrate, which is inconsistent with previous descriptive observations of the habitat preferences of this species. Clench and Turner (1956) suggested that *E. sloatianus* avoided backwater areas. The relocation site that contained the stable sand substrate was next to an island and out of the main current, which may explain why survival was lower in this habitat.

Elliptio crassidens and *Lampsilis teres* were difficult to recover, either because they died early in the experiments and were washed out of the enclosures, or because they are highly mobile and were able to leave the enclosures. This reduced the precision of estimates of their survival after relocation and limited our abilities to test for differences in survival between the experimental treatments. Although survival of *E. crassidens* was high (1.0 and 0.92) in the limestone and stable sand habitats, substrate type did not appear to have a significant effect on the survival of this species ($p = 0.391$). This is consistent with previous observations that suggest this species may be a habitat generalist, as *E. crassidens* has been reported from a range of substrate types, including mud, sand or fine gravel (Cummings and Mayer, 1992) to muddy sand, sand and rock (Heard, 1979).

Survival of the yellow sandshell, *Lampsilis teres*, ranged from 0.0 to 0.50 among the three substrates. This species was difficult to retrieve, as only seven (15%) of the 48 relocated mussels were found at the end of the experiment. It cannot be determined whether the unrecovered specimens moved, or died and were washed out of the enclosures. A significant treatment effect (i.e. effect of substrate) was not evident for this species ($p = 0.829$), but given the low number of recovered mussels the statistical power of this test may have been too low to detect differences in survival.

Although three (Sheehan *et al.*, 1989; Dunn, 1993; Layzer and Gordon, 1993) of the 33 studies reviewed by Cope and Waller (1995) evaluated the instability of sediments at relocation sites, none of them tested empirically whether mussel survival varied between relocation habitats. In this study we tested Cope and Waller's (1995) assertion that quantitative information on the habitat requirements of unionid mussels would greatly facilitate the identification of suitable relocation sites. Two conclusions were reached that have not been addressed in other relocation efforts. First, we showed empirically that microhabitat was important in the survival of relocated mussels. The conditional probability of survival ranged from complete survival to no survival, depending on the particular microhabitat (i.e. substrate type). Three of the species tested had complete survival in the limestone/sand substrate, while the fourth species had no survival. That habitat preferences differed among species was not surprising, although specific examples of the habitat requirements of individual species based on empirical studies are rare. Habitat requirements are usually based on observational or descriptive data (Clench and Turner, 1956; Heard, 1979).

Secondly, we showed that the type of habitat that mussels should be relocated into varies by species Two of the species, *Elliptoideus sloatianus* and *Megalonaias boykiniana*, appeared to be habitat specialists, while *Elliptio crassidens* appeared to be a habitat generalist. The low number of recovered *Lampsilis teres* made it difficult to evaluate the habitat preferences of this species. Based on the results of this study, *E. sloatianus* and *M. boykiniana* should be relocated into specific habitat types. Relocating *E. crassidens* into specific substrate types may not be as important as for the former two species, and some other factor, such as depth or velocity, may be a more appropriate habitat variable to consider for the purpose of relocation. This conclusion supports Cope and Waller's (1995) speculation that relocation site selection criteria could be developed for individual species if quantitative information on the habitat requirements of individual species were known.

Cope and Waller (1995) concluded that for relocation projects to be more successful as both conservation and management tools, research is needed to develop the criteria for selecting suitable relocation sites. Given our experimental results with relocated mussels, we agree that habitat type at the destination site is important in predicting the success of a relocation project, and that the development of criteria for site selection should be species specific.

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EFFECTS OF HABITAT SUITABILITY ON THE SURVIVAL OF RELOCATED FRESHWATER MUSSELS

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ABSTRACT

Freshwater mussels are often relocated from existing beds for both conservation and management reasons. In this study, we empirically tested whether the habitat type at the destination site was important in predicting the success of mussel relocation. In 1993, four species of freshwater mussels were relocated in the Apalachicola River in Florida, into three distinct habitat types: stable sand, limestone/sand and cobble. The conditional probability of survival of relocated mussels varied by species and habitat. Two species were considered habitat specialists, one species was considered a habitat generalist and recovery rates for the fourth species were too low to assess habitat preferences. We show empirically that microhabitat is important in the survival of relocated mussels and that the habitat-specific criteria for relocation is species specific. These results suggest that survival of relocated mussels can be enhanced if species-specific site selection criteria are developed using quantitative information. © 1997 John Wiley & Sons, Ltd.

KEY WORDS: freshwater mussels; relocation; habitat suitability; microhabitat; survival

INTRODUCTION

Unionid mussels are often relocated from existing beds for both conservation (US Fish and Wildlife Service, 1983; Layzer and Gordon, 1993) and management reasons (Dunn, 1993). Cope and Waller (1995) reviewed 33 relocation projects and found that few projects quantitatively characterized the habitat as a criterion in selecting potential relocation sites. In general, destination sites were often chosen based on descriptive or observational criteria, which Cope and Waller (1995) speculated may be one of the reasons for the generally poor (about 50%) mean survival rate of relocated mussels.

Although it is often assumed that mussels show strong habitat specificity, the results are often ambiguous. Some studies suggest strong habitat specificity (Kat, 1982; Leff *et al*., 1990) while others (Strayer, 1981; Holland-Bartels, 1990; Layzer and Madison, 1995) failed to find statistically significant relationships between mussels and habitat descriptors. Part of this ambiguity may be a result of the paucity of studies (e.g. Huehner, 1987, Bailey, 1989) that have empirically tested for species-specific habitat preference and specificity.

The specific habitat requirements of individual mussel species are generally unknown, although knowledge of these requirements could increase the likely success of relocation efforts (Cope and Waller, 1995). The degree to which a particular species may be a habitat generalist or specialist has generally been overlooked in relocation efforts. In this study we tested Cope and Waller's (1995) assertion that quantitative information on the habitat requirements of unionid mussels could have a direct influence on the survival and successful relocation of individual species.

METHODS

To test the importance of microhabitat in relocation efforts, four species of mussels, *Elliptoideus sloatianus* (I. Lea, 1840), *Elliptio crassidens* (Lamark, 1819), *Megalonaias boykiniana* (I. Lea, 1840) and *Lampsilis*

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teres (Rafinesque, 1820), were relocated from a sand and gravel shoal in the Apalachicola River directly below Jim Woodruff Lock and Dam (river mile 106.3) The shoal was scheduled to be dredged and removed by the US Army Corps of Engineers. Mussels were removed from the dredge site using snorkel and scuba searches during a low flow period from 26 to 28 July 1993. Mussels were placed in wet mesh bags and transported in insulated coolers to and from a temporary field station. Mussels were immediately placed in aerated buckets, separated by species, and given external marks with hand drills. While the mussels were out of water, they were placed on, and covered with, wet burlap sacks. After being marked, mussels were returned to their respective holding buckets until all were processed, which took about 1.5 h.

The effects of microhabitat on mussel survival were examined by transplanting the marked mussels to three sites that contained distinct substrates: (1) stable sand (river mile 104.6) on the east side of an unnamed island; (2) limestone/sand (river mile 105.2); and (3) cobble (river mile 100.4). At each site mussels (four of each species) were placed inside each of four 1 m^2 enclosures. Each mussel was placed with its siphons facing upstream and its body half buried. The enclosures, modelled after those used by Waller *et al.* (1993), were constructed using 5 cm PVC pipes and elbows with holes drilled into the pipes allowing them to fill with water. They were anchored to the substrate with a 1 cm diameter rebar on each side.

Relocated mussels were retrieved and counted in May 1994. Survival was not measured in July 1994 as planned, owing to tropical storm Alberto, which produced a 500-year flood and made the sites inaccessible. Because of the storm's effects, survival was estimated for the 10-month period between July 1993 and May 1994.

STATISTICAL ANALYSIS

In each replicate of the experimental treatments, three measurements were made at the end of the experiment: the number of mussels of each species that died, the number of mussels that survived and the number of mussels that were not recovered from the enclosure. Let the observed values of these three variables in the ith enclosure be $y_{0,i}$, $y_{1,i}$ and $y_{2,i}$, respectively. Because the total number of mussels per enclosure was fixed in advance of the experiment, the observed outcomes were considered to be multinomially distributed with probabilities π_0, π_1 and π_2, in which $\Sigma\pi_j = 1$. For the purposes of analysis these probabilities were parameterized in terms of θ, the probability that mussels survived, given that they were recovered from the enclosure at the end of the experiment, and λ, the probability that mussels were not recovered at the end of the experiment. Given these definitions, the multinomial probabilities can be expressed as follows: $\pi_0 = (1-\theta)(1-\lambda)$, $\pi_1 = \theta(1-\lambda)$ and $\pi_2 = \lambda$. Maximum likelihood estimates of θ and λ could have been computed by maximizing $l(\theta, \lambda)$, the kernel of the log–likelihood function for multinomial outcomes (Mood *et al.*, 1974):

$$l(\theta, \lambda) = \sum_i y_{0,i} \log[(1-\theta)(1-\lambda)] + y_{1,i} \log[\theta(1-\lambda)] + y_{2,i} \log[\lambda]$$

However, this equation can be rearranged to express $l(\theta\ \lambda)$ as the sum of two components, $l(\theta)$ and $l(\lambda)$, in which

$$l(\theta) = \sum_i y_{0,i} \log(1-\theta) + y_{1,i} \log(\theta)$$

and

$$l(\lambda) = \sum_i (y_{0,i} + y_{1,i}) \log(1-\lambda) + y_{2,i} \log(\lambda)$$

Because $l(\theta)$ does not include λ, the conditional probability of survival, θ, can be estimated by conditioning on the number of mussels that were recovered at the end of the experiment and ignoring the

