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## EFFECTS OF HABITAT AND BODY SIZE ON MORTALITY RATES OF *POECILIA LATIPINNA*<sup>1</sup>

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**Abstract.** We examined the effect of body size and habitat on mortality rates of juvenile and adult sailfin mollies (*Poecilia latipinna*) maintained in field cages that excluded predators. Mortality rates and the extent of size dependence varied among years and among seasons within years for juvenile and adult fish. When mortality rates were size dependent, large individuals had much lower mortality rates than small ones. Differences between habitats in mortality rates were present in some experiments but not others. When there were habitat effects under winter conditions, both juveniles and adults had higher survival rates in a saltwater habitat than in a freshwater one. Some adults survived through the winter in all of our experiments. Adult mortality during the growing season exhibited a similar pattern of habitat effects although at lower mortality rates. Juvenile survival to sexual maturity in the growing season showed no consistent effects of habitat. Fish born during the autumn had a much lower probability of survival to sexual maturity than those born in spring or summer, and there was a threshold time beyond which newborn fish were virtually assured of perishing over the winter, presumably due to the inability to achieve a minimum body size capable of withstanding winter conditions.

These experiments illustrate that the net direction of selection on molly body size in any generation depends on events that are stochastic on a yearly scale, such as the climatic severity of the winter and the intensity of predation pressure. Our results illustrate the complex interplay of different sources of selective mortality that operate in natural populations, and highlight the importance of ecological investigations of the different agents of mortality for a predictive understanding of the operation of natural selection.

**Key words:** analysis of variance; demography; habitat; logistic regression; mortality; natural selection; *Poecilia latipinna*; sailfin mollies; size; temporal variation.

### INTRODUCTION

Natural selection, the differential proliferation of phenotypes within a generation, is an ecological phenomenon. Ecological investigations of selective mortality or fertility in natural populations usually uncover multiple causal agents that interact additively, multiplicatively, or in opposition to each other (Kusano 1980, Tilling 1983, Hairston and Walton 1986, Weis and Abrahamson 1986, Miller 1987, Simms and Rausher 1989, Travis 1990). Because individual ecological factors such as predation pressure, abiotic stress, or resource limitation vary temporally and spatially in their impact on natural populations, it is not surprising that most repetitive studies of selection have found extensive temporal and spatial variation in its form and intensity (Berry and Crothers 1970, Hagen and Gilbertson 1973, van Noordwijk et al. 1981a, b, Price et al. 1984, Kalisz 1986, Campbell 1989, Conner 1989, Marquis 1990). Thus, a full understanding of how selection molds the distribution of phenotypic variation within and among populations of a species, which is a

major focus of evolutionary ecology, requires an understanding of each major ecological effect on vital rates, how those effects combine, and how that combination may vary spatially and temporally.

The potential complexity of this problem is especially evident when examining body size variation in the sailfin molly, *Poecilia latipinna* (Poeciliidae). Populations of these fish exhibit dramatic variation in body size in both genders within and among populations (Snelson 1985, Travis and Trexler 1987, Travis 1989) which appears to be maintained by selection (Trexler 1989). Populations differ dramatically in body size distributions on a local scale (comparisons of populations separated by <1–30 km) with only a small amount of additional variation across larger geographic scales (comparisons of groups of populations separated by as much as 800 km; Trexler 1986, Travis and Trexler 1987, Trexler et al. 1990). The average male body size and average female body size are correlated across populations (Travis and Trexler 1987), despite the fact that nearly all of the male body size variation within a population has a genetic basis (size at maturity is a Y-linked trait: Travis et al. 1992; males grow only minimally after completing maturation: Snelson 1984,

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Travis et al. 1989) and female body size variation is produced by post-maturation growth and age structure (Travis et al. 1992; J. C. Trexler and J. Travis, *unpublished data*). Sailfin mollies occupy a range of salt marsh and freshwater habitats along the southeastern coast of the United States from South Carolina, around Florida, and westward and southward along the Gulf Coast into Mexico (Simanek 1978, Lee et al. 1980, Trexler 1986). However, phenotypic plasticity cannot account for the magnitude of local differences in body size distributions in either gender (Trexler and Travis 1990, Trexler et al. 1990). The concordant distributions of male and female body size suggests that the selective agents that act on male size are also acting on female age structure through female size (Trexler 1989).

Several selective pressures have been identified that are likely to be the major causes of the observed patterns, and three of these possibilities involve direct selection on body size. First, abiotic stress, especially in winter conditions, may cause size-specific mortality of adults in some locations. Second, size-selection predation by wading birds, coupled with different risks of such predation in different locations, may mold size distributions. Third, the intensity of the sexual selection that favors larger male body sizes (Baird 1968, Simanek 1978, Luckner 1979, Farr et al. 1986, Travis and Woodward 1989) might vary across locations. The sexual selection hypothesis is problematic in two ways; it can only account for patterns in male size, and sexual selection is almost always "soft" (Wallace 1975), which means that it should be acting on relative size rather than absolute size (see discussion in Farr et al. 1986). The fourth possible selective explanation is that selection acts indirectly on body size through direct action on correlated traits. Age at maturity has a strong positive genetic correlation with body size at maturity (Travis et al. 1992) and is the most likely candidate. Selection on age at maturity can occur in two ways. First, earlier age at maturity will be advantageous in locations with low productivity because individuals that take longer to mature are disproportionately delayed by poor growth conditions (Trexler et al. 1990). Small body sizes will follow as an indirect effect. Second, locations may vary in the ratio of juvenile to adult mortality rates. High average juvenile mortality rates (or highly uncertain juvenile mortality rates) and low average adult mortality rates (or relatively predictable adult mortality rates) can favor delayed maturity (Charlesworth 1980, Stearns and Koella 1986). Selection for delayed maturity will produce larger body sizes as an indirect effect.

In this paper we describe a repetitive series of experiments designed to evaluate the role of abiotic stress as a direct selective agent on adult size and its potential to act as an indirect selective agent on adult size through its effects on juvenile mortality. Other papers address direct selection on age at maturity (Travis et al. 1992), the role of wading bird predation (J. C. Trexler et al.,

*unpublished manuscript*), and the contribution of sexual selection (Farr et al. 1986, Travis et al. 1992).

## MATERIALS AND METHODS

The experimental designs that follow test the hypothesis that abiotic stress can potentially influence adult size distributions by size-specific mortality patterns in adult or juvenile sailfin mollies. We have repeated both experiments as frequently as was feasible in anticipation of meaningful annual and seasonal variation. No attempt was made to conduct equal numbers of either juvenile or adult experiments across seasons or years; this was impossible based on the availability of animals and logistics involved in conducting these experiments. We do not envision our results as one factorial experiment. Instead, we report a collection of eight independent studies that are especially informative when considered collectively.

### *The experimental system*

Our studies were conducted in field cages maintained in two ponds in the St. Marks National Wildlife Refuge on the Gulf Coast of north Florida (Wakulla County). One of these ponds was a marshy freshwater location and the other an impounded salt marsh. Sailfin mollies are primarily herbivorous (Harrington and Harrington 1961) and in our experiments they fed on vegetable matter that grew in the cages. The ponds differ in a variety of ecologically important characteristics (Table 1) and represent the extremes of habitats in which sailfin mollies occur in north Florida (Trexler and Travis 1990). These environmental differences generate the strength and weakness of our experimental approach. They render us unable to attribute our results to any one environmental source, the approach's weakness, but the overall pattern of mortality we observe should be of broad relevance to the range of habitat effects on molly mortality patterns in nature, which is the approach's strength.

Cages were constructed of a frame covered by linear-polyethylene screen and were 75 cm long by 75 cm wide by 90 cm high and were maintained in water with a depth of approximately 60 cm. After each experiment we removed the cages from the ponds, reinforced all of their seams, scrubbed off the accumulated algae, and left them standing dry for a short time to "disinfect" them of accumulated colonizing invertebrates. In all cases, the placement of fish in cages was conducted to avoid bias from microenvironmental gradients in our study area.

Fish of different standard lengths differ in the quantity of somatic tissue present and may also differ in body composition. We used standard length as a conservative assay of size because it can be easily measured in the field with minimal handling of the fish. Live masses are susceptible to variation in water content, which could introduce bias in comparison of fish from

TABLE 1. The ranges of temperature and salinity recorded at our study sites during each experiment and sample sizes. Life stage refers to the age category studied in a particular experiment: J = juvenile, A = adult.

| Experiment  | Life stage | Freshwater pond  |                    |           | Saltwater pond   |                    |           |
|-------------|------------|------------------|--------------------|-----------|------------------|--------------------|-----------|
|             |            | Temp. range (°C) | Salinity range (‰) | No. cages | Temp. range (°C) | Salinity range (‰) | No. cages |
| Summer 1983 | J          | 23–31            | 0                  | 22        | 22–35            | 14–18              | 21        |
| Summer 1984 | J          | 24–29            | 0                  | 30        | 24–34            | 7–33               | 30        |
| Winter 1984 | J          | 10–25            | 0                  | 29        | 11–32            | 25–30              | 28        |
| Winter 1985 | A          | 10–19            | 0                  | 12        | 10–25            | 24–27              | 12        |
| Summer 1985 | J          | 20–31            | 0                  | 34        | 24–34            | 26–38              | 35        |
| Winter 1987 | A          | 12–16            | 0                  | 15        | 10–16            | 7–16               | 15        |
| Winter 1988 | A          | 9–19             | 0                  | 8         | 7–19             | 12–27              | 6         |
| Summer 1987 | A          | 26–32            | 0                  | 11        | 29–34            | 21–25              | 11        |

salt and freshwater habitats, and cannot be easily obtained in the field.

#### *Study of juveniles*

We raised sailfin mollies from birth to sexual maturity and censused them weekly starting at 3 wk of age. These fish were the offspring of field-caught, gravid females. The offspring of several different females from a population were used in each experiment, and females were collected from at least two different populations. The newborn fishes from each female were divided into two groups, one for the freshwater pond cages and one for the saltwater pond cages. Three broodmates were raised in each cage and members of each brood were placed in three different cages in each pond for a total of 18 fish per brood raised (except in 1983 when 5 broodmates were placed in each cage for a total of 30 fish per brood). The number of cages used per experiment varied with the number of families used in each experiment (Table 1). The experiment was repeated in the summers of 1983, 1984, 1985, and fall of 1984. It was difficult to obtain gravid females for the fall 1984 experiment because few females reproduce in the fall. Thus, gravid females could be obtained from only one population prior to 18 October and only from a second and third population after that date. Therefore, population of origin and date of birth are confounded in that experiment. Additional details on the ponds used for the study, the sources of the fish, and analysis of growth and maturation of surviving fish are reported elsewhere (Trexler and Travis 1990).

#### *Study of adults*

We collected sailfin mollies from natural populations and maintained them in our field cages to determine how size and environment influenced their probability of survival. We repeated this experiment in both winter and summer conditions: winter 1984–1985, 1986–1987, 1987–1988, and summer 1987. In each experiment we placed four fish that were distinguishable by size in each cage. These fish were drawn randomly from a group of fish collected the day before and assigned to one of four size classes (small, medium, large, jumbo).

We could not collect enough fish of the various size classes needed from any one population. Therefore, we pooled fish collected from several adjacent populations and chose them randomly with respect to origin for placement in cages. We pooled fish from only estuarine habitats to minimize the effect of large differences among individuals in genetic and acclimatory background (Endler 1986). The number of cages used in each experiment varied among years depending on the availability of fish in each size class (Table 1).

It was necessary that the size classes differ among experiments because the range and distribution of fish sizes available from field populations varied among years. The size ranges used were: 1984–1985, small 23–30, medium 31–40, large 41–50, jumbo 51–70 mm; 1986–1987, small 21–30, medium 35–45, large 46–55, jumbo 56–71 mm; 1987–1988, small 33–40, medium 41–50, large 51–55, jumbo 56–66 mm; summer 1987, small 23–35; medium 36–45; large 46–55; jumbo 56–61 mm. In two or three cages each experiment, it was necessary to expand the size class definition for one class and use relatively small individuals of the next larger size class to spread the sizes of fish in a cage evenly. For example, when a relatively large “small” was used, a relatively large “medium” was needed. If no such fish was available, it may have been necessary to use a relatively small “large” fish as the “medium” one. This occurred because fish within each size class were not equally abundant in field populations. We avoided expanding the size ranges whenever possible even though our repeated-measures analytical approach controlled for such differences among cages by making all size comparisons based on relative size within individual cages (see *Data analysis*, below).

Adult sailfin mollies, especially males, grow very little in summer (Snelson 1982, Travis et al. 1989) and not at all in the winter, so that we could always identify individuals within each cage. We censused the fish every other week in the winter and weekly during the summer, to determine which individuals had survived since the last census period. During the summer experiment the fish were reproducing. All newborns were removed from the cages at each census to prevent

crowding effects. In all winter experiments, the experiment was terminated when all of the fish in one cage were dead, in order to avoid bias from right-censored data (i.e., cases where sample size is inversely correlated with longevity; Manly 1985). Mortality rates were so low in the summer experiment that this endpoint was not reached before the end of summer conditions.

There is evidence that mortality rates may differ between the sexes in sailfin mollies (Snelson and Wetherington 1980). If our experimental design were to confound sex with size, then we might mistakenly identify a difference between sexes in mortality rates as a difference among size classes. We could not always obtain enough specimens of both sexes in all sizes to study the independent effects of sex and size on survival rates. We randomized the sex of fish in each size category as completely as our supply of fish permitted. We have compared the survival scores (see *Data analysis*, below) of males and females of the same size in each experiment. In all but one case, there was no difference in survival scores between males and females when compared by a Student's *t* test. In one of the experiments, winter 1984–1985, small males had higher survival probabilities than small females, but large males had lower survival probabilities than large females. Thus, no consistent evidence of bias from sex-specific mortality rates is evident in our data.

#### *Data analysis*

*Juvenile survival.*—The juvenile survival experiment provided weekly estimates of the probability of survival for fish from different populations in two different environments. We focused our attention on the dependent variables: probability of survival to 3 wk of age, and probability of survival to sexual maturity. In both cases, the data were counts of the number of fishes surviving in a cage, ranging from 0 to 3. Our analyses are designed to account for the discrete nature of these data.

The probability of survival to 3 wk of age was examined through a nested analysis of variance (ANOVA) with the angularly transformed dependent variable. This transformation is adequate for approximating normality in proportions in some cases (Cox 1970). We used the following formula to transform proportions, and to adjust for 0 and 100% survival:

$$p' = \frac{1}{2} \{ \arcsine[x/(n+1)]^2 + \arcsine[(x+1)/(n+1)]^2 \},$$

where  $p'$  is the transformed probability of survival,  $x$  is the number of fish that survive, and  $n$  is the initial number of fish in the cage. The variance among families was nested within populations in the statistical model employed. (This nesting precluded the use of log-linear models in analyzing these data; Harville and Mee 1984.) The denominator of the hypothesis test for population heterogeneity was the variation among families within population. The hypotheses of envi-

ronmental main effects and environment  $\times$  population interactions were tested over the (family within population)  $\times$  environment interaction. We report the "effect size," the ratio of treatment sum of squares to the appropriate error sum of squares, as an indication of the size of treatment effects because of the unbalanced nature of our design (Rosenthal and Rosnow 1985).

We employed logistic regression to explore how parental population, environment of rearing, and size at 3 wk of age influenced the probability of survival from 3 wk of age to sexual maturity (Hosmer and Lemeshow 1989). We were not interested in documenting family differences in this case, and tests of logistic regression models including family as a categorical independent variable, though not accounting for its nesting within population, did not indicate that it explained much of the variation observed. Logistic regression entails testing a hierarchy of statistical models and obtaining a final model based on the change in the log-likelihood ratio as each term is sequentially removed. The terms retained in the final model are those that yield a significant change in the log-likelihood ratio upon removal (Hosmer and Lemeshow 1989). The LOGIT module of the statistical package SYSTAT (Wilkinson 1990) was used for this analysis.

*Adult survival.*—Adult survival was measured in our experiments by assigning a score to each fish based on the number of census periods it survived. These scores were derived from the overall mortality rate for each census period, so that survival through periods of high overall mortality gave an individual a higher score than survival through periods of low mortality. The survival scores were scaled so that survivors of the first census period received a score of 1.0 and all individual subsequent scores were greater or less than one depending on the overall mortality rates relative to the first census period. Our scores were obtained by the formulae:

$$u_i = d_i/c_i, \quad r_i = u_i/u_1, \quad \text{and} \quad s_j = \sum_{i=1}^j r_i,$$

where  $d_i$  is the number of fish that died during interval  $i$  across all sizes and both environments,  $c_i$  is the number of fish alive at the start of interval  $i$ , which makes  $u_i$  the mortality rate at time interval  $i$ . The parameter  $r_i$  is the mortality rate of period  $i$  relative to that of the first census interval, and  $s_j$  is the cumulative weighted mortality rate up to interval  $j$ . The score  $s_j$  was assigned to each fish based the census in which it was found dead. A score of zero was assigned to those that failed to survive to the first census.

We analyzed the scores as a measure of survival for the fish of each size within each cage. The experimental unit was the cage and "fish" was a repeated measure, because the fate of each fish inside each cage was not necessarily independent of that of its cagemates. We used a repeated-measures univariate analysis of variance (ANOVA) when assumptions of this approach

were met (Tabachnick and Fidell 1983:228). These are that the variance of scores for each size fish within environments was equal (homogeneity of variance assumption) and that correlations among levels of size are constant over all combinations of levels (sphericity assumption). When either assumption was violated, we employed a multivariate analysis of variance (MANOVA) for hypothesis tests because it does not require these assumptions. The univariate test is preferred because it has greater statistical power than the multivariate approach. We chose not to test statistically for evidence of optimizing selection (Travis 1989) by examining changing patterns of variation (Manly 1985: 55–66) because our sample size in each cage was small. However, our approach permits us to determine if selection is directional or optimizing by examination of graphs of our survival scores relative to fish size. Concave patterns would be indicative of optimizing selection.

*Adult selection differential.*—The effect of selection may vary over short time periods. We tested for such “bouts” of selection using the selection differential ( $S$ ; Falconer 1981:171–177) as a measure of the effect of selection between census periods. The selection differential

$$S = \bar{X}_i - \bar{X}_{i-1},$$

where  $\bar{X}_i$  is the mean size of fish in a cage at census  $i$ . The selection differentials calculated for each cage were analyzed in a profile analysis (Timm 1975) to test for changes over time and between habitats. The profile analysis is similar to the multivariate approach for analysis of repeated measures data described earlier, but employs contrasts to test specified hypotheses of temporal change. We tested for differences between adjacent census periods as an a priori hypothesis. Growth by fish, especially females, during the summer 1987 experiment precluded the analysis of the short-term effect of selection on body size in those data.

## RESULTS

### *Juvenile survival*

Most juvenile mortality occurred prior to 3 wk of age (Table 2). The probability of survival through the first 3 wk varied among families (Fig. 1). In three of the four experiments the probability of survival differed significantly among families within populations (nested ANOVA: 1983,  $F_{6,28} = 3.71$ ,  $P = .008$ ; fall 1984,  $F_{6,39} = 4.05$ ,  $P = .003$ ; 1985,  $F_{10,45} = 5.08$ ,  $P < .001$ ), and this source accounted for  $\approx 30\%$  of the total variation in probability of survival each time. Family differences in survival were inconsistent between environments (family  $\times$  environment interaction) in summer 1984 and 1985 experiments (nested ANOVA:  $F_{9,38} = 2.81$ ,  $P = .012$  and  $F_{10,45} = 3.37$ ,  $P = .002$ , respectively). Thirty-six and 23% of the total variation were attributable to this interaction in 1984 and 1985,

TABLE 2. The number of fish alive at the outset of each age interval ( $n_i$ ) and number dying during that interval ( $d_i = n_i - n_{i+1}$ ) by environment. The summer 1983 experiment is excluded because of its short duration.

|             |       | Time (weeks) |    |    |    |    |    |    |
|-------------|-------|--------------|----|----|----|----|----|----|
|             |       | 0            | 3  | 4  | 5  | 6  | 7  | 8  |
| Summer 1984 |       |              |    |    |    |    |    |    |
| Freshwater  | $n_i$ | 90           | 62 | 57 | 52 | 45 | 39 | 38 |
|             | $d_i$ | 28           | 5  | 5  | 7  | 6  | 1  |    |
| Saltwater   | $n_i$ | 90           | 57 | 50 | 43 | 38 | 36 | 34 |
|             | $d_i$ | 33           | 7  | 7  | 5  | 2  | 2  |    |
| Fall 1984   |       |              |    |    |    |    |    |    |
| Freshwater  | $n_i$ | 69           | 35 | 19 | 9  | 7  | 5  | 4  |
|             | $d_i$ | 34           | 26 | 10 | 2  | 2  | 1  |    |
| Saltwater   | $n_i$ | 75           | 42 | 19 | 18 | 16 | 16 | 16 |
|             | $d_i$ | 33           | 23 | 1  | 2  | 0  | 0  |    |
| Summer 1985 |       |              |    |    |    |    |    |    |
| Freshwater  | $n_i$ | 102          | 80 | 74 | 69 | 66 | 62 | 59 |
|             | $d_i$ | 22           | 6  | 5  | 3  | 4  | 3  |    |
| Saltwater   | $n_i$ | 114          | 70 | 52 | 38 | 37 | 37 | 28 |
|             | $d_i$ | 44           | 18 | 14 | 1  | 0  | 9  |    |

respectively. In 1984, the families with the highest survival and those with the lowest survival switched ranks between the two environments (Fig. 1). As a general statement, differences among families, either as a main effect or an interaction with habitat, account for 50–60% of the variation in survival from birth to 3 wk of age. The range of probability of survival varied among families over two- (1983: 0.4 to 0.80) to five- (1985: 0.15 to 0.80) fold and was similar for each experiment in both habitats studied. No differences between populations or environments were observed in any year of the study.

The probability that a fish survived from age 3 wk to sexual maturity in the summer of 1984 was related to its size at 3 wk of age (Fig. 2). The hypothesis that the coefficients of size equalled zero was rejected ( $\chi^2 = 15.1$ ,  $df = 3$ ,  $P < .005$ ). Approximately 60% of the fish alive at 3 wk survived to sexual maturity in this experiment (Table 2).

In the summer of 1985 survivorship was significantly different between environments. The hypothesis that the coefficients of the independent variable (environment) equalled zero was rejected ( $\chi^2 = 28.5$ ,  $df = 6$ ,  $P < .001$ ). In this experiment, all fish alive at 3 wk of age survived to sexual maturity in 17 of 31 cages in the freshwater pond, while this occurred in only 12 of 31 cages in the saltwater pond. Conversely, in only 1 cage out of 31 in the freshwater pond did all fish alive at 3 wk of age die prior to sexual maturity, while all fish died in 14 of 31 cages in the saltwater pond. Approximately 74% of the fish alive at 3 wk survived to sexual maturity in freshwater, while only 40% of those alive at 3 wk survived to sexual maturity in the saltwater pond (Table 2).

In the experiment begun in the autumn of 1984, fish

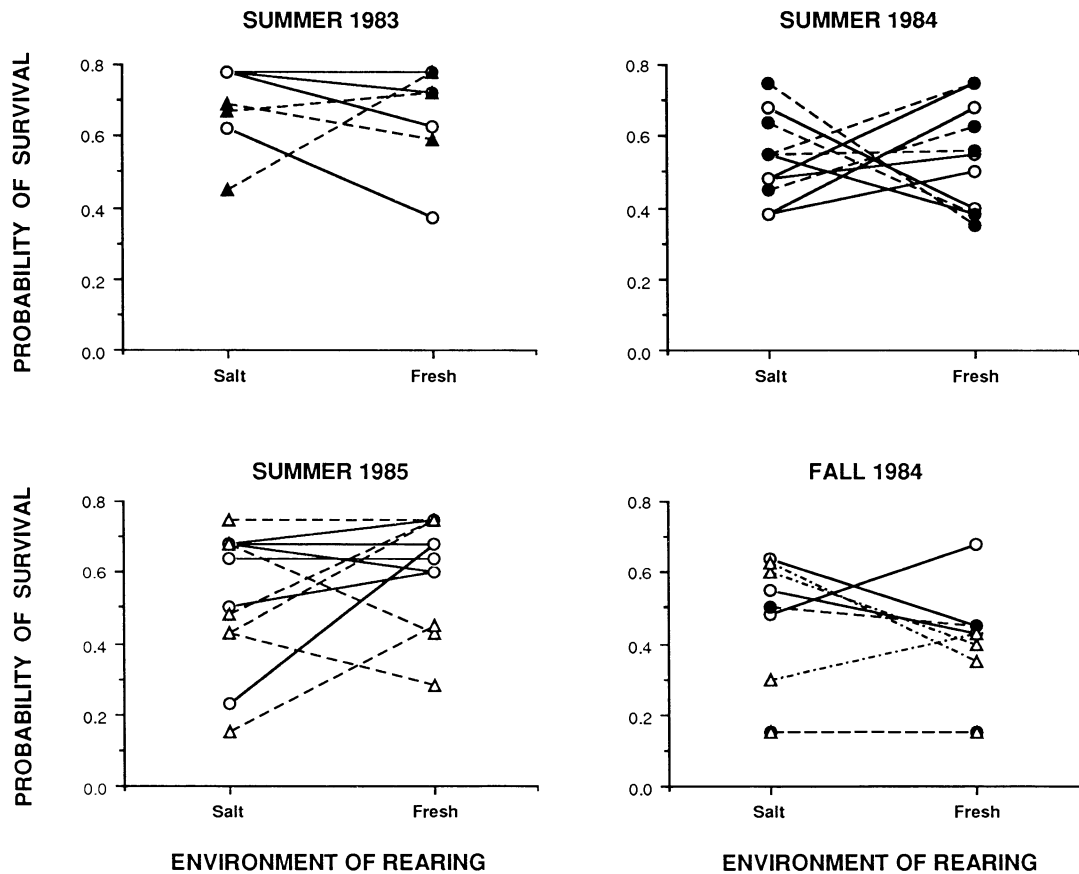


FIG. 1. Plots of the relationship between rearing environment and probability of survival to 3 wk of age, by family group and source population. Family averages are plotted. Open symbols indicate the offspring of fish collected from a saltwater habitat and closed symbols indicate offspring of fish collected from a freshwater habitat. Dashed and solid lines connect family averages from different populations. Plots with open circles and triangles indicate that fish from two different saltwater habitats were used.

born later had a lower probability of survival through the winter than those born earlier. All fish in this study born on or before 18 October were offspring of females from one population, while those born later were from two other populations. We use this confounding of

birth date and source to demarcate early and late autumn births, because there was no evidence in our other experiments that population of origin accounted for a significant fraction of the variance in probability of juvenile survival. All fish born in late autumn died

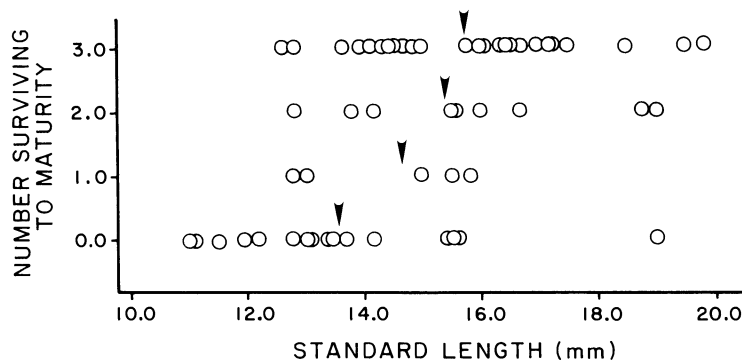


FIG. 2. The relationship of the number of fish in field cages surviving to sexual maturity and their average size at 3 wk of age. Results from summer 1984 experiment are plotted. Arrows indicate the average size of fish with each level of survivorship.

TABLE 3. Summary of results from univariate analysis of variance of transformed probability of survival scores. An asterisk indicates that data violate sphericity assumption in Bartlett's test. The effect size is the ratio of the treatment sum of squares to the error sum of squares.

| Experiment        | Factor             | Sum of squares | F      | df   | P    | Effect size |
|-------------------|--------------------|----------------|--------|------|------|-------------|
| Winter 1984–1985  | environment        | 315.593        | 14.091 | 1,22 | .001 | 0.640       |
|                   | size               | 73.914         | 1.796  | 3,66 | .156 | 0.082       |
|                   | size $\times$ env. | 10.107         | 0.246  | 3,66 | .864 | 0.011       |
| Winter 1986–1987  | environment        | 0.332          | 0.263  | 1,28 | .612 | 0.009       |
|                   | size               | 8.766          | 5.625  | 3,84 | .001 | 0.201       |
|                   | size $\times$ env. | 10.656         | 6.839  | 3,84 | .001 | 0.244       |
| Winter 1987–1988* | environment        | 123.943        | 5.169  | 1,12 | .042 | 0.431       |
|                   | size               | 39.242         | 0.840  | 3,36 | .481 | 0.070       |
|                   | size $\times$ env. | 58.942         | 1.261  | 3,36 | .302 | 0.105       |
| Summer 1987*      | environment        | 46.038         | 13.386 | 1,20 | .002 | 0.669       |
|                   | size               | 42.068         | 4.428  | 3,60 | .007 | 0.221       |
|                   | size $\times$ env. | 17.046         | 1.794  | 3,60 | .158 | 0.090       |

before 1 January. Forty percent (12 of 30) born in early autumn survived to 1 January in the saltwater pond, and 7% (2 of 30) survived to that time in the freshwater pond. These fish were born between 1 September and 18 October and were the progeny of three different females from the same population. The proportion of fish surviving to 1 January and born in early autumn differs between the fresh and saltwater ponds (test of difference between two proportions:  $A = 3.05$ ,  $P = .001$ ; Brown and Hollander 1977:180). No fish born in late autumn (0 of 57 in freshwater and 0 of 54 in saltwater) survived until 1 January. The fish born in late autumn were the progeny of two females from a second population (born on 27 October and 11 November) and three females from a third population (born between 26 October and 5 November). The mothers of these fish were collected as gravid from their natural habitats and would have given birth at the same time in nature.

#### Adult survival

In the winter of 1984–1985 we observed a 55% mortality rate during the 6-wk study period (53 of 96 fish died). A 30% mortality rate was noted in the saltwater pond, while an 81% mortality rate was noted in the freshwater pond. The sphericity assumption was not violated for these data and the results of univariate ANOVA and MANOVA were consistent. The prob-

ability of survival in the saltwater pond was significantly higher than in the freshwater one (Table 3; Fig. 3). To provide a statistically more powerful analysis, we analyzed size separately by environment, but still did not find it to be significant (Table 4).

In the winter of 1986–1987 our experiment was conducted over a 10-wk period with an overall mortality rate of 34% (41 out of 120 fish died). The level of mortality was equally distributed between the environments (37% mortality in the saltwater pond and 32% mortality in the freshwater pond). The assumptions of univariate analysis were not violated in these data and the results of univariate and multivariate analyses were consistent. Environmental differences were not significant as a main effect but did influence the survival of members of the size classes differently (environment  $\times$  size interaction, Table 3). In addition to the environment effect, the life expectancy of fishes differed with respect to body size (size effect, Table 3). Analysis of the size effect separately by environment indicated that it was significant in the saltwater pond but not in the freshwater pond (Table 3; Fig. 3).

In winter 1987–1988, the experiment lasted 13 wk and 45% of the fish placed in cages failed to survive to the end of the experiment (29 of 56). The mortality rate in the saltwater pond was 21%, while that of the freshwater pond was 75%. The sphericity assumption

TABLE 4. Summary of univariate analysis of fish size on transformed probability of survival, with each experimental environment considered separately. An asterisk indicates that data violate sphericity assumption in Bartlett's test. The effect size is the ratio of the treatment sum of squares to the error sum of squares.

| Experiment       | Environment | Sum of squares | F      | df   | P    | Effect size |
|------------------|-------------|----------------|--------|------|------|-------------|
| Winter 1984–1985 | saltwater   | 43.537         | 0.879  | 3,33 | .462 | 0.080       |
|                  | freshwater  | 40.484         | 1.236  | 3,33 | .312 | 0.112       |
| Winter 1986–1987 | saltwater   | 18.748         | 11.765 | 3,42 | .001 | 0.840       |
|                  | freshwater  | 0.674          | 0.443  | 3,42 | .724 | 0.032       |
| Winter 1987–1988 | saltwater*  | 54.925         | 0.932  | 3,15 | .449 | 0.186       |
|                  | freshwater  | 41.314         | 1.086  | 3,21 | .377 | 0.155       |
| Summer 1987*     | saltwater*  | 7.537          | 1.586  | 3,30 | .213 | 0.159       |
|                  | freshwater* | 51.577         | 3.620  | 3,30 | .024 | 0.362       |



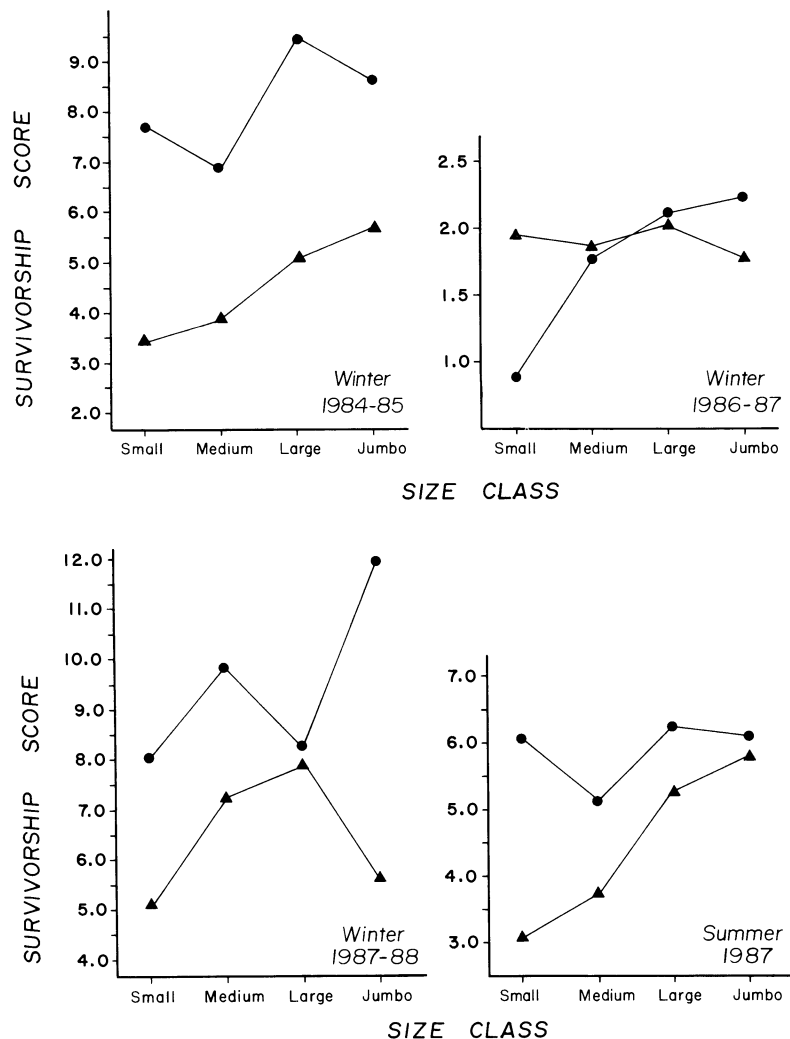


FIG. 3. Plots of survivorship scores by size class for adult survival experiments. Survivorship scores indicate the relative length of survival in experimental cages. ● results for fish maintained in a saltwater pond; ▲ results for fish maintained in a freshwater pond.

was violated (Bartlett's test = 8.313 with 3 df,  $P = .04$ ), but the results of both univariate and multivariate analyses agreed. Only the effect of environment was significant (MANOVA: environment  $F_{1,12} = 5.169$ ,  $P = .042$  and Table 3); fish of all sizes had a longer life expectancy in the saltwater pond than the freshwater one (Fig. 3). No significant effect of size was detected (MANOVA: freshwater, Wilks'  $\lambda_{3,5} = 0.480$ ,  $P = .263$ ; saltwater, Wilks'  $\lambda_{3,3} = 0.500$ ,  $P = .500$  and Table 3) when size was analyzed separately for each environment to increase the statistical power of the hypothesis test.

Survivorship was much higher in the summer 1987 experiment than in any of the winter ones. The mortality rate for the summer experiment was 31% (27 of 88 fish died). Forty-one percent (18 of 44) of the freshwater fish and 14% (6 of 44) of the saltwater fish failed

to survive the duration of the summer in our cages (23 May–19 August,  $\approx 13$  wk). One of the assumptions of the univariate analytical approach was violated (Bartlett's test of sphericity = 29.8, with 3 degrees of freedom,  $P < .001$ ), so a multivariate approach was required. There was a significant difference in the probability of survival between the two ponds (MANOVA: environment  $F_{1,20} = 46.038$ ,  $P = .002$ ), with fish in the saltwater pond surviving the longest (Fig. 3). There appeared to be an effect of size on probability of survival, also, but this was not significant by the conservative multivariate approach (MANOVA: size Wilks'  $\lambda_{3,18} = 0.736$ ,  $P = .129$ ; size  $\times$  environment Wilks'  $\lambda_{3,18} = 0.822$ ,  $P = .306$ ). Univariate analysis did indicate size to be significant (Table 3), but must be viewed with caution. When analyzed separately by environment, size is not significant in explaining survival

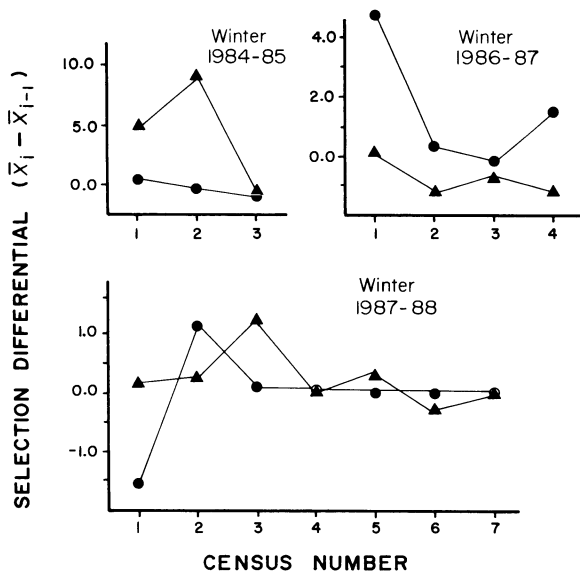


FIG. 4. The average selection differential by census period in winter experiments, where  $\bar{X}_i$  = the mean size (in millimetres) of fish in cage  $i$ . Census periods were 2-wk intervals. Positive values indicate that the average size in cages increased after selection, i.e., that small individuals were less likely to survive that census period. ● data from cages in the saltwater pond; ▲ data from cages in the freshwater pond.

in the saltwater pond, but may be significant in the freshwater one (Table 4). However, the sphericity assumption is violated by these data so that this result remains uncertain. Size was not significant in the freshwater pond when analyzed by the less powerful but more appropriate multivariate test (Wilks'  $\lambda_{3,8} = 0.662$ ,  $P = .322$ ).

There was little indication of optimizing selection for size (Fig. 3). When size-selective mortality was statistically significant, it was always in the direction of favoring large fish. Though the selection documented was directional, the fitness function was not always strictly linear, and there was usually a group of phenotypes with roughly equivalent fitness. The only indication of optimizing selection was in freshwater in 1987–1988, but it was not significant. Thus, our overall conclusion is that when selection occurred, it was directional in favor of larger fish, though probably not uniformly increasing across the range of fish size.

**Adult selection differential.**—Profile analysis revealed that selection against relatively small fish occurred in pulses only in the winter of 1986–1987 (Fig. 4). In the winter of 1986–1987, the first period differed from the second (linear contrast:  $F_{1,25} = 8.25$ ,  $P = .008$ ), but subsequent periods did not vary (linear contrasts: period 2 vs. 3,  $F_{1,25} = 0.86$ ,  $P = .362$ ; period 3 vs. 4,  $F_{1,25} = 0.61$ ,  $P = .443$ ). No comparisons indicated heterogeneity between the two study habitats in the selection differential (linear contrasts: period 1 vs. 2,  $F_{1,25} = 1.89$ ,  $P = .181$ ; period 2 vs. 3,  $F_{1,25} = 0.01$ ,  $P = .972$ ; period 3 vs. 4,  $F_{1,25} = 1.93$ ,  $P = .177$ ). During the

winter 1984–1985 experiment the average selection differential was quite different in the 2nd wk of study from that of the 1st and 3rd week in the freshwater pond. However, much inter-cage variation in this pattern rendered it statistically insignificant. Profile analysis of the winter 1987–1988 data was precluded because a large number of zeros (no change in mean size) produced rounding errors in the calculations (SYSTAT, MGLH module). Examination of the individual values indicate that biweekly changes are not likely to differ from zero (Fig. 4).

We observed no relationship between the effect of selection and the mortality rate using linear regression ( $t_{1,20} = 0.25$ ,  $P = .803$ ; Fig. 5). Both variables were transformed by taking logarithms to better fulfill the assumptions of this analysis. The residuals of this regression were funnel patterned (Zar 1984:288–289), but no transformation alleviated this problem any better than logarithms. Analysis of the absolute value of the selection differential relative to mortality rate gave similar results. Summer data were excluded from this analysis.

## DISCUSSION

Our studies of sailfin mollies provide another example of how mortality rates produced by one class of effects (abiotic stress, broadly construed) vary temporally and spatially. The data on adult mortality illustrate this well. The effects of varying mortality levels generated weekly mortality rates that varied across years and habitats from 1.6 to 13.5% (Table 5). The chief source of variation in weekly mortality rates is the freshwater habitat, in which rates varied nearly four-fold across the 3 yr. Mortality rates in the saltwater habitat were much more circumscribed. In one winter the mortality rate over the entire experiment was similar in the two habitats (37% in saltwater and 32% in freshwater in 1986–1987), but mortality in the two habitats differed dramatically in the other winters (salt-

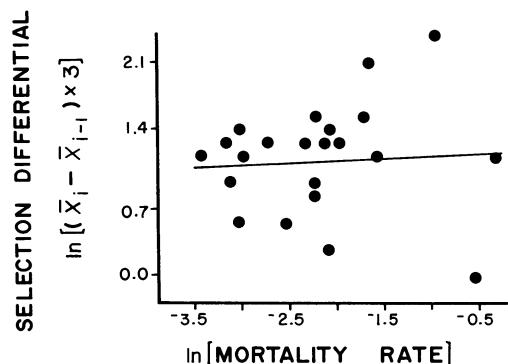


FIG. 5. The relationship of the average selection differential, where  $\bar{X}_i$  is the mean size (in millimetres) of fish in cage  $i$ , to the mortality rate at that time. Census periods with no mortality were excluded from this analysis. The line indicates the fit of a linear regression model to these data.

TABLE 5. Percent mortality per week by age of fish used in each experiment. FW indicates fish in freshwater and SW indicates fish in saltwater. The summer 1983 experiment with juveniles is excluded because of its short duration.

| Age group | Habitat | Season | Year      | Mortality rate<br>(% per week) |
|-----------|---------|--------|-----------|--------------------------------|
| Juvenile  | FW      | Summer | 1984      | 7.2                            |
| Juvenile  | FW      | Summer | 1985      | 5.3                            |
| Adult     | FW      | Summer | 1987      | 3.2                            |
| Juvenile  | SW      | Summer | 1984      | 7.8                            |
| Juvenile  | SW      | Summer | 1985      | 9.4                            |
| Adult     | SW      | Summer | 1987      | 1.0                            |
| Juvenile  | FW      | Winter | 1984–1985 | 11.8                           |
| Adult     | FW      | Winter | 1984–1985 | 13.5                           |
| Adult     | FW      | Winter | 1986–1987 | 3.2                            |
| Adult     | FW      | Winter | 1987–1988 | 5.8                            |
| Juvenile  | SW      | Winter | 1984–1985 | 9.8                            |
| Adult     | SW      | Winter | 1984–1985 | 5.0                            |
| Adult     | SW      | Winter | 1986–1987 | 3.7                            |
| Adult     | SW      | Winter | 1987–1988 | 1.6                            |

water mortality in 1984–1985 and 1987–1988 was 30 and 21%, respectively, while freshwater rates in the same years were 81 and 75%).

In contrast, average juvenile mortality rates in summer varied much less on a weekly basis, whether examined in the first 3 wk (Fig. 1) or from age 3 wk to maturity (Table 5). These rates are only slightly lower than juvenile mortality rates in winter. The weekly winter mortality rates of juveniles in the year in which we examined them were twice that of the adults censused contemporaneously in the saltwater habitat and comparable to those of adults in the freshwater habitat.

An analysis of variance on the average weekly mortality rates of juveniles and adults in each season in each habitat (averaging replicates from Table 5 before analysis of the eight averages) revealed that the dichotomy between adults and juveniles accounted for the largest fraction of the variance, 51%. The seasonal differences, summer vs. winter, accounted for 22% of the variance. Habitat differences accounted only for 9% of the variance, which left 18% of the variance attributable to the various interactions among the main effects. This analysis indicates that the impact of habitat type (freshwater vs. saltwater) is largely through its interaction with other effects and not as a factor alone that is likely to account for large demographic differences among populations.

We can propose a qualitative synthesis of these mortality patterns if we combine the data in this paper with previous work (Snelson 1984, Travis et al. 1989, Trexler and Travis 1990, Trexler et al. 1990). Juvenile mortality rates may vary with habitat type in summer, but generally vary little across years. In saltwater, most juveniles are likely to achieve maturity before winter conditions arrive; juveniles born late in the season are at severe risk of winter mortality and this effect may exert an indirect selective pressure against late breed-

ing. Individuals destined to be large males may enter winter as very large juveniles if they were born later in the season and will have the mortality risk of small to medium adults. In freshwater, juvenile growth and development is much slower and the "deadline" for birth in order to achieve maturity by the onset of winter is probably earlier unless such habitats are more productive, which would compensate for the increased demand metabolism induced by low salinities. Individuals that have not matured by the onset of winter in freshwater are quite likely to die. For adults, winter conditions bring increased mortality rates over those in summer in the same habitats. Freshwater mortality rates in winter may be much higher than those in saltwater, but this effect will vary from one year to the next.

The cause of winter mortality may be traceable to energy stress. Teleost fish decrease feeding rates at lower temperatures (Lemons and Crawshaw 1985, Prentice 1989) and rely heavily on endogenous energy stores, primarily triacylglycerols, for catabolism (Moerland and Sidell 1981). Sailfin mollies would be expected to require more energy in freshwater at a given temperature because their osmotic system is inefficient in freshwater (Evans 1973, 1975, Gustafson 1981). The lower feeding rates and reduced primary productivity typical of winter conditions may place a premium on the use of stored energy, especially in the more stressful freshwater habitat. Teleosts respond to energy demand and inability to feed by mobilizing stored triacylglycerols in the viscera (Idler and Bitners 1960, Ince and Thorpe 1976, Jezierska et al. 1982, see also reviews by Greene and Selivonchick 1987, Henderson and Tocher 1987). Death from insufficient energy stores has been shown in laboratory experiments (e.g., Newsome and Leduc 1975) and implicated in size-specific mortality patterns in other teleost fish of comparable body size to sailfin mollies (Conover and Ross 1982, Conover 1984, Henderson et al. 1988). If mollies are unable to sequester enough stored energy before winter they are less likely to survive a harsh winter in water of low salinity. The slower growth and lengthened development time of mollies in low salinities (Trexler and Travis 1990, Trexler et al. 1990) might be indicative of lowered scope for growth in those conditions and consequently reduced ability to sequester energy reserves. However, low salinity habitats that are high in productivity may allow the acquisition and retention of considerable stored energy, so correlations of mortality rates with habitat type should probably classify habitats on the basis of scope for growth, and not solely on the basis of productivity or the demand placed on the animal (Trexler 1989).

When size-specific mortality occurred, larger fish were favored, which is a result found in many other studies of comparably sized teleost fishes (Hunt 1969, Oliver et al. 1979, Toney and Coble 1979, Shuter et al. 1980, Conover and Ross 1982, Henderson et al. 1988, Post

and Evans 1989). In two cases (Conover 1984, Johnson and Evans 1991) experimental investigations have confirmed that larger fish were more likely to survive prolonged exposure to cold temperatures. Gradual losses of dry mass often occur in these species through the winter, which implicates energy stress (Conover and Ross 1982). In one case (Henderson et al. 1988) greater fat stores in larger fish were implicated as the determinant of enhanced survival probability. This result is not surprising; other fish in similar habitats decrease feeding rates at low temperatures (e.g., Prentice 1989) and rely on endogenous energy stores, primarily triacylglycerols, for catabolism (Moerland and Sidell 1981). Juvenile fish, which have little stored lipid, are especially susceptible to this source of mortality, because they often inhabit shallow microhabitats that reduce their exposure to piscivorous predators but also expose them to greater extremes of temperature. Cold-temperature stress has been implicated as a causal agent in high overwintering mortality rates in several species of cyprinodontid fishes that occur in the same coastal marshes inhabited by sailfin mollies (references in Coleman 1991). Selective mortality through abiotic stress can play a role in determining the patterns of adult body size variation in natural populations. Enhanced survivorship of larger fish can act to counter their higher risk of predation from wading birds in shallow-water habitats (J. C. Trexler et al., *unpublished manuscript*). In these situations the net direct selection pressures will create optimizing selection for an intermediate body size. The final net selection on body size will be determined by these effects plus the indirect effects generated through selection on the age at maturity. One source of such indirect effects can be variable mortality rates between juveniles and adults. In habitats with a high scope for growth, juvenile mortality rates will exceed those of adults under most conditions, at least with respect to abiotic stress. In habitats with a low scope for growth, adult rates and juvenile rates may be comparable, and adult rates may even be higher and more unpredictable. This effect could generate selection for earlier maturity and reproduction that would produce small body sizes as an indirect effect (Stearns and Koella 1986).

Two issues complicate this picture. First, the growth and development patterns of males are much less sensitive to environmental variation than those of females (Trexler et al. 1990). The demographic differences among populations may indeed select for genetic differences in male body size but they may be selecting for distinct norms of reaction to growth conditions in females (Stearns and Koella 1986). In this scenario the concordance of interdemic variation in male and female size is the result of two different processes that generate the same result. Second, it is possible that larger males can only persist in populations with larger females through the enhanced reproductive success the larger males acquire via assortative mating (Travis et

al. 1990). In this hypothesis the net selection force on male body size is itself determined by the net selective force on female size. Data are insufficient to resolve these issues at present.

The results of this study, in conjunction with our other studies of this species, illustrate the ecological complexity of natural selection. This is old news to many biologists who have studied the genesis and maintenance of genetic diversity (e.g., Cain 1988). However, it bears re-emphasizing; our knowledge of the ecology of natural selection is far from complete (Manly 1985, Endler 1986) and studies of this complex process should be an integral part of ecologists' search for the causes of biological diversity.

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