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EXPERIMENTAL EVIDENCE OF COMPETITION BETWEEN LARVAE OF  
COLORADO SQUAWFISH AND FATHEAD MINNOW

Final Report

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## Preface

This study was funded by the Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin. This program is a joint effort of the U.S. Fish and Wildlife Service, U.S. Bureau of Reclamation, Western Area Power Administration, States of Colorado, Utah, and Wyoming, Upper Basin water users, and environmental organizations.

## Abstract

Quantitative study of resource competition has been frustrated by an inability to separate effects of intraspecific and interspecific competition. Two types of experimental design are commonly used to study competition in two-species assemblages (1) replacement designs, and (2) additive designs. We used an experimental design and analysis that incorporated the positive attributes of replacement and additive designs to study resource competition between larvae of federally endangered Colorado squawfish, *Ptychocheilus lucius*, and a widely distributed non-native species, the fathead minnow, *Pimephales promelas*. Effects of competition were inferred by feeding fish known quantities of zooplankton and comparing relative growth in single- and mixed-species assemblages. Effects of intraspecific exploitative competition were accounted for by using regression to describe the density-dependent relation between relative growth and feeding regime in single-species assemblages, and then subtracting these effects from the response of relative growth in mixed-species assemblages. Relative growth of Colorado squawfish and fathead minnow in single- and mixed-species assemblages was compared using a one-sample *t*-statistic, regression analysis, and an index of competitive ability. Conclusions of statistical analyses were confirmed by study of diet overlap.

The response of each species to competition was consistent with that predicted by ecological theory: relative growth of both fishes was reduced by competition (i.e., -/-). Negative competitive effects were asymmetrical, and quantitatively greater and more frequent for Colorado squawfish than for fathead minnow. Study of diet overlap confirmed conclusions of relative growth analysis. Diet overlap was reduced in the lowest feeding regime where

resource competition was intense. Paradoxically, at higher feeding regimes diet overlap increased although analysis of relative growth suggested competition occurred at those feeding regimes as well. The insensitivity of diet overlap at higher feeding regimes may have been due to a lack of alternative prey, or may suggest that the response variable, relative growth, integrated effects of two qualitatively different competitive mechanisms without reflecting a change because intensity of competition remained relatively constant. These results emphasize the need for more detailed ecological investigations of interactions between early life stages of Colorado squawfish and potential non-native competitors. In addition, this study demonstrated that under experimental conditions, effects of intra- and interspecific competition can be separated and the outcome of exploitative resource competition can be determined.

## Introduction

Quantitative study of resource competition has been frustrated by an inability to separate effects of intraspecific and interspecific competition (Connell 1983; Schoener 1983; Strong et al. 1984; Diamond and Case 1986; and Underwood 1986). Even for the simplest case of interspecific competition (i.e., two-species assemblage), few studies allow unconfounded interpretation if experimental design and analysis are critically evaluated. Two types of experimental design are commonly used to study competition in two-species assemblages (1) replacement designs, and (2) additive designs. Strengths and weaknesses of these approaches have been summarized (de Wit 1960; Harper 1977; Connolly 1986, 1988; Underwood 1986; Rejmánek et al. 1989; Snaydon 1991), and both approaches have a degree of intuitive appeal but are either confounded or difficult to interpret. Snaydon (1991) noted "*there has been no consensus on the nature of the problems which replacement designs pose, nor of how they might be solved; neither has there been any clear recognition of the role that additive designs might play*" and suggested that bivariate factorial designs have advantages over traditional methods. We used an experimental approach that incorporated positive attributes of replacement and additive designs to study resource competition between larvae of federally endangered Colorado squawfish, *Ptychocheilus lucius*, and a widely distributed non-native species, the fathead minnow, *Pimephales promelas*. The method is equivalent to an incomplete bivariate factorial design and allows unconfounded, straight-forward interpretation of intra- and interspecific competitive effects. It also has the advantage that if competition occurs, the response of each species is consistent with that predicted by ecological theory. Theoretically, when two species compete for limited resources, the interaction

must negatively affect one or both of the species (Odum 1971; Lawton and Hassell 1981). Using standard notation for species interactions (Odum 1971), these alternative outcomes indicate competition (-/-) or a strongly asymmetrical form of competition known as amensalism (-/0).

Historically, Colorado squawfish were relatively abundant in large rivers of the Colorado River Basin, but distribution and abundance have declined. Colorado squawfish are currently restricted to warm-water reaches of the Green, Colorado, and San Juan rivers and their larger tributaries (Behnke and Benson 1983; Tyus 1991; Platania et al. 1992). Factors responsible for decline of Colorado squawfish have been associated with (1) modification and loss of habitat, and (2) introduction of non-native fishes (Stanford and Ward 1986; Carlson and Muth 1989; Minckley 1991; Tyus 1991). Studies of effects of non-native fishes on Colorado squawfish have emphasized predator-prey interactions and interspecific competition; but studies of interspecific competition have not provided convincing evidence of either negative or positive effects. Previous studies of interspecific competition for food were conducted in the field, and the potential for competition was inferred based on diet overlap (Jacobi and Jacobi 1982; McAda and Tyus 1984; S. J. Grabowski and S. D. Hiebert, unpublished report). The weakness of using diet overlap to infer interspecific competition has been discussed (Schoener 1982, 1983; Wiens 1992). However, study of diet overlap can contribute to a convincing case for the occurrence of interspecific competition if it is part of a larger study which demonstrates that exploitation of a limited resource by one species has negative effects on another (Wiens 1992).

This experiment focused on competition for food between larval Colorado squawfish and larval fathead minnow. Early life stages of Colorado squawfish co-occur with fathead minnow and share habitat and food resources. Young Colorado squawfish, and all life stages of fathead minnow, inhabit shallow near-shore habitats (e.g., backwaters and side channels) and feed on zooplankton, chironomid larvae, and detritus (Vanicek and Kramer 1969; S. J. Grabowski and S. D. Hiebert, unpublished report). At 20 to 30 mm total length, Colorado squawfish begin to consume other small fishes. Thus, intense competition for food between Colorado squawfish and fathead minnow may occur during a relatively short developmental period ranging from onset of exogenous feeding to commencement of piscivory in Colorado squawfish.

It has been shown that growth is positively related to fitness and competitive ability (Werner 1976; Mittlebach 1981; Persson 1991). Our experiment was designed to compel the fishes to compete for zooplankton so that the effects of competition on growth could be observed. We determined the outcome of interspecific competition for food between larvae of Colorado squawfish and fathead minnow by (1) estimating relative growth of each species in single-species assemblages and mixed-species assemblages; (2) estimating effects of intraspecific competition; (3) estimating effects of interspecific competition after subtracting effects of intraspecific competition; (4) determining the symmetry of competitive interactions and, if asymmetric, identifying which species was most adversely affected; and (5) confirming results by studying the relation between diet overlap and resource availability.

## Materials and Methods

### *Experimental animals*

Colorado squawfish were obtained from Dexter National Fish Hatchery and Technology Center, Dexter, New Mexico. Fathead minnow larvae were purchased from a commercial source (Aquatic Biosystems, Inc., Fort Collins, Colorado). After onset of first feeding, all larvae were fed live 24-h-old brine shrimp nauplii (Aquarium Products, Glen Burnie, Maryland) twice daily.

To ensure that larval Colorado squawfish and fathead minnow were capable of eating the same prey, the experiment was initiated when both species first began to consume brine shrimp nauplii. This was accomplished by purchasing fathead minnow that were expected to reach the developmental phase at approximately the same time as Colorado squawfish. Thus, the decision of when to start the experiment was based on functional development of foraging abilities instead of correlated measures such as body length or mouth gape. Mean wet mass and total length at start of the experiment were 4.16 mg and 8.4 mm for Colorado squawfish and 2.23 mg and 7.0 mm for fathead minnow. Initial mass and length were determined by measuring 20 fish sacrificed and preserved at the start of the experiment.

### *Experimental design and conditions*

The duration of the experiment was 14 d. Experimental treatments were assigned to replicate aquaria using a completely randomized, 3X5 factorial design. The first factor, feeding regime, had three levels (32, 80, and 200 zooplankton·fish<sup>-1</sup>·day<sup>-1</sup>). The second factor, relative abundance, had five levels (ratios) of % Colorado squawfish:% fathead minnow (100:0, 75:25, 50:50, 25:75, and 0:100). Each treatment was replicated three times and the



experimental unit was an aquarium. Forty-five 76-L aquaria (30 x 75 x 32 cm high) were housed within the same room. Cool-white fluorescent lamps were the only source of illumination, and a 12:12-h light:dark photoperiod was maintained.

Water was supplied by a well on the Colorado State University campus and had the following characteristics: dissolved oxygen,  $\geq 6.1$  mg/L; pH, 8.2; temperature,  $20 \pm 1$  °C; alkalinity, 237 mg/L as  $\text{CaCO}_3$ ; hardness, 344 mg/L as  $\text{CaCO}_3$ ; and specific conductance, 720  $\mu\text{S}/\text{cm}$ . The bottom of each aquarium was covered with approximately 2 cm of washed sand. Each aquarium was aerated continuously with a single airstone and water was added periodically to maintain a depth of 24 cm.

Zooplankton abundance levels were based on results of field studies and encompassed a realistic range of zooplankton densities (S. J. Grabowski and S. D. Hiebert, unpublished report). Zooplankton were collected from Fossil Creek Reservoir (Larimer County, Colorado) with an 80- $\mu\text{m}$ -mesh plankton net. Zooplankton were transferred to the laboratory where they were quantified by subsampling and a stock was prepared by diluting to a target density. Aliquots of stock were delivered to aquaria twice daily to obtain 2000 zooplankton per aquarium per feeding (26 zooplankton / L). Feeding-regime levels (32, 80, and 200 zooplankton·fish<sup>-1</sup>·day<sup>-1</sup>) were obtained by manipulating number of fish per aquarium rather than number of zooplankton. For example, the 32 zooplankton·fish<sup>-1</sup>·day<sup>-1</sup> treatment was obtained by delivering 2000 zooplankton twice daily into an aquarium containing 125 fish. Numbers of fish per aquarium corresponding to 80 and 200 zooplankton·fish<sup>-1</sup>·day<sup>-1</sup> were 50 and 20, respectively. This procedure allowed manipulation of zooplankton relative

abundance without facilitating or inhibiting feeding due to super-abundance or scarcity of food.

The number of zooplankton introduced into aquaria was not adjusted to account for mortality of fish because small size and rapid deterioration of dead fish made accurate counting difficult. Zooplankton abundance within aquaria was not measured. Inspection of aquaria showed that living zooplankton did not accumulate in any of the experimental treatments.

The experiment was concluded 1 h after the second feeding on day 14. Surviving fish were removed from aquaria, sacrificed by administering an overdose of anesthesia (tricaine methanesulfonate, Argent Chemical Laboratories, Redmond, Washington), and preserved in 10 % formalin. Preserved fish were sorted by species, counted, blotted, and their wet mass was determined ( $\pm 1$  mg).

Five Colorado squawfish and five fathead minnow were randomly selected from each replicate for diet analysis. Guts (from esophagus to vent) were removed by dissection. No evidence of regurgitation of gut contents was observed. Gut contents were examined under magnification, and individual food items were identified and enumerated by categories: cladocera, copepoda, rotifera, or nauplii.

### *Statistical analysis*

The response of relative growth ( $r$ ), where  $r = (w_2 - w_1)/w_1$  and  $w_1$  and  $w_2$  are mass at beginning and end of the experiment, was used to infer effects of competition. Survivorship was measured, but the experiment duration was too short to permit its use for study of competitive effects because non-feeding fish could have remained alive via internal energy reserves. Data were

subjected to Shapiro-Wilk's Test for normality and Bartlett's Test for homogeneity of variance (Zar 1984). Subsequently, relative growth was  $\log_{10}$  transformed to stabilize variance for statistical procedures.

Density-dependent intraspecific competition was studied by analyzing the relation between relative growth and feeding regime for Colorado squawfish and fathead minnow in single-species assemblages. Regression analysis was used to fit relative growth as a function of feeding regime. A significant regression suggested that intensity of intraspecific competition varied with zooplankton availability. Regression equations also allowed prediction of relative growth over a range of feeding regimes: these estimates were used in analysis of interspecific competition.

Effects of interspecific competition were estimated by comparing relative growth of fish in mixed- and single-species assemblages, at identical species-specific per-capita feeding regimes (Figure 1). For example, for the experimental treatment illustrated in Figure 1, which comprised 62 Colorado squawfish and 63 fathead minnow for a total density of 125 fish per aquarium, the response of each species was compared to that estimated from single-species regression equations at a density of 62 or 63 fish per aquarium, respectively. The difference between relative growth in mixed-species assemblages and single-species assemblages was tested by calculating a one-sample  $t$ -statistic, and comparing it to a two-tailed Student's critical value (Zar 1984). Relative growth in mixed-species assemblages was the observed value; relative growth in single-species assemblages was the expected value. A difference ( $d$ ), where:

$$d = \text{observed relative growth} - \text{expected relative growth},$$

was the effect of interspecific competition ( $\alpha = .05$  for all statistical comparisons). Values of  $d$  not significantly different from zero suggest that relative growth was equivalent in mixed-species assemblages and in single-species assemblages; negative values suggest that relative growth was reduced in mixed-species assemblages.

Conclusions of  $t$ -tests were confirmed by regressing  $d$  as a function of relative abundance (i.e., percent Colorado squawfish) within each feeding regime. A significant regression confirmed that relative growth was different in mixed-species assemblages compared to single-species assemblages and that the relationship was a function of relative abundance. Slope of the regression line described the response of each species to interspecific competition. For example, if  $d$  for species  $A$  decreased with increasing relative abundance of species  $B$ , it was concluded that growth of species  $A$  was reduced by interspecific competition.

Competitive ability of Colorado squawfish and fathead minnow was compared using an index that is identical to the relative crowding coefficient used by de Wit (1960). Competitive ability as defined by Snaydon (1991) is the ability of one species to obtain and use limiting resources, when grown in mixed assemblages with another species, compared with its ability to obtain and use those resources when grown in single-species assemblages. Competitive ability was calculated based on mean relative growth in each experimental treatment, using the formula:

$$CA = \log_{10} [(G_{cf} / G_{cc}) / (G_{fc} / G_{ff})],$$

where CA is competitive ability of Colorado squawfish, when grown with fathead minnow,  $G_{cc}$  and  $G_{ff}$  are relative growth of Colorado squawfish and fathead minnow in single-species assemblages, and  $G_{cf}$  and  $G_{fc}$  are relative growth of Colorado squawfish and fathead minnow in mixed-species assemblages. Positive values of CA suggest that Colorado squawfish were more competitive than fathead minnow; negative values, that fathead minnow were more competitive than Colorado squawfish.

Diet overlap of Colorado squawfish and fathead minnow in mixed-species assemblages was calculated using Schoener's (1970) measure:

$$\text{percent similarity} = 100(1 - \frac{1}{2} \sum_i |P_{x,i} - P_{y,i}|),$$

where  $P_{x,i}$  is the proportion of the  $i^{\text{th}}$  prey in species  $x$ , and  $P_{y,i}$  is the proportion of the  $i^{\text{th}}$  prey in species  $y$ . Abrams (1980, 1982) argued that Schoener's measure has several advantages over other indices for comparing similarity of resource use between species. Because of a relatively large number of empty guts (32 % of Colorado squawfish and 20 % of fathead minnow), results from replicate aquaria were pooled and diet overlap was calculated based on the mean frequency of each prey type in an experimental treatment. For comparison, diet overlap of Colorado squawfish and fathead minnow in single-species assemblages was also calculated for each feeding regime. Diet overlap of fish in mixed-species assemblages and single-species assemblages was compared by inspection.

## Results

No evidence of intra- or interspecific interference competition (i.e., agonistic behavior) was observed in any of the experimental treatments. This was consistent with previous observations made while rearing larval Colorado squawfish and fathead minnow (D. W. Beyers, unpublished data). Lacking evidence of interference competition, subsequent analyses were devoted to study of intra- and interspecific exploitative competition.

### *Intraspecific exploitative competition*

Maintenance of fish densities and relative abundances was problematic because survival increased directly with feeding regime. Mean survivorship in 32, 80, and 200 zooplankton·fish<sup>-1</sup>·day<sup>-1</sup> feeding regimes was 68, 80, and 86 % for Colorado squawfish and 34, 56, and 75 % for fathead minnow, respectively. However, because the duration of the experiment was relatively short, it is likely that initial densities and relative abundances were maintained for most of the experiment. This assumption was supported by the consistent relation between relative growth and feeding regime in single-species assemblages (Figure 2). These relationships would probably have been more variable if fish densities deviated from target numbers early in the experiment.

Intraspecific competition in single-species assemblages diminished (i.e., became less intense or severe) as zooplankton availability increased. Relative growth of Colorado squawfish and fathead minnow increased significantly ( $P = .0001$  and  $P = .0003$ ) with zooplankton availability

(Figure 2). Relative growth of Colorado squawfish was less than that of fathead minnow in all experimental treatments.

*Interspecific exploitative competition*

Negative effects of interspecific competition were greater for Colorado squawfish than for fathead minnow. One-sample *t*-statistic comparisons showed that Colorado squawfish grew significantly slower in four of nine mixed-species treatments than in single-species assemblages (Table 1). Of the remaining five mixed-species treatments, four had non-significant negative effects on Colorado squawfish growth. The 25:75, 32 zooplankton·fish<sup>-1</sup>·day<sup>-1</sup> experimental treatment was the only one in which Colorado squawfish growth was not negatively affected; however, this response was not significantly positive, suggesting that growth in mixed- and single-species assemblages may have been equivalent. In contrast to Colorado squawfish, fathead minnow growth was significantly reduced by competition in only one experimental treatment. Of remaining mixed-species treatments, three had non-significant negative effects and five had non-significant positive effects on fathead minnow growth.

Inspection of tabulated *d* values showed that significant responses did not occur more or less frequently as a function of relative abundance or feeding regime (Table 1). There was a weak tendency for non-significant positive values at low feeding regimes, and non-significant negative values at high feeding regimes. No consistent trends were apparent within feeding regimes. However, *t*-tests are inadequate for detection of quantitative relationships within data sets (e.g., *d* as a function of relative abundance)

and regression analysis provided a more detailed description of quantitative relationships.

Regression analysis showed that the response of  $d$  as a function of relative abundance within each feeding regime was variable (Table 2). For Colorado squawfish in the two highest feeding regimes, there was a significant reduction in growth as the relative abundance of fathead minnow increased. In the lowest feeding regime, the regression was not significant, suggesting that there was no relationship between Colorado squawfish growth and relative abundance, or that the relation was not detected by statistical analysis. The response of fathead minnow in the highest feeding regime was similar to that of Colorado squawfish: growth declined as the relative abundance of the competitor increased. No statistically significant relationship was detected in the intermediate feeding regime. In the lowest feeding regime, growth of fathead minnow increased significantly with relative abundance of the competitor. This response is inconsistent with ecological theory because it implies that fathead minnow grew faster in mixed- than in single-species assemblages (i.e., the interaction had the form  $+/0$ ). The cause of this anomalous response is uncertain, but may have resulted from failure to maintain initial fish densities and relative abundances in the lowest feeding regime. In that regime, fathead minnow survival ranged from 22 % to 53 %. Because growth was slow in the lowest feeding regime, deviations of food ration due to mortality may have had relatively large effects.

#### *Competitive ability*

In contrast to  $t$ -test and regression methods which detected competitive effects by intraspecific comparisons of growth in mixed- and single-species



assemblages, the index of competitive ability permitted interspecific comparison of ability of each competitor to obtain limited resources. Values of competitive ability were negative for seven of nine mixed-species treatments suggesting that fathead minnow were superior competitors in those experimental treatments, and that Colorado squawfish were superior in the remaining two experimental treatments. These conclusions are consistent with those from analysis of *d*. Competitive ability values were positive for two of the three experimental treatments where *d* values for Colorado squawfish were greater than those for fathead minnow.

#### *Diet overlap*

Diet overlap estimates based on Colorado squawfish and fathead minnow in single-species assemblages ranged from 0.92 to 0.99 (Table 1). These values provide a basis for comparing diet overlap in mixed-species assemblages by showing the range of responses that occurred in absence of interspecific resource competition. There was a variable response of diet overlap in mixed-species assemblages to resource availability. In the two highest feeding regimes there was no relation between diet overlap and resource availability or relative abundance. Overlap at these feeding regimes ranged from 0.70 to 0.98, and four of six values were greater than or equal to 0.91. In contrast, diet overlap in mixed-species assemblages in the lowest feeding regime ranged from 0.66 to 0.88 and was reduced compared to single-species assemblages. There was no apparent relation between diet overlap and relative abundance.

## Discussion

### *Symmetry of competition*

Patterns of distribution and abundance of organisms may depend on the relative importance and intensity of intraspecific and interspecific competition. The symmetry of these interactions is of interest because effects of one may outweigh those of the other under certain circumstances (Underwood 1986). In this experiment, effects of intraspecific exploitative competition were accounted for by using regression to describe a density-dependent relation between growth and feeding regime in single-species assemblages, and then subtracting these effects from the response of relative growth in mixed-species assemblages. Thus, interpretation of interspecific effects was simplified because  $d$  and the index of competitive ability only reflect effects of interspecific competition. Several authors have argued that competition is usually not symmetrical and that one species is typically more affected than the other (Lawton and Hassell 1981; Connell 1983; Schoener 1983; but, see Underwood 1986). This experiment showed that competitive effects between Colorado squawfish and fathead minnow were asymmetrical, and that negative effects were greater and more frequent for Colorado squawfish than for fathead minnow.

It is uncertain why the outcome of competition varied and fathead minnow were superior in only seven of nine mixed-species experimental treatments. The most likely explanation we have presented, attributes variable outcome of the experiment to our inability to compensate for mortality of study fish. Alternatively, statistical sensitivity to number of replicates, variability of data, and selected level of significance may have contributed to low statistical power and an inability to detect experimental treatment effects.

### *Resource limitation*

The response of relative growth gave no indication that resource limitation was reduced at higher feeding regimes. The highest feeding regime was thought to represent a superabundance of prey relative to number of fish, but relative growth increased at all resource levels suggesting that zooplankton were limiting. Rotifera and nauplii were the most abundant types of zooplankton in collections and made up an average of 61 % total zooplankton. However, rotifera and nauplii were identified in only 3 % of fish guts. It is uncertain whether the low occurrence of these food items in fish guts resulted from our inability to discern them from other contents, or because they were not consumed by study fish. It was anticipated that rotifera and nauplii would be consumed, at least at the beginning of the experiment when fish were small. If they were consumed early in the experiment, but not at the end, diet analysis would have shown similar results to those observed. Alternatively, if rotifera and nauplii were too small to be consumed by fish (i.e., were not available), zooplankton availability was overestimated. If zooplankton availability estimates are adjusted assuming that rotifera and nauplii were not available to fish, then the actual feeding regimes were 12, 31, and 78 rather than 32, 80, and 200 zooplankton·fish<sup>-1</sup>·day<sup>-1</sup>, respectively.

### *Diet overlap*

Diet overlap varied slightly in response to changes in resource availability. Diet overlap only decreased in the lowest feeding regime where survival and growth responses indicated that resource competition was intense. However, relative growth at other feeding regimes showed that competition

occurred in those treatments as well. Several explanations can be offered to account for the insensitivity of diet overlap under the experimental conditions. First, diet overlap may have been insensitive to changes in resource availability because only one type of food, zooplankton, was introduced into aquaria. Wild Colorado squawfish and fathead minnow larvae also consume benthic invertebrates, phytoplankton, and detritus. Lack of alternative prey may have compelled study fish to partition what would normally be perceived as one resource type. Consequently, diet overlap would not be expected to change until competition was extreme.

An alternative explanation for the insensitivity of diet overlap is related to its uncertain relation to resource availability (Schoener 1983; Wiens 1992). Diet overlap may not decrease monotonically with resource availability. As resource availability declines, competition may foster decreasing overlap, or, if a resource is scarce (as was the case in the lowest feeding regime), increasing overlap. This hypothetical relation, and example data, are depicted in Figure 3. The relative position of example data correspond to those observed in our experiment. The position of the response at the lowest feeding regime is uncertain and cannot be assigned without additional information (i.e., more responses where the slope is non-zero). At the lowest feeding regime, zooplankton availability may have been sufficiently low to push the response of diet overlap into the realm of starvation. Indeed, growth and survival were poor in the lowest feeding regime. Simultaneously, the two highest resource availabilities may have corresponded with opportunistic responses, and an intermediate response may not have been observed. This interpretation implies that competition for zooplankton did not occur at the two highest feeding regimes; however, analysis of relative

growth showed that competition did occur. This lack of corroboration by diet analysis is confusing, but may suggest an alternative hypothesis. That is, the intensity of competition was consistent in all feeding regimes, but the quality of competition changed. Wilson and Tilman (1991) presented this hypothesis to explain plant competition along a nitrogen gradient: a similar mechanism may be governing competitive interactions in our experiment. Fierce competition in the lowest feeding regime may have manifested normally insignificant, functional feeding differences that were reflected by reduced diet overlap. At higher feeding regimes, functional differences may have been of less importance, but competition remained intense because of differential growth efficiencies. Thus, relative growth could have integrated effects of two qualitatively different competitive mechanisms without reflecting a change because intensity of competition remained relatively constant.

#### *Possible implications*

Some attributes that facilitate competitive superiority of one species over another include: feeding efficiency, functional morphology, efficiency of conversion of resource to biomass (growth efficiency), and body size (Schoener 1983; Werner 1992). Although identification and description of characteristics that provided a competitive advantage were not objectives of this research, results of this experiment allow insight into possible mechanisms. Feeding efficiencies and functional morphology of the fishes were similar based on their consumption of the same food items and ability to capture brine shrimp nauplii. At the beginning of the experiment, Colorado squawfish had a size advantage but grew slower than fathead minnow suggesting that the size differential did not provide a competitive advantage. Thus,

growth efficiency may have been responsible for observed differences between Colorado squawfish and fathead minnow.

The hypothesis that growth efficiency was responsible for the competitive advantage of fathead minnow over Colorado squawfish is consistent with the life-history strategies of the fishes. Colorado squawfish are long lived, have large body size, and delayed reproduction. Fathead minnow are short lived, have small body size, and early reproduction. Implicit in these characteristics is one other correlate of life-history theory: short-lived species have rapid development compared to long-lived species (Pianka 1970). Faster development implies greater growth efficiency, provided that both species eat similar prey and are exposed to identical environmental conditions. Thus, natural selection may have provided fathead minnow with a competitive advantage over larval stages of Colorado squawfish.

Because fathead minnow are not native to the Colorado River Basin, there has been no coevolution with Colorado squawfish to facilitate development of partitioning mechanisms that would allow coexistence. Assuming Colorado squawfish do not become extirpated in the wild, two important implications of the lack of coevolution are related to (1) effects of non-native fishes on habitat selection by young Colorado squawfish and (2) ultimate evolutionary effects of the introduction of non-native fishes into the Colorado River Basin. Mechanisms of nursery-habitat selection used by young Colorado squawfish are unknown, but it is plausible that food availability plays a role. The species that is most efficient at capturing and converting food resources to biomass will be able to persist in an environment for a longer time as resources become scarce (Tilman 1982). For larval Colorado squawfish, the alternative to living in a backwater habitat that has become unsuitable is

to leave the habitat, venture into the river proper, and search for a new nursery area. This process is inherently risky and an alternate nursery area may not be found. Colorado squawfish probably inhabit nursery habitats where food is abundant so that growth is maximized. However, when resources are limited, and competitors are present, food availability for Colorado squawfish is diminished. This resource reduction may cause a corresponding increase in (1) time to size of reproductive maturity, and (2) mortality because of longer time spent in smaller size classes in which fish are more vulnerable to predators and other mortality factors (Werner 1984; Thompson et al. 1991). The species with greatest growth efficiency has an advantage because it can maintain a higher growth rate as resources become scarce, and can persist in a resource-poor environment for a longer period of time. Less efficient species like Colorado squawfish may be forced to abandon nursery habitats more frequently when superior competitors are present, a consequence which may reduce survival.

Ultimately, the impact of non-native fishes may influence the life-history strategy of Colorado squawfish. Historically, adult Colorado squawfish attained larger size compared to fish captured recently. The cause of this change is unknown but has been attributed to a variety of factors including: elimination of historical prey (Behnke and Benson 1983), and modification of historical temperature regime (Vanicek and Kramer 1969; Kaeding and Osmundson 1988). An alternative explanation is that, because of competition with non-native fishes, natural selection has favored Colorado squawfish offspring with a life-history strategy that results in smaller adults, and smaller size at first reproduction. This response is consistent with predictions of life-history theory for organisms that simultaneously

incur reduced growth rates and increased adult mortality (Stearns and Crandall 1984; Wootton 1991; Roff 1992). Three other species of *Ptychocheilus* (*P. oregonensis*, *P. grandis*, and *P. umpqua*) achieve smaller adult sizes than Colorado squawfish (Lee et al. 1980). If modern Colorado squawfish have retained the genetic basis, or phenotypic plasticity for this alternative life-history strategy, a decrease in size of adult Colorado squawfish is a predictable consequence of the introduction of non-native competitors.

Extrapolation of conclusions of this laboratory experiment to field localities is, as always, questionable. We demonstrated that, if larvae of Colorado squawfish and fathead minnow share an environment where food resources are limiting, growth and survival of Colorado squawfish is reduced; but the experiment lacked the physical and biological complexity of the natural environment. Larval fathead minnow are not the only potential competitors with young Colorado squawfish. Other life stages of fathead minnow, and other non-native fishes (e.g., red shiner, *Cyprinella lutrensis*), are widely distributed within the Colorado River Basin. These non-native species warrant further study because they are abundant and well adapted to habitats that Colorado squawfish use during early life. Results of this experiment can be used to make predictions about the outcome of future studies. Semi-controlled field experiments could provide a framework for testing predictions, while yielding new information about the interaction of biotic and abiotic variables on the potential for competition between Colorado squawfish and non-native fishes.



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Table 1. Summary of the statistic  $d$ , competitive ability, and diet overlap for larvae of Colorado squawfish and fathead minnow in 15 experimental treatments (N=3).

Treatment		$d^a$			
Relative Abundance <sup>b</sup>	Feeding Regime <sup>c</sup>	Colorado Squawfish	Fathead Minnow	Competitive Ability	Diet Overlap
0:100	32	NA	0.0367	NA	0.95
25:75	32	1.99	0.825	0.106	0.69
50:50	32	-0.179*	1.21	-0.0834	0.66
75:25	32	-0.326*	2.55	-0.168	0.88
100:0	32	-0.0333	NA	NA	0.95
0:100	80	NA	0.0274	NA	0.99
25:75	80	-2.15*	1.43	-0.137	0.95
50:50	80	-0.669	1.35	-0.0864	0.98
75:25	80	-0.396	-0.467	-0.0336	0.70
100:0	80	0.211	NA	NA	0.99
0:100	200	NA	0.0496	NA	0.92
25:75	200	-8.41*	-1.54	-0.112	0.87
50:50	200	-0.644	-4.69	0.0447	0.91
75:25	200	-0.389	-36.1*	-0.0767	0.92
100:0	200	-0.200	NA	NA	0.92

<sup>a</sup> $d$  = relative growth in single-species assemblage - relative growth in mixed-species assemblage.

<sup>b</sup>% Colorado squawfish:% fathead minnow.

<sup>c</sup>Zooplankton·fish<sup>-1</sup>·day<sup>-1</sup>.

NA = not applicable, treatment was a single-species assemblage.

\*Significantly different by t-test, alpha = .05.

Table 2. Summary statistics for linear relation between relative growth and relative abundance (% Colorado squawfish:% fathead minnow) at three feeding regimes. Slope, probability value for the hypothesis  $H_0$ : slope = 0, and  $r^2$  estimates for the linear regression equation:

$$\log_{10}\text{relative growth} = \text{intercept} + \text{slope}(\% \text{ Colorado squawfish}).$$

Feeding Regime <sup>a</sup>	Colorado squawfish			Fathead minnow		
	Slope	<i>P</i>	$r^2$	Slope	<i>P</i>	$r^2$
32	-0.00934	.3	0.11	0.0292	.03	0.40
80	0.0259	.001	0.72	-0.00501	.8	0.004
200	0.0787	.02	0.44	-0.302	.01	0.53

<sup>a</sup>Zooplankton·fish<sup>-1</sup>·day<sup>-1</sup>.

## Figure Legends

Figure 1. Diagrammatic representation of the experimental design used to study exploitative competition between larval Colorado squawfish and fathead minnow. Solid diagonal lines denote standard replacement series at three densities. Dashed diagonal lines denote equivalent relative-abundance experimental treatments, % Colorado squawfish:% fathead minnow. Arrows illustrate method for comparing relative growth in mixed- and single-species assemblages.

Figure 2. Observed data and fitted regression lines for Colorado squawfish and fathead minnow relative growth in single-species assemblages.

Figure 3. Hypothetical relation of diet overlap for species sharing a resource, as a function of resource availability. Relative position of three data points correspond to observed experimental responses. Location of response for lowest feeding regime is uncertain and alternate positions are indicated. Modified from Wiens (1992), with permission.





