TROPHIC POLYMORPHISM AND BEHAVIORAL DIFFERENCES DECREASE INTRASPECIFIC COMPETITION IN A CICHLID, *HERICHTHYS MINCKLEYI*

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Abstract. Resource polymorphisms, or morphological variations related to resource use, are common in fishes and are thought to be a possible step in speciation. This study experimentally tests the hypothesis that fitness (as estimated by growth rates) is increased by the presence of multiple trophic morphotypes (or morphs) within a population. Cage experiments were used to quantify the intraspecific competitive interactions between morphs of the polymorphic cichlid *Herichthys minckleyi* in Cuatro Ciénegas, Mexico. Results suggest that competition is reduced between morphs in mixed-morph treatments relative to equal-density single-morph treatments. Field studies revealed that the morphs feed in different microhabitats and use different feeding behaviors within these microhabitats. These results suggest that the polymorphism is maintained in the population because it decreases competition between the morphs, and that differences in feeding behavior facilitate resource partitioning.

Key words: cichlid; competition; ecological speciation; feeding behavior; Herichthys minckleyi; *intraspecific variation; polymorphism; resource partitioning.*

INTRODUCTION

Trophic polymorphisms, intraspecific variations in feeding structures, are hypothesized to be important in speciation (Skúlason and Smith 1995) and to reduce intraspecific competition (McLaughlin et al. 1999). This reduction in intraspecific competition, attributed to differential resource use, could be a mechanism maintaining these polymorphisms (Skúlason and Smith 1995, Tregenza et al. 1996, McCann 1998). If morphotypes (or morphs) specialize on different food resources, character displacement may separate morphs into distinct ecological niches affecting community structure (Roughgarden 1983, Rummel and Roughgarden 1983, Robinson and Wilson 1994). In addition to morphological differences, morphs may use different habitats and feeding behaviors (Robinson and Wilson 1996). Differences in feeding behavior may constitute an early stage in the evolution of polymorphisms and be integral to their maintenance (Skúlason and Smith 1995, McLaughlin 2001).

The Cuatro Ciénegas cichlid, *Herichthys minckleyi*, endemic to the spring-fed pools of the Cuatro Ciénegas basin in Coahuila, Mexico, demonstrates at least three distinct morphological types (Minckley 1969, Kornfield and Taylor 1983, Stephens and Hendrickson 2001). The two most abundant morphs are distinguished by extreme differences in pharyngeal jaw morphology. The third morph, a piscivore, shows a different body form, but can have pharyngeal jaw mor-

phology similar to either of the other two morphs. The papilliform morph has narrow, needle-like teeth, gracile pharyngeal jawbones, and small pharyngeal jaw musculature (Liem and Kaufman 1984). This morph feeds primarily on detritus, algae, and soft-bodied invertebrates (Smith 1982). The molariform morph has large, molar-like teeth, robust pharyngeal jawbones, and hypertrophied associated musculature. In addition to detritus, algae, and soft-bodied invertebrates, this morph also eats snails (Smith 1982, Liem and Kaufman 1984, Hulsey et al. 2001). The molariform morph is generally less frequent in the population than the papilliform morph (Kloeppel 2002; D. A. Hendrickson, *personal observation*).

Polymorphism in *H. minckleyi* is proposed as an adaptation for resource partitioning and reduced intraspecific competition (Kornfield and Taylor 1983, Liem and Kaufman 1984). Jaw morphology in other polymorphic fish changes in response to resource abundance; a response that is both genetically and environmentally induced (Meyer 1989, Mittelbach et al. 1992) This response is consistent with the theory that trophic polymorphisms are adaptations for partitioning resources, but does not directly test if competition is reduced between morphs. We quantified competitive interactions in *H. minckleyi* using growth rates as proxy for fitness (after Pritchard and Schluter 2001). We estimated within-morph (or intra-morph) competition and between-morph (or inter-morph) competition to test the hypothesis that intraspecific competition is reduced in a population containing multiple trophic morphs. To examine the proximate mechanism of resource partitioning between morphs, we examined feeding behaviors in the field. We tested the hypothesis that there are

differences in the microhabitat used for feeding and/or feeding behavior used between the morphs.

METHODS

The competition experiment was conducted in Mojarral Este, an ~2 m deep pool with an area of ~11 642 m², in the Protected Area for Flora and Fauna in Cuatro Ciénegas, Mexico. Cages ($n = 25$) 1 m³ were constructed of 0.56-cm (0.25-inch) Vexar brand aquaculture mesh (DuPont Canada, Incorporated, Mississauga, Ontario, Canada) and polyvinyl chloride (PVC) tubing. Cages were arbitrarily placed along the periphery of the pool in <1 m of water, and randomly assigned to one of five treatments: 1) molariform high-density, with four molariform individuals, 2) molariform low-density, with two molariform individuals, 3) papilliform high-density, with four papilliform individuals, 4) papilliform low-density, with two papilliform individuals, and 5) a mixed high-density treatment, with two individuals of each morph. Each treatment had five replicates for a total of 25 cages and 80 fish. Densities within the cages (fish per square meter) mimicked the upper range of ambient fish density (Kloeppel 2002). Previous researchers have suggested that variation in feeding morphology is most important in times of low food availability because individuals with alternative morphology are able to switch to a suboptimal food source (Boag and Grant 1981, McKaye and Marsh 1983, Liem and Kaufman 1984, Robinson and Wilson 1998). Thus, the experiment was designed to generate intense competition for food resources within the cages.

Fish were captured using hook and line and gill nets, and anesthetized with ~20 drops of clove oil in ~8 L of water (Munday and Wilson 1997). Individuals with standard lengths (SL) between 70 and 100 mm were categorized by morph by examining pharyngeal teeth through an otoscope with categories defined by Kornfield and Taylor (1983), measured (mass, SL), photographed, and marked with an fin clip code. There was no significant difference in fish length among treatments ($F_{4,60} = 0.146$, $P = 0.96$). Most individuals within the population could be categorized into a distinct morph based on pharyngeal tooth morphology. Some individuals have intermediate morphology; however, their abundance in the population is relatively low. For these experiments, only individuals with pronounced molariform or papilliform morphology were selected. (It is unclear whether the polymorphism is genetically based or environmentally determined and if the intermediates represent a continuum in morphologies or ontogenetic development towards the molariform morph.) Fish were placed in cages on 28 and 29 May 2001. Fish were collected on 10–12 August 2001 using bubbled CO_2 (as anesthesia) and dip nets. Individuals were identified, then weighed, re-photographed, and released. Changes in mass were calculated by subtracting pre-experiment mass from post-experiment mass, and converted to growth rates by dividing by the duration of the experiment in weeks (change in mass over time was used as growth rate for this experiment). Growth rates were compared among treatments using ANOVA with the random effect of cage nested within the fixed effect of treatment.

For the behavioral study, feeding events were recorded in Mojarral Oeste, a 5 m deep pool with an area of ~1298 m², which contains multiple distinct microhabitat types. Surrounding the large inflow spring is an area of stromatolite travertine deposit, which forms a hard shelf covered with filamentous cyanobacteria and diatoms. The margins of the pool are covered with thick, soft, flocculent material, with high densities of hydrobiid snails (Minckley 1969). The pool also has patches of gravel substrate and submerged and emergent water lilies. We used this pool because it has distinct microhabitats, and a limited fish population in a confined area, increasing the likelihood of observing tagged fish. Individuals of *H. minckleyi* were caught on 4 and 5 January 2001 and processed as above (70 individuals: 34 molariform and 36 papilliform). Fish were measured (SL) and labeled with unique, numbered, plastic tags sutured to the epaxial musculature near the rostral base of the dorsal fin with absorbable dental sutures. We were able to identify these for up to one week; after which the sutures softened and the tags fell off.

Behavioral observations were recorded from 7–11 January 2001 using a digital-video camera in an underwater housing. Recordings were made for one-hour periods four times per day, for five consecutive days. Feeding events were recorded by arbitrarily moving around the pool and video taping tagged fish. The observer was blind to morph while recording feeding events. The digital videotapes were examined and each feeding event was scored for microhabitat use. A total of 362 feeding events were analyzed: 163 observations of molariform individuals and 199 observations of papilliform individuals. Five categories were used to identify microhabitat type: 1) water surface (hereafter surface), 2) submerged vegetation (vegetation), 3) gravel substrates (gravel), 4) travertine shelf (hard), and 5) flocculent bottom sediments (soft). An expected contingency table was constructed using the total number of feeding events in each microhabitat and the total number of feeding events by each morph. A χ^2 test was used to test whether the frequencies of observed feeding events differed from the null model of no difference between the morphs in microhabitat use. This design tested whether there was a difference between the morphs in frequency of feeding in microhabitat, irrespective of microhabitat availability.

A subsample of these events ($n = 111$) with exceptionally clear digital images were visually categorized into four feeding behaviors: (1) ''suction feeding,'' where the fish produced suction to capture food items; (2) ''scraping,'' where the fish pressed its jaws against
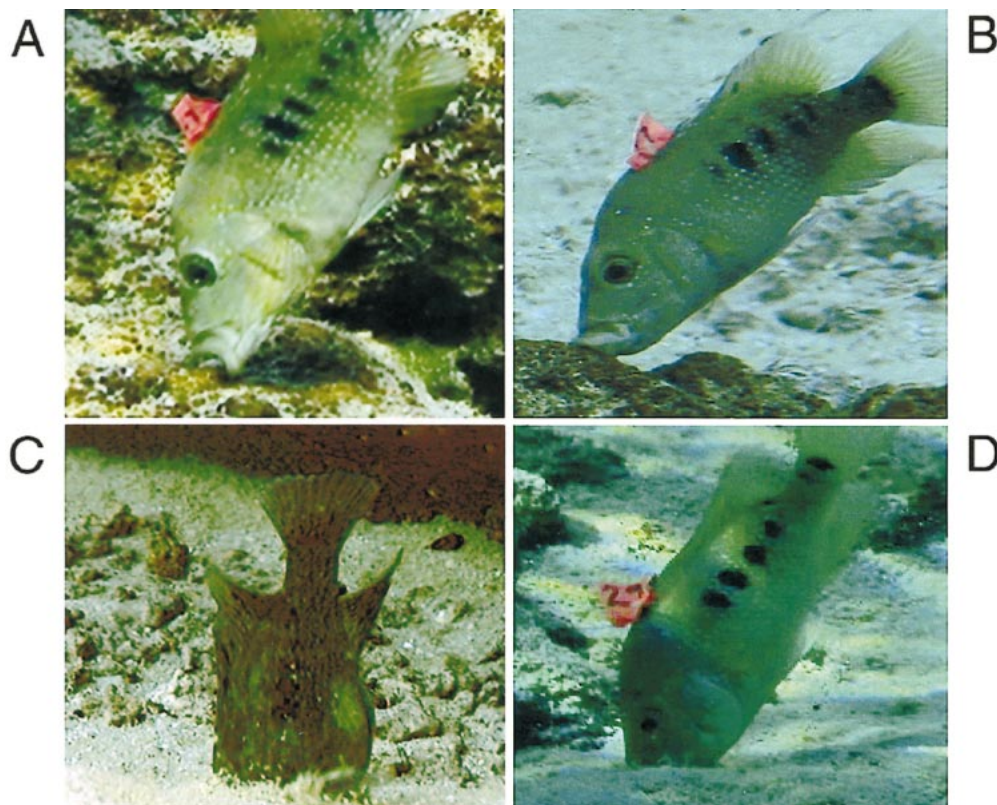
FIG. 1. Video images representing the four feeding behaviors observed in *Herichthys mincklleyi* during the study period. (A) Suction feeding consists of the fish using suction to acquire food from any substrate. (B) Scraping consists of the fish pressing its jaws against a hard substrate and using friction to remove material from the surface. (C) Diving consists of the fish diving into the soft substrate to grab a mouthful of flocculent material. (D) Scooping consists of the fish gathering sediment off of the surface of the soft substrate.

a hard surface and removed food items with friction; (3) ''diving,'' where the fish dove and inserted a large portion of its body into soft sediments; and (4) ''scooping,'' where the fish acquired a mouthful of soft sediment off of the bottom (see Fig. 1). Sequences of sufficient quality were used to quantify feeding behavior using Didge software, version 2.3, Beta 1. Kinematic variables calculated included gape, gape angle, angle of interaction with the substrate, premaxillary protrusion, and depth into the substrate. These variables were compared among behaviors to verify that behavioral categories were based on consistent, measurable differences in feeding movements. Additional events were added to the behavior data set for a total of 314 events. A χ^2 test was used to determine if the morphs used behaviors at different frequencies. Because certain behaviors can only occur within a particular microhabitat (e.g., scraping only occurs on hard substrates and diving only occurs in the soft sediment), we used separate χ^2 tests on soft and hard microhabitats to test if the morphs use different behaviors within a given microhabitat.

RESULTS

The results of the cage experiment suggest that competition between morphs is reduced relative to competition within morphs. (Intra-morph competition was assessed by comparing the high- and low-density treatments within a morph. Inter-morph competition was assessed by comparing high-density treatments to the individuals of the same morph in the mixed treatment.) There was no cage effect in the nested ANOVA ($F_{18,63}$ = 1.18, P = 0.323). Fish in all cage treatments lost weight during the competition experiment, which confirmed that the relatively high densities used in the experiment elicited strong competitive interactions among individuals. Fish in high-density (single morph) treatments lost more weight than the low-density treatments or the mixed treatment ($F_{4,18}$ = 3.04, P < 0.05; Fig. 2). Growth rates for the molariforms were lowest in the high density, intermediate in the mixed, and highest in the low-density treatments ($F_{2,12}$ = 7.48, P < 0.01; Fig. 3), indicating that inter morph competition is less than intra-morph competition. There were no statistically significant differences between papilliform treatment growth rates ($F_{2,15}$ = 2.03, P = 0.18; Fig. 3). However, because of incidental death and/or escape, the number of replicate cages in the high-density papilliform treatment was reduced from five to three. The trends for the papilliform treatments were similar to the molariform treatments, with the fish in the high-
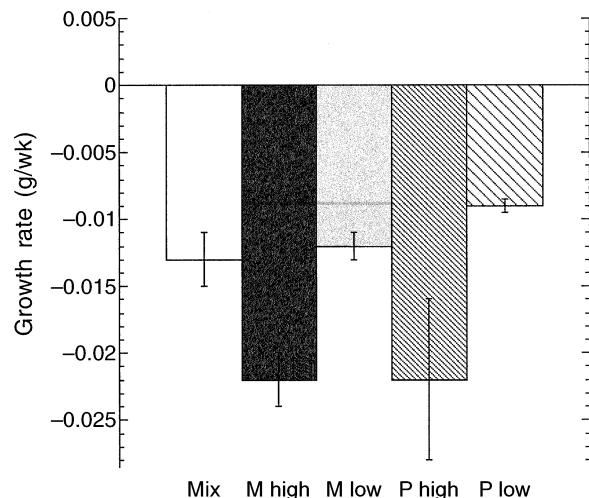
FIG. 2. Mean growth rates ± 1 SEM for all five treatments in the competition experiment. "M high" cages contained four molariform individuals, and "M low" cages contained two molariform individuals. "P high" cages contained four papilliform individuals, and "P low" cages contained two papilliform individuals. "Mix" cages contained two individuals of each morph.

density cages losing more weight than the fish in the low-density or the mixed morph cages. A two sample Student's t test revealed that papilliforms lost significantly less weight than the molariforms in the mixed treatments ($t_4 = 2.95$, $P < 0.05$).

Morphs differed in microhabitat use ($\chi_4^2 = 56.3$, $P < 0.01$). The molariforms used the soft sediment microhabitat more than expected, and the papilliforms used the hard travertine substrate more than expected (see Appendix A). The morphs also performed feeding behaviors at different frequencies ($\chi_3^2 = 35.0$, $P < 0.01$). Molariforms used the diving behavior more than expected, whereas papilliforms used the scraping and the scooping behaviors more than expected (see Appendix B). Within a given microhabitat (e.g., hard substrate or soft substrate), the morphs also used behaviors at a frequency different from random ($\chi_1^2 = 4.67$, $P < 0.05$ for hard substrate; $\chi_2^2 = 18.46$, $P < 0.05$ for soft substrate). On the hard substrate, the papilliforms used the scraping more than expected, and in the soft sediments, the molariforms used the diving behavior more than expected (see Appendix C). In summary, molariforms feed more frequently in the soft flocculent sediments where snails are abundant, and papilliforms feed more frequently on the travertine shelf in the pool, which is covered with algae and soft-bodied invertebrates.

DISCUSSION

Resource partitioning has been hypothesized to cause character displacement and to reduce competition in closely related species (Pacala and Roughgarden 1982, Roughgarden 1983, Robinson and Wilson 1994, Pritchard and Schluter 2001). Similarly, trophic mor-

photypes may allow reduced competition within a species (Skúlason and Smith 1995, McLaughlin 2001). However, without an individual fitness advantage to being part of a polymorphic population, one of the morphs is expected to be rapidly lost (Hedrick et al. 1976). This study demonstrates that polymorphism reduces competition, conferring an advantage to maintaining polymorphic populations, similar to that observed in competition experiments conducted with different age classes of the same species (Webster and Hixon 2000), and between closely related species (Bengtson 1985).

We observed reduced weight loss (a proxy for fitness, see Pritchard and Schluter 2001) in treatments containing both morphs when compared to treatments at the same density containing only a single morph. The individuals in the mixed treatment had growth rates intermediate between the high- and low-density single-morph treatments, indicating that intraspecific competition is reduced, but not eliminated, across morphs in this polymorphic population. Decreased intraspecific competition in a polymorphic population relative to a
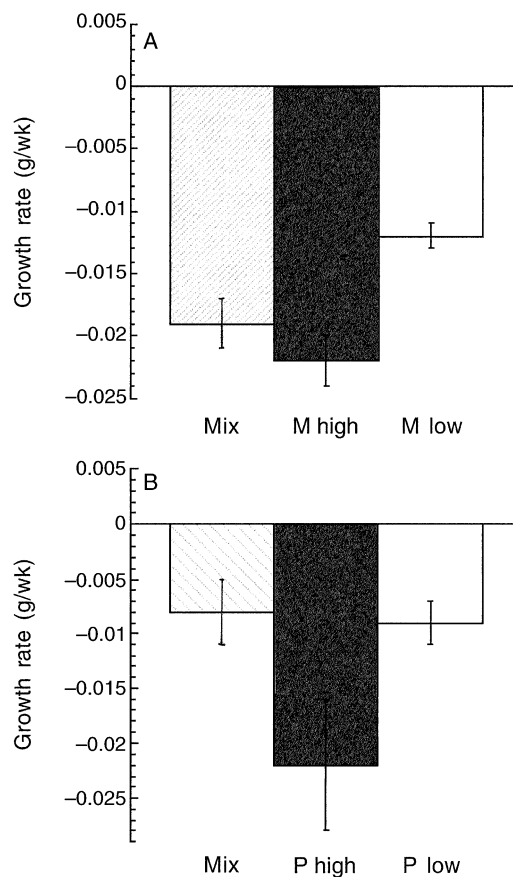

FIG. 3. (A) Mean growth rates ± 1 SEM for molariform fish in each treatment containing molariform morphs. (B) Mean growth rates ± 1 SEM for papilliform fish in each treatment containing papilliform morphs. Densities and abbreviations are given in Fig. 2.

monomorphic population (exemplified by the mixed treatment and the high-density treatment, respectively) will increase individual fitness if the reduction in competition translates into either lower mortality or higher fecundity (Smith and Skúlason 1996). Polymorphism in cichlid pharyngeal jaw morphology is common (Meyer 1989); however, this is one of the first experiments to demonstrate a selective mechanism that could be responsible for the maintenance of these polymorphisms.

Although our experimental densities were high, this served as a model for periods of limited food resources when competition should be very intense. Liem and Kaufman (1984) hypothesized that the polymorphism in *H. minckleyi* may have evolved during, and may be maintained by, periods of low food availability. This pattern of competition and resource partitioning only during relatively infrequent stressful periods (see Weins 1977) is also seen in interspecific interactions of cichlids (McKaye and Marsh 1983) and ground finches (Boag and Grant 1981). Density did not influence the outcome of competition experiments using juvenile *H. minckleyi* and an exotic cichlid, which showed the same competitive patterns at low and high densities. This suggests that, had we conducted this experiment at lower densities, we would have found consistent patterns, but reduced competition (Williamson et al. 2001).

Within the mixed morph treatments, the papilliforms lost less weight than the molariforms, suggesting that under conditions of low food availability, the papilliform individuals may be better at acquiring rapidly renewable resources such as algae, detritus, and soft-bodied invertebrates. Molariforms, which are able to crush large snails (Liem and Kaufman 1984), may be at a disadvantage when snail populations are low. Similarly, populations of *Lepomis* species express molariform morphology when snail resources are available, and a more generalized morphology when snails are depleted (Mittelbach et al. 1992). These results, combined with field observations that the molariform morph is less abundant than the papilliform morph (Kloeppel 2002), suggest density-dependent selection. In this situation, resource partitioning benefits both morphs as long as the density of the molariforms is not so high that it depletes snails. Exclosure experiments in this system show that fish can significantly reduce snail populations (Kloeppel 2002). In some scale-eating cichlids, the fitness of the rare morph (left- or right-handed scale eating) is higher than the common morph, which results in the frequencies of the morphs oscillating ~50% (Hori 1993). In contrast, the frequency of morphs in *H. minckleyi* is skewed, with molariform morphs rarely reaching 50%. If this is an example of frequency- or density-dependent selection, it provides a possible mechanism for the maintenance of the trophic polymorphism (Wimberger 1994, Smith and Skúlason 1996). To more thoroughly understand the density- and frequency-dependent interactions between the two morphs, it will be necessary to conduct further experiments varying the relative densities of the morphs. We expect that the rare morph, if it has relatively abundant food resources, should have a selective advantage over the more abundant morph. Additional experiments are currently underway to test this hypothesis.

Previous work on trophic polymorphism has suggested that individuals with different morphologies also segregate resources behaviorally (Skúlason and Smith 1995, McLaughlin 2001). This study provides evidence that different morphotypes partition resources by using different microhabitats (Ross 1986, Pritchard and Schluter 2001) and different feeding behaviors (McLaughlin et al. 1999, McLaughlin 2001). Molariform individuals more often used a diving behavior in the soft sediment, which would provide access to snails living deep within the sediment. Papilliform individuals more often used the scraping behavior, which removes filamentous algae and diatoms from the surface of the travertine. These differences between the two morphs provide a behavioral mechanism by which they can partition available food resources. Indeed, behavioral exposure to different resources may generate differences in diet, irrespective of differences in feeding performance (Liem 1979, 1980, McLaughlin 2001). These observed differences in feeding behavior may be one of the first stages in the evolution of different trophic morphs and may be integral to the maintenance of this diversity (Skúlason and Smith 1995, McLaughlin 2001).

Literature Cited

Bengtson, D. A. 1985. Laboratory experiments on mechanisms of competition and resource partitioning between *Menidia menidia* (L.) and *Menidia beryllina* (Cope) (Osteichthyes: Atherinidae). Journal of Experimental Marine Biology and Ecology **92**:1–18.

Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. Science **214**:82–85.

Hedrick, P. W., M. E. Ginevan, and E. P. Ewing. 1976. Genetic polymorphism in heterogeneous environments. Annual Review of Ecological Systematics **7**:1–32.

Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. Science **260**:216–219.

Hulsey, C. D., J. C. Marks, D. A. Hendrickson, A. E. Cohen, and C. A. Williamson. 2001. Role of prey functional disparity in maintenance of fish pharyngeal jaw polymorphism. American Zoologist **41**:1478A.

Kloeppel, H. 2002. Molluscivore (*Herichthys minckleyi*) effects on snail (*Mexipyrgus carranzae*) densities and size in Cuatro Ciénegas, Mexico. Thesis. Northern Arizona University, Flagstaff, Arizona, USA.

Kornfield, I., and J. N. Taylor. 1983. A new species of polymorphic fish, *Cichlasoma minckleyi*, from Cuatro Ciénegas, Mexico (Teleostei: Cichladae). Proceedings of the Biological Society of Washington, Washington, D.C. **96**:253–269.

Liem, K. F. 1979. Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. Journal of Zoology, London **189**:93–125.

Liem, K. F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. American Zoologist **20**:295–314.

Liem, K. F., and L. S. Kaufman. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. Pages 203–215 *in* A. A. Echelle and I. Kornfield, editors. Evolution of species flocks. University of Maine Press, Orono, Maine.

McCann, K. 1998. Density-dependent coexistence in fish communities. Ecology **79**:2957–2967.

McKaye, K. R., and A. Marsh. 1983. Food switching by two specialized algae-scraping cichlid fishes in Lake Malawi, Africa. Oecologia **56**:245–248.

McLaughlin, R. L. 2001. Behavioral diversification in brook charr: adaptive responses to local conditions. Journal of Animal Ecology **70**:325–337.

McLaughlin, R. L., M. M. Ferguson, and D. L. G. Noakes. 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sit-and-waiting and actively searching. Behavioral Ecology and Sociobiology **45**:386–395.

Meyer, A. 1989. Cost of morphological specialization: feeding performance of the two morphs in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*. Oecologia **80**:431–436.

Minckley, W. L. 1969. Environments of the bolson of Cuatro Ciénegas, Coahuila, Mexico, with special reference to the aquatic biota. Pages 1–65 *in* Science Series. Texas Western Press, El Paso, Texas, USA.

Mittelbach, G. G., C. W. Osenberg, and P. C. Wainwright. 1992. Variation in resource abundance affects diet and feeding morphology in the pumpkinseed sunfish (*Lepomis gibbosus*). Oecologia **90**:8–13.

Munday, P. L., and S. K. Wilson. 1997. Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. Journal of Fish Biology **51**:931–938.

Pacala, S. W., and J. Roughgarden. 1982. The evolution of resource partitioning in a multidimensional resource space. Theoretical Population Biology **22**:127–145.

Pritchard, J. R., and D. Schluter. 2001. Declining interspecific competition during character displacement: summoning the ghost of competition past. Evolutionary Ecology Research **3**:209–220.

Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: a neglected literature. The American Naturalist **144**:596–627.

Robinson, B. W., and D. S. Wilson. 1996. Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (*Lepomis gibbosus*). Evolutionary Ecology **10**:631–652.

Robinson, B. W., and D. S. Wilson. 1998. Optimal foraging, specialization and a solution to Liem's paradox. The American Naturalist **151**:223–235.

Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia **1986**:352–388.

Roughgarden, J. 1983. Competition and theory in community ecology. The American Naturalist **122**:583–601.

Rummel, R. D., and J. Roughgarden. 1983. Some differences between invasion-structured and coevolution-structured competitive communities: a preliminary theoretical analysis. Oikos **41**:477–486.

Skúlason, S., and T. B. Smith. 1995. Resource polymorphisms in vertebrates. Trends in Ecology and Evolution **10**:366–370.

Smith, D. C. 1982. Trophic ecology of the cichlid morphs of Cuatro Ciénegas, Mexico. Thesis. University of Maine, Orono, Maine, USA.

Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annual Review of Ecology and Systematics **27**:111–133.

Stephens, M. J., and D. A. Hendrickson. 2001. Larval development of the Cuatro Ciénegas cichlid, *Cichlasoma minckleyi*. The Southwestern Naturalist **46**:16–22.

Tregenza, T., M. A. Hack, and D. J. Thompson. 1996. Relative competitive success of unequal competitors changes with overall density. Oikos **77**:158–162.

Webster, M. S., and M. A. Hixon. 2000. Mechanism and individual consequences of intraspecific competition in a coral-reef fish. Marine Ecology Progress Series **196**:187–194.

Weins, J. A. 1977. On competition and variable environments. American Scientist **65**:590–597.

Williamson, C. A., J. C. Marks, D. A. Hendrickson, and B. O. Swanson. 2001. Aliens invade Mexico: proof of their impact on native cichlids. American Zoologist **41**:1627.

Wimberger, P. H. 1994. Trophic polymorphisms, plasticity, and speciation in vertebrates. Pages 19–43 *in* D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia, South Carolina, USA.

APPENDIX A

A table of microhabitat use by morphotypes of *Herichthys minckleyi* is available in ESA's Electronic Data Archive: *Ecological Archives* E084-036-A1.

APPENDIX B

A table of feeding behaviors used by morphotypes of *Herichthys minckleyi* is available in ESA's Electronic Data Archive: *Ecological Archives* E084-036-A2.

APPENDIX C

A table of feeding behaviors in the two most commonly used microhabitats by *Herichthys minckleyi* is available in ESA's Electronic Data Archive: *Ecological Archives* E084-036-A3.