Feeding specialization in *Herichthys minckleyi*: a trophically polymorphic fish

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Diet specialization in the trophically polymorphic cichlid fish *Herichthys minckleyi* was examined using gut contents. Individual *H. minckleyi* were categorized as having molariform, papilliform or undetermined pharyngeal jaws. The presence of enlarged flattened pharyngeal jaw teeth was used to categorize *H. minckleyi* as molariform, and the possession of only small pencil-like pharyngeal teeth was used to classify fish as papilliform. Undetermined individuals (<50 mm standard length, L_S) were not assigned to one of the two larger morphotypes. Arthropods were found to be generally rare in *H. minckleyi* gut contents, but when present, they were most frequently recovered from undetermined individuals. The percentage of plant material consumed by undetermined *H. minckleyi* was not as great as papilliforms ingested on average, and snail crushing by undetermined *H. minckleyi* was not evident. A significantly greater mean percentage of plant detritus was recovered from papilliforms compared to molariforms. Snails were crushed by molariforms more frequently than by papilliforms. When only molariforms and papilliforms that had crushed snails were compared, a greater number of snails were crushed by molariforms. No relationship was found between molariform L_S and the number of snails crushed, but greater molariform tooth number, adjusted for L_S, was indicative of recent snail crushing. The maintenance of *H. minckleyi* pharyngeal jaw variation could be promoted by intraspecific diet differentiation. © 2006 The Authors

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Key words: Cichlidae; Hydrobiidae; individual specialization; Mexico; teeth.

INTRODUCTION

Trophic polymorphisms have been advocated as model systems for understanding how intraspecific differences in jaw morphology translate into diet variation (Smith & Skúlason, 1996). Multiple examples of trophic polymorphism have

been observed in fishes (Meyer, 1990; Wainwright *et al.*, 1991), but perhaps the most extreme trophic polymorphism known is the morphological variation found in *Herichthys minckleyi* (Kornfield & Taylor). The extent to which *H. minckleyi* pharyngeal jaw variation is associated with dietary specialization remains unclear (Smith, 1982; Liem & Kaufman, 1984). In order to examine the association between jaw variation and feeding specialization within *H. minckleyi*, it was determined whether fish with different pharyngeal morphologies exploit different prey.

In *H. minckleyi*, like most fishes, prey is captured with the oral jaws (Wainwright *et al.*, 2001; Swanson *et al.*, 2003), and prey is processed by modified gill arches known as pharyngeal jaws (Hulsey *et al.*, 2005). Unlike most fishes, at least two distinct pharyngeal jaw morphologies have been diagnosed in *H. minckleyi* (Kornfield & Taylor, 1983). Pharyngeal jaws with enlarged flattened teeth are exhibited by 'molariform' *H. minckleyi* (Fig. 1) and 'papilliform' *H. minckleyi* are characterized by the presence of only small pencil-like teeth on the pharyngeal jaw (Liem & Kaufman, 1984). The *H. minckleyi* pharyngeal morphotypes were originally thought to be two different species (Minckley, 1969). Evidence that the two morphotypes represent alternative phenotypes in a single species, however, has been provided by allozyme studies (Kornfield & Koehn, 1975; Sage & Selander, 1975) and observations of interbreeding in the wild (Kornfield *et al.*, 1982). Both morphotypes have also been found in all known populations that have been examined in the small Cuatro Ciénegas valley in Mexico where *H. minckleyi* is endemic (Hendrickson *et al.*, in press),

Because the extreme morphological variation in this one species is apparently being maintained within populations (Schoener, 1986), stark differences in prey use among the *H. minckleyi* pharyngeal morphotypes might be expected. Discrete differences in diet, however, have not been identified. Previous studies indicate detritus, algae, macroinvertebrates (Sage & Selander, 1975; Smith, 1982) and snail shells (Sage & Selander, 1975; Smith, 1982) are consumed by both molariforms and papilliforms. Despite this qualitative overlap in diet, the papilliform pharyngeal jaw has been suggested to enhance the shredding of arthropods and plants (Sage & Selander, 1975; Liem & Kaufman, 1984; Hulsey *et al.*, 2005),

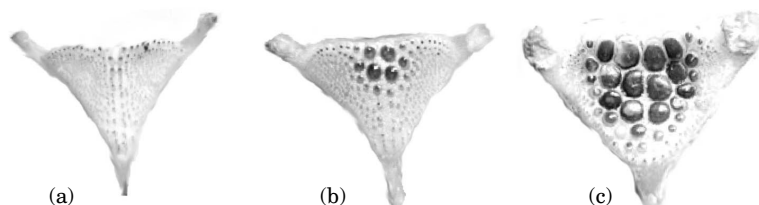(a)   (b)   (c)

FIG. 1. Lower pharyngeal toothplates of *Herichthys minckleyi*. (a) Small pointed teeth and slight pharyngeal morphology characterize papilliforms. (b), (c) The presence of enlarged flattened pharyngeal jaw teeth was used to categorize *H. minckleyi* as molariform. Although tooth number generally increases with size, substantial variation can be found in molariform tooth number. A substantial number of molariform teeth can be found on the pharyngeal jaw of some molariforms, but many fewer molariform teeth can also be exhibited on the pharyngeal jaw of similarly sized individuals. In smaller individuals (not shown), <50 mm L_S, the pharyngeal morphology is difficult to determine definitively.

and the massive teeth of molariforms have been hypothesized to be modified for crushing durable snail shells (Kornfield & Koehn, 1975; Sage & Selander, 1975; Hulsey *et al.*, 2005). Morphotype niche differences could be uncovered through more extensive quantification of prey use.

Previously cryptic diet differences might be detected if the specific snail species exploited by each morphotype were identified. In the diverse Cuatro Ciénegas gastropod fauna (Taylor, 1966; Hershler, 1985), several unusual snail species that exhibit extensive ribbing and sculpturing (Vermeij & Covich, 1978) may be crushed exclusively by molariforms. Alternatively, several more delicate appearing snail species (Minckley, 1969; Hershler, 1985) may be exploited primarily by papilliforms. Because the substratum of most of the Cuatro Ciénegas habitats are covered with the shells of dead snails (Taylor, 1966; Hershler, 1985; Johnson, 2005), evaluation of whether live snails are being crushed or empty shells are being accidentally consumed seems critical to determining if *H. minckleyi* morphotypes are segregated in their utilization of snails as prey.

The diet of *H. minckleyi* may also be influenced by morphological variation other than the simple presence or absence of molariform teeth. Fish >100 mm standard length, L_S, have been the focus of previous *H. minckleyi* diet analyses (Sage & Selander, 1975; Smith, 1982). Prior studies of *H. minckleyi* feeding specialization may have been biased as a result of observations made during only these later ontogenetic stages (Osenberg & Mittelbach, 1989; Wainwright *et al.*, 1991; Osenberg *et al.*, 1992; Wainwright, 1996). By examining feeding in smaller individuals (<50 mm L_S), at the stage when the pharyngeal morphology is difficult to determine, an ontogenetic contrast to the diet of the fully developed molariform and papiliform morphotypes could be made. How feeding may change with morphological variation that occurs within the *H. minckleyi* morphotypes may also not have been adequately appreciated in previous diet studies. For example, extensive variation in molar number is exhibited by molariform pharyngeal jaws (Sage & Selander, 1975), and within morphotype feeding specialization might be associated with this variation (Bolnick *et al.*, 2003).

To evaluate if pharyngeal morphology is associated with diet differentiation within *H. minckleyi*, gut contents of wild-caught fish exhibiting molariform, papilliform and undetermined pharyngeal jaw morphology were analysed. The proportional contribution and frequency that major prey types were recovered from the gut contents was determined. Whether the amount of plant material consumed and number of snails crushed were significantly different between papilliforms and molariforms was also assessed. Which species of snails were crushed and whether molariform L_S was correlated with the number of snails consumed was also investigated. Finally, the relationship between the number of molars (N_M) on the lower pharyngeal jaw and whether molariforms had recently crushed snails was examined.

METHODS

Gut contents of 178 *H. minckleyi* were examined in March 2002. Fish were collected from 11 pools in the Cuatro Ciénegas valley over several years (June 1999 to March 2001) (Fig. 2) and placed immediately in 95% ethanol for long-term storage. Most collections for a pool were made on a single day during the summer months. Eight fish collected
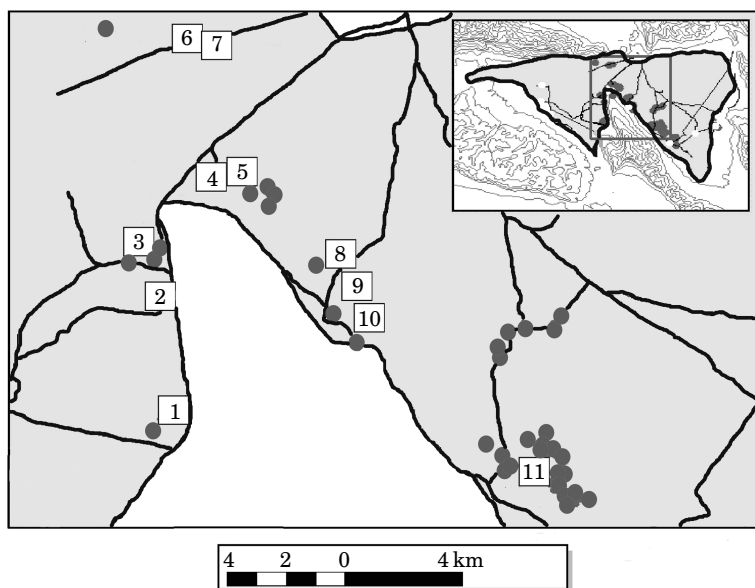
FIG. 2. Cuatro Ciénegas valley. In the top right corner inset, the entire valley (■) and the topography of the surrounding mountains (□) are depicted. A magnified view of the portion of the valley with the greatest number of pools is shown. ●, Pools present in the valley but not sampled. The eleven pools from which fish specimens were analysed for gut contents in this study are numbered: 1, Churince; 2, Becerra; 3, Juan Santos; 4, Mojarral Oeste; 5, Mojarral Este; 6, Poza Anteojo; 7, Anteojito; 8, Escobedo; 9, Poza Negro; 10, Tio Candido; 11, Poza Azules.

haphazardly throughout the sampling period, however, were also included in the analyses. The pools Anteojito ($n = 9$), Anteojo ($n = 13$), Azules ($n = 16$), Becerra ($n = 17$), Churince ($n = 12$), Escobedo ($n = 17$), Juan Santos ($n = 4$), Mojarral Este ($n = 14$), Mojarral Oeste ($n = 18$), Negro ($n = 9$), and Tio Candido ($n = 29$) were the sites where collections were made. These sites were chosen because they encompass the biotic and abiotic diversity of pools *H. minckleyi* inhabits. Diet analyses were performed on individuals combined across all pools potentially providing a robust view of differentiation, but unfortunately masking any differences among pools. Fish L_S was measured to the nearest 0·1 mm. For the gut analyses, fish were identified as having one of three pharyngeal jaw morphologies. Fish were classified as having either molariform jaws, if they possessed molariform teeth on the lower pharyngeal jaw ($n = 73$), papilliform jaws if they did not exhibit molariform teeth ($n = 85$), or as undetermined ($n = 20$). The last group of individuals included all fish <50 mm L_S whose pharyngeal jaw morphology was difficult to distinguish (Stephens & Hendrickson, 2001). All specimens have been deposited in Texas Natural History Collection of the Texas Memorial Museum, and catalogue numbers are available.

    The volume of diet items found in the entire digestive tracts of fish as well as the frequency of occurrence of prey types were quantified. The volumetric contribution was measured using water displacement, and frequency was defined as the percentage of a morphotype containing a particular prey type. Diet items were identified to the lowest practical taxonomic level (Hershler, 1985; Merritt & Cummins, 1996). Detritus in the gut contents was differentiated into two categories: (1). plant detritus (including algae) and (2). detritus (non-plant). Calcium carbonate, a common and presumably inedible component of the stromatolites and substratum in many of the pools, was commonly encountered in the gut contents and was referred to as 'travertine'. A χ^2 test was used to determine if dominant prey items differed between the gut contents of molariforms

and papilliforms. For plant detritus, which comprised an extensive proportion of the diet of both morphotypes, a two-tailed t-test was performed on its proportional contribution to the gut contents. Because the proportions violated assumptions of normality, arcsine transformations were performed on the data prior to the statistical analysis.

Frequency of snail crushing was also assessed for both molariforms and papilliforms. When snails are crushed by *H. minckleyi*, smashed shell may either be consumed or winnowed from the soft snail tissues and subsequently ejected from the buccal cavity (C. D. Hulsey, pers. obs.). Therefore, the degree of feeding specialization on snails may be misleading when based on the volumetric amount of snail shell in the gut. Because a snail's operculum is firmly attached to its soft edible parts, the number of snails eaten should be accurately assessed by counts of this keratinous opercular covering of the shell aperture recovered from the digestive tract (Wainwright, 1987). All snail opercula were isolated from the gut contents of *H. minckleyi*. Snail species were identified based on opercular traits that are diagnostic for each species (Hershler, 1985), and the opercula recovered from each fish were also enumerated. A t-test was used to determine if molariforms and papilliforms with snails in their guts differed in the number of snails crushed.

Several aspects of snail crushing within only the molariforms were also examined. The relative number of opercula from the three species *Mexithauma quadripaludium* (Hershler), *Nymphophilus minckleyi* (Hershler), and *Mexipyrgus churinceanus* (Taylor) recovered from the molariforms' guts was enumerated. It was then determined if there was a relationship between L_S of molariforms and the number of snails crushed. Also, to test if molariforms that had recently crushed snails had a significantly greater N_M, the number of molars present on the pharyngeal jaw of individuals that had recently crushed snails ($n = 25$) was tallied. Using an ANCOVA, these tooth numbers were compared to the N_M on the jaws of individuals that had not recently crushed snails ($n = 24$). Because N_M generally increases with body size (Sage & Selander, 1975), fish L_S was used as a covariate to compare the size specific N_M between the two groups of molariforms differing in the presence of snail opercula. Both L_S and N_M are counts and non-normally distributed, therefore, they were $\log_{10}$ transformed prior to the ANCOVA.

RESULTS

The three pharyngeal morphotypes differed in their gut contents (Figs 3 and 4). The combined total per cent volumetric contributions for prey types in order of decreasing contribution found in the *H. minckleyi* guts were: plant detritus 33·6%, detritus 30·0%, travertine 14·4%, snail shell 11·6%, Odonata 2·0%, fishes 1·4%, *Palaemonetes* sp. 1·2%, Chironomidae 1·2%, *Hyalella* sp. 1·1%, Ostracoda 1·0%, Hymenoptera 0·7%, Coleoptera 0·4%, Ephemeroptera 0·2%, Lepidoptera 0·2%, fish scales 0·2%, mites 0·1%, Diptera other than Chironomidae 0·1% and Hemiptera 0·1%. Arthropods accounted for a small amount of the total gut volume (Fig. 3). Chironomidae, *Hyalella* and Ostracoda were the arthropods most frequently ingested (Fig. 4), but their contribution to the gut contents of any pharyngeal jaw type (Fig. 3) was not substantial. Arthropods were not eaten significantly more frequently by either molariform ($n = 73$) or papilliform ($n = 85$) *H. minckleyi* (χ^2 test, d.f. = 1, $P > 0.05$) although there was a tendency for molariforms to ingest this prey type more frequently (70%) than papilliforms (40%). Additionally, fishes accounted for a small fraction of the diet of all morphotypes (Fig. 3). The vast majority of the gut volume was composed of snail shell, travertine, detritus and plant detritus.

The majority of the undetermined individuals' gut contents were filled with both types of detritus (Fig. 3). Only *c.* 20% of gut contents in these small individuals were composed of plant detritus, which was similar to the proportion
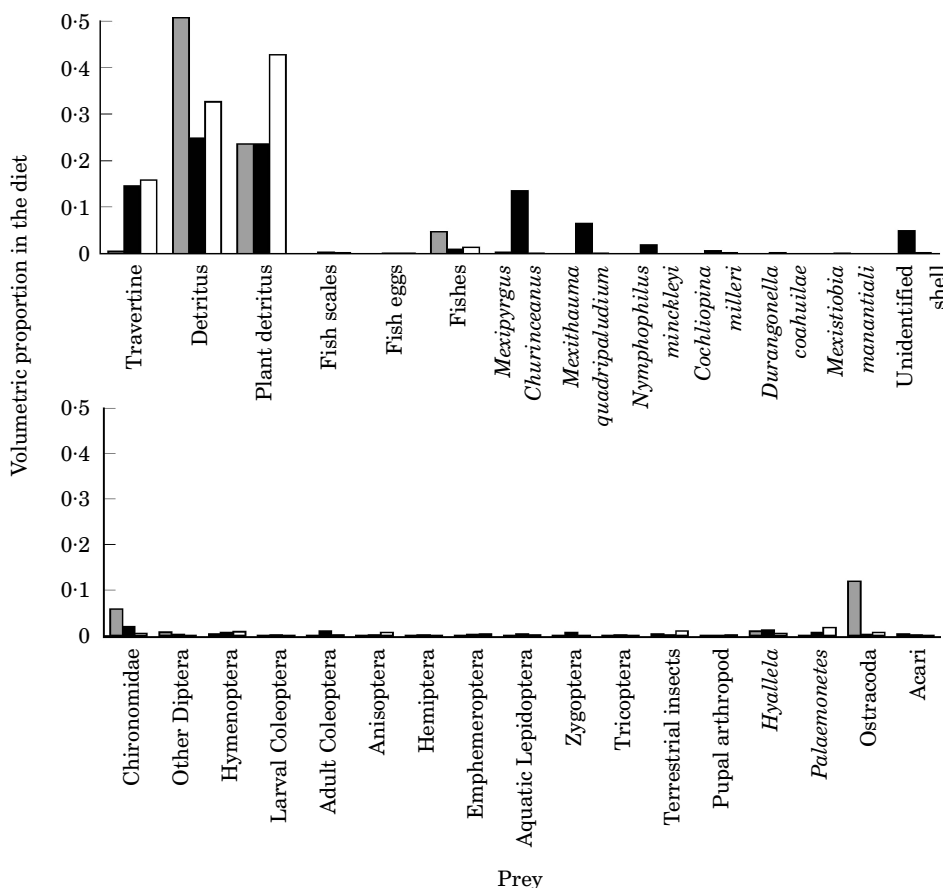
FIG. 3. The volumetric contribution of prey to gut contents of undetermined ■ ($n = 20$), molariform ■ ($n = 73$) and papilliform □ ($n = 85$) pharyngeal morphotypes of *Herichthys minckleyi*.

ingested by molariforms. In particular, Ostracoda and Chironomidae were both commonly consumed by these small fish. No snail opercula were recovered from these undetermined individuals.

Approximately 90% of *H. minckleyi* examined contained detritus as well as plant detritus in their gut (Fig. 4). Detritus did not occur with any greater frequency within papilliforms ($n = 85$) or molariforms ($n = 73$) (χ^2 test, d.f. $= 1$, $P = 0.975$). This is true for plant detritus in the same individuals (χ^2 test, d.f. $= 1$, $P = 0.650$). When the percentage of plant detritus contributing to the gut contents of these molariforms ($21 \pm 4\%$ mean $\pm$ S.E.) and papilliforms ($36 \pm 3\%$ S.E.) was compared, papilliforms consistently consumed a greater percentage of plant detritus (two-tailed *t*-test, papilliform $n = 85$, molariform $n = 73$, $P = 0.001$).

Ingestion of snails was non-randomly distributed among the pharyngeal jaw morphotypes (Figs 3 and 4). Snail shell accounted for a small percentage of the gut contents of papilliforms ($<0.5\%$) and only three papilliform guts contained opercula. In molariforms, 28% of the total gut contents were constituted of snail
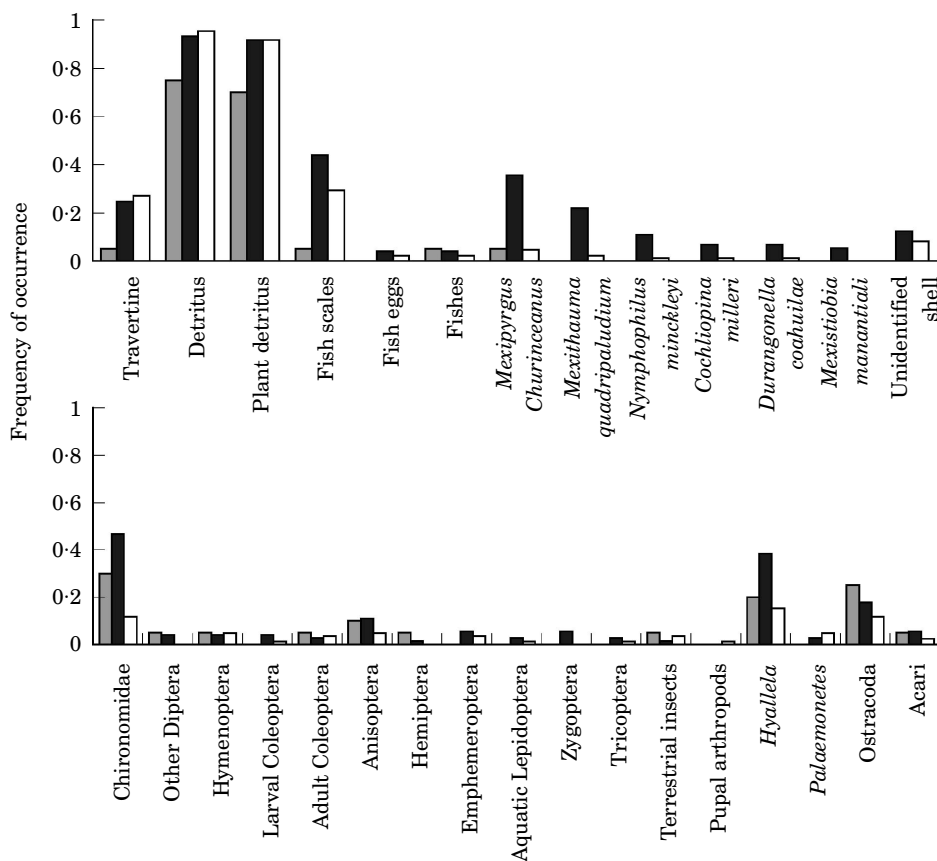
FIG. 4. The frequency of occurrence of prey in the gut contents of undetermined ▦, molariform ■ and papilliform □ pharyngeal morphotypes of *Herichthys minckleyi*. Samples sizes are as in Fig. 3.

shell, and snails were crushed with a significantly greater frequency by molariforms (χ^2 test, d.f. = 1, $P < 0.001$). Less than 4% (three of 85) of papilliforms contained snail opercula whereas 45% (33 of 73) of molariforms appeared to have crushed snails based on the presence of snail opercula. Furthermore, when examining only those papilliforms ($n = 3$) and molariforms ($n = 33$) with snail opercula recovered from their gut contents, molariforms ingested a significantly greater number of snails than did papilliforms (Fig. 5) (two tailed *t*-test, $n = 36$, $P < 0.001$). All three papilliform individuals with snail opercula in their digestive tracts contained only a single snail operculum. The mean ± S.E. number of snails inferred to have been crushed by molariforms, as indicated by snail opercula, was 14.9 ± 11.2 and the maximum number recovered from an individual was 52 opercula.

The most frequently encountered snail species in the molariform guts (57.0% of the snails crushed) was found to be *M. churinceanus*. The opercula of *M. quadripaludium* (29.7% of the snails crushed) and *N. minckleyi* (12.5% of the snails crushed) were also commonly recovered. There was a small amount of *Cochliopina riograndensis* (Pilsbry & Ferriss) shell but no opercula of this species
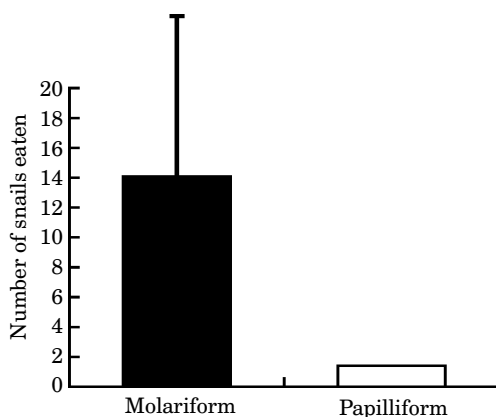
Fig. 5. Morphotype snail crushing. A greater number of snails were crushed by molariforms than by papilliforms even when comparing only those individuals that crushed snails (*t*-test, molariforms: $n = 33$ of 73, papilliforms: $n = 3$ of 85, $P < 0.001$).

were found in the gut contents. Notably, the small, thin-shelled *Mexistiobia manantiali* (Hershler) and *Durangonella coahuilae* (Hershler) were not often crushed when recovered from the guts, and when found in the papilliforms, they were never crushed. These two non-operculate snails accounted for <2% of the gut contents of molariform *H. minckleyi* (Fig. 3).

Size of the molariforms, L_S, and the number of snails eaten was not found to have a significant association (correlation; $n = 33$; $P = 0.838$). A strong relationship, however, was found between M_N on the lower pharyngeal jaw, as adjusted by L_S, and whether a snail had recently been ingested by a molariform (Fig. 6). Once L_S was factored out as a covariate, there were significantly more
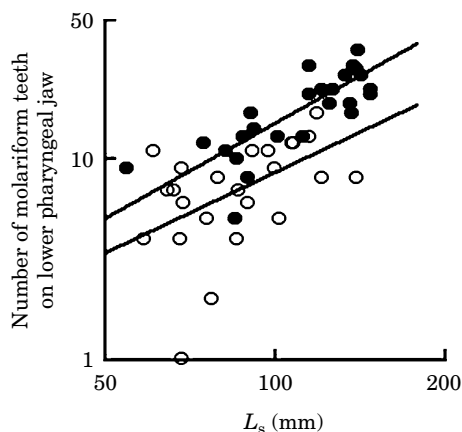

Fig. 6. Diet related phenotypic difference in molariform *Herichthys minckleyi*. Once L_S was accounted for in an ANCOVA, molariforms that contained snail opercula in their gut contents (●) were found to have on average more molariform teeth than molariforms that did not contain snail opercula (○). The curves were fitted by: $\log_{10} y = 1.43 \log_{10} x - 1.68$ (snail opercula in the gut) and $\log_{10} y = 1.20 \log_{10} x - 1.49$ (no snail opercula in the gut).

molariform teeth (ANCOVA; $n = 25$ molariform that contained opercula, n = 24 molariform that did not contain opercula, $P < 0.001$) on the lower pharyngeal jaw for individuals ingesting snails ($\log_{10} M_N = 1.43(\log_{10} L_S) - 1.68$) as compared to molariforms that had not ($\log_{10} M_N = 1.20(\log_{10} L_S) - 1.49$).

DISCUSSION

Prey use differed substantially among the *H. minckleyi* pharyngeal morphotypes. Plants and snails were not exploited extensively by undetermined *H. minckleyi*. The same percentage of plant material recovered from molariforms was found in the undetermined guts (Fig. 3), and snails were never crushed by this smaller morphotype. The pharyngeal jaws of *H. minckleyi* <50 mm L_S have not yet fused and their teeth and muscles have not been fully developed (Stephens & Hendrickson, 2001). Because of their undeveloped jaws and teeth, shredding plants and crushing snails are probably not a viable means of prey processing by undetermined *H. minckleyi*.

Both molariform and papilliform *H. minckleyi* have been found experimentally to favour feeding on arthropods over crushing snails (Liem & Kaufman, 1984). Extensive exploitation of arthropods in the wild by *H. minckleyi* is not strongly suggested by the volumetric proportion or frequency of this prey type in the diets. Cuatro Ciénegas is characterized by a strikingly low abundance of aquatic arthropods (Dinger, 2001), and the low prevalence of arthropod prey in the diets of *H. minckleyi* (Fig. 4) may be a result of this low availability. The advantage of feeding on plants or snails may be increased by the low arthropod density in Cuatro Ciénegas.

Plant material was consumed by papilliforms to a greater extent than by molariforms (Fig. 3). The ability of papilliforms to effectively shred and manipulate plant material when compared to molariforms (Hulsey *et al.*, 2005) may be due to their more gracile pharyngeal morphology and small pointed teeth. If plant detritus is more extensively shred by papilliforms, nutrients from this difficult to digest food may be more efficiently extracted (Horn, 1989). Further trophic niche differentiation within *H. minckleyi* could be identified by finer taxonomic categorization of the plant material that both morphotypes ingest.

Snails rarely or perhaps were never crushed by papilliforms, but all three common and robust Cuatro Ciénegas snails (Fig. 5) were frequently crushed by molariforms. *Mexipyrgus churinceanus* was ingested most frequently, but both *M. quadripaludium* and *N. minckleyi* were also often crushed by molariforms. There was no relationship between molariform L_S and the number of snails crushed. Also, snails were crushed by less than half of the molariforms examined and a mere 28% of the molariform gut contents was constituted of snail shell (Fig. 3). This low snail utilization may be due to the shell strengths of these robust snails (Hulsey *et al.*, 2005) that would make it more favourable for molariforms to eat alternative prey when available. Prey availability throughout the year in Cuatro Ciénegas should be assessed further because feeding behaviours in the *H. minckleyi* morphotypes do vary seasonally (Cohen *et al.*, 2005). As the frequency of morphotypes varies among habitats (Hendrickson *et al.*, in press), more intensive examination of differences in prey availability among pools might also be informative about *H. minckleyi* trophic specialization.

A fundamental question regarding *H. minckleyi* trophic biology that has not been conclusively answered is if the presence of molariform teeth is determined genetically or is induced as a plastic response to environmental conditions (Kornfield & Taylor, 1983, Trapani, 2003). In *H. minckleyi* with at least one molariform tooth, however, total molar number appears to be influenced by snail crushing. Breeding studies indicate that *H. minckleyi* have lower M_N when compared to individuals in the wild (Trapani, 2003). Also, a correlation between M_N and the presence of crushed snails in the diet was shown in this study. Increasing molarization of the jaw in response to snail crushing has been found in other fishes as well (Wainwright *et al.*, 1991; Mittelbach *et al.*, 1992). In the future, molecular markers should be developed to confirm what aspects of morphological variation in the *H. minckleyi* pharyngeal jaw have a genetic basis. If these genetic tools were coupled with further laboratory analyses of the prey characteristics that induce the variation in *H. minckleyi* pharyngeal dentition, the mechanistic underpinnings of this trophic polymorphism could be determined.

Understanding what components of a predator's feeding morphology are novel and adaptive is aided by documenting what prey are utilized in a predator's native habitat (Wainwright, 1996). Even when discrete trophic phenotypes exist within a species, it is not a guarantee that qualitatively different prey will be utilized by alternative phenotypes (Smith, 1982; Schoener, 1986; Robinson & Wilson, 1998). Unexpected insights into trophic differentiation may be provided by explicitly linking morphological variation to ecological differences as attempted in this study (Wainwright *et al.*, 2001; Hulsey & Wainwright, 2002; Bolnick *et al.*, 2003). Which factors originally favoured and preserve the pharyngeal variation in this polymorphic fish could be resolved through further studies of *H. minckleyi*.

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