TROPHIC ECOLOGY OF THE CICHLID MORPHS
OF CUATRO CIENEGAS, MEXICO

By

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Requirements for the Degree of
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An Abstract of the Thesis Presented in Partial
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Observations of resource utilization and feeding behaviors of the endemic cichlid ecomorphs of Cuatro Cienegas, Coahuila were made in three consecutive summers. Comparison of diets between the two major morphs of this species (by gut content analysis and the Schoener index of diet overlap) indicated that ecological differences are not as great as expected on the basis of distinct trophic morphologies. A lack of dietary specialization was shown in the season when food was presumably most abundant, a finding which is apparently not consistent with optimal foraging theory.

Previous workers inferred real and continuous ecological differences between these morphs, and the hypothesis was presented that molariform cichlids may "track" snail abundance over time. The data presented here suggest rather that snails may constitute a competitive refugium for molariforms as food becomes scarce, or that the present polymorphic system is an historical artifact not dependent on present snail populations.

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Introduction

The endemic cichlids (genus Cichlasoma) of the Cuatro Cienegas basin in Mexico have been of interest to evolutionary biologists since their discovery by E.G. Marsh, Jr. in 1939. Taylor and Minckley (1966) reported the existence of three cichlid species in the Cuatro Cienegas valley which preyed on snails, organic detritus, and fish, respectively. They concluded that these trophic forms represented adaptations to adjacent ecological niches. Taylor and Minckley also raised the possibility of sympatric speciation in this fauna due to the absence of temporally sufficient geographic isolation within the valley for allopatric differentiation to have occurred. In a detailed analysis of comparative cichlid morphology, LaBounty (1974) concluded that actually four species were present: a molluscivore, a detritivore, and two cryptic piscivorous forms. Kornfield and Koehn (1975) examined the two major morphs (mollusc-crusher and detritivore) for biochemical differentiation and found virtual electrophoretic identity between them. Although they discussed the possibility of a single biological species, Kornfield and Koehn concluded that these forms represented closely related species which differed in some restricted portion of their genomes, not reflected in the isoenzyme data. Based on evidence of concordant geographic variation in allele frequencies between morphs, Sage and Selander (1975) proposed the hypothesis that trophic polymorphism rather than speciation was represented in these cichlids.

Recent work on the reproductive biology of these fish has provided additional compelling evidence in support of the single species hypothesis. In particular, concordant temporal as well as geographic variation in allele frequencies, the absence of differential post-zygotic mortality in intermorph versus intramorph crosses, and demonstration of random mating between morphs in nature provide direct evidence for this theory (Kornfield, et al. in press). The existence of dichotomous arrays of functionally interrelated characters and the high degree of morphological divergence in trophic adaptations between these morphs was the original impetus for recognition of separate species. The major differences involve the relative size of the tooth-bearing pharyngeal plates and head musculature associated with these elements, the size and number of the pharyngeal teeth, and the relative gut length of the two forms (LaBounty 1974; Sage and Selander 1975; Hoogerhoud and Barel 1978). These characters are only evident upon internal examination; otherwise, the morphs are externally indistinguishable. This magnitude of differentiation parallels that seen between many congeneric cichlids of the species flocks in the African rift lakes, and many of the standard taxonomic characters used to distinguish these Old World species are involved in the divergence of the Cuatro Cienegas morphs. Taxonomists have generally used similar levels of morphological specialization as indicators of systematic differentiation (Fryer and Iles 1972; Greenwood 1974).

Sage and Selander (1975) suggested that this morphological and trophic polymorphism was genetically controlled by a regulatory "switch" gene. They predicted that the molariform or snail-crushing phenotype would be recessive to the papilliform or detritus-eating phenotype, thereby ensuring the survival of the molariform type in the population even at low snail densities. The molluscivore would be expected to "track" the environment (snail density) and might be most numerous in localities with many snails. In effect, the polymorphism was presumed to have had the effect of broadening the among-phenotype niche width of the species along the food axis (sensu Roughgarden 1972), by opening up a resource unavailable to or not effectively exploited by the presumed generalist precursor species.

This study was prompted in part by the paucity of data concerning resource utilization by these morphs. Speculation about the origin and maintenance of the trophic polymorphism presupposed real and continuous ecological differences between forms. Previous work on food habits was cursory (Taylor and Minckley 1966; LaBounty 1974; Sage and Selander 1975), and indicated only the general food categories utilized. No comparisons of dietary similarity were possible since neither numbers of food items nor volumes of food categories was reported. Critical examination of the trophic ecology of these cichlids may be pertinent to niche theory, and may increase understanding of the striking adaptive radiations observed in the family Cichlidae (Fryer and Iles 1972).

General ecological setting

Three major localities were examined in the Cuatro Cienegas basin: Laguna Churince, Pozos de la Becerra (South), and Laguna El Mojarral (for precise locations, refer to Minckley 1969). (These localities are hereafter referred to as Churince, Becerra, and El Mojarral, respectively.) Each study site is dominated by a submerged area of detrital aggregate (composed of fish and snail feces, dead and crushed snail shells, decaying plant matter, and associated love algae, diatoms and bacteria). Interspersed in the detrital sediment are beds of stoneworts (Utricularia) and blue-green algae (Chara). Firmer substrates consist of travertine ledges, and densely packed snail shells near stream outflows.

Churince is the smallest and most eutrophic of these locales, with approximately 50% of the bottom covered by plants or algae. Reeds are abundance about the entire perimeter, while dense beds of Utricularia predominate in shallow areas. Water depth ranges from 0.5 - 3.0 m. Nymphaea (waterlilies) are absent from this locality.

Becerra is relatively devoid of vegetative cover, which comprises 20% or less of the bottom area. A narrow band of waterlilies on the east bank and scattered eelgrasses in shallows along the west bank form the bulk of the aquatic macrophytes. No beds of stonewort or algae occur here. This site was disturbed by construction of a canal in 1964 which lowered water levels by more than a meter (Minckley 1969). In addition, this lake is in constant use as a "swimming hole" in summer by the local populace. This appears to have little impact, however, on behavior or reproduction of the fishes. The central area is almost 5 m deep and, owing to numerous submerged springs, the sediment layer is in constant agitation.

El Mojarral, a small lake, comprised the largest study area.

Nymphaea is the dominant vascular plant at this locality. Wide beds of waterlilies occur in the shallows, along the entire southern perimeter and around the stream outflow from the lake. Approximately 40% of the bottom is vegetated. Aside from lily beds, large mats of *Utricularia* and *Chara* are the most common types of plants. Other dominant substrate types include large open areas of flocculent detritus in the deepest water (5-6 m), and broad rocky ledges of travertine where high currents sweep away the sediment layer. A schematic map of El Mojarral is provided in Fig. 1.

Snail habitats

The dominant snail species at each of these three localities belong to the endemic genera *Mexipyrgus* (six species in the basin), *Mexithauma* (one species), and *Nymphophilus* (one species) (Taylor 1966). *Mexipyrgus* is copraphagic, apparently capable of digesting diatoms, algae, or bacteria inhabiting the fecal pellets of snails and fishes. It is abundant in the top 2-3 cm of the detrital aggregate layer. Reproduction is apparently continuous throughout the year, by ovoviviparity (young are expelled completely formed). The typical size range for adults is from 4-7 mm. The shells appear highly variable in sculpturing and banding pattern.

Mexithauma reaches sizes up to 8 mm and is much less variable in color and form than *Mexipyrgus*. The shell is highly sculptured and the bristly periostracum forms a dark spiral banding pattern. These snails appear to browse on particulate matter, diatoms and microorganisms on firm substrates (on undersides of stones or tufa, or on firm, shelly bottom). Reproduction is again continuous by ovoviviparity.

Nymphophilus is quite large by comparison, up to 10 mm in length, and is typically found in association with *Nymphaea*. It grazes on epiphytes of the stems and leaves, and possibly also utilizes substrates proximal to these plants. This species lays single encapsulated eggs which often are found on shells of live *Nymphophilus* (Taylor 1966).

Correlated cichlid trophic adaptations

The oral dentition (premaxillary and dentary) of both morphs consists of relatively unspecialized caniform teeth (LaBounty 1974). The pharyngeal jaws of these cichlids (comprising a lower element representing the fused fifth ceratobranchials, and the paired upper epipharyngobranchials 2,3,4) are markedly different. The papilliform morph has very fine villiform teeth on the occlusal surfaces and a relatively narrow lower pharyngeal element. The molariform fish have broad flat molars on the pharyngeal plates which are surrounded by a small number of papilliform teeth. The entire structure is proportionately much more massive than that of the papilliform, and the extrinsic branchial musculature associated with movements of the pharyngeal elements appears hypertrophied in molariform fish. The neurocranial apophysis or articulation of the epipharyngobranchials 3,4 also shows immediate differences between morphs, it being much broader and saddle-shaped in the molluscivore (Hoogerhund and Barel 1978). A trend towards greater head width in this form has been noted, traceable to this hypertrophy of branchial elements and head musculature.

Gut length (GL) also appears to be correlated with these trophic characters and differs significantly between morphs. The average GL for papilliforms is about 3.3 times the standard length (SL) of the fish (range: 2.5-4.5 x SL), while for molariforms the relationship is approximately 1.6 x SL (range: 1.0-2.5 x SL) (LaBounty 1974, Table 6; personal observation).

In addition to the two major morphs, individuals with pharyngeal dentition intermediate between them have been identified. LaBounty (1974) reported that the incidence of intermediate forms appeared to increase "at various localities" in successive collections from 1958 to 1972, although neither numbers nor proportions of intermediates in the samples was reported. Gut length of these individuals appears to be intermediate between that of the other two morphs, with considerable overlap (mean GL = 2.1 x SL; range: 1.0-4.0 x SL) (LaBounty 1974, Table 6).

Our own collections yielded a frequency of intermediates in the general population of ≤5%. The criteria used for recognition of intermediate individuals was: 1) presence of enlarged teeth along the central rows only of the pharyngeal plates, and 2) presence on these small molars of a pointed cusp (rather than the completely flattened teeth of the molariform).

Materials and methods

Cichlid feeding behavior in situ

General observations of cichlid feeding repertoires were made in July and August of 1979 and 1980, at Churince, Becerra and El

Mojarral. Areas of intensive feeding activity were observed by skin divers, and typical foraging behaviors were catalogued. More detailed quantitative measurements of feeding activity were made at El Mojarral in July, 1981. Individual fish feeding in deep sediment were followed and the temporal sequence of discrete behaviors associated with foraging was recorded. The following measurements were taken: 1) the total time (seconds) of observation; 2) time between feeding bouts; 3) relative depth in the substrate at which the fish foraged (to the level of its mouth, eye, posterior margin of the operculum, or anterior margin of anal fin); and 4) whether the fish discharged sediment ("winnowed") through the mouth or gills after feeding. The individual under observation was captured by speargun after several feeding attempts to determine the morphotype. Data were gathered for four papilliforms and nine molariforms, feeding in one area.

Resource utilization

Preliminary results on cichlid food habits were obtained at Churince in July, 1979, utilizing a stomach flushing technique (Foster 1977). Thirty-five cichlids were captured with hand nets at various hours of the day, or at one hour after dark. Standard length, sex (by examination of genital papilla), and pharyngeal tooth type were recorded for each fish. Stomach contents were fixed in 10% buffered formalin and stored in numbered vials. The samples were sorted under a stereomicroscope in the laboratory and individual prey items were counted.

A general collection of cichlids was made in July and August of 1979 at all three study sites. A variety of sampling methods was employed: speargun, hand net (generally after dark), and fyke net. Each fish was identified at time of capture by insertion of a numbered, color-coded tag (Dennison clothing tags) into the dorsal musculature. Fish were preserved in the field in 10% formalin, and later transferred to 50% isopropanol. A representative sample of both morphs was chosen from this general collection for gut content analysis. Entire intestinal tracts were excised and gut length (GL) was measured to the nearest centimeter, by gently straightening the intestinal coils on a centimeter scale. The average of three independent GL measurements was recorded, as well as SL, sex, morphotype, and capture location. Eighty-one fish were examined.

The entire intestinal contents were sorted, identifed to lowest possible taxon, and counted. Volumes (by dry weight) of major food types were measured for stomach contents only, in order to circumvent possible differential rates of digestion of prey items as food moved through the intestine. Statistical calculations on gut contents were made as follows: 1) Frequency of occurrence (FO%)--the percentage of guts containing a particular food item; 2) Average number (Ave. no.)--the mean number of organisms in guts containing that organism; and 3) Mean percent volume ($\overline{V}\%$)--the average percentage that each food category contributed to the total volume (weight) in each stomach. A large proportion of stomachs (36%) contained no food (possibly attributable to sampling methods employed, or a rapid evacuation rate of food from the stomach). These stomachs were excluded from calculations of volume percentages. Due to small sample sizes, no subdivision of analysis by sex was performed.

A smaller collection of fish at El Mojarral was made in July, 1980 by selectively speargunning individuals actively feeding in one of two distinct habitat types. Regions of intensive feeding activity were chosen for sampling on different substrates (travertine ledge in relatively shallow water, or deep flocculent detritus). These areas are indicated in Fig. 1. Fish were eviscerated in the field and the entire gut was stored in formalin. SL, sex, morph, date of capture, and habitat type were recorded. Gut contents were analyzed as above. Due to occurrence of only minute quantities of food, or complete lack thereof, in stomachs previously examined and in these samples, the entire gut and stomach contents were pooled for direct volumetric measurements of major food types in each gut. Ten fish were examined by this method.

A large sample of juvenile cichlids (SL < 60 mm) was collected, also in 1980 at El Mojarral, by placing unbaited metal minnow traps on firm substrate where numerous small cichlids appeared to congregate and feed. Fish were preserved whole in 10% formalin in numbered jars. Entire intestinal tracts were analyzed for FO% and Ave. no. Sex was indeterminable in most cases. The pharyngeal tooth type was determined by dissecting out the upper and lower pharyngeal elements, staining them lightly in alizarin red in 1% KOH, and examining the tooth plates under a stereomicroscope. A total of 41 juvenile cichlids was examined.

Gut evacuation rate determinations

An attempt was made to compare the average evacuation rate or passage rate of food through the gut of papilliform versus molariform cichlids. Adult fishes were shipped in August 1979 and 1980 from the field to wet lab facilities at the University of Maine at Orono. Fish were maintained singly in 160 l tanks at 32° ±1°C, under a 14:10 light:dark photoperiod, and were fed a diet of commercial trout pellets. Thirteen fish (9 papilliform and 4 molariform) were tested to determine the time to first excretion after feeding. Fish were starved at least 48 h prior to testing to ensure complete evacuation of the gut, then fed to satiation; excess food was then removed. Tanks were checked hourly to determine the interval during which the first excretion of the consumed ration occurred. Up to 10 trials per fish were run. SL, sex, and morphotype were recorded for each. Six of these fish were sacrificed upon termination of these experiments; for these, GL was measured directly. For the remainder, GL was computed from a regression analysis of GL on SL for each morph. The data were expressed as the average evacuation rate or passage rate of food through the gut (cm h^{-1}).

Comparative gut morphology and histology

Entire guts from two specimens of each morph were fixed in the field in Bouin's solution. The stomach sac and midgut region were embedded in paraffin, sectioned at 10µ , and stained with hematoxylin and eosin, and Alcian blue. A graded series of specimens of various standard lengths was utilized in examining gross morphology and development of the gut.

Snail abundance measurements

In an effort to characterize the abundance of the dominant snail prey, *Mexipyrgus*, five samples were taken within one contiguous area of intensive feeding activity (Fig. 1) at El Mojarral, in August, 1980. A 50.8 cm diameter hand net (8 mm mesh) was held parallel to the substrate, the lip was inserted approximately 2 cm into the detritus, and the net was scooped forward one diameter. This yielded an approximate volume of 4 l of material. The detrital aggregate was fine enough to filter through the mesh; all larger particles of shell debris, whole snails, invertebrates, and plant matter were retained. Samples were bagged and preserved in 10% formalin.

Two 30 ml portions from each sample were examined for presence of live snails. The number and dry weight of live snails was recorded, as well as the dry weight of all remaining debris. Debris consisted primarily of dead snail shells, shell fragments, and decayed plant matter. Additional potential prey items, including ostracods and amphipods, were present in most samples. Also noted were several cichlid pharyngeal teeth and trematode cercariae. The data are expressed as the percentage of live snails (by weight) of the total weight, and the average number of live snails per 30 ml portion is given. The total volume of shell material and plant debris in each sample was measured to compute approximate snail abundances (number per square meter) within the top 2 cm of substrate.

Snail behavior in situ

To characterize possible anti-predatory strategies of Mexipyrgus in El Mojarral, snail behaviors were observed in August, 1980. Movements of Mexipyrgus were demonstrated by marking live snails with waterproof ink, and placing ten snails each in several glass culture dishes. (The height of the sides was 5 cm.) Dishes were placed on various substrates (rock ledge, flocculent sediment, or tufa stones) in the morning such that snails remained uncovered by detritus. Snails were checked for migration in the afternoon and again on the following morning. The numbers of new (immigrant) snails and the marked snails remaining were noted.

Behavior of Nymphophilus was characterized by visually counting snails on upper and lower leaf surfaces and stems of ten separate leaves of Nymphaea plants. Twenty water lilies were marked and checked during daylight and again after dark (using underwater lamps and waterproof notepads). Sixty-two observations were made during the daytime in this manner, and 34 at night.

Snail crushing experiments

A graded series of snails, Mexipyrgus multilineatus, Mexithauma quadripaludium, and Nymphophilus minckleyi, all endemic to El Mojarral, were crushed on an Instron weight loading machine to measure the force necessarily exerted by cichlids in cracking snail shells. The wet weight of individual snails (which bears a direct linear relationship to shell length) was graphed versus the force (in Newtons) required to crush them. For comparison, the marine species Littorina littorea is included on this graph.

Results

Cichlid feeding behavior in situ

In areas of deep sediment, fish dip into the substrate at an angle of approximately 45-60 degrees, engulf a mouthful of detritus, and often winnow out coprapel and shell fragments through the opercular openings. In beds of Chara and Utrilcularia, and on other submerged macrophytes, fish appear to pick stems and leaves (possible cropping epiphytic diatoms and algae). Around submerged upwellings, smaller cichlids sometimes congregate to pick out dislodged "Aufwuchs" from the water column. On travertine ledge, small sichlids appear to feed by picking at the thin detrital layer, fissures in the substrate, or occasionally by rolling small stones, presumably searching for cryptic arthropods.

A marginally significant difference between morphs in the time between feeding attempts was revealed (Mann-Whitney U test, P=0.10, one-sided test) (Table 1). Observations on the depth in the substrate at which the fish foraged ranged from the level of the mouth up to the anal fin but no significant difference between papilliform and molariform was indicated. The frequency of winnowing flocculent material through the mouth and gills also appeared to be the same for both morphs.

Resource utilization

Five major food types were found to occur in cichlid guts, which were subdivided as follows:

1) Plant matter

   a) Algae - Chara, filamentous blue-greens, and some brown algae were most common;

   b) Vascular plants - stems and leaf fragments (fresh and decayed) of Nymphaea, Utricularia, and sedges;

2) Arthropods

   a) Acari - brown and blue water mites were occasionally present in abundance. The species were not identified;

   b) Amphipoda - Hyalella azteca was the only species noted;

   c) Arachnida - all appeared to be terrestrial spiders;

   d) chironomid larvae - were occasionally highly abundant;

   e) Diptera (adult) - mostly midges, some possibly emergent forms;

   f) Formicidae - occurred in few guts;

   g) Odonata - appeared to be dragonfly naiads and pupae;

   h) Ostracoda - probably Chlamydotheca; appeared to be widespread in the sediment but low in abundance;

   i) miscellaneous - included unidentifiable fragments (legs, wings, ommatidia) encountered in guts;

3) Gastropods--An attempt was made to distinguish snails ingested live and then crushed from shells which were old and dead by searching for 1) pigmented snail flesh adhering to the whorls, and 2) presence of operculi with shell fragments. Snails were enumerated by counting the last whorls (apex) of crushed shells.

   a) Mexipyrgus - appeared to be the most abundant snail at all localities and in guts overall;

b) Mexithauma - occurred only rarely in guts;

c) Nymphophilus - also rare in guts;

d) fragments - included all old shell debris and, if no evidence was found that the snail had been ingested live, any other fresh snail fragments;

4) Fish

a) eggs - the size of fish eggs in guts matched the typical size of cichlid eggs (1-2 mm).

b) scales - both cycloid and ctenoid scales were found; only cichlids and largemouth bass (Micropterus salmoides) have ctenoid scales at these localities.

c) whole fish - were generally too digested for positive identification, but were probably Gambusia or Cyprinodon (as associated scales were cycloid);

5) Detritus--bottom sediment composed of snail and fish feces (with its associated microflora), minute shell fragments, and occasional bits of algae-encrusted travertine.

Frequency of occurrence (FO%) and average number (Ave. no.) of food items identified in the guts of adult cichlids are presented in Table 2 for the three study sites. The presence of detrital aggregate and some plant matter was common to almost all fish examined. Fish parts, especially scales, occurred in a substantial number of specimens, but the average numbers in guts were low. Live snails and shell fragments were more common in molariform fish than papilliforms, but again the mean number per gut is low (less than 5). In an effort to determine the magnitude of dietary similarity between morphs, an index of diet overlap was calculated (Schoener 1970) as follows:

$$\alpha = 1.0 - 0.5\ (\underset{i=1}{\overset{n}{\ }}\ p_{ix} - p_{iy}\ ),\ \text{where:}$$

p_{ix} = proportion of food type i in morph x (molariform);
p_{iy} = proportion of food type i in morph y (papilliform);
n = number of food categories (5).

The proportional measure used was the mean of the volume (weight) percentages (V%) for the five major food types (for discussion, see Wallace 1981). Diet overlap and V% measures are presented in Table 3 for the 1979 collection. Data are presented for each locality separately and for all trophically identical morphs pooled over localities (due to small sample sizes). Diet overlap values ranged from $\alpha = 0.58$ at Churince to 0.77 at Becerra. The Schoener index ranges from 0 (no overlap) to 1.0 (indicating complete dietary similarity). Overlap in this index is generally considered significant at levels exceeding 0.60 (Wallace 1981). The α value for pooled specimens was 0.85, thus indicating a very high degree of diet similarity overall.

Table 4 includes FO% and Ave. no. for all cichlids (adults and juveniles) collected in 1980 at El Mojarral. Adult molariforms feeding on travertine shelf appeared to utilize a greater number of snails and insect larvae (chironomids and odonates) than papilliforms feeding sympatrically. This is better illustrated by the volumetric measurements of these food categories (see Table 5) and a relatively low level of diet overlap ($\alpha = 0.44$). By contrast, utilization of the arthropod resource in flocculent sediment is essentially equivalent for both morphs (Tables 4 and 5). Again, molariforms took more snails more often in this habitat type than papilliform fish. Overall, diets appeared more similar here, with $\alpha = 0.74$.

Detritus, plant matter, and fish scales occurred in most guts of juvenile cichlids from El Mojarral (Table 4). Molariforms appeared to prey on snails slightly more often than juvenile papilliforms, but it is notable that all three major snail species are utilized by both morphs. Compared to adult cichlids feeding in a similar habitat type, the spectrum of foods chosen by juveniles appears to be identical, but the average numbers and frequency of occurrence of most items are less.

Gut evacuation rates

The comparative rates of passage of food through the gut is presented in Table 6 for both morphs. A marginally significant difference in evacuation rate between morphs is indicated (Mann-Whitney U test, $.05 < P < .10$).

Comparative gut morphology and histology

The gross morphology of the intestinal tract of the morphs appears identical. The gut consists of a highly muscular esophagus leading into a simple sac-like stomach, which itself empties via the same opening into the proximal intestine. No pyloric valve was observed. The walls of the proximal intestine are highly folded and appear very muscular. No intestinorectal valve occurs, but the rectum can be distinguished from the distal intestine by lack of wavy mucosal folds prominent in the latter part. Histological sections of the stomach sac and mid-gut region revealed no major differences in the gastric mucosa or intestinal walls between the morphs.

Gut length was regressed on standard length for both morphs. For papilliforms the relationship is described by:

GL (cm) = -8.736 + 0.300 x SL (mm); and for molariforms:

GL = -2.297 + 0.192 x SL (see Figure 3).

An F-test comparison of slopes indicated a very significant difference (F = 10.58**, df = 1,34, .005 < P <.010). The regression lines intersect one another at about 60 mm (SL); below this size, GL is approximately equivalent for both morphs, and approaches the standard length of the individual. The general ontogeny of gut development is shown in Figure 2 for both morphs, as drawn from a graded series of specimens. The elongation and coiling of the intestines of larger papilliform fish is quite marked compared to that of molariforms of equal size.

Snail abundance measurements

Table 7 summarizes snail abundance data for Mexipyrgus in five microhabitats of El Mojarral. These data indicate the extreme patchiness of the snail resource within the bottom sediments, even in contiguous microhabitats. Factors affecting the distribution of snails in the detrital layer are not known. Although the abundance of the other two major snail prey species has not been measured quantitatively, the habitats utilized by Mexithauma and Nymphophilus do not appear as extensive as that of Mexipyrgus. In general, the abundance of Mexithauma beneath stones and in interstices of travertine appears low. No local congregations of this species have been noted. Similarly, waterlilies harbor few individuals of *Nymphophilus* per plant.

Nocturnal vertical migrations of *Mexipyrgus*, *Nymphophilus*, and possible *Mexithauma*, apparently associated with cryptic feeding behaviors, are indicated in Table 8 . (Over 30% of snails entering dishes placed on travertine were *Mexithauma*; the remainder were *Mexipyrgus*.) No daytime movements of either species were observed. The substantial nocturnal movements, coupled with the extreme shell hardness in this snail fauna, suggests the possibility of coevolution of these snails with their cichlid predators. Figure 4 graphs the shell strength (Newtons) versus the wet weight of shells (which bears a direct linear relationship to shell size) for the three dominant snail species of Cuatro Cienegas. For comparison, the local marine species, *Littorina littorea* is included as representative of thick-shelled marine gastropods.

Discussion

Previous workers inferred a high degree of diet specificity in these cichlids, based on distinct trophic morphologies. Taylor and Minckley (1966) noted the presence of snails in guts of molariform fish in X-ray photographs, and reported that snails are the main food of this form and are not eaten by papilliforms. Sage and Selander (1975) found snails in the intestines of 35 molariform and one papilliform fish, in a sample of 128 fish from the Cuatro Cienegas basin. They postulated that the molariform morph might track snail abundance over time, assuming a high specificity of molariforms on snails. In contrast, the above data on diet overlap indicate a high degree of similarity in food items selected by both forms, rather than a clear-cut dietary separation. For example, the Schoener index of overlap computed for all 1979 specimens overall yielded α = .85. Values for closely related sunfish species (_Lepomis_ _gibbosus_ and _L_. _megalotis_ _peltastes_) ranged from less than 0.10 to 0.48 in various lake habitats (Laughlin and Werner 1980). Overlap between Mississippi silversides (_Menidia_ _audens_) and juvenile largemouth bass (_Micropterus_ _salmoides_) seined concurrently from a single river, computed by the same method employed here, yielded α = 0.43 (Wallace 1981). In the absence of information on resource abundance, the Schoener index appears to be a useful measure of diet similarity (Wallace 1981). The relatively high α value for pooled specimens reflects the similarity of food items selected by these cichlid morphs over all three major localities of Cuatro Cienegas. When broken down by locality, the α

values ranged from 0.58 to 0.77, apparently reflecting the resource abundance specific to each locale. Of particular interest is the analysis of diet differences in different habitat types (El Mojarral, 1980). Although diet overlap is quite high for fish feeding in deep sediment ($\alpha = 0.74$), on travertine ledge the spectrum of food items selected appears to diverge ($\alpha = 0.44$). When pooled over both habitats, however, the morphs appear to exhibit significant overlap ($\alpha = 0.65$), thus obscuring dietary differences noted in discrete habitats. The Schoener index, utilizing the appropriate measure of overlap, appears to be sensitive to small changes in diet which may reflect different spectrums of resource abundance in different habitats. Where sufficient data on resource abundance are lacking, researchers should be careful to sample animals from discrete homogeneous habitat types for comparisons of trophic overlap.

No evidence for habitat segregation in these morphs exists, rather, individuals of both types were captured while feeding sympatrically. Few adult cichlids greater than 100 mm were observed feeding in shallow water on travertine ledge. Conversely, juveniles (20-60 mm) were most common on this substrate, while sub-adults (60-100 mm) appeared to frequent both travertine and flocculent substrates. These observations may indicate habitat segregation between adults and juveniles, with a progressive shift to deeper areas with age (size). The relatively discrete diets between morphs in sub-adults feeding on travertine ledge can be traced in the juveniles as well (Table 4), as a slightly greater usage of the snail and arthropod resources by molariforms.

Unfortunately, no observations on the manner of "hunting" prey in travertine habitats have been made. Habitat partitioning may be accomplished by discrete feeding behaviors (foraging at a specific depth in the sediment; acceptance or rejection of various potential prey items encountered (by "winnowing"); different modes of handling various prey types). Based on our field observations, these possibilities appear unlikely. Similar feeding behaviors were noted, however, between morphs in deep sediment habitat, except for a marginally significant increase in time between feeding bouts for molariforms. This may indicate an increased handling time with certain prey items, perhaps snails. In areas of flocculent detritus, tactile and possibly olfactory cues, rather than visual searching, must be responsible for the ability to distinguish live snails from dead or broken shells. From the extreme patchiness of live snails and the preponderance of shell debris (Table 7) in deep sediments, it is apparent that if all shells encountered by molariform fish were accepted, few live snails would be found in guts. Since, in fact, the reverse is found (many live whole or crushed snails, and few old, dead shells) a sorting process can be inferred which would necessarily increase handling time. The extreme hardness of the shells in the Cuatro Cienegas snail fauna relative to most other freshwater species (Fig. 4) would demand manipulation of snails into proper position in the pharyngeal mill to prevent damage to the tooth-bearing surfaces. (Pharyngeal teeth of both morphs were encountered in sediment samples and intestinal tracts, and examination of a large number of pharyngeal plates revealed many with cracked or missing teeth.) Some snails, especially very tiny ones, escaped crushing and were swallowed whole. Often the digestive processes did not seem to have significantly affected these snails, which could be found even in the endgut virtually intact.

The extent of shell sculpture and hardness in these gastropods is somewhat exceptional for freshwater snails, although such features are common in marine snails (Vermeij and Covich 1978). A high ambient concentration of calcium carbonate may allow developed of massive shell structure, but this shell armor may have evolved partly in conjunction with predation pressures imposed by molluscivorous cichlids. Coadaptation of snails with their predators has proceeded furthest in geologically old lakes (Vermeij and Covich 1978), which may testify to the age and stability of the Cuatro Cienegas ecosystem. The existence of cryptic feeding behaviors (nocturnal vertical migrations) in Mexipyrgus, Nymphophilus, and possibly Mexithauma (Table 8) may present further evidence that the molariform cichlids have imposed substantial selective pressures on their snail prey.

Considering the degree of divergence in trophic morphology in these cichlids, the lack of specialization in diet overall is unexpected. Optimal foraging theory would predict that in a stable environment, the specialization of the morphs should increase over time, or more precisely, that the within-phenotype component of niche width should decrease in variability (Cody 1974; Stenseth and Hannson 1979). Abundance evidence testifies to the apparent stability of this ecosystem and the climate through time. Taylor (1966) estimated that freshwater habitats continuously suitable for snails may have existed since the late Tertiary. The major structural features of the Cuatro Cienegas basin were probably formed by the Paleocene (Minckley 1969). Meyer (1973) presented evidence derived from sediment core analyses that local habitats have existed for the past 30,000-40,000 years, that stream and pond habitats have been extant since early Tertiary, and that the basin floor has been a relatively stable environment throughout the Quaternary. The divergence of various taxa within the basin from other living relatives (particularly in the molluscs, crustaceans, and turtles), and the especially high degree of endemism inferentially testify to a long history of continuous isolation of the aquatic habitats.

Models of optimal diets in homogeneous environments also predict diet expansion as resource abundance decreases, or as patchiness increases (Emlen 1966; Cody 1974). Smith, et al. (1978) noted a lack of correspondence between many field studies and these predictions, however, and found that diet overlap between related finch species was reduced seasonally as food became scarce, due to qualitative changes in the spectrum of available foods. Preferred foods of all finch species declined to near-zero, and diet shifts occurred to food types that reflected each species' morphological and behavioral adaptations. Seasonal sampling of the cichlids of Cuatro Cienegas may reveal similar diet shifts, as the present study focused on summer months when food was presumably most abundant. Cursory examination of a portion of the gut contents of 12 specimens of each morph collected in March 1975 indicated a high frequency of occurrence of detritus and some plant matter in all fish. Almost 60% of molariforms contained snail shells, while only 8% of papilliforms had consumed gastropods. Only a single fish (molariform) contained arthropod remains. It is of interest that for the pumpkinseed sunfish Lepomis gibbosus, which also has massive pharyngeal plates endowed with molar teeth, the preferred food may be odonate and mayfly nymphs, while snails constitute a competitive refugium (Laughlin and Werner 1980).

Extrapolating predictions of competition theory (as expressed by Smith, et al. 1978) to the Cuatro Cienegas situation, three alternative hypotheses emerge: 1) if intermorph competition determines resource partitioning, then diets should diverge as food becomes scarce; 2) if intramorph competition is stronger, then diets should expand and overlap more as food abundance decreases; and 3) if no competition occurs when food is most scarce, then diet shifts should be in response to changes in the nature of the available foods. Sufficient data to distinguish between these predictions would entail quantitative determinations of relative food abundances within discrete habitats compared to food items selected, carried out on a seasonal basis. Patchiness in distribution of food resources even within a habitat would present difficult logistical problems in conducting such a study. Observations on search and handling times and comparative feeding behaviors between morphs are likewise incomplete, but the intensive time commitment involved in observing and capturing feeding cichlids by the methods utilized in this study may outweigh the usefulness of further study.

Tracking of snail abundance by molariforms suggests a specialization on this resource not borne out by the results of this study. The proportion of snails in the diet (by frequency of occurrence, average number, or percent volume) appears low during the season at which food would presumably be most abundant, and at a time at which optimal foraging theory predicts maximal diet specialization would occur. The present polymorphic system, in which the proportions of the morphs vary from locality to locality, may be an historical artifact rather than dependent on current snail populations. Factors other than food resources may limit total population sizes and morph frequencies (e.g. size and number of male territories and breeding sites). More detailed correlations of snail abundance to molariform frequencies over localities would resolve the question of the selective advantage of molariform dentition. Demonstration of random fluctuations in relative morph frequencies over localities unrelated to snail abundances would indicate absence of such a selective advantage, or a time lag in response of the molariform populations to past snail abundances. Distinguishing between these interpretations might be impossible.

Current work on the mode of inheritance of trophic characters may expose the mechanisms for maintenance of the polymorphism and for production of individuals with intermediate dentition. Sage and Selander (1975) reported that molariform dentition can be expressed in the absence of gastropods or other hard foods in the diet, suggesting genetic control of the polymorphism not dependent on environmental factors. Wild-caught specimens as small as 25 mm exhibited well developed molars, indicating a probable very early hypertrophication of the pharyngeal elements.

Although not as strikingly dichotomous until fish are relatively large, gut length is significantly correlated to trophic type. Comparison of a number of cichlid species reveals a trend for long get lengths in herbivores, relatively short tracts in carnivores, and intermediate lengths in omnivores (Fryer and Iles 1972, p. 40-41). Cichlasoma cyanoguttatum, the Texas cichlid, appears to be a close relative of the Cuatro Cienegas endemics, and is reported to have a GL:SL ratio of from 5.00-6.12 (N=21) (Buchanan 1971). The relatively short guts of the Cuatro Cienegas cichlids (which appear to vary from close to half the total length in some molariforms up to twice total length in papilliforms), would tend to place them in the carnivorous to omnivorous range.

To assess the adaptive significance of the differences in gut lengths, additional work on digestive efficiencies of various food types would be required. In the laboratory, molariforms showed a slight tendency to pass food through the gut at a slower rate than papilliforms (Table 6). In view of the elongate nature of the papilliform gut, with its many folds in larger fish, it might be expected that food would pass slower through such a gut than the relatively straight tube of the molariform. A slower passage rate might enable more complete digestion and assimilation of food in its short gut, with its corresponding small surface area.

Unfortunately, no data exist on the relative food values of the categories encountered in this study, since such information could determine the importance of the detrital aggregate in the diet of this species. (Detritus occurred in virtually all guts examined, and often accounted for up to 50% of total food volumes.) Work on various herbivorous and detrivorous species has shown that lysis of diatoms, bacterial and algal cell walls and subsequent digestion of cell contents can be accomplished by trituration by pharyngeal plates (Payne 1978; Spataru 1978), by secretion of acid in the stomach, producing a pH < 2 (Moriarty 1972; Bowen 1976; Payne 1978), and by ingestion of decaying plant matter colonized by cellulase-producing bacteria (Prejs and Blaszczyk 1977). Similar mechanisms may be involved in the ability of these fish to extract nutrients from the detrital aggregate. Recent work of Bowen (1980) on rapid growth of the cichlid Sarotherodon mossambicus by efficient utilization of the non-protein amino acid component of detritus has raised the interesting possibility of a similar phenomenon in these cichlids. Where two food groups provide equal food values (that is, net energy intake per time) a stable polymorphism could be maintained in a constant environment (Stenseth and Hannson 1979).

The high incidence and percent volume of scales (fish parts) in stomachs of fish in 1979 samples may be partly an artifact of collecting methods. Where fish were captured by trap net, agonistic interactions may have been heightened in the confined space of the trap. Coupled with a possible slow rate of passage of scales through the stomach (scales were often found clumped in stacks), this would tend to inflate this food category's importance. The samples taken in 1980 by speargun exhibited a similar frequency of occurrence as the earlier samples, but overall numbers of scales in guts tended to be small. Noakes (1979) stressed the high nutritive value of scales and associated mucus. Scales are probably nipped off in intra- and interspecific agonisitc interactions. A female captured while guarding eggs contained 116 scales in its stomach sac. Aggressive interactions between juvenile cichlids appeared to be common, but between adult males in adjacent territories, generally only ritualized aggressive behaviors were observed (including opercular displays and patrolling of territorial boundaries in parallel). Territorial male pupfish, Cyprinodon bifasciatus, were frequently observed actively defending their territories against even adult cichlids.

The degree of diet overlap in these morphs contrasted with their remarkable specializations in trophic morphology raises an important consideration on the validity of extrapolating directly from observations on structure to function. Anatomical trophic specializations need not imply a narrow range of operation, but rather may improve exploitation of a resource not as accessible to individuals lacking the specialization, without reducing the overall scope of operation (Liem 1979). Broad interspecific diet overlap and opportunistic feeding have been reported in a number of cichlid species (Fryer and Iles 1972; Greenwood 1974; Liem 1979), thus the trophic overlap in the Cuatro Cienegas cichlids is not without precedent. As Karel Liem (1980) has aptly stated: "The greatest paradox emerging from the study on intra- and interspecific differences in feeding repertoires of cichlid fishes is that the most specialized taxa are not only remarkable specialists in a narrow sense, but also jacks-of-all-trades."

Table 1. In situ observations of feeding behaviors in papilliform (Pap) and molariform (Mol) cichlids at El Mojarral, 1981.

	Pap	Mol
No. observations	4	9
Mean duration of observations (sec)	76.9	88.7
Mean times between foraging bouts (sec)	4.64	6.15
Range	3.75 - 5.93	2.75 - 11.33

Table 2. Summary of frequency of occurrence (FO%) and average number (Ave. no.) of food items in guts of papilliform and molariform cichlids from three major sampling locations, 1979.

Food items	Churince				Becerra				El Mojarral			
	Pap		Mol		Pap		Mol		Pap		Mol	
	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.
Plant matter												
Vascular plants	100	-	100	-	61.5	-	63.6	-	94.4	-	81.8	-
Algae	88.9	-	100	-	23.1	-	31.8	-	22.2	-	27.3	-
Arthropoda												
Acari	11.1	4							33.3	10		
Amphipoda	33.3	3.7					4.5	1	16.7	3	9.1	1
Arachnida	11.1	1	50	1								
Chironomid larvae	22.2	2	50	1	38.5	1.2	22.7	3.8	22.2	2	27.3	2.3
Diptera (adults)					7.7	1					18.2	1
Formicidae			50	1					11.1	1		
Odonata												
Ostracoda	44.4	4.3	50	3	7.7	1	4.5	5	27.8	1.4	9.1	3
Other	33.3	-	100	-	23.1	-	4.5	-	50	-	27.3	-
Gastropoda												
Mexipyrgus	22.2	1	50	5			27.3	5.2	11.1	1.5	63.6	4
Mexithauma											9.1	6
Nymphophilus												
Snail fragments	77.8	-	50	-	15.4	-	50	-	33.3	-	90.9	-
Osteichthyes												
Eggs	66.7	1.2					9.1	5	5.6	118*	9.1	6
Scales	77.8	2.1	100	4	76.9	15.2	63.6	9.9	50	21	27.3	6.7
Whole fish											9.1	1
Organic detritus	100	-	100	-	100	-	100	-	100	-	100	-
Mean SL(mm)±s.e.(n)	125.1±11.3 (9)		93.0±19.0 (2)		70.0±7.1 (22)		68.0±4.8 (13)		106.9±3.6 (18)		105.5±5.5 (11)	
Range	72.0-160.0		74.0, 112.0		42.9-120.6		40.2-110.0		76.4-145.4		65.6-128.0	

* This represents a single female, captured while guarding eggs.

Table 3. Summary of volume percentages of major food types in guts of cichlid morphs sampled in 1979. Diet overlap (α) was computed by the method of Schoener (1970).

	Churince		Becerra		El Mojarral		Pooled	
Food category	Pap	Mol	Pap	Mol	Pap	Mol	Pap	Mol
Plants	14.9±3.8	40.3	10.9±4.7	15.9±8.7	16.9±12.1	24.9±16.0	13.7±4.2	19.8±7.3
Arthropods	2.0±1.2	22.2	2.9±2.5	-	4.6±2.8	11.0±11.0	3.2±1.4	5.0±3.4
Gastropods	-	-	-	5.4±4.7	-	15.4±15.4	-	9.1±5.4
Fish	22.7±14.2	-	46.9±11.2	23.0±9.5	23.3±12.2	35.4±16.4	34.0±7.3	30.6±8.6
Detritus	53.0±13.5	37.5	39.4±10.5	48.0±11.3	55.1±14.9	13.3±11.8	47.4±7.2	37.1±8.8
No. specimens	6	1	12	13	8	6	26	20
Diet overlap (α)	0.581		0.771		0.582		0.846	

Table 4. Summary of frequency of occurrence (FO%) and average number (Ave. no.) of food items in guts of adult and juvenile cichlid morphs from El Mojarral, 1981. Sampling was performed over two major substrate types: open travertine shelf, or deep flocculent ooze.

Substrate type:	Adults								Juveniles			
	Travertine				Flocculent				Travertine			
	Pap		Mol		Pap		Mol		Pap		Mol	
Food items	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.	FO%	Ave. no.
Plant matter												
Vascular plants	100	-	100	-	100	-	100	-	72.0	-	64.3	-
Algae	33.3	-	0	-	66.7	-	50	-	16.0	-	14.3	-
Arthropoda												
Acari	33.3	1	100	1.5							14.3	1
Amphipoda	66.7	30.5	100	8	100	223	100	3.5	16.0	2	35.7	2.2
Arachnida												
Chironomid larvae	66.7	101.5	100	184.5	100	6.3	100	11	60.0	10	71.4	8.7
Diptera (adults)					33.3	1						
Formicidae												
Odonata	33.3	12	100	59	33.3	1	50	11	4.0	4		
Ostracoda	33.3	4	100	6	66.7	20	50	20.5	16.0	1.8	42.9	1.5
Other	33.3	-	50	-	66.7	-	100	-	4.0	-	28.6	-
Gastropoda												
Mexipyrgus	33.3	13	100	175.5	66.7	1	100	73.5	4.0	3	14.3	8
Mexithauma	33.3	4	100	9			50	18	4.0	1	21.4	1
Nymphophilus					33.3	2			8.0	1	21.4	1.7
Snail fragments	66.7	-	100	-	66.7	-	100	-	32.0	-	35.7	-
Osteichthyes												
Eggs												
Scales					66.7	2	50	1	40.0	7.7	57.1	7
Whole fish	33.3	1							4.0	1		
Organic detritus	100	-	100	-	100	-	100	-	88.0	-	78.6	-
Mean SL(mm)±s.e.(n)	80.0±5.6 (3)		80.2±0.8 (2)		83.3±4.5 (3)		91.0±17.0 (2)		39.9±1.7 (25)		41.3±2.8 (14)	
Range	73.0-91.0		79.5, 81.0		75.5-91.0		74.0, 108.0		25.4-63.5		25.6-57.1	

Table 5. Summary of volume percentages of major food types in guts of adult cichlid morphs from El Mojarral, 1981, sampled over two substrate types.

	Travertine		Flocculent		Pooled	
Food category	Pap	Mol	Pap	Mol	Pap	Mol
Plants	30.2±7.3	2.8±1.4	33.0±10.0	8.9±2.4	31.6±5.6	5.9±2.2
Arthropods	6.1±5.9	34.3±0.5	13.4± 9.5	11.9±9.5	9.7±5.3	23.1±8.0
Gastropods	0.6±0.5	28.5±5.3	0.7± 0.2	16.7±14.7	0.6±0.2	22.6±7.2
Fish	4.6±4.6	-	0.1± 0.1	-	2.3±2.3	-
Detritus	58.5±11.9	34.4±6.2	52.8± 9.1	62.5±23.3	55.6±6.8	48.4±12.8
No. specimens	3	2	3	2	6	4
Diet overlap (α)	0.439		0.743		0.647	

Table 6. Summary of passage rates of food through intestinal tracts of papilliform and molariform fish.

	Pap	Mol
Mean passage rate ($cm \cdot h^{-1}$)±s.e.(n)	4.10 ± .34 (30)	3.03 ± .17 (17)
Range of passage rates	1.65 - 8.56	2.0 - 4.73
No. specimens	9	4
Mean SL (mm)	123.0	132.2
Range of SL	103.4 - 157.3	117.0 - 170.0

Table 7. Summary of snail abundance data for *Mexipyrgus* in 5 microhabitats in El Mojarral. Sampling sites are identified in Figure 1.

	Sample Portions (30 cm³)				
	1	2	3	4	5
Ave. no. live	6.5	76	72	7.5	28.5
% (by weight) ± s.e.	0.96±.004	27.4±.07	17.03±.05	0.45±.002	6.17±.04
Abundance ($\cdot m^{-2}$)*	280	2260	3120	510	880

* in the top 2 cm of detrital layer.

Table 8. Summary of snail migrations in day and night observations for Mexipyrgus and Nymphophilus.

		Day	Night
Mexipyrgus			
Mean no. per leaf surface	Top	.006	.57
	Bottom	.43	.165
	Stem	0	.14
No. observations		62	34
Nymphophilus			
Mean % emigration		0	54.7
Mean no. immigrants		0	2.6
No. observations		12	12

Figure 1. Diagrammatic map of Laguna El Mojarral (East) indicating habitat locations from which feeding cichlids were captured. Floc=area of deep flocculent sediment; Trav=open travertine shelf. Dark circles mark approximate sampling sites for Mexipyrgus in sediment. Feeding obs=area in which observations of feeding behaviors were made (deep sediment habitat in the deepest part of the lake).

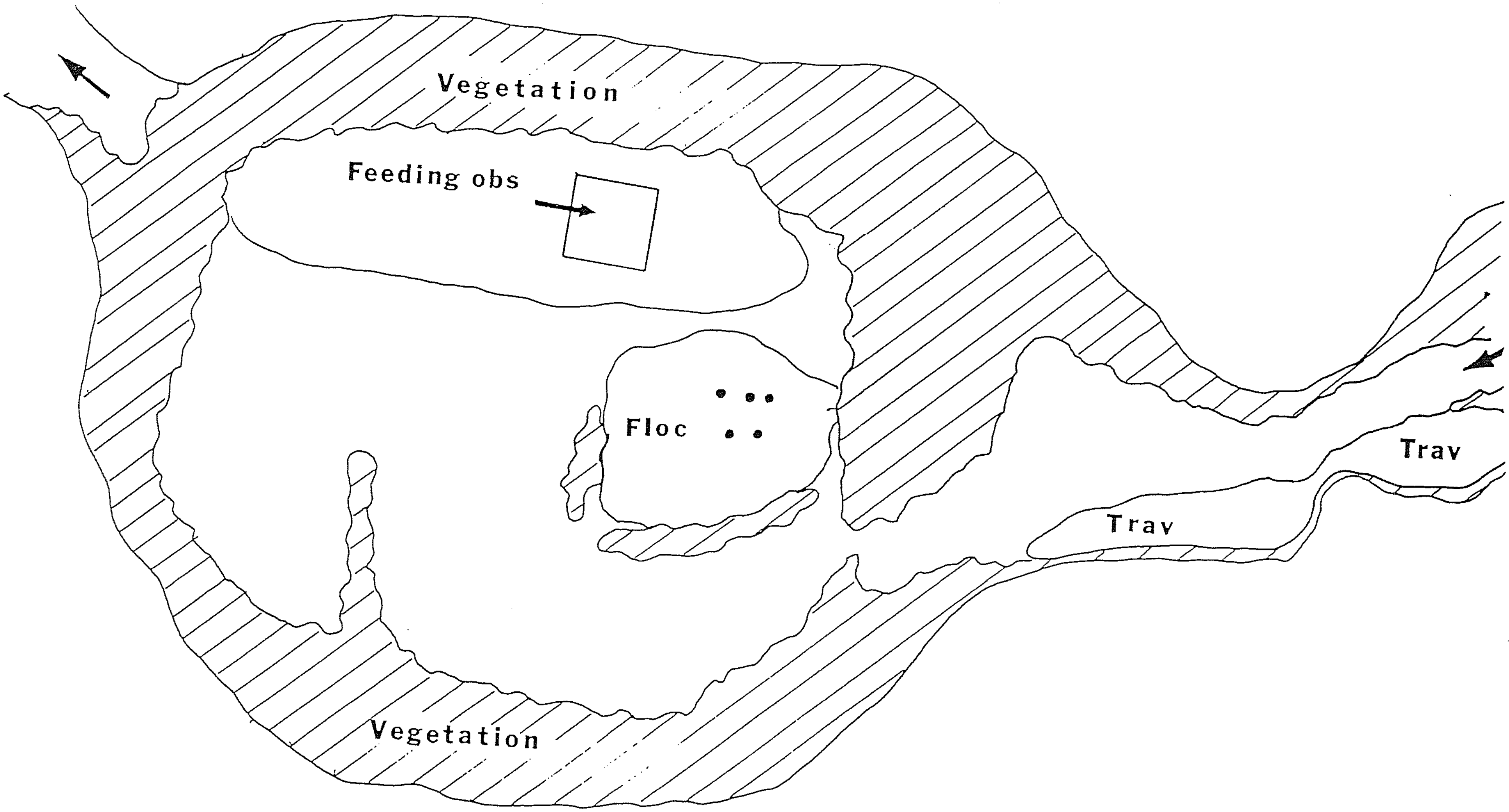
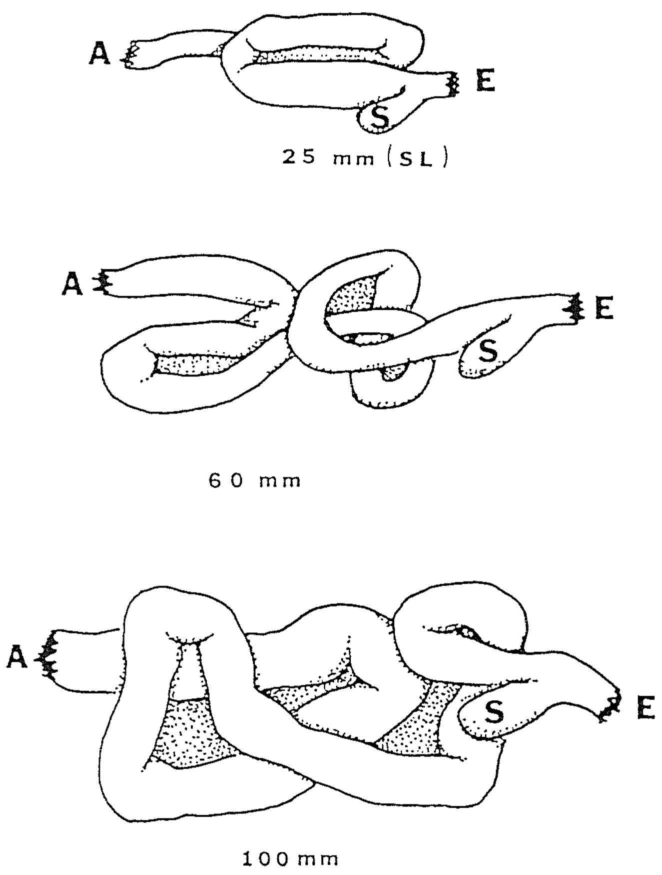
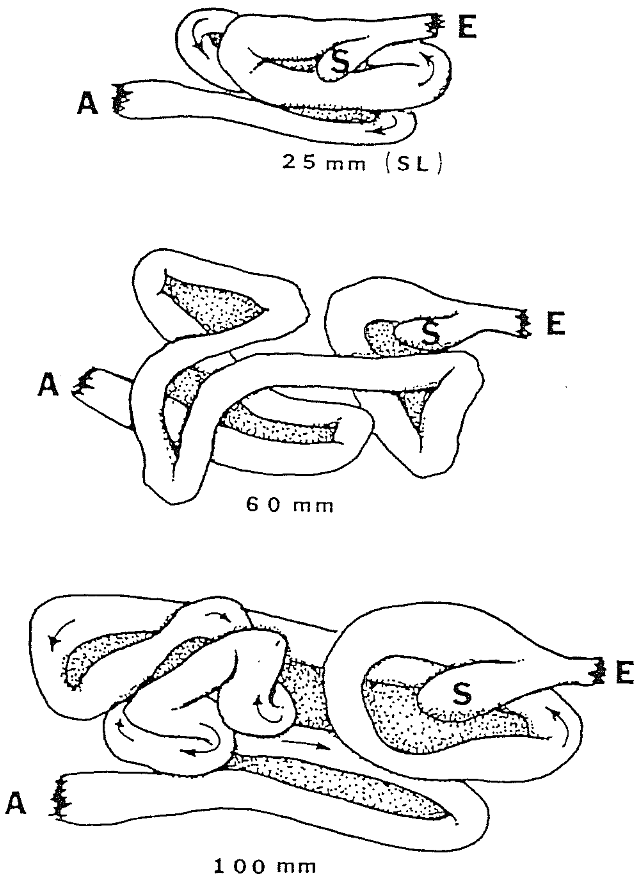

Vegetation
Feeding obs
Floc
Trav
Trav
Vegetation

Figure 2. Comparative development of general gut morphology in molariform and papilliform cichlids. A=anus; E=esophagus; S=stomach sac.



Molariform



Papilliform

Figure 3. Graph of gut length (cm) versus standard length (mm) for papilliform and molariform cichlids.

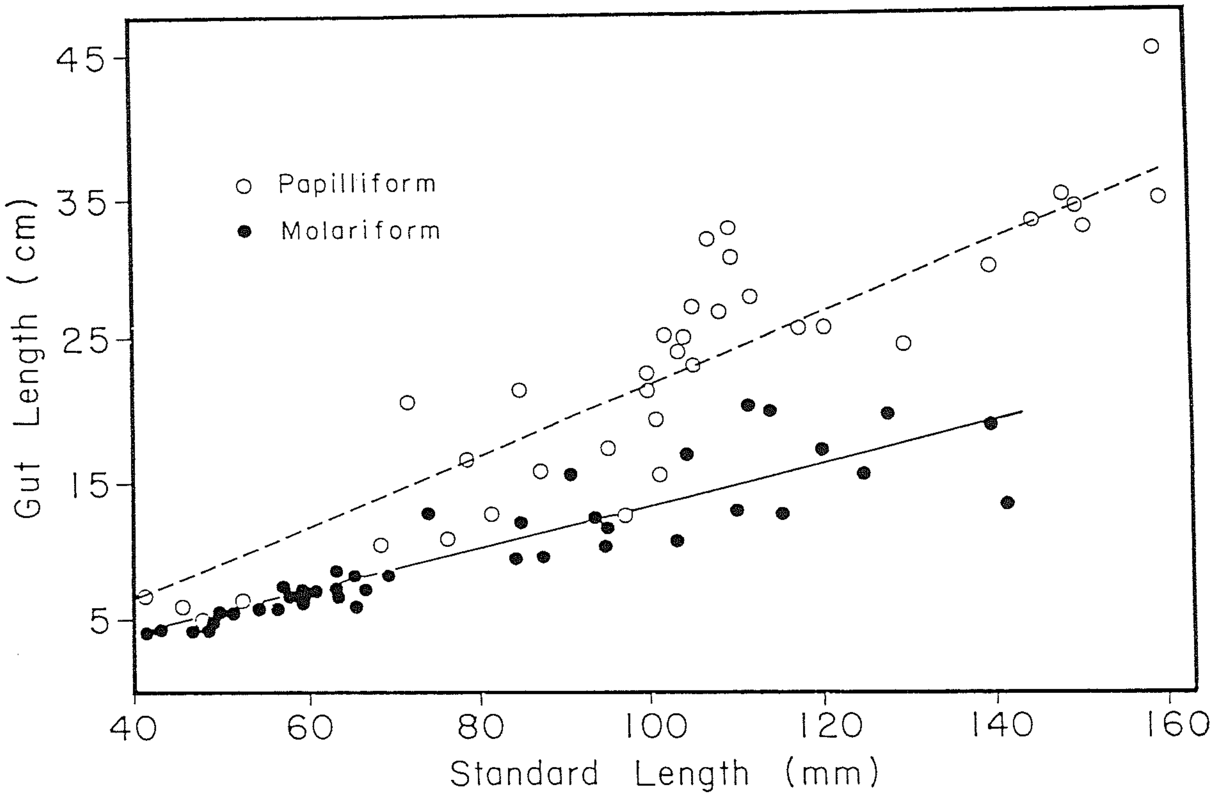
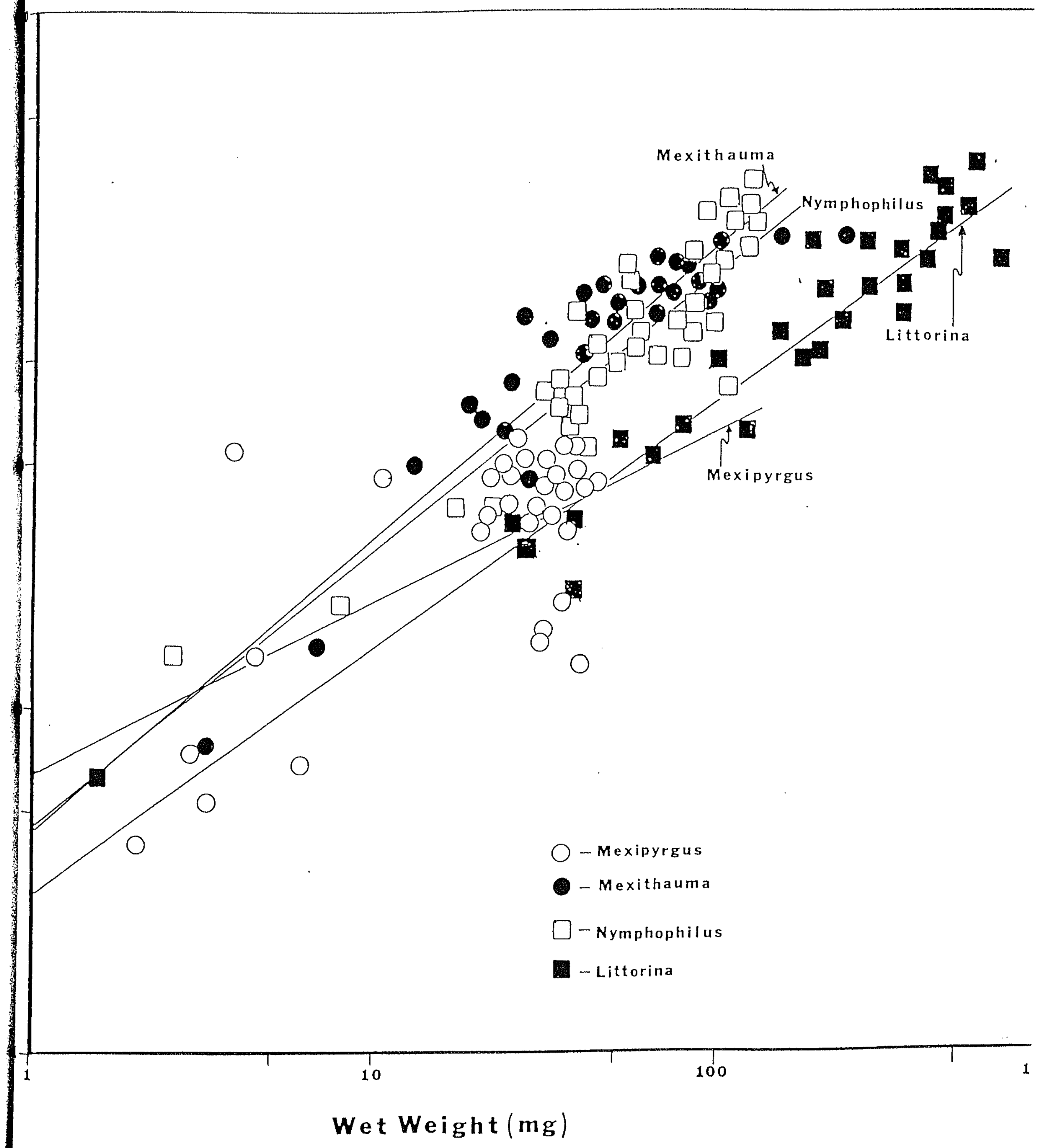

Papilliform
Molariform
Gut Length (cm)
45
35
25
15
5
40
60
80
100
120
140
160
Standard Length (mm)

Figure 4. Graph of crushing force (Newtons) versus the size (wet weight) of three species of endemic snails, *Nymphophilus*, *Mexithauma*, and *Mexipyrgus* from El Mojarral. Also included is *Littorina littorea*, a common hard-shelled marine gastropod for comparison.


Mexithauma
Nymphophilus
Littorina
Mexipyrgus
○ – Mexipyrgus
● – Mexithauma
□ – Nymphophilus
■ – Littorina
1
10
100
1
Wet Weight (mg)

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