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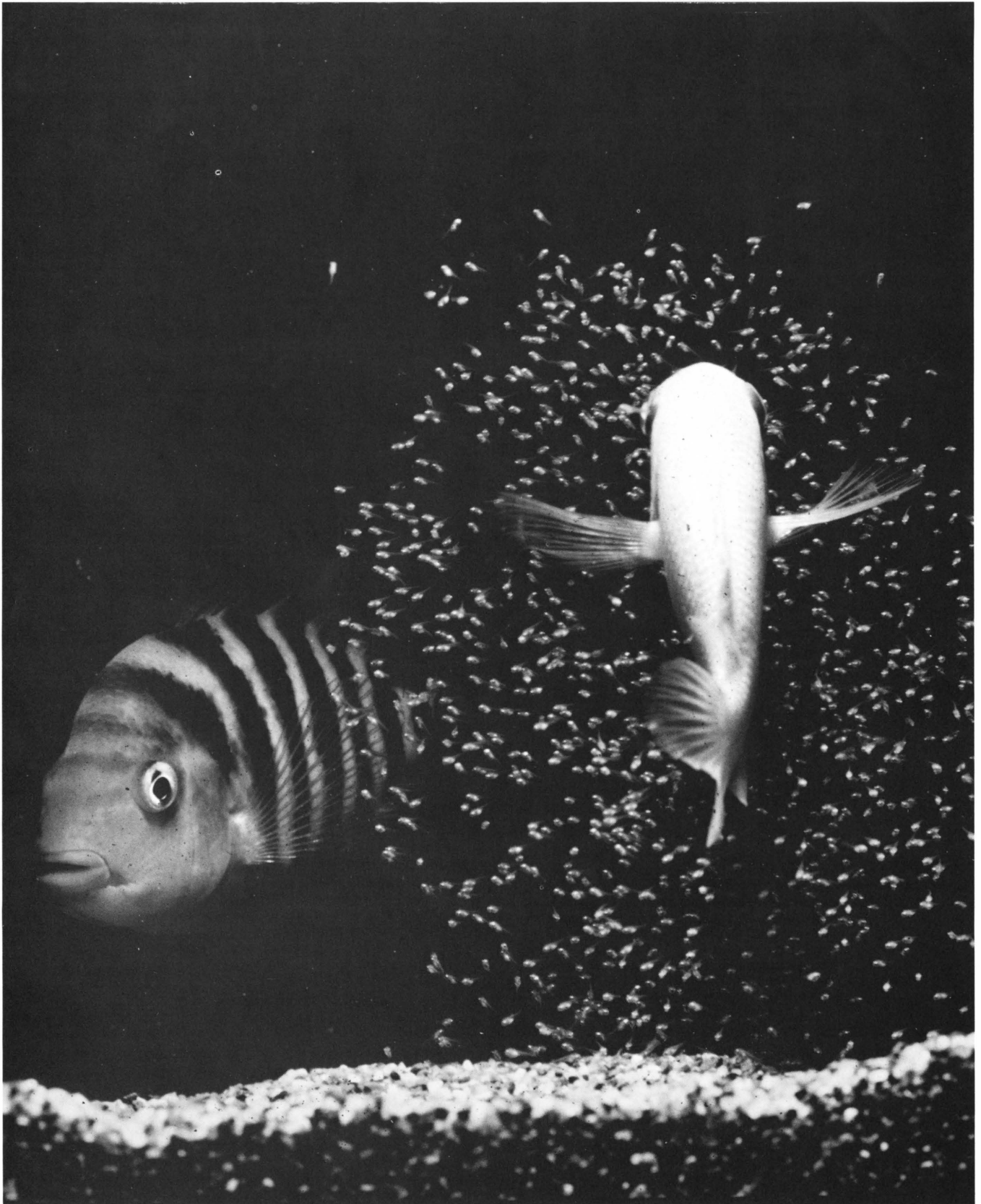
More study has been devoted to the polychromatic Midas cichlid, *Cichlasoma citrinellum*, than to any other teleost of Nicaraguan lakes. In the illustrated pair, the male (left) exhibits the "barred" pattern and the female is a gold morph. Their fry have been swimming for one day. Photograph by George W. Barlow. Courtesy American Association for the Advancement of Science (Science 179(4075): cover photograph, 23 February, 1973).

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INTRODUCTION

"Once upon a time, if stories are true, there lived a king called Midas, whose touch turned everything into gold. Whenever I see goldfish, I wonder if, perhaps, King Midas were not a Chinese and if he perchance did not handle some of the little fish in orient streams. But common man has learned a magic as wonderful as that of King Midas, although it does not act so immediately, for it is through his agency in selecting and breeding that we have gained these exquisite fish for our aquaria. In the streams of China the goldfish, which were the ancestors of these effulgent creatures, were safe green colors like the shiners in our brooks; and if any goldfish escaped from our fountains and ran wild, their progeny returned to their native olive-green color. There are many of such dull-colored goldfish in the lakes and rivers of our country. It is almost inconceivable that one of the brilliant-colored fishes, if it chanced to escape into our ponds, should escape the fate of being eaten by some larger fish attracted by such glittering bait." (Comstock, 1967: 144–145).

Goldfish-colored fishes occur in a variety of species and in unrelated groups. Usually, but not always, such brilliant coloration is confined to but a few individuals in a given species. The Midas cichlid, *Cichlasoma citrinellum* (Günther), is exceptional in this respect: while most of the adults in Nicaragua are relatively drab, a fair proportion of them are unpatterned and are brilliantly colored, much like the common goldfish.

For a number of reasons the Midas cichlid offers an unusual opportunity to study the phenomenon of polychromatism. As just stated, it is relatively common in nature. It is also easily bred in captivity. And, as is so typical of cichlid fishes, it has complex social behavior that is accessible for study. This allows the possibility of experimental analyses, correlating behavior and polychromatism. I have been engaged in such laboratory research for the past several years (*e.g.*, Barlow, 1973). But those studies are not the subject of this article, although the results from some of them will be mentioned where appropriate.

The Midas cichlid also affords the opportunity to study the ecological relationships, and hence the evolutionary significance, of competition between the various color morphs. The regular occurrence of such brilliantly colored fish presents a challenging intellectual problem. One would like to know which factors favor the survival of such conspicuous morphs, and which work against it. Before analysis begins, however, there must be description. Here this means the natural history of *Cichlasoma citrinellum*.

Basic information on the natural history of the Midas cichlid is also important for the welfare of the citizens of Nicaragua. They eat more Midas cichlids than any other species of fish caught in the Great Lakes Basin of Nicaragua (INFONAC, 1971). Surprisingly, however, virtually nothing is known about the basic biology of this species. Such information is vital to the proper management of the small fishery that now exists, and for the possible cultivation of this species in the future.

The objective of this article is to supply as much information as possible about the natural history of the Midas cichlid. Much of the knowledge I have is fragmentary. The pieces, however, should provide a framework in which the major features become obvious. Further, the existence of this outline will make obvious the areas where research is especially needed and should lead to implementation and revision of the report that follows. It should become especially apparent that the greatest need is for year-round studies which, iiven my vocation, are impossible for me. These could easily be done by Nicaraguan biologists. I hope this article stimulates them to undertake a sustained programmatic study of their most important food fish.

ENVIRONMENT

Among the nations of Central America, Nicaragua has the most inland water, estimated as high as 12% of the surface area (Riedel, 1964). The most striking limnological feature is the Great Lakes Basin (Fig. 1), occupied by two large bodies of water, Lakes Nicaragua (Cocibolca) and Managua (Xolotlán) (see Cole, 1976, for details of limnology). There are also sunken craters in the basin; many occur in relatively level land near the two Great Lakes and at a similar elevation. These craters have few or no streams running into them, but they act as wells, forming a number of discontinuous crater lakes.

There is little vegetation in most of the lakes. In some of the marshy areas, particularly around the Great Lakes, there is a rich flora; but in the lakes proper one encounters only an occasional *Typha* or *Scirpus* (Riedel, 1964). In Lake Apoyo *Chara* grows in luxuriant beds starting at a depth of 3-4 m and continuing down to 18 m. The rocks in all the lakes are carpeted by *Aufwuchs*, but its richness varies among them.

Phytoplankton is prevalent in some lakes; it is the main agent of decreased visibility in the water (Bengoechea, pers. comm.); it is exceedingly and continuously abundant in the Great Lakes Nicaragua and Managua, almost equally so in Lake Masaya, moderately present in Lake Jiloá, and sparse in Lake Apoyo. This is reflected in the Secchi disc readings from these lakes (Table 1). The apparent color of the water in the Great Lakes varies locally and with time; to me, it usually appears yellowish brown with traces of maroon. On
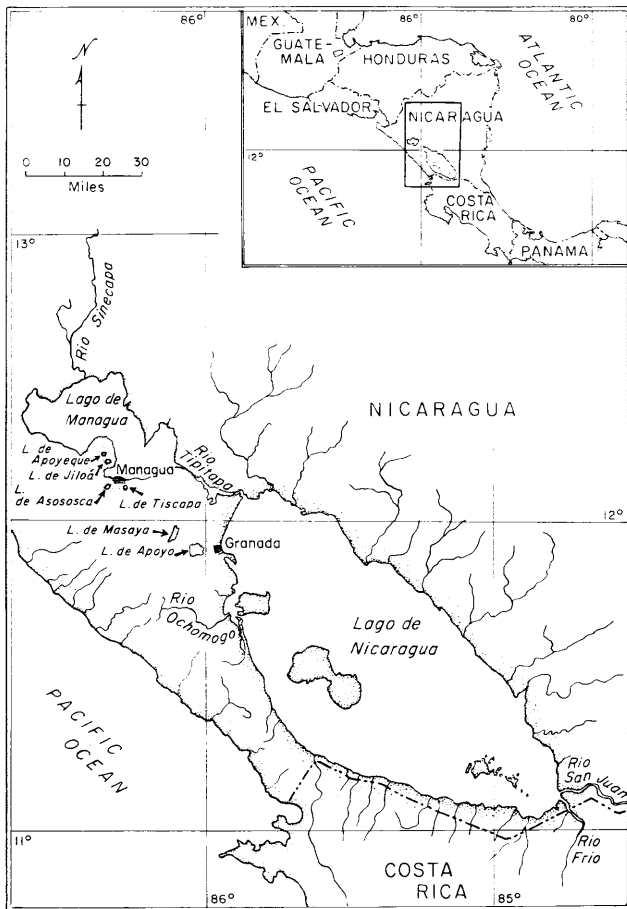
Fig. 1. Map of the Great Lakes Basin of Nicaragua, showing the lakes and rivers referred to in the text.

Table 1. Resumé of some of the physical characteristics of selected lakes in Nicaragua.

	L. Nicaragua	L. Managua	L. Masaya	L. Jiloá	L. Apoyo
Surface area (km²)	7,740	1,050	8.4	3.8	21.2
Average depth (m)	15-20	8	— — —	— — —	— — —
Maximum depth (m)	50	30	82	92	(>92?)
Clarity (Secchi disc, m)	0.25-0.35	0.25-0.35	0.25-1.0	3-5	3.5-9.5

A complicating factor is "chromatic adaptation" as shown by humans and thus possibly fishes. For example, an object perceived as yellow at the surface still seems yellow at a depth of 30 m in oceanic water; but if the spectral radiance of that object at that depth were reproduced at the surface, it would give the visual sensation of green or blue-green (Lythgoe, 1968). On theoretical (*loc. cit.*) and on practical grounds (Luria and Kinney, 1970), however, there is reason to believe that orange through red objects are most readily detected in shallow freshwater, *i.e.*, to depths of 18 m. Lythgoe (1968) reasoned that yellow objects, on the other hand, would appear grey and difficult to see because of insufficient mismatch with the prevailing green of the background radiation. Along these lines, Luria and Kinney (1970) reported that white objects tend to take on the color of the water where they are found.

A further complication lies in the eyes of cichlid fishes. Many Amazon species, but not all, have photostable yellow pigment in their corneas, lenses, and retinas (Muntz, 1973). That would effectively screen out blue light. None of the cichlids in Nicaragua have been examined in this respect.

In comparing the various bodies of water, Lakes Managua and Nicaragua can be treated collectively in many respects (Table 1). The former drains into the latter intermittently by the shallow Río Tipitapa. Both lakes are large, shallow, well-mixed, highly turbid, and have a diverse fauna. Much of their coasts consists of local sloughs, or sand and gravel beaches. The profile of the bottom is gentle, wave action is continuous, and cover for fishes is often scarce. In many places there are rocky outcroppings. There the bottom profile is steep until the rocks encounter the soft bottom.

The crater lakes, taken together, differ in some notable ways from the Great Lakes (Table 1; see also Barlow, Baylis and Roberts, 1976). They are relatively wind protected and comparatively deep, with the slope of the bottom plunging steeply toward the depths. In most places the bottom profile appears to follow the relaxation slope of the substrate. Thus, where the beaches are sandy or gravelly the bottom angles toward the depths at about 30°-40°, whereas when the bottom consists of rock slides the slope may be 50° or 60°; in some places, sheer rock faces descend to depths in excess of 50 m (Alfonso Solórzano, pers. comm.).

Typically the bottom profile is characterized by a wave-cut bench 5-10 m wide. When the beach is rocky, the shoreline consists of jumbled boulders so that one is in water approximately 1.5 m deep upon entering. At the edge of the wave-cut bench, where it drops off, the water is about 2 m deep. The situation varies depending on whether you are in one of the many coves or at a headland, the profile being steeper along the headland than in the cove.

To a naturalist, one of the most disappointing features of the crater lakes is that invertebrate animals are so difficult to find. My colleagues and I went to considerable effort to locate invertebrates, digging in the bottom at a variety of

the other hand, the water of Lake Masaya seems yellowish green. The crater lakes are usually murkiest during the dry season. During the rainy season clarity increases, reaching a maximum in December (although clarity may drop right after a heavy rainfall).

Because the focus of this article in on a xanthomorphic cichlid fish, the problem of the perception of hues in water needs to be explored, however briefly. In clear oceanic water shorter wavelengths such as blue and green penetrate to depths (Fig. 2). The longer wavelengths are filtered out in proportion to their wavelengths. Thus red disappears within the first 5-10 m.

Coastal and fresh waters generally contain a number of natural contaminants (Mertens, 1970). Many of these result from the decay of vegetable matter such as algae and are called "yellow substances." Particles such as these scatter the short wavelength more than the long ones (Fig. 3). "The yellow substances absorb the short wavelength (blue) light as it penetrates through the water, whilst the water itself absorbs the long wavelength (red) light. Thus only the middle (green) part of the spectrum reaches deep into fresh and inshore water." (Lythgoe, 1968).

The problem is how to interpret such information when trying to decide whether the color of a fish will make it visible or, conversely, difficult to see. Each body of water may have different visual properties, and these may change over time and depth.
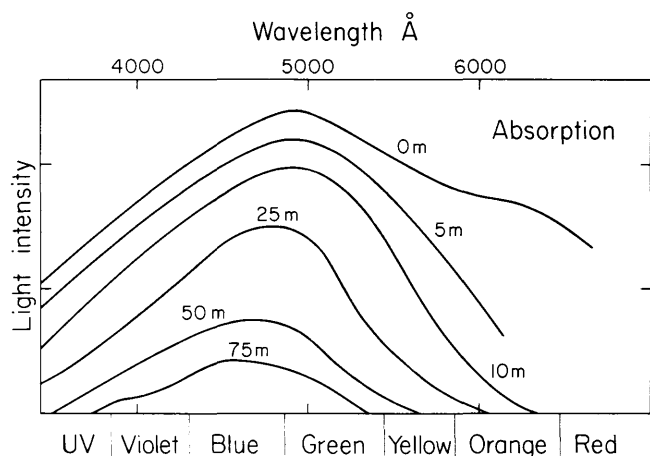
FIG. 2. Absorption of hues of different wave lengths at increasing depths of water. Based on measurements in the eastern Mediterranean Sea by Ivanoff (1955).

depths while diving with SCUBA gear. We found little. Night diving with a flashlight was slightly more profitable. A few insect larvae occasionally entered the beam of the flashlight. During the day the tiny snails that live in the lakes were not to be seen, but at night they emerged in numbers. Their abundance is demonstrated by the sand of the beaches which consists almost entirely of snail shells. Diving at night, one also encounters numerous large crabs, *Potamocarcinus nicaraguensis* (Fig. 4). Thus, the invertebrate fauna of the crater lakes consists predominantly of tiny snails and large crabs, both of which are nocturnally active.

There are also few vertebrates in the crater lakes other than fishes. The toad, *Bufo marinus*, breeds in Lakes Jiloá and Masaya, and their tadpoles are found in the very shallow warm water. Turtles (probably *Pseudemys scripta*) are seen occasionally in Lake Jiloá.

Because of themes to be developed further on, and in the article by Barlow and Munsey (1976), I must point out three ways in which a gradation of conditions can be seen, proceeding from the Great Lakes to the crater lakes. The first is physical resemblance. Lake Jiloá lies directly next to Lake Managua and is separated from the large lake by a sandy but stable barrier; the two lakes must have been connected at one time (Villa, 1968). In the region of the barrier, the bottom profile of Lake Jiloá slopes gently and thus shows at least some of the features of much of the shore of the larger lake. But in the remaining parts of Lake Jiloá, the bottom profile and other conditions are characteristic of the other crater lakes. Thus Lake Jiloá is transitional between the Great Lakes and the crater lakes with regard to the bottom conditions.

The second ordering of lakes involves the richness of the fauna. The Great Lakes have a wide variety of species, although the larger marine fishes are excluded from Lake Managua. Other vertebrates, such as cayman and a number of turtles, occur in both lakes.

As one would expect, the fauna of Lake Jiloá is similar to that of Lake Managua, although many species are missing (see Villa, 1968). Lake Jiloá is well endowed with cichlid fishes, containing all the species found in Lake Managua with the exception of *Cichlasoma maculicauda* Regan, *C. labiatum* (Günther) and *Herotilapia multispinosa* (Günther). The piscivorous cichlid, *C. managuense* (Günther), is present (Villa, 1968, 1971) but it is rare; in all our diving in that lake
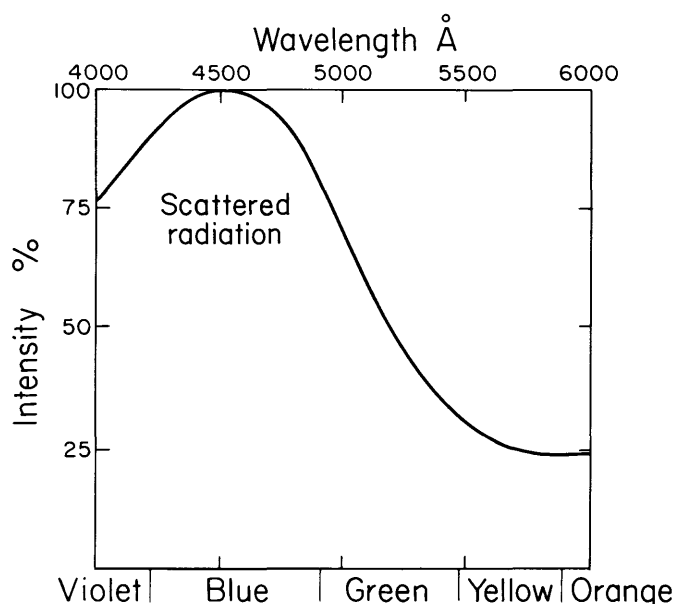

FIG. 3. The percent scattering of light by particles in water in relation to the wave length of the light. After Schenk and Kendall (1954).

we have had only a few uncertain sightings of that species; recently Kenneth R. McKaye located three breeding pairs. Lake Jiloá also contains the catfish, *Rhamdia nicaraguensis* (Günther), the atherinid, *Melaniris sardina* Meek, the poeciliid, *Poecilia sphenops* (C. and V.), the lurking predatory gobioid fish, *Gobiomorus dormitor* Lacépède, and a shad, *Dorosoma chavesi* Meek (Riedel, 1964; J. R. Baylis, pers. comm.).

The fish fauna of Lake Masaya consists of yet fewer species. Among the cichlids are both of the large piscivorous species, *Cichlasoma dovii* (Günther) and *C. managuense*, the smaller species, *C. longimanus* (Günther), *C. citrinellum* (Günther), *C. nigrofasciatum* (Günther), and the small herbivorous species *Neetroplus nematopus* (Günther). The three other fish species are *Poecilia sphenops*, *Melaniris sardina*, and *Gobiomorus dormitor*.

Lake Apoyo is even more impoverished, having only five species of fish. These are *C. managuense*, *C. citrinellum*, an undescribed species of *Cichlasoma* (see Barlow and Munsey, 1976), *Poecilia sphenops* and *Melaniris sardina*.

It is particularly germane to point out that the progressive reduction in faunal diversity is paralleled by a reduction in the species of potential predators on the Midas cichlid (Table 2).

TABLE 2. Occurrence of potential predators on Midas cichlids; + = present, − = absent, ? = probable, but not confirmed.

	Lakes				
	Nicaragua	Managua	Masaya	Jiloá	Apoyo
Fishes:					
Gobiomorus	+	+	+	+	−
C. dovii	+	+	+	+	−
C. managuense	+	+	+	+	+
marine fishes	+	−	−	−	−
Other vertebrates:					
Turtles	+	+	?	+	?
Cayman	+	+	−	−	−

FIG. 4. A *Potamocarcinus nicaraguensis* showing anti-predator threat display in Lake Apoyo. Photo by the author.

The lakes can also be ordered according to turbidity (Table 1). The Great Lakes of Nicaragua are so murky that underwater observations are impossible. These lakes have probably always been murky (*e.g.*, Meek, 1907). Lake Masaya is presently too turbid for underwater observations, although I was able to carry out some work there in 1965; occasionally it may still be clear enough to permit limited underwater observations. Possibly Lake Masaya was once clear and has become increasingly turbid due to the nutrients provided by sewage from the town of Masaya. Fortunately, Lake Jiloá is clear enough for observations, although it is rather murky at times. Lake Apoyo is usually exceedingly clear; on some occasions, however, the water becomes moderately turbid.

FINDINGS

Economy:

The cichlids, taken together, are the important food fishes of interior Nicaragua (Schuster, 1957; Lin, 1961; Riedel, 1964). The most desirable are two large species that reach lengths of 500 mm and more. They are eaten baked or as filets. The slightly smaller species is *Cichlasoma managuense*, called the *guapote*. The larger species, *C. dovii*, is called the *lagunero* or the *guapote blanco*. These species are sometimes confused by the fishermen who tend to call the largest specimens *laguneros* and the smaller ones *guapotes*. Both species are at the top of the trophic pyramid, being piscivores, and therefore are not abundant.

More numerous are the cichlids collectively called *mojarras*. Most of these species reach, maximally, about 200 mm standard length and these are eaten in soup. In the market one sees a few specimens of *Cichlasoma granadense, C. longimanus, C. nicaraguense, C. centrarchus,* and *C. rostratum.* However, marketed *mojarras* consist mostly of *C. citrinellum* and, to a lesser degree, *C. labiatum.*

The major markets for cichlid fishes are two. Those from Lake Nicaragua are sold primarily in the city of Granada, while those from Lake Managua are offered chiefly at the capital city of Managua. However, most of the catch is distributed locally before it ever reaches the market place (unpublished F.A.O. Report).

There have been attempts to introduce other species of food fishes. I mention two because of their possible interaction with endemic cichlids. The first is the largemouth black bass, *Micropterus salmoides*, from North America; apparently it has not survived. The other species is the African mouthbreeding cichlid, *Tilapia mossambica*. While *Tilapia* has thrived in managed ponds, it does not appear to fare well in competition with native cichlids. We have dived in at least three lakes where this species has been planted; I have never encountered any but Jeffrey R. Baylis believes he sighted one in Lake Apoyo.

The local people are said to have introduced fish into sterile lakes prior to the advent of modern fisheries biologists (Astorqui, pers. comm.). They may have put fishes into the crater lakes, either because the lakes lacked fish, or because the fish had been killed by lava. However, the mix of species found in these crater lakes is such that it is improbable that man consciously selected them. The very delicate atherine, *Melaniris sardina*, is one of the most ubiquitous species, as is the molly, *Poecilia sphenops*, a species of no importance to man and of little value as a forage fish for larger species. Furthermore, the cichlids found in these crater lakes are often small species, and/or highly adaptable species commonly found in bodies of water that are difficult to enter. But, while the species composition of the crater lakes is that which one would expect from natural causes, the situation nonetheless may have been altered by man.

Occurrence:

Cichlasoma citrinellum and *C. labiatum* are uncommon in rivers, at least during the dry season. A few specimens of *C. citrinellum* were collected then, and some seen, in larger rivers (*e.g.* Ochomogo and Sinecapa) flowing into the Great Lakes. These fish, however, were juveniles (with one exception), as were even those taken close to the lakes.

During the dry season pools form in the headwaters of rivers, and these connect with one another to varying degrees. Water in such pools is clear enough to census fishes there. Among the cichlids, I saw or caught a number of species, to wit, *C. dovii, C. managuense, C. rostratum, C. nicaraguense, C. centrarchus, C. longimanus, Neetroplus nematopus,* and the most ubiquitous cichlid species of the rivers and streams, *C. nigrofasciatum.* However, no *C. citrinellum* or *C. labiatum* were detected in these pools.

Perhaps *C. citrinellum* moves into the rivers during the wet season when there is more water, but I doubt that they ever do so in numbers. William Bussing has collected some from the very large Río San Juan. J. R. Baylis and Catherine R. Bleick made a number of collections near the head waters of the Rí San Juan, in the marshy area of the Río Frío around Los Chiles, Costa Rica. They caught a variety of cichlid fishes, but I found no *C. citrinellum* or *C. labiatum* in their collections; one adult *C. citrinellum* was caught there but released.

The distribution of *C. citrinellum* in lakes stands in contrast to their absence in rivers. It is the most ubiquitous species in the lakes. It is found in more of the lakes than any of the other cichlids, and it occurs in the widest variety of habitats. It can be taken in small numbers over beaches whose bottom is mud, sand or gravel. Occasionally the Midas cichlid is seen in groups up in the water, even just under the surface. When disturbed, however, it flees toward the bottom, a species-typical characteristic separating it from a close, yet to be described, relative. When it reaches

the bottom, it proceeds toward cover. But if there is no cover, it then swims toward the depths, moving close to the bottom.

Typically this species stays near the substrate and the number of individuals rises sharply around cover. Cover may consist of sunken bushes or trees, particularly along open beachs, or of rock piles. The affinity of *C. citrinellum* for cover, especially jumbled rocks, is apparent when one dives to depths. This species occurs from water so shallow that the fish can barely swim, down to a depth of at least 30 m (we could detect fish still further down at about 35 m, and they probably occur yet deeper). It seems to be most abundant in water shallower than 30 m but it was still abundant at greater depths so long as cover was available. A few fish were encountered in the open, but the numbers always went up when cover was reached.

The Midas cichlid makes good use of cover, disappearing into nooks and crannies. If there is no exit, it lodges itself among the rocks, head in. The fish cannot be pulled out because it locks itself in place with the spines of the median fins.

The importance of cover is also demonstrated by the frequent occurrence of small excavations in more open situations. The fish dig these pits with their mouths, depositing a sill on the downhill side. These holes are dug beneath logs, beside buried rocks, or in beds of *Chara*. They range in completeness from slight excavations under the branch of a log to well excavated pits with steep sides. The holes are deep enough to admit a Midas cichlid in a normal upright position and have a diameter slightly greater than the length of the fish.

This species was also observed at night in Lakes Jiloá and Apoyo by diving with SCUBA gear and flashlights. About 30–60 min. prior to darkness most of the *C. citrinellum* disappeared from view, apparently moving into holes and crevices among the rocks. However, even when illumination was so faint as to barely permit observations (less than 0.3 lux) some movement by the fish from hole to hole was detected. Most of the Midas cichlids slept in holes, but many were also found lying on the bottom in the open.

There is no clear relationship between the size of the fish and where it occurs in the lakes. Perhaps juveniles are encountered more frequently in small groups in the open.

In spite of its predilection for lakes in Nicaragua, *C. citrinellum* is found in other, but similar, habitats. Gilbert and Kelso (1971) collected this species in the Tortuguero area on the Caribbean coast of Costa Rica. They were most abundant along the west shore of an estuary where there was little cover. Some were also taken along its east shore where cover should have made it difficult to capture them. A few Midas cichlids were also taken in the streams mouthing into its estuary.

Thus the picture based on occurrence is one of an unspecialized cichlid, except for its absence from rivers. It occurs in a variety of habitats at various depths in still water where there is sufficient light, well oxygenated water, and ostensibly food, though it is associated with the bottom and is inclined to stay near cover. This generalized character is found in most Central American cichlids, doubtless reflecting their evolutionary recency (Barlow, 1974). In this respect they make a remarkable contrast to the highly specialized communities of cichlid fishes in the relatively old rift lakes of Africa (Fryer and Iles, 1972).

Aggregations:

Cichlasoma citrinellum starts life as schooling fry, thus as a highly aggregated species. When they leave the parents they appear to maintain the integrity of the school, judging by the similarity in size and numbers of the fry still seen protected by the parents. Juveniles tend to form closely knit aggregations. This is evident in groups on the move where one encounters, for example, 5, 20, 50, 100 or more juveniles swimming in a common direction close together. Adults, on the other hand, are inclined to space out a little more in loose but coherent aggregations.

The most common situations in which both juveniles and adults are seen aggregated in large numbers (500–1,000) is over rock piles or sunken trees, or within rocky canyons. Here they laze above the bottom in a loose assemblage at varying distances from one another and not having a common orientation (Fig. 5).

A noteworthy difference in behavior between aggregations of Midas cichlids in nature and those in aquaria is their aggressiveness. Leaving aside the territorial breeding adults, aggregated fish in the wild tolerate being close together with little expression of aggression. They do spar over food when working the bottom; but these outbreaks are brief, with one fish making a quick, short charge at the other, which generally swims away. But a few moments later, when moving about or hovering as a close group, the same two fish may resume the spatial proximity that prevailed when one attacked the other. Midas cichlids behave the same way in captivity in a spacious pool. But the fighting in aquaria conveys an entirely different view of their aggressiveness.

When kept in small groups, say two to seven fish, in aquaria of 100 to 400 l capacity, there is almost continual fighting. This results in injury and ultimately the death of weaker individuals. There appear to be three factors contributing to this. First, the subordinate fish cannot move far enough away from the attacker, as it would in nature. Second, being confined to the same place, the fish tend to become territorial, which often leads to breeding, and thus they are not in the same behavioral set as schooling wild fish. Third, in small groups the dominant fish seems to sustain its attacks on selected individuals. Given that the fish must be held in aquaria, their damaging aggressiveness can be held in check in two ways: (1) There should be no objects on the bottom, such as terra cotta pots or large rocks, that the fish can use as a focal point of territorial activity; and (2) ideally, the aquarium should have no corners. In combination with this, but much more effective, the fish should be crowded, say one adult per 15 to 25 liters in a large aquarium. This technique works well, but with crowding one must manage the water chemistry with considerable care.

In conclusion, while the Midas cichlid occurs in relatively pacific groups in nature, it has the potential of being an injuriously aggressive species. Under conditions of ample space *or* crowding, aggression is minimal.

Food Habits:

Underwater observations on *C. citrinellum* revealed that this species takes food in a variety of ways. Individuals can be seen sifting gravel or sand when feeding in the open areas, or sifting the detritus taken from crannies among the rocks. When over sand, they first tilt, then plunge the snout

FIG. 5. An aggregation of *C. citrinellum* in shallow water along a rocky shore of Lake Apoyo. Photo by the author.

into the substrate, rebounding to the horizontal position. They hold the mouth closed and churn the contents, straining the material for edible objects. Then the contents of the mouth are spat out and the procedure is repeated. Interspersed with these feeding movements are bouts of vigorous mouth-digging whereby the fish excavates a small pit, apparently exposing food items. Presumably these objects are tiny snails and insect larvae. In the laboratory the Midas cichlid avidly devours snails of the genus *Planorbis* and *Physa*, and their eggs. The snails are crushed between the pharyngeal teeth.

In Lake Apoyo this cichlid was observed biting off strands of the alga, *Chara*, and devouring them. Evidently there is enough animal matter on the *Chara* to make this nutritionally profitable.

In the rocky areas, and where large logs abound, *C. citrinellum* can be seen rasping *Aufwuchs* from the hard substrate. This is done with a simple emphatic bite at the rock or log.

Food objects are also taken in open water. I have seen this species strike at insects at the water surface, and also catch eggs falling from spawning atherines *(Melaniris sardina)*.

Native fishermen hook *C. citrinellum* using *Melaniris* as bait. I have caught Midas cichlids by using a fish-simulating lure (golden spinner). This species also hovers near schools of young cichlids being protected by their parents (Fig. 13). It will devour the young, even of its own species, if the parents are chased away or removed.

Preliminary studies of the gut contents of Midas cichlids from Lake Masaya indicated a diet consisting predominantly of an amorphous blue-green substance, the algae

making up the *Aufwuchs*. Some remains of snails and insects were also found. In 1972 J. R. Baylis examined 29 fish collected with rotenone in Lake Masaya (Table 3). Only the contents of the lower gut were used since the fish might have eaten small fish stunned by the ichthyocide before they themselves succumbed. These data reveal that algae are the most commonly found food, followed by insects, then snails; some fish remains were also detected. An analysis based on the volume of different foods in the guts might lead to a different rank ordering, for one prey item can make up the bulk of the contents, yet at least a small amount of algae is found in almost all the fish.

A few large individuals were speared in Lake Apoyo and their stomachs were examined by C. R. Bleick. The fish contained remains of small cichlids and atherines, plus occasional strands of the alga, *Chara*.

Riedel (1964) commented in passing that the cichlid fishes found in this part of Nicaragua, excluding the two large piscivorous species, are not predaceous, but that *C. citrinellum* occasionally takes shad *(Dorosoma)*. Gilbert and Kelso (1971) examined the gut contents of 19 *C. citrinellum* collected in an estuary in Costa Rica. They found "orange

TABLE 3. Gut contents of 29 *C. citrinellum* from Lake Masaya. Number of fish and percentage of total in whose lower gut such items were found.

	Algae	Insects	Snails	Fish	Empty	Sand
n	27	21	8	4	2	1
%	93.1	72.4	27.6	13.8	6.9	3.4

slime," well macerated plant material, one small eel and mud and sand.

The very young fish that are still protected by their parents feed on the plankton carried past them by the gentle currents of the lake. They also forage on the *Aufwuchs* on the rocks, apparently capturing tiny animals there, such as copepods. In addition, the fry swim to their parents from time to time to eat mucus from their sides (Noakes and Barlow, 1973).

Thus, the pattern that emerges is of a highly omnivorous and opportunistic feeder. It starts life as a predaceous fry but soon shifts to an omnivorous way of life, consuming appreciable amounts of plant matter. But as it approaches maximum size it appears to shift toward being more piscivorous.

Length-Weight Relationships:

Ideally this section would deal with age and growth of the Midas cichlid. Information on rate of growth, age at sexual maturity, and longevity are fundamental both to understanding the phenomenon of polychromatism and to enlightened fisheries management. It would provide the basis for determining regulations aimed at ensuring the maximum sustained yield, such as setting the minimum permissible size at whcch fish could be taken (see Fryer and Iles, 1972, for an excellent treatment of this fisheries problem in African cichlids). While the gathering of such data is a straight-forward undertaking, it can only be done adequately by a team of biologists residing in Nicaragua.

I have assembled some data on the relationship between length and weight in two populations of Midas cichlids (Fig. 6). This information will be of help in planning an age-growth study. Over the size range considered, standard lengths of from 40 to 200 mm, there are two obvious stadia, the fish shorter than 70 mm having a much lower slope than the larger fish. Because so few fish of the smaller sizes were available for comparison, they were left out of the calculation by least-squares method of the linear equations (Table 4), although the data are shown in Fig. 6.

TABLE 4. Linear equations describing the log of the weight of the fish (y′) as a function of the log of its standard length (x′), for Midas cichlids longer than 70 mm ; r = correlation coefficient; (A), (B), (C) key the equations to the lines in Fig. 6.

Lake	Year	Total n	n>70 mm	Equation	r
Masaya	1970	159	132	(A) $y' = -9.81 + 2.95x'$	0.98
Masaya	1969	70	57	(B) $y' = -10.95 + 3.15x'$	0.98
Apoyo	1969	105	65	(C) $y' = -9.05 + 2.76x'$	0.92

Three obvious conclusions emerge: (1) Weight is reliably correlated with length (r = 0.92 to 0.98). (2) Midas cichlids from Lakes Masaya and Apoyo have the same length-weight relationship. (3) Males and females have the same length-weight relationship.

Laboratory observations and an analysis of length-frequency data from Lake Masaya yield some information on growth. In the laboratory, males grow faster than females. This is probably why the larger adults in Lake Masaya, and evidently in the other lakes, are predominantly males (Fig. 11).

Although there are no differences in the length-weight relationship of populations from Lakes Masaya and Apoyo, there does seem to be a difference in rate of growth. Under the same conditions in the laboratory, the fish from Lake Apoyo grow faster than those from Lake Masaya and reach
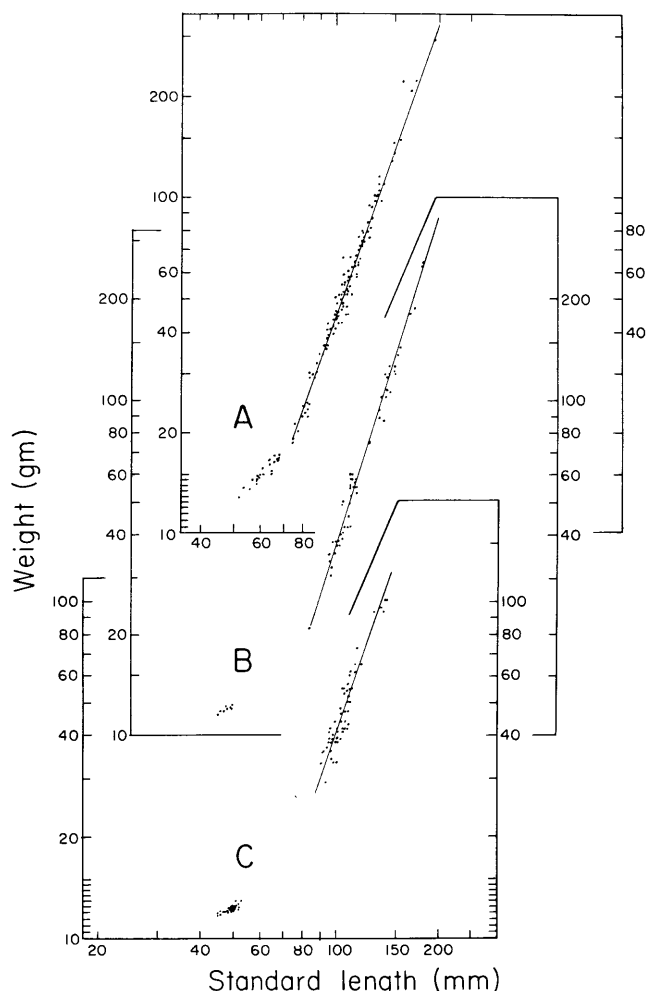

FIG. 6. The relationship between the log of the standard length and the log of the weight in the Midas cichlid. Three panels have been telescoped into one figure to facilitate comparisons; the scales of the abscissa are aligned but those of the ordinates are shifted up for each set of data. Lake Masaya, 1970 = A, 1969 = B; Lake Apoyo, 1969 = C. See Table 4 for the parameters of the linear equations.

larger size. Two laboratory-raised males of Lake Apoyo stock were so much larger than those of Lake Masaya stock that they were measured out of curiosity. One was 232 mm S.L. and weighed 720 gm, and the other 239 mm and 793 gm. I have no data on maximum size in the field, but our impression from diving is that the largest Midas cichlids occur in Lake Apoyo and the smallest in Lake Jiloá. This point warrants careful investigation because of its potential importance to conservation of irreplaceable natural resources, in this case possibly a genetic strain of larger size and faster growth.

Disease and General Health:

Information about the health of Midas cichlids from various populations can be useful in at least two ways. First, since predation on large adults seems to be slight (see section on predation), it becomes important to assess the contribution of disease to the mortality of adults and, in a less direct way, to the younger fish; this could have significant

consequences if correlated with coloration. Second, the management of a fishery requires knowledge of the diseases of the fish and the appropriate treatments.

Lake Masaya was first visited during two days in January, 1965. A dry, dead *C. citrinellum* was encountered every few meters of shoreline in the coves. A few dead fish floating on the surface washed ashore. Observing underwater, many *C. citrinellum* could be seen to have bits of whitish fluff on their fins. Some fish were captured alive and taken to the laboratory. All of these either had, or subsequently developed, in their fins the nodules typical of lymphocystis. Since lymphocystis is commonly accompanied by secondary bacterial and fungal infections, this probably accounted for the whitish fluffs on the fins in nature. (After a number of treatments were tried, the fish were finally cured by keeping them in water containing 12.5 mg/l of terramycin.)

I doubt that the lymphocystis was responsible for the numerous deaths, but suspect rather that it was a secondary correlate of a more general debilitation of the population. I thought the primary cause was overpopulation. However, when Lake Masaya was visited in 1969, and again in 1970, the population density seemed at least as high, if not higher, and there was no indication of illness or mortality among the Midas or other cichlids.

In Lake Jiloá I occasionally found a dead *C. citrinellum* floating at the surface in 1969 and 1970. Many of the fish encountered underwater were noticeably ill. For example, while free diving to recover a gill net, I successively captured with one free hand six fish that were too weak to

escape. One could only turn in tight circles against the bottom in its futile attempt to swim away. I also saw fish with copper-green patches of skin, commonly on the side of the head or body; while these seemed thinner and not as active as most of the Midas cichlids, there was no obvious correlation between the green discoloration and the fish that I could grasp.

In Lake Apoyo I never encountered any recognizably sick *C. citrinellum*, though superficial wounds were common during the breeding season. These consisted of occasional torn fins and scratches on the sides, of the type made by the teeth of rivals, and abraded areas above and below the lips as though the fish had been engaging in mouth fighting. When there was no breeding such wounds were not seen.

It is worth noting that, while the Midas cichlids do well in Lake Apoyo, the *C. managuense* there appear to have a unique problem. Large paired adults are common (Fig. 7), and apparently breed the year around (C. R. Bleick, pers. comm.). As a consequence, young of *C. managuense* less than about 100–150 mm standard length are abundant. However, intermediate *C. managuense*, i.e., just larger than this but smaller than full grown adults, are rather rare. On several occasions I encountered emaciated *C. managuense* of this intermediate size lying on the bottom, apparently dying of starvation; some were easily captured by hand. There seems to be a gap in the abundance of prey fishes of the size these intermediate *C. managuense* can feed upon. The most appropriate species, the atherine *Melaniris*, is not present in great numbers. Those *C. managuense* that reach adulthood
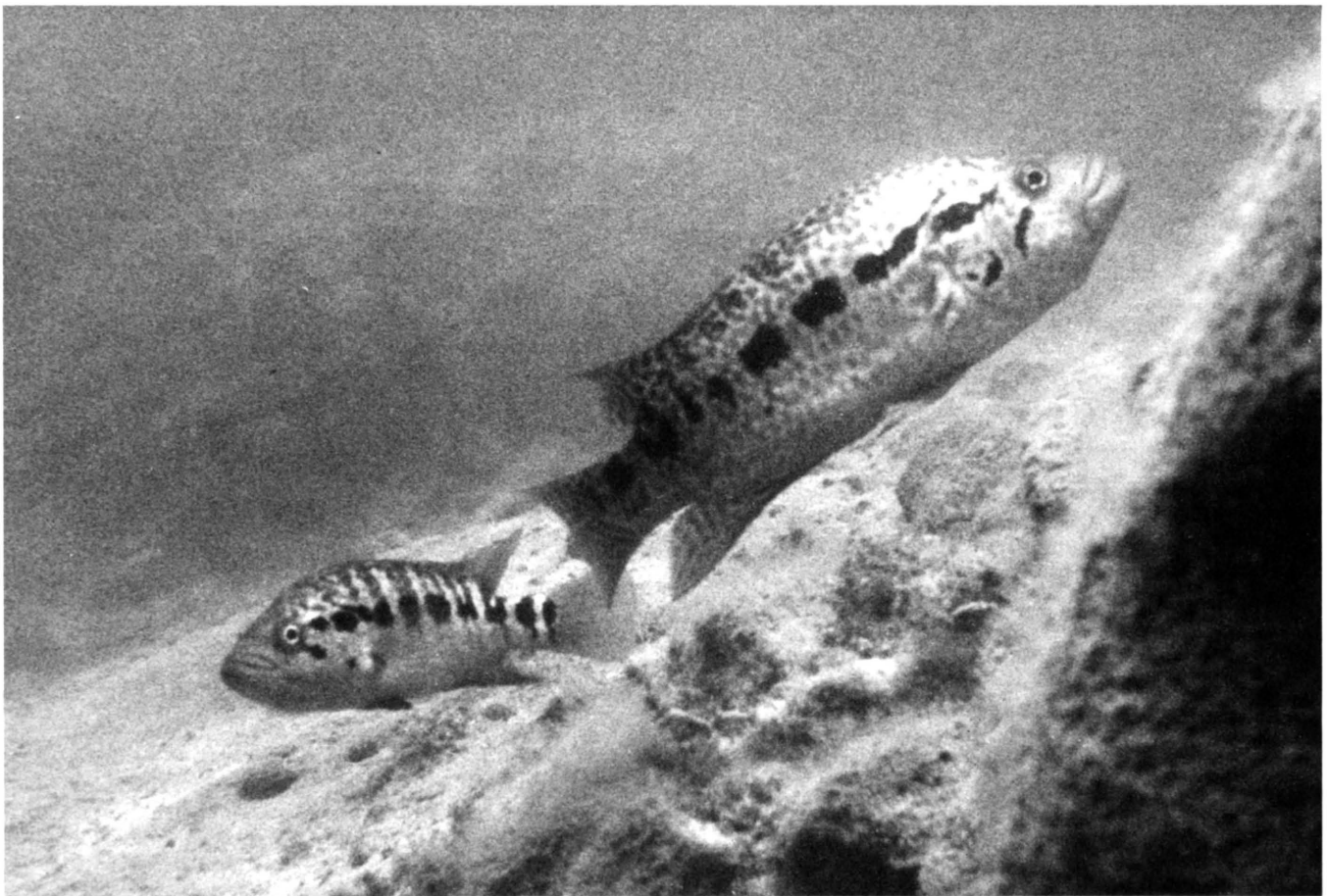

FIG. 7. A pair of *C. managuense* in Lake Apoyo; the female is to the left. Photo by the author.

probably feed primarily on atherines and on *C. citrinellum* that are too large for the *C. managuense* of intermediate size. The economy of this lake might profit, therefore, from the introduction of a small herbivorous forage fish, such as *Neetroplus nematopus*, that could sustain *C. managuense* during this critical phase of its growth.

Coming back to the Midas cichlid, its culture in the laboratory presents few problems because, as is typical of many of the *Cichlasoma*, it is a robust species that appears resistant to most common aquarium diseases. However, when our laboratory fish, which are predominantly of Lake Masaya stock, are kept under crowded conditions, a sickness appears that we first thought to be fish tuberculosis. They become weak and a red inflammation often appears at the base of all the fins. Some individuals show a severe distention of the abdomen, with or without the red inflammation. One specimen with a greatly distended abdomen was sent to Montserrat Educational and Scientific Company (M.E.S.C.O.) of Kansas City, Missouri, for diagnosis. The gut of the fish contained the bacteria *Pseudomonas fluorescens*, and two species identified only to genus, *Aeromonas* and *Nocardia*. The symptoms of nocardiosis are similar to those of tuberculosis. The treatment recommended by M.E.S.C.O. is 25 mg of kanamycin per liter of water. Since the adults are presently all in good health, we have not yet put the treatment to the test.

A greater problem has been presented by a disease that strikes the fry of the Midas cichlid when they are about 1–3 months of age. One by one, individuals stop growing, become thin and develop large abdomens. They lie listlessly on the bottom for a few days before dying. Some of these are now being diagnosed. The syndrome suggests nocardiosis again.

A potentially important but inconclusive finding is that fry from gold pairs appear to be more resistant than those in which both parents were normal in color. The consequence is that we regularly have large numbers of gold adults that we have raised in the lab but relatively few that are normal in color. I attempted to test the proposition that fry of normal pairs experience greater mortality than those of gold pairs. This was done by placing five batches of 100 fry each, and of both colors, in separate aquaria. In that way the starting number was clearly known and the mortality could be followed. But when the fry were spaced out in this manner they did not develop the disease. While the results were inconclusive, the observations suggest that the gold coloration might be genetically linked to greater resistance to this particular bacterial infection. Along similar lines, Ewers and Rose (1966) reported that in the snail, *Vel-acumantus australis*, individuals of the rare white-banded morph are more resistant to infection by parasitic trematodes than are nonbanded snails.

Color Patterns:

That which attracted attention to *C. citrinellum* and led to its vernacular, the Midas cichlid, is its polychromatism—the occurrence of colorful goldfish-like morphs. But the bulk of the fish are relatively drab, as we are accustomed to thinking of freshwater fishes. To appreciate the significance of the conspicuous morphs, I shall describe first the markings on the normal fish, and their ability to change patterns, with an eye to their role in concealment and communication.

Normal phase.—The normal color patterns of *C. citrinellum* are similar to those of the more generalized cichlids in the
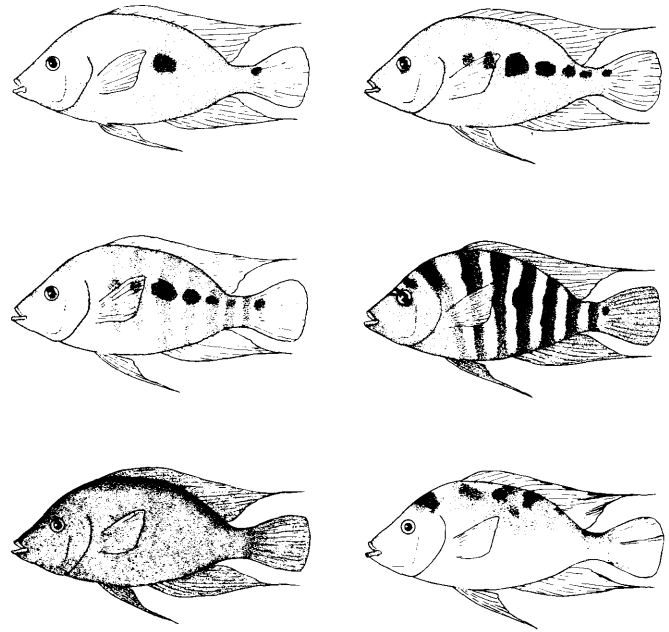

FIG. 8. Six color patterns shown by the Midas cichlid. The upper left pattern is called Spotted, the upper right, Striped. The middle left is intermediate to those in the upper row and the middle right is called Barred. The lower left is Black, seen so far only in fish from Lake Apoyo. In the lower right is a conspicuous morph that lacks the markings shown in the upper two rows but bears dark irregular blotches dorsally and some spots in the median fins.

genus *Cichlasoma*. The nonbreeding fish are cryptic: they match the darkness of the substrate, are countershaded, and can be difficult to see. The fish change their markings from moment to moment, adding or removing spots or bars. (Lacking this information, systematists have often relied on such differences when erecting new species.)

Although intermediates exist, the color patterns of the "normal" fish can be assigned to three groups, *spotted, striped,* and *barred* (Fig. 8). In the color patterns spotted and striped, the ground color is a dull mix of brown and grey with a light green to blue cast. There is considerable variation, however, in the intensity and the color of the wash in these brownish grey fish. Some have a yellow or even an orange tinge, while others have a slightly copper-green cast. The throat is variously neutral brownish grey to yellow, orange, or even red. Similar variability in eye color is shown, some fish having black eyes, while in others portions or all of the eye are variously yellow, orange, or red. Thus within the basic brownish grey color there is a varying degree of expression of yellow through red coloration (see below and Table 5), not to mention green and blue.

The species-typical markings are black, though when not fully expressed they appear as shades of grey. There is also variation in the spotting. The large median spot is about twice the size of the other spots and is larger than the eye of the fish; it is located just above and slightly to the rear of the mid-point of the fish. The median spot is always present. The caudal spot is the smallest of the spots, being equal to or less than the pupil of the eye; it is situated at the base of

TABLE 5. The occurrence of different colorations of *C. citrinellum* in three populations, sampled in different ways, and at different times. "Colorful Normals" refers to normal fish suffused with yellow, orange, or gold, while "Bright Morphs" refers to fish lacking the species-typical dark markings; colorful and plain normals are separated only in the first two entries.

		Plain Normals	Colorful Normals	Bright Morphs	Total
Collection					
L. Apoyo					
Gill nets	n:	56	17	6[b]	79
	%:	70.9	21.6	7.6	
L. Masaya					
1) Gill nets	n:	60	31	8	99
	%:	60.6	31.3	8.1	
2) Ichthyocide[a]	n:	– – –	314	– – –	26	340
(April, 1970)	%:		92.4		7.6	
3) Ichthyocide[a]	n:	– – –	44	– – –	5	49
(July, 1972)	%:		87.5		10.2	
L. Nicaragua					
Market[a]	n:	– – –	151	– – –	12	162
(August, 1972)	%:		93.1		7.4	
Market[a]	n:	– – –	1,432	– – –	133	1,565
(August, 1973)	%:		90.7		9.3	

[a]Fish 86 mm S.L.; plain and colorful normal morphs not separated.
[b]"Bright Morph" here refers to brilliant yellow fish with the median and caudal peduncle spots present.

the upper half of the caudal fin and it, too, is always present. From time to time a given fish shows two more spots of intermediate size falling in a horizontal line just anterior to the median spot. Or it may show just one spot of intermediate size directly behind the median spot.

Occasionally the fish carries two spots anterior to the median spot, and three spots between the median and caudal spot. Taken together, these form a longitudinal stripe on the fish. This phase is termed striped.

The functional significance of the variation in the appearance of the spots is not altogether clear. The spotted pattern and its variants characterize gregarious nonbreeding fish lazing about in the water just over the substrate (Fig. 5). The striped pattern is apt to be seen on fish farther up in the water. However, in a single large aquarium containing many juveniles it is possible to note at any moment the various spotted patterns in different individuals as well as a few fish that are striped. Since these fish are all experiencing the same physical environment, the differences in coloration are most likely related to interindividual communication.

These fish may also manifest seven vertical black bars. The first, lying at the posterior margin of the head, does not run through a spot on the body. The other six bars, when present, overlap the spots. The caudal spot, however, remains distinct.

There are gradations in the barred pattern. The bars are commonly visible as shadows in the spotted phase (Fig. 8, middle left). Then the interspaces between the bars are neutral grey and contrast little with the bars; the boundaries between the bars and interspaces are indistinct, grading from one to the other. This pattern is characteristic of fish that are either freshly captured or attacked by larger *C. citrinellum* in aquaria. The muted barring probably helps to camouflage the fish.

When breeding, Midas cichlids develop intensely black bars, with well-defined edges, and with almost white interspaces. In some individuals the interspaces are light yellow or even orange, the more so ventrally. This pattern is rich in contrast, and as a consequence the fish are conspicuous at close range; it probably signals other fishes to avoid the aggressive breeding pairs.

In Lake Apoyo only, breeding fish also show a *black* phase. When parental and in the open with their fry, these fish are usually barred. But when they swim back into a cave they most often immediately become uniformly sooty black and thus almost impossible to see. The black pattern, however, is sometimes shown by breeding fish away from caves.

There are also sexual differences in the utilization of color patterns. Females tend to become barred as soon as they are paired. Males, on the other hand, frequently delay the barring until parental, especially (in captivity) if it is their first breeding. In Lake Apoyo, males were often seen to show a wider range of color changes than females. A male might be black in the cave, barred in the open with the school, then immediately become spotted as it moves away from the family. However, since the females never left the families, it is not possible to say whether or not they would also be capable of developing the spotted pattern at that time.

Conspicuous phase. — Several questions arise when considering the conspicuous, or bright, morphs: With what frequency do they occur? Does that frequency vary with population, habitat, size, or sex, and is it stable through time? What is the nature of the differences in colors among the bright morphs? These and related questions will be treated here, but not all of them will be satisfactorily answered.

Meek (1907) commented on the occurrence of red or partially red cichlids in Nicaragua, and referred to the phenomenon as "rubrism." Those species said by Meek to have red morphs, which apparently included white through yellow and orange fish, although this was not made clear, are *C. citrinellum, C. labiatum* and *C. erythraeum* (=*labiatum*). "Red morphs" of these were taken from Lakes Nicaragua, Managua, Asososca, Apoyo, and Masaya by Meek, but he collected none from Lake Tiscapa or Lagoon Jenicero. We have found xanthomorphic *C. citrinellum* in the Great Lakes, and in Lakes Masaya, Jiloá, Apoyeque and Tiscapa. No brightly colored morphs of *C. citrinellum* were encountered in Lake Apoyo (see below), and we have not been able to examine Lake Asososca. Furthermore, I have found no evidence of *C. labiatum* in lakes other than Managua and Nicaragua.

Other species of cichlids in Nicaragua sometimes have gold morphs, but such fish are rare. Alfonso Solórzano sent a photograph of a golden female *C. managuense* that he had speared in Lake Apoyo. Gerald H. Meral and William Bussing have both seen gold *C. dovii* in the rivers of nearby Costa Rica (pers. comm.). I encountered specimens of *C. nicaraguense* in the Granada market that were nearly all gold but had weakly developed spots so typical of its species; one such pale blue morph of this species was also seen. A single gold male of *C. nigrofasciatum* was sighted by K. R. McKaye (pers. comm.) at a depth of about 13 m in Lake Jiloá. Farther north, in British Honduras, I have observed xanthomorphic *Petenia spendida* Günther, a large piscivore.

Returning to the Midas cichlid, one of the more recent laboratory developments will be reported first because it is so fundamental to what follows. The chemical basis of the polychromatism was explored, using laboratory-raised fish
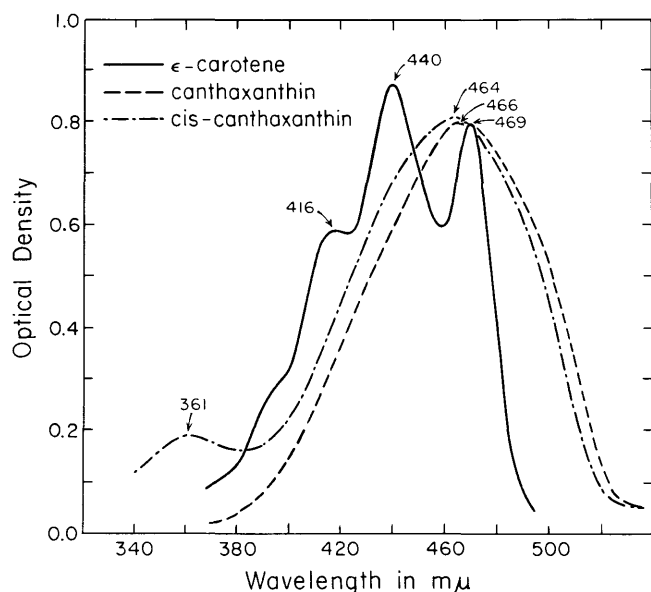
FIG. 9. Absorption spectra of carotenoid pigments isolated from *C. citrinellum*. The intense absorption from 350-500 mμ produces the yellow through red hues of the fish skin. From Webber, Barlow and Brush (1973).
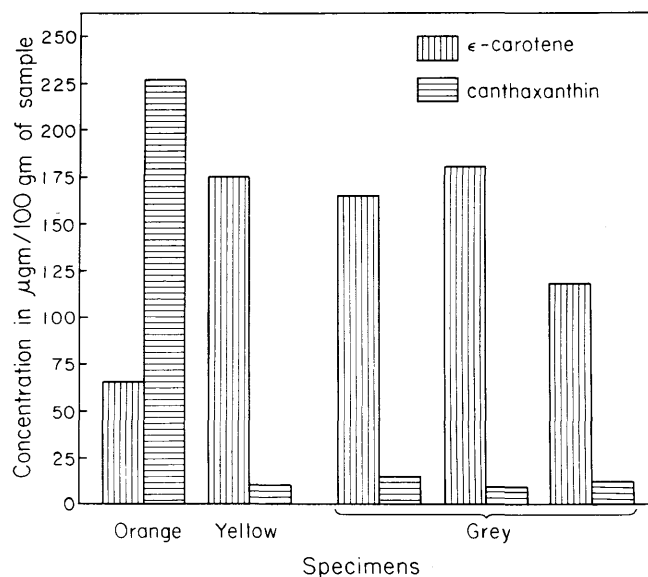

FIG. 10. The concentration and type of pigment in the skins of five *C. citrinellum*, one orange, one yellow and three grey (normal) morphs. From Webber, Barlow and Brush (1973).

of the Lake Masaya stock (Webber, Barlow and Brush, 1973). Three pigments of two types were found in all the fish (Fig. 9). One is ε-carotene, which is an orange pigment. The other two pigments are the xanthophyll called canthaxanthin and its isomer cis-canthaxanthin; these are red pigments, and are treated as one here.

The perceived color of the skin varies with the concentration and the mix of pigments. Thus skin that contains carotene at low concentrations appears yellow rather than orange. Likewise low concentrations of canthaxanthin give a pink hue. Mixes of the two pigments in varying concentrations could account for the range of apparent hues, from lemon yellow through orange to bright red (see below).

Lake Masaya fish bred in the laboratory generally appear to be either yellow or orange. The yellow one examined had some canthaxanthin in its skin, but most of the pigment was carotene (Fig. 10). Conversely, the orange fish had mostly canthaxanthin but some carotene; in nature, with a better diet, this fish would probably have been red or dark orange. The three normal grey fish studied had both pigments, which were present in the proportion found in the yellow individual. Since normal colored fish have variously yellow, orange, or red on them, further analysis of normal fish of the Masaya stock would probably reveal some individuals with mostly canthaxanthin but some carotene.

The difference between the conspicuous and the normal cryptic morph, then, is that melanin masks the orange and red pigments that are also present in the normal colored fish. The conversion from a normal to a yellow or red Midas cichlid therefore must entail removal of the masking melanin.

Initially all fry are of the normal cryptic color, irrespective of the color of the parents. The first sign of color metamorphosis in captivity is a slight paling of the fish, usually unevenly, giving the animal a mottled appearance. As more of the fish pales, it assumes a "dirty" light grey coloration. This is coupled with the disappearance of the

species-typical markings. Gradually the bright colors emerge. In the laboratory stock from Lake Masaya, most of the fish become orange, some slightly more yellow and some slightly more red than others; this coloration is referred to collectively as gold.

Occasional gold morphs become almost entirely chalky white. They are not albinos, for their eyes are pigmented and their skin is not pink. A few individuals, however, passed directly from the normal coloration to the white phase. The basis of the white coloration has not been investigated, but they lack the orange and red pigments, as do some normal morphs (Brush, pers. comm.).

Immediately after becoming brightly colored, inky black spots or patches usually appear, mostly on the fins, lips, and dorsum (Fig. 8). With time, most of these splotches disappear and the fish become immaculate. Occasionally, even long after metamorphosis, flecks of black reappear, especially in the fins, and following no particular pattern. After a fight, damaged areas on the lips and fins slowly become black, then later fade. A few individuals retain black markings, and some preserve a grey wash on the dorsum; they are rare in the laboratory, however. Thus, the conspicuous morphs retain the biochemical competence to produce melanin, but do not use it in the skin in the normal way.

Aquarists have told me that differences in the environment seem to trigger metamorphosis. I have seen no evidence of this, but the question is an important one and deserves investigation. Fox and Vevers (1960) noted that in general, light favors deposition of carotenes, and low temperatures may interfere with it. However, Midas cichlids kept in the laboratory under uniform conditons have shown a great range in the timing of metamorphosis. Perhaps if some missing environmental factor were present, there would be less variation. The age at metamorphosis in the laboratory is usually continuously variable. Within siblings, one can commonly find yet another individual transforming after the previous fish has changed color. The progeny

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of different pairs of the same color start metamorphosing at different times, indicating that this difference in timing is genetic.

Some examples follow of the timing of color transformation in relation to parentage. When Midas cichlids were first brought back from Lake Masaya, three pairings were carried out: both parents gold, both parents normal, and one parent gold and one parent normal. In the fully gold pair, the first juveniles changed color at an age of three months, but four years later some were still normal in color. In the mixed color pair, the earliest transformation also occurred at three months, and eventually most of the offspring became gold. In the pure normal pair none of the young metamorphosed within four years.

In another pure gold pair of Lake Masaya fish, the first young did not metamorphose until an age of one year. On the other hand, among the progeny of yet another gold × normal cross (both parents being offspring of a Lake Masaya gold × gold pair), 90% of the offspring had turned gold within one year.

In a number of pairings of gold fish, a small percentage of the offspring has been white. (They are also rare in Lake Masaya; Table 6). One F_2 cross was made using a white male and white female. Most of the fish eventually changed to the gold color, but any increase in the percentage of white offspring was not obvious. Thus multiple loci are probably involved. The alleles controlling the expression of white are probably recessive.

Characteristic patterns repeat within the offspring of a given pair, suggesting a genetic similarity. A recurring arrangement in one group of siblings was a white fish with bright orange rings around the eyes and around the bases of the pectoral fins. Another pattern from a different pair was a white body with orange on the head and median fins.

These fragmentary and nonquantitative findings indicate a polygenic system regulating the color patterns in C. citrinellum. There must be (1) a complex genetic system determining the color pattern of the normal phase, (2) a system setting age, or stage of development, at metamorphosis, (3) a system regulating the removal of melanin, (4) a system determining the proportion of carotene and canthaxanthin, (5) a system directing the placement of the bright colors, such as the orange rings around the eyes (a genetic mosaic?), and finally, perhaps, (6) an additional system controlling the saturation of the bright pigments. Moreover, the alleles for the gold morphs are dominant to those of the normal morph.

The saturation of pigments in the skin, however, appears to depend primarily on diet. Fishes do not synthesize carotene and xanthophylls. They depend rather on plants for the basic molecules which they may or may not modify, for example by increasing the number of double bonds or by the addition of radicals or protein molecules; this changes the absorption of the pigment and hence the wavelengths it reflects (Fox and Vevers, 1960).

Individual Midas cichlids vary in the intensity of their coloration in nature. When the most deeply colored, presumably most saturated fish are brought into the laboratory, their colors slowly fade over a few months and the differences in hues are lost. Adding water-soluble beadlets of β-carotene and canthaxanthin to their diet causes a partial recovery of coloration. Live adult brine shrimp (Artemia salina) as food are more effective in restoring colors but are too expensive to use extensively. Evidently the Midas cichlid's diet in nature is liberally laced with the necessary

TABLE 6. Hues of bright morphs of C. citrinellum.

Lake		White	Yellow	Orange	Pink	Red	Mix	Σ
Masaya	n:	1	5	24	1	4	1	36
(1969 + 1970)	%:	2.8	13.9	66.7	2.8	11.1	2.8	
		2.8	80.6		13.9		2.8	
Nicaragua	n:	11	14	37	--	--	1	63
(1971)	%:	17.5	22.2	58.7	--	--	1.6	
		17.5	80.9				1.6	

pigments. In the Great Lakes almost all the species of fishes show a tendency toward yellowing of white areas, including the nocturnal catfishes. Perhaps this is somehow related to the extremely dense phytoplankton in those waters, literally saturating the food chain with pigments.

The intensity of coloration of the bright morphs also varies somewhat in relation to their reproductive state. Fish held in the laboratory become noticeably more colorful after pairing and as spawning approaches. (The same intensification of bright colors can be observed in breeding normal morphs.) Beyond that, the bright morphs are unable to change their color patterns, in marked contrast to the normal colored fish. One gold female, however, showed a vestige of the color change of barring in the normal morphs: When parental, the areas on her side corresponding to the spaces between the bars on a breeding normal fish became slightly paler, creating the impression of faint orange bars.

Observations on the incidence of brightly colored Midas cichlids in nature are beset with frustrations. Because the morphs occur at a low frequency, one would have to collect an exceedingly large sample to get an adequate number of brightly colored fish. More discouraging, there appears to be a positive correlation with the turbidity of water, both in percentages of fish that are conspicuously colored and in the variety of color types. Thus, where the morphs are the most abundant they are the least observable. (Another problem is that collections of specimens that have been preserved in spirits are of limited use. All hues are eventually lost and one has only colorless fish with grey markings.)

In the clearest lake, Lake Apoyo, all the Midas cichlids have the species-typical spots or bars. (J. R. Baylis has bred normally colored fish that came from Lake Apoyo in this laboratory. In the first group of siblings three fish have metamorphosed to the gold phase. Therefore Lake Apoyo C. citrinellum carry the genes for gold morphs.) A few fish were seen underwater in Lake Apoyo that were obvious because of their striking lemon yellow color; but they still had the simple spotted pattern. I suspected that patternless gold morphs might be adapted to the light at greater depths and therefore present there while absent from the shallows. To test this we made two SCUBA dives to a depth of 30 m in Lake Apoyo; no gold morphs were seen, but the possibility remains that they exist at depths in that lake.

By means of gill nets (2″ and 3 ″ mesh) in the shallows (to 10 m) of Lake Apoyo, 35 males and 44 females were caught, ranging from 95 mm standard length (S.L.) and 28 g, to 140 mm and 100 g. Of these, 7.6% (5 males plus one female) were conspicuously yellow or orange although bearing the species-typical markings (Table 5). Additionally, 17 of the 73 normal fish had a distinct suffusion of
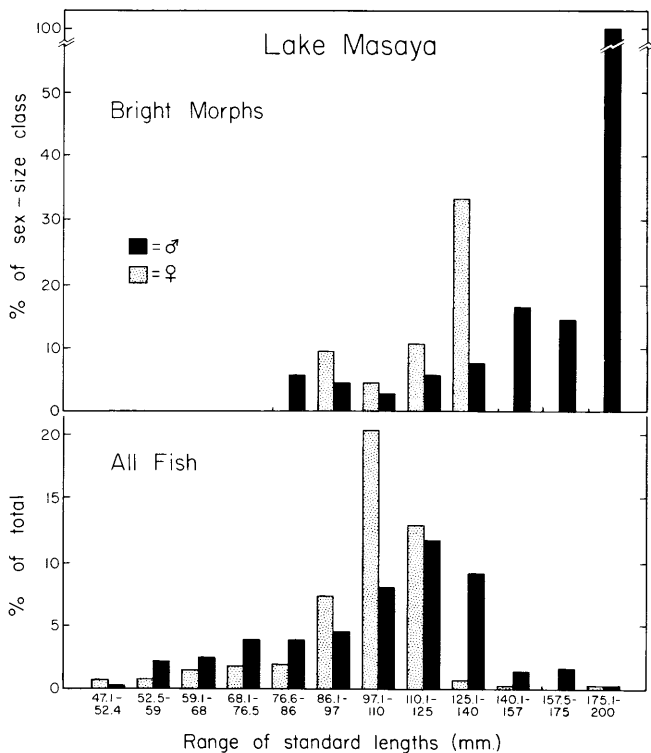
FIG. 11. The lower panel shows the percent of the total number (438) of *C. citrinellum* in each sex-size class. The upper panel shows the bright morphs in each sex-size class, as the percent of the number of all fish in that particular class.
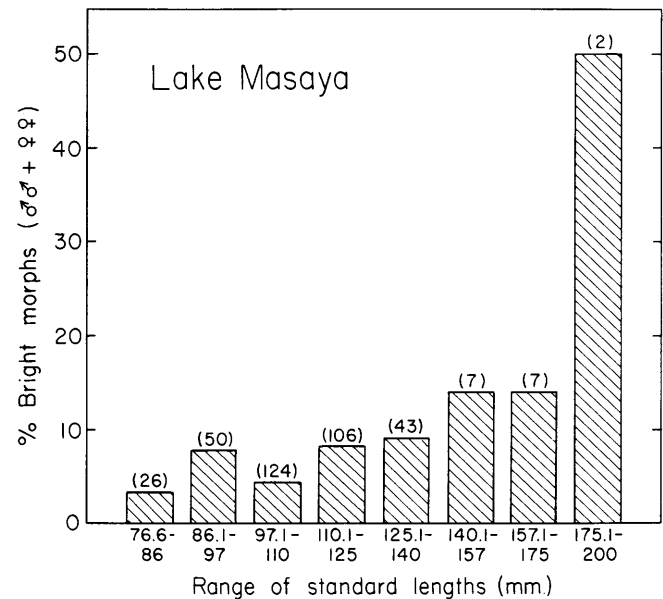

FIG. 12. The combined number of male and female bright morphs in each size class, shown as the percent of the number of all fish in that particular size class.

yellow or orange. One fish had a patch of bright orange on one side; a similarly marked fish was seen underwater but with the orange patch on its head. Thus Lake Apoyo can be characterized as having no true gold morphs, although almost 8% of the individuals are bright yellow and 22% are suffused with yellow or orange; furthermore, the genes for fully developed bright morphs are present but are not ordinarily expressed.

The water of Lake Jiloá is less clear than that of Apoyo. While diving there I encountered about one fish in several hundred that appeared lemon yellow or white and lacked the species-typical markings. Again, one fish had a patch of orange on its face, but was otherwise normal. In general, the bright morphs seen in the shallow waters of Lake Jiloá are not well or completely developed. Many retain fragments of the normal color pattern.

G. H. Meral encountered a higher proportion of bright morphs in Lake Jiloá (pers. comm.). He saw a number of yellow or orange fish, usually singly and always occurring at depths of 3-4 m or more. He noted a group of about 100 fish, in 7 m of water, that had two gold and one orange member, plus two others with orange on their heads. Recently J. R. Baylis and K. R. McKaye (pers. comm.) independently estimated that about 10% of the *C. citrinellum* in Lake Jiloá are conspicuous morphs; they made more extensive use of SCUBA and consequently worked in deeper water; they also included all degrees of development of conspicuousness. All three of these observers dived in a different part of the lake than I did. Since Meral and Baylis accompanied me on the dives in which few gold morphs were seen, it is likely that the differences are due to location and depth, rather than to the observers.

My involvement with the Midas cichlid commenced in 1965 with a two-day visit to Lake Masaya. By way of a start, I made an underwater census of the conspicuous morphs there. Of 368 large adults, 9.5% were bright colored morphs. Because they are more conspicuous than the normal fish in murky water (visibility was about 2-3 m horizontally), I may have overestimated their abundance. In July, 1972, K. R. and K. H. McKaye observed 311 adult fish underwater, 18% of which were brightly colored morphs. In my subsequent visits, Lake Masaya has never been clear enough to permit underwater observations (it was only marginally so in 1965). Estimates of the frequency of conspicuous morphs that follow are based on captures.

Gill-net catches in Lake Masaya in 1969 resulted in 55 males and 44 females, ranging from 84 mm S.L. and 21 g, to 180 mm and 245 g. In this catch 8.1% were brilliantly colored and lacked the species-typical markings, a percentage remarkably close to that (7.6) of bright yellow fish in Lake Apoyo (Table 5).

Up to now I have ignored the problem raised by the metamorphosis of normals into golds as it impinges on estimates of relative frequency of occurrence of bright morphs. If there are selective advantages or disadvantages to being so brightly colored, the proportion of gold morphs might reflect this, particularly if the fitness of gold morphs varies as a function of their size.

A large collection of *C. citrinellum* provides the only data bearing well on this point. The fish were taken from Lake Masaya, Rotarian's Beach, by C. R. Bleick, J. R. Baylis, and me on 14 April, 1970, with the use of rotenone. The Midas cichlid is highly susceptible to this ichthyocide, so we got a good cross section of the population. Sex was determined later through microscopic examination of the gonads. To compare the data with gill-net catch statistics, only specimens larger than 86 mm were used in Table 5. In Figure 11 all 438 fish were employed, those classes less than 76.4 mm S.L. not having any gold morphs.

The abcissas of Figure 11 and 12 call for some explanation. The intervals grow larger from left to right, but they were derived from equal-distance increments on a log scale. This gets around the difficulty, inherent in natural populations, of progressively fewer larger (older) members. Nonetheless, the largest classes still suffer from too few members; hence, estimates of the proportions of gold morphs in them are more subject to sampling error.

The analysis of the frequency of occurrence of bright morphs at different sizes is meaningful only in relation to the distribution of sizes in the population as a whole (Fig. 11, lower panel). At small sizes the males appear to outnumber the females; this probably resulted from errors in sexing the small fish, for the ovaries of immature females can be mistaken for testes. Clearly, however, females peak in numbers in the class 97.1-110 mm S.L. After that, loss exceeds recruitment, and there are few females longer than 125 mm. The males peak in the next larger class, 110.1-125 mm and only a few are found longer than 140 mm.

In the April, 1970, sample the smallest bright morph fell in the class 76.6-86 mm S.L. This corresponds well with the minimum sizes of bright morphs caught and shipped back alive to the laboratory in previous years. However, late in July, 1972, J. R. Baylis collected 120 C. citrinellum at the same beach and among these were four unusually small bright morphs ranging from 62 to 66 mm S.L.

Both in the females and in the males, the proportion of bright morphs increases with size. And in each sex, the very high proportions occur at sizes markedly exceeding those of the most frequent size class, when mortality is obviously greater than recruitment (Fig. 11); but extreme caution is called for in interpreting these results because so few very large fish were taken; considerable sampling error may be involved.

Since the Midas cichlid was so difficult for us to sex at that time, the more so when hurried, as in the field, many of the data on frequency of occurrence of the bright morphs are based on counts in which sex was not determined. To facilitate comparisons, the data for males and females from the collection of 14 April, 1970, were combined (Fig. 12). Up to a length of around 140 mm, 7 to 8% of the fish are bright morphs. Above that, the percentage goes up. In fact, a general rising trend can be seen across the size groups that projects to around 15% bright morphs in the largest class. But if the proportion is calculated only from fish of gill-net size, then a figure of 7.6% bright morphs is obtained. This agrees well with the 8.1% bright morphs caught in gill nets in previous years (Table 5). Using the "gill net" sizes from the 1972 collection by Baylis, however, the higher value of 10.2% is found (Table 5).

The Midas cichlids in Lake Masaya differ further from those in Lakes Apoyo and Jiloá in that the bright morphs exhibit a greater range of color types. Most are golden orange, but there are also white lemon, and medium red individuals. Multicolored specimens are present as well; most of these are predominantly orange with mixtures of white and yellow. Assignment to a particular color type is often difficult and therefore arbitrary. The incidence of normal colored individuals with patches of bright color on them seems greater than in the clearer lakes, although no data are available.

While the fish were still fresh, color types of 27 bright morphs taken on 14 April, 1970, were tallied in the field (Table 6). White, pink, and mixed colors were infrequent, with orange predominating (67%), followed by yellow and

red. Since the term gold refers both to yellow and orange, their numbers were combined, yielding a figure of 81%.

These 27 bright morphs also offered the opportunity to examine the distribution of the dark markings that seem so haphazard in their placement. Sixty-seven percent had black or grey splotches. Black was found as follows: dorsal fin — 33%, caudal fin — 50%, lips — 78%, and eyes — 83%. Thus, black markings are found predominantly on the median fins, lips, and eyes, not on the body. To simplify, black marks tend to be on the periphery of the fish and on its eyes.

Ten of these bright morphs (56%) had large areas of grey; in every case, the grey fell on the dorsal surface of the body. Among the bright morphs there was also a tendency toward lighter coloration ventrally. In many individuals the ventral surface approached white. Hence there is a variable but obvious development of counter-shading in these brilliantly colored fish. Note, too, that black splotches were not found on the ventral profiles of these specimens, although black has been seen on the anal and pelvic fins of fish in the laboratory.

Lakes Nicaragua and Managua are the last to be considered in this progression, being the culmination of a trend from clear to turbid bodies of water. Meek (1907) commented that about 8% of the fish in the market were red, but he did not distinguish between the different polychromatic species, nor did he explain what he meant by red. The fish from Lake Nicaragua, and also those I have seen from Lake Managua, show the greatest range of hues of any population. While most of the fish are normal in color pattern many of these appear to be bleached out. This could result either from the pre-market holding conditions, or from the extremely turbid water from which the fish came. Many normal fish have patches of bright color.

Among the brilliant morphs from the Great Lakes, individuals are white, yellow, brassy (a blend of yellow and brown), orange, or multicolored. Thus the Midas cichlids from Lake Nicaragua differ from those in Lake Masaya in the presence of a brassy morph and in the absence of morphs showing shades of red (see below).

The situation is further complicated by the variations seen in successive visits to the market. On one visit one year several brassy morphs were seen, but none was sighted in a week of visiting the market in the following year. Interobserver differences have arisen in estimates of the abundance of white morphs, and of red specimens of the species C. labiatum. These differences could stem from differences in criteria or perception, for the color categories are an arbitrary division of a continuum, or from the contributions to the market of different fishermen, bringing their catches from divergent locales. They could also indicate annual or seasonal differences. In August, 1972, J. R. Baylis counted 162 C. citrinellum, of which 12, or 7.4%, were bright morphs (Table 5). (Fish of marketable size are commensurate with those caught in gill nets.) In August of the following year K. R. McKaye, K. H. McKaye, and P. Sharkey tallied nearly all the Midas cichlids (over 1,000) in the Granada market and found that the proportion of bright morphs came to 9.3%. These two estimates are therefore well within the range of percentages found in the fish collected from the crater lakes.

The interesting difference in the Midas cichlids in the Great Lakes lies in the shift in color types away from red and pink toward gold. In April, 1971, I counted 1,175 fish in the Granada Market. Unfortunately, I believed at that

time that *C. citrinellum* and *C. labiatum* were the same species. I have since established that the pink and red morphs in the Great Lakes are not *C. citrinellum*. While the gold individuals collectively made up 81% of the bright morphs of *C. citrinellum*, there was a decrease (relative to Lake Masaya) in orange morphs (67 to 59%, and an increase in yellow (14 to 22%) and white morphs (3 to 18%) (Table 6). Still, some caution is in order. When McKaye, McKaye, and Sharkey censused the market in 1973, only one percent of the nonred morphs was white, and 72% were orange. Some of the difference may be between the observers, but I suspect that at least the difference in white morphs is real.

Comparing the lakes by going from clear waters to turbid, in summary, there appears to be a gradient in (1) the frequency of occurrence of conspicuous color phases, and (2) the diversity of types of colors. This progression starts as a suffusion of yellow or orange in the clearest lake. It is characterized by white through orange morphs, many incompletely developed, in an intermediate lake, and culminates in a variety of more fully developed color types in the population in turbid bodies of water. Ignoring the degree of development of the color type, there appears to be a remarkably consistent penetrance of bright coloration, ranging from about 7 to 10% of the adult population.

Predation:

The brilliantly colored morphs should be obvious to predators. It is difficult to get data on differential predation in the field, however, for a number of reasons. The skin of the prey and its pigments are rapidly digested in the gut of any predator. This problem is heightened if the predator is a cichlid because cichlids macerate their prey with their pharyngeal teeth (Fryer and Iles, 1972). Also, a large percentage of predators have nothing in their stomachs when captured. Since the conspicuous morphs occur at a low frequency, one would have to examine a vast number of predators with freshly devoured prey to estimate the relative frequency with which the prey are taken. Consequently estimates of differential predation must be either inferential from relative frequency of occurrence of the color types, or be projected from laboratory experiments. If experiments are to be done, it is important to know which are the appropriate predators.

One of the difficulties is that some of the predators that could have played a role in the evolution of the conspicuous morphs are no longer present in effective numbers. Fish-eating diving birds were common in fairly recent times (Riedel, 1964). Now they are rare, perhaps having succumbed to the chemical pesticides that are so generously applied to cotton crops in the vicinity. Furthermore, tropical otters may have preyed on this species, but otters are not now known in the area.

Another consideration is the difference in occurrence of various predators among the lakes (Table 2). There is a gradient in the number of kinds of predators, proceeding from the large lakes to the crater lakes of Masaya, Jiloá, and Apoyo. In Lake Nicaragua there are also extremely large fish predators such as the sawfish *Pristis perotteti* and the shark *Carcharhinus leucas*.

One should not speak of predation in general here but rather predation in relation to the size of the prey. The smaller the prey the more vulnerable it is to a wider variety of predators. The fry of *C. citrinellum* are eaten by all the species of cichlids with which they occur, including the

mostly herbivorous *Neetroplus*. Characins are particularly effective predators on cichlid fry, judging from earlier observations in Panama. Characins are abundant in the Great Lakes but they are either absent or not apparent in the crater lakes.

Not only are the smaller fish exposed to more predatory species, but they are also vulnerable to more individuals of a given species. For example, small individuals of *Gobiomorus dormitor* cannot eat adult Midas cichlids but only their young, whereas larger *Gobiomorus* take both juveniles and fry. In general, the larger the *C. citrinellum* the fewer its predators.

The main visual predators on *C. citrinellum* appear to be three species, the eleotrid fish, *Gobiomorus dormitor* and the two large cichlids, *C. dovii* and *C. managuense*. This conclusion stems from observations on their behavior, and from the fact that these piscivores are common where *C. citrinellum* occurs.

Bleick (1970) reported in passing on the capability of *C. managuense* to ingest large prey. She found that an adult can devour another cichlid fish (*Tilapia mossambica*) up to 38% its own length, or about 6% its own weight. This was doubtless the maximum size that the *C. managuense* could devour, for it took 8 hr to swallow the prey, and much of the time the tail of the prey protruded from the mouth of the predator. In an aquarium, a piscivorous African cichlid (*Haplochromis longirostris*) took cichlid prey whose maximum standard length ranged from 22 to 30% and weight from 2.4 to 4.8% that of the predator (Buruga, 1967).

Bleick also reported that the largest specimen of *C. managuense* that she took in Nicaragua was 298 mm long and weighed 618 g; this is representative of the average *largest* specimen one encounters in the crater lakes. By calculation, the biggest *C. citrinellum* such a fish could eat would be about 113 mm and weigh around 37 g. *Cichlasoma dovii*, however, grows even larger than *C. managuense*, 1000 g being not unusually large for a male. Such a *C. dovii* should be able to devour *C. citrinellum* up to about 120 mm long and weighing approximately 60 g. The largest *Gobiomorus* could be expected to take similarly large Midas cichlids. While some unusually large *Gobiomorus* have been seen in Costa Rica (G. H. Meral, pers. comm.), most of the large *Gobiomorus* I have seen in Nicaraguan lakes are about 250 mm long.

These sizes and consequent calculations are based on the maximum size of predator, a size reached by only a few specimens. Even at those sizes such large prey are difficult to capture and might present to the predator the hazard of lodging in its throat. Note that while Buruga (1967) found that *Haplochromis longirostris* could ingest a cichlid prey up to 30% of its own length, such prey in wild-caught *H. longirostris* ranged from only 7 to 11% the length of the predator (although only five fish with prey were examined). Most of the predation, furthermore, is done by appreciably smaller predators.

While the maximum length of *C. citrinellum* that could be expected to be taken would be around 110-120 mm, the major impact of predation falls upon smaller individuals. Predation is therefore probably directed largely to Midas cichlids that have not yet reached reproductive maturity.

Seasonality:

Seasonality here refers to reproduction and, to a lesser degree, to fluctuation in local abundance, which might be a consequence of reproductive behavior. Since our visits to

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Nicaragua have been so few and so brief, conclusions reached here must be regarded as particularly provisional. Our experience indicates that there is considerable variation from lake to lake in the degree to which seasonal variation can be detected. Even within a given lake, some species appear to be more seasonal than others.

In Lake Masaya, *C. citrinellum* was found breeding in good numbers during both the wet and dry seasons. Because of the extreme turbidity, however, it was not possible to gauge the frequency of breeding pairs. But the impression gained from the frequency of stumbling upon breeding pairs in the murky waters of that lake, while diving, is that breeding goes on year-round.

In Lake Jiloá, too, breeding pairs were observed in the wet and in the dry season. But it seems that more of the pairs breed during the wet season. To illustrate, one transect, followed at a constant depth near the shoreline, indicated a density of breeding pairs of 2.5 per 100 m of shoreline (both J. R. Baylis and K. R. McKaye have found much higher densities). This transect was fairly representative of other stretches of shoreline in Lake Jiloá at that time. During the dry season, in contrast, only occasional breeding pairs were seen.

The seasonality of breeding was more pronounced in Lake Apoyo. During the wet season of July and August, thus at the same time the census was conducted in Lake Jiloá, a similar transect survey was carried out. It yielded the high figure of 27 breeding pairs per 100 m of favorable shoreline, roughly ten fold that observed in Lake Jiloá. Yet in a subsequent year Baylis could find no fish reproducing in Lake Apoyo during the wet season. During the dry season I found no breeding pairs.

This variation in number of breeding pairs in Lake Apoyo was also accompanied by obvious variations in local abundance of *C. citrinellum*. During the wet season over a favorable reef I saw thousands of adults, many in pairs. In the dry season, at the same reef, I saw only a few fish, and these were scattered about. Since this species doubtless is long lived, it is reasonable to assume that the sparsity of fish during the dry season is due to local movements. Either they move to depths, or they are simply more uniformly dispersed through the lake.

Lake Apoyo is also interesting in that the *C. managuense* there give little indication of seasonality in their breeding. In contrast to *C. citrinellum*, this large fish-eating species appears to breed year-round in about equal numbers.

In conclusion, there is some seasonal variation in *C. citrinellum* in that breeding appears to occur more frequently during the wet season than during the dry, when it may cease in some populations. But this aspect of the Midas cichlid's biology needs much more and sustained observation. The unpublished data of J. R. Baylis and of K. R. McKaye indicate a more complex situation and in some ways contradict the relationship I suggest here.

In the laboratory, this species breeds at any time of the year, so long as conditions are favorable.

Territoriality and Reproduction:

This account of territoriality and breeding in *C. citrinellum* is based chiefly on observations made while diving, but without SCUBA gear, in Lakes Jiloá and Apoyo in August, 1969. I shall describe first some of the physical attributes of the territories and then the behavior of the breeding fish.

Most of the territories were found in shallow water, 1-1.5 m deep, and directly against the shoreline among the jumbled boulders there. Territory-holding pairs were seldom found on the wave-cut bench,but were encountered again as deep as we dived (10-15 m). Pairs may have been less abundant in the deeper water where we dived simply because less cover was available there. Proper substrate seems the most important factor determining where *C. citrinellum* breeds.

In April, 1970, we dived to depths of 20 to 30 m in Lakes Jiloá and Apoyo. No breeding pairs whatsoever were encountered in Lake Apoyo, and the few found in Lake Jiloá were mostly in shallow water directly against the shoreline. Other cichlids in Lake Jiloá were breeding at almost all depths, although *C. dovii* was breeding only at depths greater than 10-15 m.

With a little experience in finding breeding pairs it soon becomes possible to predict where one will encounter a territory-holding pair, based on the characteristics of the substrate. In general, rock slides consisting of large boulders are most favorable. Within these, breeding pairs are encountered at small caves, particularly those situated at the base of a pile of rocks and having a mouth whose width measures about twice its height (Table 7 and Fig. 13). One pair, however, occupied a cave whose mouth was 10 cm wide and 30 cm high.

Another sign of a breeding pair is the audience of potential predators hovering nearby, often pointed toward the cave. Additionally, a breeding pair is immediately recognized by the contrast-rich banded color pattern (Fig. 8 and 13, and section on color patterns) and their more often erect median fins (female in Fig. 13).

The distance between breeding pairs differed in the two lakes (Table 7). In Lake Apoyo, where there were many more breeding pairs, there appeared to be more demand for suitable caves. The distance between pairs was commonly as little as 1-1.5 m. In Lake Jiloá, in contrast, there was much less breeding, and many caves that looked appropriate for breeding were unused; the shortest distance between pairs was 10 m.

One of the most remarkable features of the territories was that while the center was clearly defined by the cave entrance, it was not possible to identify the boundaries. The best that could be done was to tally the estimated distances that the parental fish swam out to attack potential predators. This attack distance was variable (Table 7). Another type of evidence for the lack of boundaries was the degree to which neighboring pairs tolerated one another within what appeared to be their territory, as defined by the paths they swam to attack predators. Breeding fish were seen to

TABLE 7. A resumé of data characterizing breeding pairs of *C. citrinellum* in two crater lakes. "Cave mouth" refers to the dimensions of the cave where the eggs were laid. "Predators repelled" is the distance swum to ward off intruding potential predators. "Nearest neighbor" refers to other conspecific breeding pairs. The last row indicates the range of lengths of females relative to their mates.

	Lake Jiloá	Lake Apoyo
Cave mouth (x̄, width × height)	36 × 18 cm	40 × 25 cm
Predators repelled	10 − 100 cm	10 − 100 cm
Nearest neighbor	≥ 10 m	1-4 m
$\frac{♀ \text{ length}}{♂ \text{ length}}$ (100)	75 − 90%	65 − 90%

FIG. 13. A breeding pair of Midas cichlids in Lake Apoyo standing with their young before their cave; the male is to the left and the female to the right. A group of Midas cichlids hovers at the periphery of the territory in the background and a molly, *Poecilia sphenops*, passes through the territory, to the right, unmolested.

swim through the area cleared by the neighboring pair to attack a potential predator without eliciting attack from the neighbors. Thus what I have been calling a territory in this species does not conform well to the general model for territory among vertebrates.

Another noteworthy feature of their territory, deducible from the foregoing, is its small size. In most instances, the territory encompasses only about 1–2 m³, which is unexpectedly small for so large a species.

The small size of the territory, plus the closeness of pairs when many are breeding, suggests a tendency toward coloniality. Currently, however, I am unable to distinguish, in the clumping of pairs, between social attraction and preferred habitat.

Some of the pairs in Lake Apoyo and Lake Jiloá bred in open, rather sandy areas, although this happened relatively infrequently. Such pairs dug post-hole-like pits in the bottom, generally about 30 cm in diameter and 20 cm deep. These pits were always dug against some hard vertical surface, such as a buried rock. Little territorial defense was seen, probably because such pairs were widely spaced. These more exposed fish seemed shyer than those in the rock piles. The fry of these pairs are probably more vulnerable to predators because the school can be approached from all sides.

Before describing the major features of courtship and reproductive behavior I will digress briefly to take up the

matter of sexual dimorphism. If two fish of opposite sex and equal size are examined when not breeding it is difficult to establish which is the male and which the female. The length of the trailing filaments of the dorsal and anal fins is not a reliable indicator of sex in the Midas cichlid, although it is in other *Cichlasoma* such as *C. nigrofasciatum*.

If sexually mature, the sex can be ascertained by a close examination of the genital papilla (Fig. 14). There is considerable individual variation in the morphology of the papilla, some of which is due to the reproductive state of the fish. The sexual differences are heightened, and thus more obvious, as a fish approaches spawning and the papilla becomes more turgid. In a live fish, details of the papilla are obscured by mucus and its attendant interfering reflections. In a nonbreeding fish the flacid papilla lies more completely in a depression, making it even more difficult to make out. For the illustration, a male and a female papilla were chosen (from preserved fish, in which it is easier to see) that clearly demonstrate sexual differences; some of the details, however, are not relevant, such as the size and shape of the vent (the lowermost orifice shown in the illustration).

The papilla of the male is the more conical, tending to be pointed, and has the single orifice at its tip. The female's papilla is broader and semilobate, tending to be flat; the terminal, presumably urinary, orifice usually lies just short of the end of the papilla. The female's papilla has a second
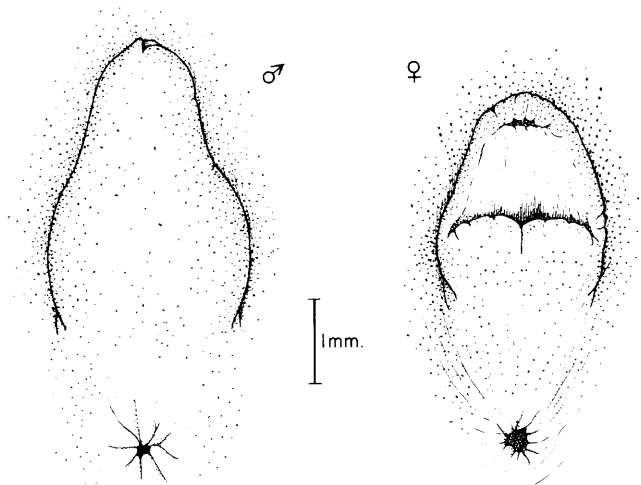
FIG. 14. The genital papilla of a male (left) and a female (right) *C. citrinellum*, in ventral view; anterior corresponds to the bottom of the figure.
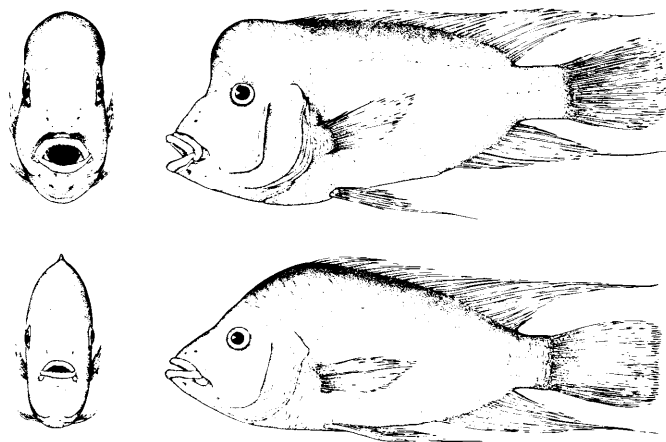

FIG. 15. Drawings of two freshly preserved laboratory-reared Midas cichlids of the same size, the upper of which has developed a nuchal hump and a swollen throat. The differences in the mouths and cheeks are due to accidents of preservation.

opening near its center, apparently for oviposition, which is marked by an elaborate transverse lip; this may be difficult to make out in a hand-held fish, but its presence or absence can be verified with a small blunt probe (thanks are due C.R. Bleick for pointing out this convenient and reliable test and some of the details of the anatomy).

As the fish come into breeding a remarkable sexual dimorphism appears. The forehead of the male starts swelling, producing a nuchal hump; the throat in the region of the isthmus also expands (Fig. 15). The swelling is soft to the touch, and is caused by local edema (C.R. Bleick, pers. comm.). The female may also develop a nuchal hump, but it is much smaller than the male's and is relatively inconspicuous. This dimorphism results in the male having a profile that is blunt anteriorly and tapers to the rear, while the profile of the female is tapered at both ends.

The factors determining the presence and size of the nuchal hump are complex, but they tend to assure that maximum dimorphism occurs at the time of pair formation. A typical progression makes the point: a male with no nuchal hump is brought into the laboratory and put into a situation conducive to breeding. Within a few days he develops a large hump. Then he is paired with a female. The hump recedes during the one or two weeks of courtship. Sometimes it diminishes rapidly, in less than one day, just before spawning (C.R. Bleick, pers. comm.). It stays reduced through the parental phase. If the pair completes the rearing of young and commences another breeding cycle, the male does not develop a large nuchal hump this time. But if the female is taken away at this point for a few days and is then returned, or replaced with a new female, the hump develops anew in the male. Here the elaboration of the nuchal hump is stimulated by the factors associated with thwarted sexual behavior and pair formation.

Groups of males kept without females in large tanks regularly develop enormous nuchal humps that persist. The humps on such males often become grotesque, and far exceed anything seen in nature. The behavior of these males suggests that aggressive behavior might be involved in stimulating the development of the hump. Aggressive activity is also an important aspect of courtship behavior, particularly during pair formation. We need systematic studies

of isolated and of interacting pairs, together with quantitative correlations of levels of aggression and development of the nuchal lump.

In freely formed captive pairs the male is always larger than the female. Attempts to form pairs with the female larger than the male were unsuccessful. In the field, too, males are larger than their mates. I estimated by eye that the modal size relationship is for the female to be around 80 to 85% the length of the male, although pairing is possible with appreciably smaller females (Table 7; see also McKaye and Barlow, 1976).

In a sense the population is dimorphic for size. The largest size class of females in Lake Masaya in 1970 was 97 to 110 mm S.L., with few females exceeding 125 mm (Fig. 11). The largest class of males was 110 to 125 mm, with a few surpassing 140 mm. Since females mate with larger males, and since there appear to be fewer males than females in the next class larger than the peak for females (Fig 11), there might be an excess of breeding females over breeding males; such a situation could lead to competition among females for males. To test this, one would have to establish clearly which sizes of males and females are breeding and relate this to the size structure of the population under consideration. My impression is that breeding is done predominantly by the largest fish in the population, but this can serve as little more than a hypothesis to spur the collection of needed data (K.R. McKaye is accumulating data that appear to confirm this).

Returning to reproductive behavior, pair formation in the field is difficult to document because one never knows whether the fish are meeting for the first time, and because they are so much more easily disturbed by an observer than when parental. The little information on pair formation or courtship was garnered by viewing at an appreciable distance. A few pairs stayed in their territories even when approached closely, but then ceased courting. The scheme from such fragmentary observations is that pairs form while in groups, but that pair formation is facilitated by the two fish being over substrate propitious for breeding. Pairs were seen to display while moving into the mouths of caves. Evidently pair formation and territory formation are concurrent (McKaye's observations suggest that pair formation

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precedes establishing a territory); the male does not establish a territory to which the female then comes.

One spawning was observed and a few clutches of eggs were found. This species places the eggs preferentially on an oblique part of the ceiling of a cave. Those fish that nest in pits in the open obviously have no ceiling; this is probably why they nest adjacent to a hard surface, depositing the eggs on the vertical wall.

Fanning of the eggs was never seen in the field. When I approached close enough to observe such behavior I disturbed the parents so much that no fanning was done. In the laboratory, however, the species vigorously fans its eggs. One pectoral fin is held close to the clutch and the forward component of the beat pushes water past the eggs. Almost all fanning is done by the female.

No information on the wriggler phase was obtained in the field. In the laboratory, under simulated natural conditions, the parents do not dig clearly defined small pits to hold the larvae as do so many other cichlid fishes. They dig prodigiously, however, commonly removing all the gravel from the bottom of the aquarium and piling it high into the corners of the tank. They remove gravel and sand from crevices and from under rocks. There they place the newly hatched larvae out of view. Then the only way to locate the larvae is to watch where the parents direct the stream of water when fanning. The wrigglers are difficult to find even in an aquarium if the stituation permits the parents to hide them. In the field, the wrigglers are doubtless secreted in crannies inside the cave.

The 1,000–5,000 swimming fry form a compact school just before the entrance of the cave where they feed (see section on food habits). When danger threatens, e.g., the approach of a diver, one or both parents withdraw into the cave. (If only one parent was in the cave, it was invariably the female, the male having fled. In some instances the male was never seen. This may have been because the male deserted the female, but I suspect rather it was because he was too timid to approach while I was in the vicinity.) The parent or parents in the cave signalled the fry by simultaneously jerking the head to one side and snapping the pelvic fins out to the extended position. The fry then schooled more tightly and under the parents and moved into the cave. (In contrast, only during their first few days do fry in aquaria school as tightly as those in nature. Thereafter, they school loosely. However, when predators are present in the aquarium the fry continue to school tightly.) When not disturbed, the parents spent most of their time before the mouth of the cave patrolling within the school (Fig. 13), often moving to its outer edge. The potential predators lurked 1.5–2 m away. From time to time one of the parents rushed out at a predator, attempted to ram it, and then dashed back to the school.

In Lake Apoyo the predators on the fry were primarily young C. managuense that lurked and crept along the bottom, and juvenile to adult C. citrinellum that hovered in the water near the school (Fig. 13). When the parents were removed, conspecific juveniles and C. managuense immediately attacked and devoured the fry (see also Bleick, 1970). In Lake Jiloá almost all of the small species of cichlids, or the young of the larger species, hovered about the schooling fry and their protective parents. Once I chased the parents away from their fry. One parent wedged itself into its cave, but with its fins showing. At once several Neetroplus nematopus dashed in and fed on the fry, as did a number of C. nigrofasciatum. Some of the latter even bit out pieces of the hiding parent's fins.

As with its beginning, the end of the breeding cycle was difficult to observe. As the fry approached the young juvenile stage, say about 20 mm long and 4–6 weeks of age, they became more mobile. Increasingly, they moved away from the cave into the open. This process seemed to occur earlier in Lake Jiloá than Lake Apoyo, probably because of the less dense breeding population in Lake Jiloá. In Lake Jiloá parents were observed to move their schools of young along the shoreline when the fry were only about 2 weeks of age, whereas in Lake Apoyo the young were much larger, or older, before leaving the area around the home cave. Both J.R. Baylis and K.R. McKaye found that when breeding occurred at high densities in Lake Jiloá the fry were not moved about. The mobility of the families therefore appears to be related to density of breeding pairs, being permitted at low but constrained at high densities.

As families approached dissolution, the numbers of young were greatly diminished, ranging from less than 100 to several hundred. At this time there was usually only one parent with the fry, presumably the female. Also presumably, and in part based on aquarium observations, it is the parent that forsakes the fry, not the other way around. McKaye, however, is finding in Lake Jiloá that it is the fry who forsake their parents; he believes the difference again relates to the density of breeding pairs. On three different occasions in Lake Jiloá I observed a single adult, apparently a female, swimming rapidly and being followed by a small group of fry about half again as large as those normally associated with parents. These fish were in the open and in deeper water (5–10 m deep). When I approached, the parent swam rapidly off and the young fish scattered. At this size, however, the young are not so vulnerable to the many small cichlids that ordinarily hover about attempting to devour fry.

Color in Relation to Mates and Size of Territory:

One of the main goals of the field trips to Nicaragua in 1969 and 1970 was underwater observations on behavioral differences related to polychromatism. While doing experiments on families of C. citrinellum from Lake Masaya, David L.G. Noakes discovered in this laboratory that it is difficult to form a pair in which the male is gold and the female normal in color. For that reason I expected assortative mating by color types, the combination gold (bright morph) male x normal female being particularly infrequent.

Other experiments in the laboratory had established, prior to these trips, that under most circumstances fish that are gold dominate those that are normal. Therefore, I also anticipated that bright-colored fish would have larger territories than those normal in color. Unfortunately, as mentioned, the water in the lakes where the gold phase was encountered in numbers was too turbid to permit observations.

By rare good luck I chanced upon a seminatural population of Midas cichlids breeding in clear water. While awaiting departure from the Los Mercedes Airport in 1969 I noticed two new ornanental fish pools at the entrance to the airfield. The pools were stocked with cichlid fishes. Each pool is L-shaped, about 35 cm deep and 3 m wide, with each limb of the L about 15 m long on its shortest ("concave") side. Then, and again in 1971, I recorded the breeding pairs by color. I also made repeated samples, totalling over

200 fish each time, to calculate the proportion consisting of bright morphs. I estimated, as well, the sizes of the territories held by the pairs. In 1969 and in 1971 only one pool was suitable for observations, the other being too crowded on one occasion and having sick fish on the other. During each visit I had trouble gaining access to the pools, and on the second visit I was allowed too little time to observe the sizes of the territories.

I calculated the colors of mates one would expect by chance, separately for each visit before combining the data (Table 8). Unfortunately there is no appropriate statistical test for these data. Methods such as the Fisher Exact Probability Test carry the assumption that all cells are equally probable. But since the bright morphs are relatively rare, equal occurrence of all color types of pairs would be an important finding. The critical observation is the extent to which the types of pairs depart from their expected frequencies of occurrence, as calculated from their occurrence in the population as a whole. The Chi-Square Test is designed to test such an hypothesis, but larger data fields are needed for its application. Furthermore, because of the weakness of the premise of the naturalness of this serendipitous experiment, a statistical test seems inappropriate.

Although this was an artificial situation, the conclusions flowing from it gain validity in further consideration. First, the fish had had a normal history in the lakes. Second, the proportion of bright morphs (12.5% in 1969, 13.9% in 1971) was similar to that occurring in nature, since the fish in the pools were very large. Additionally, the combination of sex and colors was not selected by me and thus did not reflect any predispostion of mine.

The distribution of mating types shows two major departures from that expected by chance (Table 8). First, pairs with both sexes bright morphs were 6.5 times more abundant than expected. Second, pairs with normal females mated to bright-morph males were only 0.29 the expected frequency.

For each breeding pair in 1969 I estimated the dimensions of the territory by observing the bottom area that was kept clear of other fish by attacking them, even though the boundaries were not precisely defined. I then calculated the areas and their mean values. In the normal x normal pairs, the mean value was about 1 m², thus close to that of normal colored fish breeding in Lakes Apoyo and Jiloá. In the pairs having normal males and bright-morph females, however, the mean value was 3.3 m², i.e., a 3-fold increase. (In 1969, there were no pairs having a bright-morph male paired with a normal female.) The territories were even larger in the pairs in which both fish were bright morphs; the mean value was 6.0 m², or about 6 times that of the normal x normal pairs.

These observations on assortative mating and size of territory are tantalizing but inconclusive. That the bright morphs appear to prefer mating with one another is confirmed by laboratory experiments (and normal colored fish prefer mates of their own color), and now by field studies in Lake Jiloá by J.R. Baylis and K.R. McKaye. Other experiments underway suggest, tentatively, that pairs having a gold male and a normal female are more apt to break up than any other combination. Paradoxically, McKaye is finding that when mixed-color pairs occur in Lake Jiloá they usually have a normal female mated with a bright-morph male. The resolution of this difference could lie in demographic factors. For example, there might be an excess of bright-morph males in the largest size class. Or a dispropor-

Table 8. Color of mates in a pool at Los Mercedes Airport. Data from samples in 1969 (18 pairs; 12.5% of population bright morphs) and 1971 (20 pairs; 13.9% bright morphs). The upper data are the frequencies of pairs, while the lower data in parentheses are the frequencies expected by chance for the given percentage of color types in the population.

| | COLOR | FEMALES | |
		Normal	Bright Morph
MALES	Normal	18	7
		(22.4)	(7)
	Bright	2	11
		(7)	(1.7)

tionate number of bright-morph males might breed because they are better able to compete for females.

Discussion

In some ways the Midas cichlid finds its counterpart in the African mouthbreeding fishes of the genus *Tilapia*. Fryer and Iles (*e.g.*, 1969) have compared several aspects of the biology of *Tilapia* with that of the small cichlid species that have so successfully radiated in the great lakes of Africa. Inspired by the writings of Margalef (*e.g.*, 1959) they characterized *Tilapia* as an "initial" or colonizer species in contrast to the highly specialized cichlids that live in mature communities. Since *Tilapia* has also proved so important as a cultivated source of food for humans, the comparison with the Midas cichlid seems doubly germane.

As *Tilapia*, the Midas cichlid is an omnivore that is able to subsist on a predominantly plant diet. Unlike *Tilapia*, it is not a good colonist. Because it appears to avoid entering rivers, it is not easily dispersed. This could account for its limited geographical distribution. The lakes provide a stable environment, which again differs from the situations in which *Tilapia* seems to succeed. But within the lakes the Midas cichlid is the most ubiquitous cichlid species. Additionally, it abounds both in eutrophic and in oligotrophic bodies of water, whereas *Tilapia* favors eutrophic situations. Part of the difference might be due to the relative newness of the geological situation in Nicaragua (Miller, 1966; Myers, 1966), or even to human intervention. The Midas cichlid may have been introduced into the various crater lakes in Nicaragua by the people living there.

One characteristic of *Tilapia* is that it tends not to speciate, but it forms hybrids relatively easily. The Midas cichlid has also hybridized, for instance in Lakes Masaya and Jiloá (Barlow and Munsey, 1976). While the populations in different lakes are recognizably different, the extent of this differentiation has not reached the species level, probably because of the recency of the situation.

Tilapia may live several years, grows rapidly, and under proper circumstances becomes sexually mature at a small size. The Midas cichlid, being a substrate breeder, is much more fecund than *Tilapia* at a given spawning. But it grows more slowly (comparisons in this laboratory) and does not reach sexual maturity until at least one year of age. As *Tilapia*, it is also long lived. Where *Cichlasoma* species have been used for farm culture they have shown stunting as a result of rapid over-population (Riedel, 1965); the same applies to *Tilapia*.

A potentially relevant line of comparison between African and Central American cichlids is the occurrence of

polychromatism in both. It has been reported in at least twenty species in six genera in Africa (Fryer, 1959, 1961; Fryer and Iles, 1972; Greenwood, 1956a, 1956b, 1957; Lowe-McConnell, 1956) and doubtless more instances will be found. The most common morphs look like goldfish, ranging from white through orange, and are variously immaculate, or peppered or blotched with black; these morphs are sometimes locally abundant. Blue morphs occur in both sexes of some of the species, and black morphs have also been mentioned.

Greenwood (1957) and Fryer (1959) were at a loss to explain polychromatism in the African cichlids. Both opined that the conspicuous color patterns might be linked genetically to some other trait that is adaptive. But the concomitant conspicuousness is thought not itself sufficiently handicapping to override the linked advantage.

There are some parallels between polychromatism in the African and Central American cichlids. There is no reason to believe, however, that the same selective forces must be operating in each instance. Furthermore, there are some noteworthy differences. In Africa the bright morphs are almost limited to females, whereas in Central America they occur about equally in both sexes. Many of the polychromatic African species are small, especially those from the clear waters of Lake Malawi. Apparently the presence of polychromatism is not confined to the larger adults, even in the small species. In contrast, in Central America polychromatism is limited almost entirely to the larger species and to the larger individuals within those species. Polychromatism in the African cichlids occurs in species that inhabit the rocky reefs in clear waters of the Great Lakes there as well as in cichlids living in murky lakes. In Nicaragua, polychromatism in the Midas cichlid, and in its close relative, *C. labiatum*, is associated with turbid waters. However, both of the very large species, *Petenia splendida*, in Belize, and *C. dovii*, in Costa Rica, inhabit clear waters, although bright morphs occur at a much lower frequency than noted for the Midas cichlid.

Given the wide occurrence, in many unrelated fishes, of conspicuous color morphs resembling the goldfish (see references in Webber, Barlow, and Brush, 1973), it is surprising that there has been so little attempt to explain the phenomenon. Breder (1959: 408) suggested that bright morphs might act as leaders, but cited only anecdotes. A writer of popular articles on fishing (Cannon, 1966: 184) claimed that gold morphs of the grouper *Mycteroperca rosacea* play a key role in keeping schooling prey from escaping. But Edmond S. Hobson (pers. comm.) refuted this hypothesis through lengthy underwater observations.

The only published careful exploration of polychromatism in fishes deals with the threespine stickleback *(Gasterosteus aculeatus)*. The breeding male in most populations of this widely distributed species had a red throat and abdomen. But in some populations in the Pacific Northwest of North America only 13% to 17% of the males have red throats; other males have variously silver, dark, or blotched throats. Red throated males are evidently more frequent in deeper water (Semler, 1971). Given a choice in the laboratory, females spawned 2.5 times as often with red throated as opposed to nonred males. Red marked males are thought to have a further advantage in that their color is presumed to help intimidate intruding sticklebacks who commonly steal eggs (Semler, *l.c.*).

Since red male sticklebacks are infrequent, there must be counterselective forces keeping their numbers down.

Semler *(l.c.)* suggested that differential predation by rainbow trout *(Salmo gairdneri)* works to the detriment of the red morph. Moodie (1972) confirmed that in another lake the cutthroat trout *(Salmo clarkii)* is an effective predator on a population of black sticklebacks, about 14% of which are red throated.

These studies indicate that in the absence of predation, red throated males are favored. But it would be a mistake to assume that the female's preference is the ultimate explanation of the male's redness. Rather, his red color indicates to the female that he is the most fit to defend her eggs. And his fitness may well derive from his superiority in aggressive behavior addressed to other males, as Semler has suggested but no one has shown. Such an interpretation would also be more in keeping with the relationship between aggression and gold coloration in the Midas cichlid.

Returning to the cichlids, a paramount question is how did the polychromatism originate? Many cichlid species, not to mention other fishes and birds, employ the colors yellow or orange through red in communication, particularly where aggression and reproduction are involved (Barlow, 1974). For example, reproductively active females of *Cichlasoma nigrofasciatum* and *C. spilurum* carry a gold patch low on their sides; when the mate threatens, the female presents her side to him, which seems to inhibit further aggression by the males. Females of the African cichlid *Pelmatochromis kribensis* have a red abdomen which they display to their males in a remarkably parallel fashion. In the cichlids of Central America gold through red is common in both sexes, particularly on the lower parts of the fish and in its eyes and it becomes more intense when breeding, as in the Midas cichlid. In fact, some species become entirely yellow with black markings when parental, *e.g.*, *Herotilapia multispinosa* (Baylis, 1974) and *C. salvini*. Leong (1969) demonstrated that in the African cichlid *Haplochromis burtoni* an orange patch on the side of a territorial male inhibits aggression in other males. Similarly, the gold morph of the Midas cichlid appears to inhibit aggression in rivals by virtue of its color (Barlow and Wallach, 1975). Since the normal morphs are adorned with gold or red in a way that suggests the markings function as signals, it is reasonable to assume that the all-gold morph is essentially a super-normal releaser, inhibiting attack, *i.e.*, releasing incompatible fear responses.

These bright colors come from pigments such as carotene and canthaxanthin. Since all of the Midas cichlids possess these pigments irrespective of whether they are bright morphs, all that is necessary to produce a xanthomorphic individual is to remove the black pigment, melanin. Such a mutation probably originated in old individuals whose reproductive value was low. From that point selection operated primarily on the timing of the expression of the mutation. Probably all Midas cichlids have the genes to become xanthomorphic, but most never live long enough for the "timer gene" to operate. But with the advent of populations of the Midas cichlids in either turbid or deep water, selection favored the earlier metamorphosis to the bright morphs.

What then, are the advantages associated with xanthomorphism? I have already touched upon the inconclusive data that suggest the gold morphs may be more resistant to disease. As shown in laboratory experiments, gold morphs regularly dominate normal morphs of about equal size (Barlow and Ballin, 1975). Put in competition for food, the gold morph grows faster than does the normal (Barlow,

1973). The gold morph has an advantage where direct aggressive contests are involved, but it is not because the gold morph is inherently more aggressive but because it inhibits attack in the other fish (Barlow and Wallach, 1975). It is also possible that for similar reasons the gold morphs have the upper hand in obtaining mates and breeding sites. But observations on breeding populations in nature, such as those currently being done by McKaye (*e.g.*, McKaye and Barlow, 1976), will have to provide the answer to this question.

At one time I reasoned that the occurrence of the gold morph should be an important factor in regulating population density. If a population were to reach the upper limit of the environment's carrying capacity there would be intense intraspecific competition for food and other resources. As a consequence most if not all the adults would have difficulty getting enough to eat to sustain life and probably would not obtain sufficient food to meet the additional metabolic demand incurred by reproduction; this would be crucial to females because of the large amounts of ovarian tissue they have to lay down. Such a population might not reproduce for one or more years, until the number of adults had dropped to a level permitting some of them to get enough food to breed. Yet since the fry and small juveniles do not compete with the adults for food, if any pair were to breed during periods of overpopulation their offspring could provide an unusually large proportion of the next adult breeding population, all else being equal.

This is where the ability of the gold morph to dominate in contests over food becomes significant. It should be particularly important for gold females, for reasons given in the preceding. (In time, the occurrence of xanthomorphism might become limited to females, as in the African cichlids. The situation in Africa is not altogether comparable, however, because the reproductive roles in those cichlids are more highly differentiated, the mouthbreeding females being responsible for all the parental care.) This hypothesis about population regulation predicts fluctuations in the abundance of gold morphs in relation to population density, a rise in gold morphs following shortly after a population peak, if such occurs. Unfortunately, I have been unable to obtain data confirming or refuting this hypothesis. The generally stable proportions of gold morphs in the various lakes through time either speaks against the hypothesis, or indicates a steady-state situation with the populations held near the carrying capacity of their environments. Any fluctuations that might be observed should, on this view, be relatively small. The slightly higher percentage of gold morphs, and of smaller sizes, in the Lake Masaya population that Baylis collected in 1972 could be an example in support of the hypothesis. Recent observations in Lake Jiloá, furthermore, indicate that gold morphs actually do breed more successfully when the population density is high (McKaye and Barlow, 1976).

The dominance of gold morphs depends on their ability to communicate in turbid or deep water. To be effective as a signal they should be highly visible. In shallow or murky water the colors orange through red are thought to be the best seen (Luria and Kinney, 1970; Lythgoe, 1968). Recall that in the turbid Great Lakes and in Lake Masaya the most frequently occurring bright morphs are orange through red (see also Barlow and Munsey, 1976). Following Lythgoe (*l.c.*), the yellow and white morphs should be *relatively* inconspicuous there. The relationship in Lake Jiloá, a

slightly turbid lake where green light must prevail, is not so easily discussed because of scanty data on the colors of the morphs, and the generally greater depths where they are found. But the same logic applies — the orange morphs should stand out, whereas the yellow and white ones should look grey and therefore inconspicuous. Normal morphs are, nonetheless, better camouflaged because they have disruptive bars and spots, are better countershaded, and are often suffused with yellow or green.

If the xanthomorphic fish have these advantages, why are not all the fish gold? In part it is because the advantage of being gold is relative to having normal morphs to compete with. For example, when gold morphs are held with morphs only of their own color in the laboratory, they grow no faster than do normal morphs held only with their own colors (Barlow, 1973). If the gold morphs were to become increasingly abundant, the advantage of being gold could well become outweighed by its disadvantages. In support of this are laboratory studies (Barlow, Bauer, and McKaye, in prep.) indicating that the attack-inhibiting effect of the gold morph decreases through experience with it.

One of the main disadvantages of being a gold morph is the loss of the ability to change color patterns and consequently a marked loss in flexibility of communication. The fish also loses its species-identifying pattern. Additionally, and perhaps more importantly, crypticity may be lost. There is, nonetheless, some compromise in this respect: When darker colors are present, they tend to be more on the back, while the belly tends to be lighter whatever the hue or markings. Thus even the most brilliant morphs have a degree of countershading.

One of the greatest needs is for information on the interaction between the Midas cichlid and its predators. If we accept the search-image hypothesis that if the conspicuous morph is infrequent enough the predator overlooks it (Clarke, 1962), then we must know both how relatively and absolutely infrequent the morph must be for this phenomenon to operate. It could account for the rather stable proportion of brightly colored morphs of around 7% to 10% in the adult population. On the other hand, it is possible that the predator operates on the oddity principle (Pielowsky, 1961; Mueller, 1968).

Using the search-image hypothesis, it is difficult to account for the virtual absence of small, brightly colored morphs in the Midas cichlid; their absence suggests total selection against them below a certain size, for the genetic potential is there. I have learned from the aquarist, Guy Jordan, that it is possible in the laboratory to select for Midas cichlids that metamorphose into the gold phase while still fry. Therefore, the species has the genetic capability of producing gold fry, leaving out the normal phase. The same argument applies to the absence of bright morphs in clear lakes such as Apoyo where the genetic potential for such morphs exists.

Size in relation to predator is an important factor. Calculations support the view that full grown Midas cichlids are too large to be eaten by their common visual predators. In support of this, recall that a number of sick, weak adults were caught by hand in Lake Jiloá. They were obviously vulnerable to predation, but the *C. dovii* there would have found them too large to devour. Size must also be considered in relation to water clarity. The clearer the water, the greater the distance over which the predator can detect its prey (see below). Thus one would predict that the smallest sizes at which gold morphs occur would be larger in clearer

water; I have insufficient data to test this hypothesis. The nature of the relationship would depend on the spectral properties of the light, according to depth and turbidity. Finally, comparative evidence should be considered. All the cichlid fishes in Central America that have gold morphs in nature are large when of breeding size. The smaller species, e.g., *C. nigrofasciatum* and *C. severum*, have produced gold morphs in aquaria. But these are apparently eliminated by predators in nature, or are limited to rare, very large adults.

An additional disadvantage is that bright colored morphs might attract predators to the offspring. This seems unlikely because the normal parents assume a contrast-rich pattern when breeding, but the hypothesis merits testing.

Turbid waters are evidently permissive of the gold morphs in the Midas cichlid, rather than causative. In waters of limited visibility, the predators' visual detection distance may be so small that the coloration of the prey is not a factor in attracting it to the prey. Once close enough to make an effective strike, the deciding factor could be the quickness of the prey. And the larger the prey the greater is its absolute speed. An adult Midas cichlid might be able to move out of the predator's field so quickly that color is not important. But the smaller the prey the slower its speed and consequently the greater the relative distance it would have to swim to exit from the predator's sphere of detection. In that interval the predator could respond differentially to the brightly colored morphs.

It is important, too, to recall that most predators will favor the smaller Midas cichlids simply because they can handle them better. In the case of really large predators that can easily devour adults, such as the sawfish and shark in Lake Nicaragua, vision may not be important and color of prey therefore may be of little moment. Elasmobranchs are often nocturnal feeders and are known to detect the odor or electrical field of their prey.

The fact that the Midas cichlid transforms into conspicuous morphs at a relatively advanced size raises some interesting questions about assortative mating. As mentioned, both laboratory and field studies indicate that this species tends to mate assortatively in relation to its color. It is not yet possible to decide whether the choice is based on an awareness of one's own color, or a phenomenon much like that of imprinting deriving from the coloration of the fish's parents or siblings (*e.g.,* Sjolander and Ferno, 1973). Many of the normal adults could have had gold parents. With whom, then, would they mate? With fish of their own color? Or of their parents' color? If such a fish mates according to its current coloration, that would produce dissortative mixing of the genes. Such a phenomenon could keep the genes for the gold morphs at a relatively low frequency so long as metamorphosis occurs late in life. If breeding occurs prior to the time that gold morphs are abundant, then dissortative mating should prevail. But if breeding is done only by the very large fish, when the probability of being gold is great, then assortative mating would be more effective. On the other hand, it is possible that the size class of the breeding males presents an excess of available gold males relative to the size of breeding gold females. Then dissortative mating would again be promoted because some gold males would have to mate with normal females. This also presupposes that gold males are more effective as breeders, whether by virtue of being able to get more food to be competent to breed, or by competing for breeding sites. The laboratory results suggest that both could operate.

There are of course economic considerations here as

well. The Midas cichlid is an obvious candidate for aquaculture in Nicaragua. There would be no worry about their escaping into the local waters and disrupting the endemic fauna, as would be the case with exotic species such as the peacock cichlid *Cichla ocellaris* (Zaret and Paine, 1973) or *Tilapia*. The Midas cichlid is a desirable food fish because of its fine taste and firm flesh. It would be easy to cultivate because of its high fecundity, but we need to know more about its rate of growth. Clearly it is adapted to local conditions. Importantly, it is omnivorous and much of its diet consists of plant matter, particularly that in *Aufwuchs*. There is consequently a short food chain between the primary producers, algae, and the consumer, here the Midas cichlid. This results in high trophic efficiency.

The locally preferred fishes for eating, although fewer of them are available for food, are *C. managuense* and *C. dovii*. They are larger species having more accessible meat and are hence easier to eat. But both species are predators. Thus, there is a problem in feeding them. Each is the culmination of a long and therefore relatively inefficient food chain. Additionally, individuals in both species are widely spaced in nature and, predictably, highly and damagingly aggressive when confined; this applies especially to *C. dovii*.

The cultivation of Midas cichlids in managed pools should be relatively straightforward. They would need quality water, preferably from a flowing well. There should be rocks for the growth of *Aufwuchs* and for breeding. Water at a depth of about 2-4 m would probably provide sufficient thermal stability while being shallow enough for strong light to reach the bottom for an adequate growth of algae. Ideally there would be a drain at one end of the pool to lower the water rapidly for harvesting, transferring, or treating the stocks.

The gold morphs might prove to be the best type for cultivation so long as no predators were allowed into the ponds. First, they may be less susceptible to disease. Second, they would be easier to monitor. Finally, their social behavior might be more tractable, since the color gold appears to inhibit aggression.

When discussing cultivation it is also wise to bear in mind the importance of having available a variety of populations from different lakes. There are, doubtless, useful genetic differences between them. Some may prove more resistant to one disease, and another population more resistant to another. Some populations, such as in Lake Apoyo, reach a larger size than do those from Lakes Masaya or Jiloá. The Masaya and Jiloá fish could be smaller because of the presence among them of genes from the slightly smaller species, *C. labiatum* (Barlow and Munsey, 1976); or the Midas cichlids in Lake Apoyo could be larger as a consequence of living in a body of water free of competitors.

Research into the consequences of hybridization might also lead to promising developments, particularly if unisexual offspring could be produced. The Midas cichlid can be induced to hybridize with *C. labiatum* and other related cichlids if it has no choice (J. R. Baylis, unpublished data).

It should also be possible to improve the yield of Midas cichlids in natural waters. As mentioned, it is ubiquitous in the lakes but its numbers are low where there is no cover, particularly if rocks are absent. It should be possible at modest expense to provide cover where open gravel, sand, or mud bottom prevails. Optimally, boulders about 1 m across could be dumped at selected points. These would provide a surface for *Aufwuchs* and refuge and nest sites. The boulders should be smooth because gill nets are then

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not apt to snag on them. Gill nets are probably the most effective means of capturing the Midas cichlid, but they are almost impossible to use around jagged lava boulders. Furthermore, the use of gill nets makes it possible to control the size of the fish caught and therefore to manage the fishery better. These man-made reefs should be placed at depths of 3-8 m and indicated by buoys or shore markers to guide the fishermen.

The Midas cichlid has enormous potential as a source of protein for the people of Nicaragua. With proper management and cultivation it might even be possible to export this fish. A better understanding of the biological significance of the gold morph could facilitate such a fishery.

SUMMARY

Cichlasoma citrinellum (Günther), the Midas cichlid, is the most important food fish in the Great Lakes Basin of Nicaragua. It occurs in the majority of the lakes, where it is the most ubiquitous cichlid fish, but it is uncommon in the rivers. The fry are carnivorous while the juveniles and adults are omnivorous, eating mostly *Aufwuchs*, snails, and fish. The Midas cichlids suffer from a number of diseases in nature and in the laboratory, including lymphocystis and nocardiosis. Potential predators vary from sharks and sawfish in Lake Nicaragua, to just one cichlid relative in one crater lake; in Lake Managua and the crater lakes the large adult Midas cichlids face little danger from predators.

Most Midas cichlids are of the normal cryptic coloration, but about 7 to 10% are brilliantly colored. These bright morphs lack the species-typical markings and have lost the ability to change their patterns; they range in hues smoothly from white through yellow, orange and red, though yellow through orange prevail. All start life normal in color, but at highly variable ages they lose most or all of their melanin, revealing the bright hues that most of them possess. The degree of development of this xanthomor-phism varies among the lakes and appears to be positively correlated with turbidity of the water.

Some populations may breed year-round but the general pattern is apparently one of reproducing during the rainy season. The sexes are almost isomorphic, although males are generally larger than females of the same age; there are also differences in the genital papillae; males, and to a lesser degree females, develop a nuchal hump and swollen throat at the start of breeding. Pairs set up small territories centered around a rock cave where they spawn and defend the eggs, then larvae, and finally the swimming fry. The fry supplement their feeding by eating from the dermal mucus on their parents. Laboratory experiments and field studies from Lake Jiloá indicate that the fish mate assortatively according to color; fish of a pair are more apt to be of the same color than would be predicted by chance. Further, the "gold" morphs dominate those of normal color and grow faster when the two types are reared together. Some implications of these findings are discussed and comparisons are made with polychromatism in African cichlids.

RESUMEN

Cichlasoma citrinellum (Günther), el cíclido Midas, es el pez de tipo alimenticio mas importante de la cuenca de los lagos de Nicaragua. Se encuentra en la mayoría de los lagos, donde es el cíclido mas ubicuo, pero no es común en los ríos. Las craías son carnívoras, pero los jóvenes y los adultos son omnívoros, comiendo materia vegetal (*Aufwuchs*), caracoles y peces. El cíclido Midas padece de varias enfermedades en su medio y en el laboratorio, incluyendo linfocistis y nocardiosis. Sus depredadores potenciales varían desde el tiburón y el pez sierra en el Lago de Nicaragua, hasta sólo un cíclido emparentado, en una de las lagunas volcánicas. En el Lago de Managua, y en las lagunas volcánicas, el cíclido Midas adulto tiene poco peligro de depredación.

La mayoría de los cíclidos Midas son del color críptico normal, pero existe un 7 a 10% de individuos de color brillante. Estos morfos carecen de los diseños típicos de la especie, y han perdido la habilidad de variar sus diseños; el color varía desde blanco a amarillo, anaranjado y rojo, aunque los mas comunes son los amarillos y anaranjados. Todos nacen con la coloración normal, pero a edades muy variables pierden mucha o toda de su melanina, revelando los brillantes tonos que todos poseen. El grado de desarrollo de este xantomorfismo varía entre los lagos, pero parece relacionado positivamente con la turbidez del agua.

Algunas poblaciones se reproducen durante todo el año, pero parece que generalmente se reproducen durante la época lluviosa. Los sexos son casi isomórficos, aunque los machos son generalmente mas grandes que las hembras de la misma edad; también existen diferencias en la papila genital; los machos, y en menor grado las hembras, desarrollan una joroba en la nuca y un cuello hinchado al comienzo de la reproducción. Las parejas toman pequeños territorios centrados en huecos o cuevas de piedra, donde desovan y defienden los huevos, larvas y crías. Las crías suplementan su alimentación comiendo el mucus dérmico de sus padres. Experimentos en el laboratorio y estudios en la Laguna de Jiloá indican que estos peces se aparean de acuerdo con su color; cada pareja tiende a ser del mismo color con mas frecuencia que la que sería al azar. Más aún, los morfos dorados dominan a los de color normal y crecen más rapidamente cuando ambos se crían juntos. Se discuten las implicaciones de estos hallazgos y se comparan con casos de policromatismo en cíclidos africanos.

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