Field observations of the ecology and habits of mangrove rivulus (*Rivulus marmoratus*) in Belize and Florida (Teleostei: Cyprinodontiformes: Rivulidae)

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This report provides a synopsis of field studies of *Rivulus marmoratus* from two population surveys of mangrove islands adjacent to the Belize barrier reef and observations made over fifteen years at several sites in South Florida. Florida populations consist nearly exclusively of hermaphrodites (> 99%), while the Belize populations contained a significant proportion (10-25%) of males. Our combined observations demonstrate that this species is not "rare" as previously thought, but elusive and highly adapted to microhabitats within mangrove forests. Standard ichthyological collecting techniques are ineffective in this habitat and have previously failed to reveal the strength of the association of *R. marmoratus* with the mangral ecosystem.

Introduction

The mangrove rivulus, *Rivulus marmoratus*, has an extensive distribution throughout the Caribbean and is the only member of its speciose and diverse neotropical genus to reach the Florida peninsula. Until recently, the majority of publications concerning *R. marmoratus* have reported results of laboratory studies involving its reproduction by "selfing" (synchronous internal self-fertilization) and consequent production of homozygous clonal offspring (Harrington, 1961; Kallman & Harrington, 1964; Harrington & Kallman, 1968) and potential and actual applications for toxicological research (Davis, 1986, 1988). Numerous authors (Snelson, 1978) have repeated the consensus notion that the species is rare in nature, and the paucity of museum specimens would appear to support this idea. However, there are reasons to suggest that standard fish collecting techniques are simply ineffective in capture of this species. *Rivulus marmoratus* has become semi-terrestrial, a specialization for survival in the temporal pools and burrows in mangrove habitats. Structural specializations include a unique epidermal capillary bed, (Grizzle & Thiyagarajah, 1987). These epidermal capillaries facilitate aerial respiration, used during terrestrial locomotion and escape from anoxia/hydrogen sulfide common in their habitat. This feature apparently also assists escape from nets and evasion from ichthyocides as well. Epidermal

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chloride cells (King et al., 1989) apparently assist *R. marmoratus* to survive the wide ranges of salinity that typify mangral ecosystems (Macnae, 1968).

The few field observations have been intriguing but inconclusive. Ogden et al. (1976) reported *R. marmoratus* as an item in the diet of wood storks. Huehner et al. (1985) captured 51 *R. marmoratus* (a large number for this species) under logs and leaf litter and described the habit of "flipping" as a means of terrestrial locomotion. C. C. Koenig (pers. comm.) took more than 150 specimens on a second visit to a site during a field trip to Collier Co., southwest Florida. Only a few specimens had been captured on the initial visit earlier the same day but the search had churned the detrital sediments releasing inevitable hydrogen sulfide into the shallow stagnant pools. Hydrogen sulfide will cause *R. marmoratus* to emerge from water (Abel, 1981; Abel et al., 1987) or from substrate hiding places. Taylor (1988, 1989, in press) describes capture of *R. marmoratus* from burrows of the land crab, *Cardisoma guanhumi*, in infrequently flooded mangrove habitats along the Indian River Lagoon on the central eastern coast of Florida. These burrows have yielded many fish captures. Although crab burrow associations have been investigated by arthropod specialists (Bright & Hogue, 1972), they have seldom been examined by fish collectors. These findings suggested that *R. marmoratus* numbers were probably more abundant than previously assumed.

Therefore, following a rumored sighting of *R. marmoratus* on Twin Cays, Belize, we undertook...
two preliminary surveys to test our ideas and develop new collection methods. Twin Cays are two small adjacent mangrove islands, 5 km from Carrie Bow Cay (Fig. 1), a field station of the Smithsonian Institution Caribbean Coral Reef Ecosystems Project (CCRE). This report summarizes and compares our collective observations and experiences investigating the biology and ecology of this unique fish.

We are aware that Seegers (1984) has synonymized *Rivulus marmoratus* with the earlier described *R. ocellatus* (from Brazil). This proposed taxonomic change has been formally challenged on substantive grounds by M. Smith & K. Lazara (pers. comm.) who have petitioned the International Commission on Zoological Nomenclature to designate *R. marmoratus* as the valid name for this species. In their compilation of common names, Robins et al. (1980) list *R. marmoratus* as simply “rivulus”. However, through most of its range this common name is ambiguous, for there are numerous other *Rivulus* species with equal claim to it. Therefore, we refer to *R. marmoratus* as the “mangrove rivulus” in recognition of its characteristic association with Western Atlantic mangrove ecosystems.

**Method and materials**

The surveys of Twin Cays and adjacent mangrove islands were conducted to determine whether the population of *R. marmoratus* was sufficiently large to warrant long-term study. During 29 July to 13 August, 1988 and 4 to 19 July, 1989 various mangrove “micro-habitats” were sampled using a variety of techniques. A substantial population of hairy-legged or mangrove land crab, *Ucides cordatus* inhabits the mangroal on Twin Cays. Frequently, standing water occurred at the mouth of the crab burrow. Use of a miniature fish hook (<12 or <15 mm) baited with a small worm, (with its tail free), would typically elicit a response from
any fish in the burrow within two minutes or less, as described by Taylor (1988). This technique was particularly useful in scouting and evaluating new areas for potential trapping. The readiness of *R. marmoratus* to strike and attempt prey capture is one behavioral clue revealing the presence of the fish in crab burrows. Careful stalking is essential for the success of the technique. Our observations in Belize and Florida suggest that *R. marmoratus* is very sensitive to any ground tremor or movement which is efficiently transmitted in the water-saturated peat substrate of the mangal. Surveying for *R. marmoratus* with hook and line represents a miniaturization of baitfishing yet to be discovered by elite sports fishermen, but it does not provide adequate sample sizes to fulfill the needs of biological research and population assessment.

Small funnel-mouth traps are the most efficient method to capture sufficient numbers. Initially, we constructed traps as conceived and used by Taylor (1989), using plastic drinking glasses fitted with plastic funnel mouths held in place by hooks and rubberbands. Holes were drilled in the base and sides to allow water passage. These traps were successful, especially for capture of fish in land crab burrows. The design was expanded to utilize a wide variety of containers, including plastic pipe, various plastic bottles (from the new-age sediment deposits), bamboo sections or virtually any cylindrical object which could be fitted with funnel mouths constructed of plastic insect screening and silicon cement. Traps were set in mouths of crab burrows as well as any other pools of standing water, choice of trap type governed by appropriateness to size and shape of the microhabitat. Traps frequently captured several fish at a time, once the investigator has developed proficiency.

A reference transect line (N-S, 160 m) was estab-
Table 1. Captures of *Rivulus marmoratus* at the Papa Gabriel site, Twin Cays, Belize summarized by Julian day (JD) and number of traps (in brackets), indicating the ratio of hermaphrodites/males (x/y) caught in traps or by hook and line (H & L), and total capture each day for 1988 and 1989.

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<th>Total</th>
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Total "trap nights": 280
Total trap capture: 98
Capture rate: 0.35 fish/trap set

Total "trap nights": 1208
Total trap capture: 119
Capture rate: 0.097 fish/trap set

lished on Twin Cays at the "Papa Gabriel's" site (Fig. 1), the most productive capture site. This transect crossed an area which included both disturbed and relatively undisturbed vegetation, and had many crab burrows and several small pools. This site was an area where the dominant landward plant species, black mangrove (*Avicennia germinalis*), had been cut down in previous years. The gentle slope from the inner island to the shore fringe of red mangroves (*Rhizophora mangle*) supported regrowth of black mangrove saplings and a thick cover of saltwort (*Batis* sp.). The reference transect began in the uncut border at the north end of this clearing and extended into the uncut border at the south side for a distance of 160 meters (Fig. 3).

During the 1988 visit, the area had apparently not been disturbed for 2-3 years judging from the thick saltwort cover. Before our return in 1989, many of the new-growth tree saplings had been cut and much of the saltwort had been burned and cleared away as part of construction of a dwelling on the island. In 1989 we retrapped across this redisturbed area to compare capture rates with the previous year. At the Papa Gabriel transect, traps remained in place and were check-
ed on a 24-hour basis; new areas were visited and trap-sampled for 2- to 4-hour periods. Nocturnal visits were made to the transect site to conduct observations and assess fish and land crab activity. Newly captured fish were rinsed free of the inevitable fine detritus then placed in "zip-loc" freezer bags or "whirl-pac" polyvinyl sterile sample bags with minimal site water (< 4 ml). Bagged fish were transported to the laboratory in shaded buckets for examination, photography and external sex classification. Routine records were made of air and water temperature and salinity (measured by refractive index).

In addition to daily examination of traps set along the transect, surveys were conducted to locate other sites on Twin Cays and nearby mangrove islands including Tobacco Range and Blue Ground Range.

**Results**

The overall number of *R. marmoratus* captured exceeded 150 in 1988 and 170 in 1989. Data from the Papa Gabriel site are summarized in Table 1. Trapping effort was much greater in 1989 than 1988, while the catch per trap unit for the second survey was much lower than the first. Several
environmental factors differed between 1988 and 1989 which may have contributed to the different catch rates. The 1989 survey was conducted during an unusual drought event, which caused as much as +10°C higher surface pool-water temperatures and higher salinities in the crab burrows (ranging 35-55 ppt [parts per thousand] in 1989 vs 21-32 ppt in 1988) and especially high (40-65 ppt) in shallow surface pools. As noted, the vegetative ground cover over the center of the sampling site had been removed, and the increased insolation caused higher temperatures and evaporation than the adjacent areas with uncut vegetation. The effect was particularly evident with one shallow pool (20 cm deep and 4-5 m long) which had yielded 30-40 fish in 1988, but had dried and produced no captures in 1989. (It should be noted that at the close of the 1988 survey, 80% of the captured fish had been released in this pool). Also, in 1988, full moon occurred as we began our sampling effort, so in addition to the frequent (normal) rainfall events, we also were trapping during flooding tides.

During the 1988 visit, virtually no fish were captured inside the red mangrove intertidal zone, whereas in 1989 several tidally flushed pools and burrows in this area yielded significant numbers of fish, and these fish included larger specimens; temperatures in this area were 25-27°C and salinities were 28-34 ppt. During the exploratory surveys in 1989 we noticed on several occasions fish flipping into water of a burrow or grotto adjacent to a log, in response to approach of the observer. After a short (<1 min.) quiet period and ignoring the bait worm, the fish would flip out of the water onto an adjacent surface, where it would remain if not disturbed. This is interpreted as a response to the prevailing stagnant conditions of these microhabitats during the 1989 survey.

Nocturnal observations were made both years. We were startled to find the fish very active in the

Fig. 5. Pipette points at mouth of mangrove landcrab burrow from which 1 male and 2 hermaphrodite fish had been captured; crab is emerging to irrigate its gill chamber.
mouths of flooded burrows in 1988, around the legs of *U. cordatus* as these nocturnally active crabs moved in and out of their burrows. These active fish were observed picking/feeding upon small objects floating by in the tidal current. (Attempts to feed nocturnally in the laboratory have typically produced no feeding response). In contrast, during 1989 crab burrows often were stagnant with signs (odor and milkiness) of sulfide bacteria. The *R. marmoratus* inhabitants sometimes had a white coating which would slough off after capture. We suspect that this milky coating represents a mucous/epidermal reaction to stagnant water stress or possibly bacterial growth on the mucous of the fish. We repeatedly observed fish emersed and adhering to the edge of the burrow. Taylor first noted, soon after developing the burrow trapping technique, that traps which became completely submerged often contained dead fish, implying drowning. This "drowning" response may also reflect hydrogen sulfide concentrations fatal to fish unable to emerge from stagnant habitats. During emersion, fish are quiescent, making no gill or other body movements. Emersion observed in the laboratory had previously been assumed to be an option, but our field observations suggest that certain conditions in nature make it obligatory. On the final day of our 1989 survey, after traps had been removed, lunar flood tide inundated our transect area. A final handline survey demonstrated *R. marmoratus* actively attacking worm bait, as we had routinely observed during the 1988 surveys. Tidal flushing of the stagnant waters from the crab holes perhaps induced the fish to readiness to feed.

The food habits of *R. marmoratus* reported by Harrington and Rivas (1958) and Huehner et al. (1985) both listing insects and the latter author additionally finding fragments of annelid worms and fish scales. Our observations and those of Huehner et al. (1985) indicate that *R. marmoratus* readily leaves the water to pursue prey (via leaping or flipping), but always returning to ingest captured prey in water. It is logical, therefore, that feeding may only occur while dissolved oxygen is adequate in the burrow water. Success with hook and line undoubtedly is also correlated with these water conditions.

**Discussion**

Each of the present authors had developed individual notions of the ecology of *R. marmoratus* based upon his previous collecting experience and the published literature. The synergy of the Belize Cays survey revised our concept of the adaptive nature of *R. marmoratus* specializations to the rigorous demands of survival in the mangral. Mangrals typically are in a dynamic balance with sea level and tidal cycles. The mangral accretes through accumulation of detritus and trapped sediment and functions as a natural composting area (Macnae, 1968; Ruetzler, 1967; Lugo & Snedaker, 1974). The different localities and habitats where we have captured *R. marmoratus* demonstrate definable variations within the broad theme of mangrove ecology. Following is a brief comparison of Florida sampling sites:

Since the initial discovery and capture of *R. marmoratus* in the East Central region of Florida (Harrington & Rivas, 1958), Taylor (1989, in press) has captured nearly 500 specimens along the Indian River Lagoon (Indian River & Brevard Co.). Taylor’s captures have been exclusively from the burrows of the great land crab, *Cardisoma guanhumi*, which occur in or adjacent to estuarine salt marshes. As many as 26 specimens have been captured in a single burrow. Depths of the burrows correspond to the water table depth at each site but *R. marmoratus* were typically captured in shallow burrows (<1 m). Provost (1977) described the drastic alteration of vegetation, including loss of many black mangrove trees after construction of "mosquito control" impoundments in this region. Land crab burrows now occur only in unimpounded marshes, primarily at 30 cm elevation above mean sea level. These areas are presently vegetated predominately by the halophytic plants glasswort (*Salicornia* spp.) and saltwort (*Batis* sp.). At this elevation only rare tidal flooding of crab burrows occurs (Taylor, 1988). Apparently, *R. marmoratus* may be restricted to the burrows most of the year. Movement between burrows may occur during minimal short-term rain flooding which provides a damp substrate for terrestrial flipping as described by Huehner et al., 1985).

In Southwest Florida the Everglades and Rookery Bay (Collier Co.) contain the least disturbed
mangroals in North America. Annual and monthly tidal regimes are quite different between the east and west coasts of Florida (Provost, 1973). Cardi­somia guanhumi burrows are uncommon or non­existent in these areas, although smaller fossorial crabs (Uca spp.) are present and their much smaller burrows may be found in most localities where R. marmoratus abound. Capture sites are generally isolated, often temporary pools inland of the berm. Ritchie and Davis (1986) described the appearance of newly hatched R. marmoratus after rain inundation of one of these pools, following a November to May drought. The substrate of the mangral is a thick layer of mangrove leaves and pneumatophores often over a deeper layer of detrital clay. Temporary pools frequently form during summer thunderstorms, or as a result of lunar or storm tides. Some of these pools have >1 m deep, detrital-filled holes which hold water or are moist during the driest periods. More than 400 R. marmoratus have been captured in this area since 1975. During rainy periods, puddles in adjacent abandoned roads made of shell have contained these fish as well. Since these same puddles are dry during winter months, we speculate that the fish invaded from adjacent red mangrove areas, probably by flipping.

We have visited the locality in south Dade Co. described by Thomerson (1966) which probably represents an extreme example of disturbed but surviving mangral. In addition to having been ditched for "mosquito control", it subsequently has received incredible amounts of trash and refuse. Cardi­somia guanhumi burrows are frequent, but fish were captured without use of traps from coconut hulls, cans, under debris or in the ditches. Other specimens of R. marmoratus have been occasionally captured at several sites along the shore of Biscayne Bay and a specimen was suctioned from a land crab burrow in Broward Co. The southeast and southwest regions of Florida have yielded the only (ca 6) wild-captured male R. marmoratus from North America.

In the Florida Keys R. marmoratus populations have been sampled at four sites. However, there is every reason to believe that the species is abundant throughout mangroves of the Everglades and the Keys. Huehner et al. (1985) describe habitat and the capture of 51 specimens from under logs and leaf litter on Mangrove Key, an undisturbed island adjacent to Big Pine Key. One of us visited this site during a lunar flooding tide (May 1986), and found specimens in coconut hulls and semi-submerged beer cans. This site most resembles areas surveyed among Belize Cays. Close to Mangrove Key, on No-Name Key, more than 80 specimens were captured (two trap sets of 22 traps; May 1989) during a period of drought. Rivulus marmoratus specimens were inhabiting a roadside ditch under red mangroves in a stagnant pool with specimens of Gambusia, Pecilia latipinna, Fundulus confluentus and a few other uncollected species. Yet, R. marmoratus specimens were in robust condition and several released eggs in the observation bags. The substrate under the detritus was oolitic limestone, with many solution pits. The terminus of this man-made ditch was 10 m or less from the shoreline of open bay-water. Rivulus marmoratus was not captured in the better flushed sites under mangroves along the shore.

Hurricanes as well as man drastically alter mangroals. One recent example, hurricane "Donna" (1960), defoliated and killed great numbers of the mangroves in the middle Florida Keys. Some of these localities, where housing development has been restricted, now have regrown a lush dense canopy of mangroves. On Lower Matecumbe Key, the regrown 5-8 m canopy height has created a deeply shaded leaf-litter humous substrate, with few burrows. Only the algal line on ancient mangrove logs reveals the potential water level in isolated pools filled during lunar tides. In May, 1989, we set traps before lunar flood tide and subsequently captured 25 R. marmoratus during tidal flooding. This tide occurred during a prolonged severe drought and represented the first flooding of the site (since the previous lunar tide). These fish were especially emaciated, three so weak that they died minutes after transfer to the observation bag. Surviving fish subsequently rapidly recovered as they were fed mosquito larvae. These specimens certainly represent fish emerging from prolonged aestivation in leaf litter or burrows in the substrate. In laboratory observations, fish left in moist artificial substrates for two months were more robust than these emer­gents (Davis, unpublished).

The strong association of R. marmoratus with both the mangrove forest and mangral decapod bur-
rows is clear from the results of trapping. It is tempting to suggest that the species is a prime example of a tropical Atlantic mangrove-dependent form (sensu Milward, 1982). Although this may be correct, it is worth noting that one or more of the apparently unique characteristics of *R. marmoratus* have been observed in other species of the genus. Seghers (1978) described aestivation and emersion of *R. hartii* in mountain streams during drought on Trinidad. Fromm (1986) documents aestivation, terrestrial locomotion and/or terrestrial egg stranding for *R. chacunique*, *R. hartii*, *R. isthmensis*, *R. limoncochae*, *R. uroflammeus* and *R. stagnatilis*. Several other species are well known to South American fish specialists as colonizers of marginal or ephemeral habitats (e.g. Vaz-Ferreira & Serra, 1972). We have collected *R. tenuis* both in fresh and brackish water (10 ppt) within 5-10 m of the coast in Belize and Guatemala; some specimens captured from *C. guianum* burrows. Thus, *R. marmoratus* has successfully invaded the rigorous mangal environment with a combination of specializations established among other species within the genus and additionally, physiological tolerance to high and varying salinities.

We have no data which address the adaptive significance of selfing hermaphroditism in *R. marmoratus*. However, selfing may be a worthwhile specialization in an oviparous species that does not store sperm, and which has dispersed widely through the challenges of the mangal habitat. The species has an enormous geographic range (greater than that of any rivuline with the possible exception of the Amazonian *R. urophthalmus*). Caribbean records include Bahamas, Caymans, Puerto Rico (Erdman, 1967) and St. Maarten (de Beaufort, 1940: record listed as *R. cylindraceus*; specimens not examined) and Curacao. *R. marmoratus* has successfully colonized the islands of the Caribbean, and the South and Central American coastline more widely than any other killifish species. Perhaps then, we are examining a direct relationship between selfing and ability to successfully disperse and colonize. Until further studies are completed to elucidate the population genetics of this species, we can only speculate.

The high proportion (10-25 %) of "phenotypic males" (Fig. 2) (it is not yet possible to distinguish primary and secondary males [sensu Harrington, 1971] in the field) captured in both surveys of the Belize Cay is noteworthy. In 1989, newly captured males courted and appeared to spawn with selected hermaphrodites in aquaria. Other newly captured hermaphrodites readily released fertile eggs and subsequently have continued to spawn in the laboratory without males. Generally, the Belize Cays males have died off sooner than hermaphrodites during subsequent captivity. Males are very rare in Florida populations. Florida hermaphrodites readily produce male progeny in the laboratory with or without specific environmental manipulation (Davis, unpublished). Kristensen (1970) reported capture of males from the Netherlands Antilles in 1960 collections but did not obtain them in 1961-1965. To our knowledge they have not been taken there since, although collections have been neither regular nor well documented. Kristensen noted that the males were "very large ones". Males captured on the Belize Cays represented a full range of sizes, excepting the largest hermaphrodites (> 45 mm). Whether Kristensen's observations were of older fish, or as he seems to imply, secondary males transformed from hermaphrodites (sensu Harrington, 1971) is not clear. We cannot now explain the apparently persistent presence of a large number of males on the Belize Cays and/or their virtual absence from Florida populations. In the laboratory Harrington (1967, 1968, 1971, 1975), produced primary males by low-temperature treatment of later stage embryos, and secondary males by prolonged exposure of adult hermaphrodites to shortened photoperiods. Although this suggests that some environmental factor is correlated with incubation temperature or photoperiod, how this relates to a higher production of males in the Belize Cays than in Florida remains a fascinating unanswered question.

**Conclusions**

*Rivulus marmoratus* demonstrates with concordant physiological and behavioral specializations a strong association with mangrove ecosystems of the Western Atlantic. The presumed rarity of the species has resulted from the inadequacy of standard ichthyological collecting methods. Through use of trapping techniques, especially in land crab burrows and temporal pools, we have
found *R. marmoratus* to be relatively common, albeit elusive in microhabitats where low dissolved oxygen and increased hydrogen sulfide concentrations restrict survival of other fish species. Disturbances which alter the salinity and temperature, such as vegetation removal, may reduce the presence of the fish. However, regrowth of vegetation apparently results in recolonization by the species. Ecological events such as drought apparently are met with utilization of waters of crab burrows or aestivation in moist substrate utilizing an epidermal capillary system for aerial respiration. Return of water through rains or tidal flooding results in emergence of the fish and dispersal to temporal puddles and pools for exploitation of new food resources.

Male fish are extremely rare in Florida populations but greater in Belize populations, although sexual mating has never been demonstrated.

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