The Status of the San Marcos Gambusia, *Gambusia georgei*

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INTRODUCTION

The San Marcos gambusia, Gambusia georgei, was first recognized in 1968 in the unusually diverse San Marcos River system of central Texas. Of the three species of Gambusia native to the San Marcos River, G. georgei has always appeared to be much less abundant than either the endemic largespring gambusia, G. geiseri, or the widespread mosquitofish, G. affinis, a circumstance clearly noted in its original description (Hubbs and Peden 1969).

Because the San Marcos Springs emerge within the San Marcos city limits, the stream environment has been intimately associated with changes in the city itself. It was feared, shortly after the San Marcos gambusia had been described, that the increasing intensity of flooding of the San Marcos River might negatively impact G. georgei populations in this aquatic environment. Following a major flood in 1970, efforts were conducted to ascertain the abundance of the San Marcos gambusia, and this study located only a single specimen (Whiteside, pers. comm.).

Presently, G. georgei has been proposed for listing as an endangered species by the United States Department of the Interior (Federal Register Vol. 43(136): 30316-30319). Additionally, the Texas Parks and Wildlife Department has restricted collection of this species (Texas Parks and Wildlife Code 127.30.09.001-.006).

The purpose of this report is to provide a compendium of information on the known status of the San Marcos gambusia, including habitats and factors influencing the abundance and survival of this species in the San Marcos River environment.

Physiography, Hydrology and History of the San Marcos River Area

Physiography

The Balcones Fault Zone is the principal geological feature characterizing the San Marcos area. This fault zone separates the Edwards Plateau vegetation region, to the west, from the Blackland Prairie and Coastal Plain regions, to the east (Fig. 1). These divisions correspond to the Balconian and Texan biotic provinces, respectively, of Blair (1953). The headwaters of the San Marcos River issue from a series of five large fissures and numerous smaller solution openings along the San Marcos Springs fault (Puente, 1976). At one time, early Spanish explorers estimated that a series of 200 springs made up the main spring (Brune 1975). This spring-fed stream flows primarily southeastward for approximately 120 km toward the Guadalupe River which it joins in the vicinity of Gonzales, Texas. The San Marcos River has the appearance of a spring run from its source to the junction with the Blanco River; the reach between the Blanco and the Guadalupe has fewer attributes of a spring run. A generalized physical diagram of the San Marcos area is shown in Figure 2. The highly dissected nature of the Edwards Plateau, as well as a sharp rise in altitude, is noticeable to the northwest and the rolling hills of the Blackland Prairie, which dip slightly to the southeast, are evident on the downthrusted portion of the fault zone to the southeast.

Hydrology

The Balcones Fault Zone extends as a series of fracture lines from the vicinity of Bracketville in Kinney County east to San Antonio (Bexar County) and then northeast to near Kyle (Hays County). A major underground aquifer (Edwards Aquifer) underlies this fault zone and is the source of water for the San Marcos Spring (Figure 3). Runoff from the southern and eastern portions of the Edwards Plateau recharge this aquifer through the porous Cretaceaus-aged limestones found in this region. Water from this recharge flows along the fault zone from west to east and then northeast. Numerous other major springs are located along this fault system, including the two largest springs in Texas, Comal Springs in New Braunfels (Comal County) and The San Marcos Springs in San Marcos (Hays County). Other significant springs include the large springs in Brackettville, San Antonio and Austin (Brune 1975).

Spring flows of the San Marcos River have been monitored at least periodically since 1894 (Puente 1976). On an annual basis, an average of 249.9 m^3/min (107,690 acre-feet/year) of water flows from the springs (Brune 1975). During drought years (especially during the mid-1950's when Comal Springs did not flow for part of one year) much lower flows occurred. The lowest recorded yearly flow in San Marcos was 111.4 m^3/min (48,000 acre-feet/year) (Guyton et al. 1979). The lowest measured daily flow rate occurred on 15 and 16 August 1956 when the San Marcos River flowed at only 77.3 m^3/min. Maximum daily flows can be greater than 500 m^3/min, especially following high local rainfall and runoff (Puente 1976).

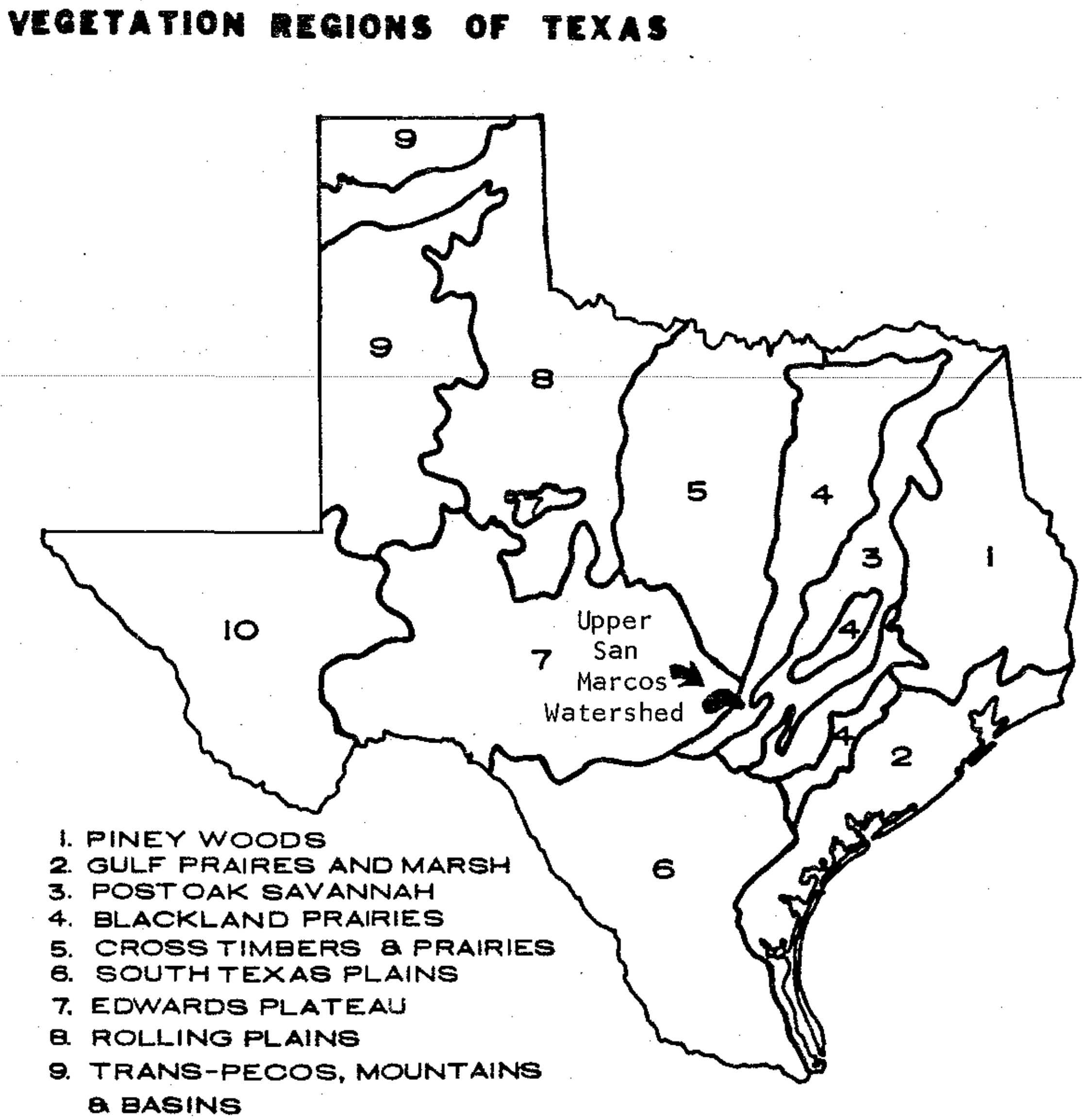
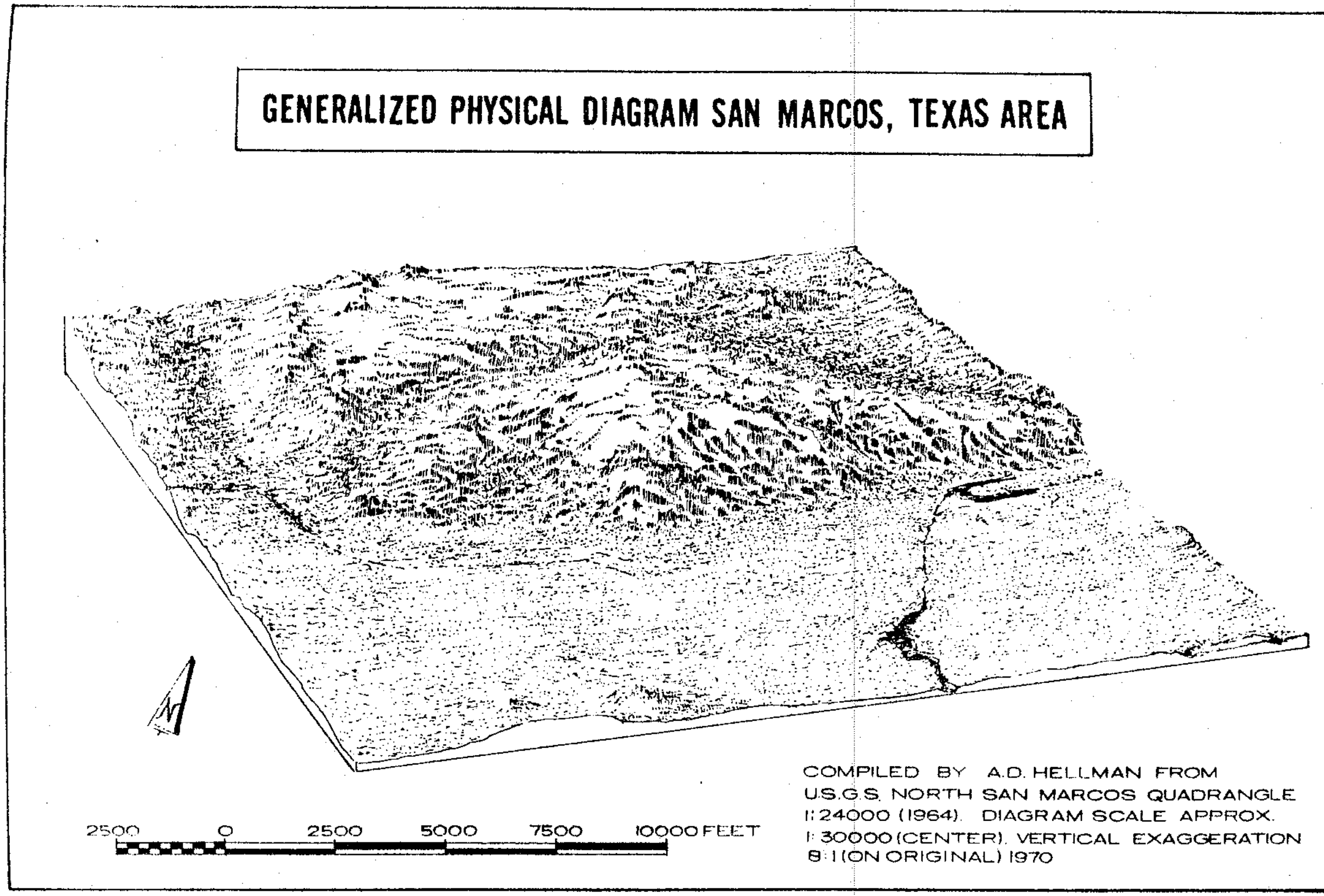


Figure 1

Adapted from Gould (1962).


GENERALIZED PHYSICAL DIAGRAM SAN MARCOS, TEXAS AREA
N
2500 0 2500 5000 7500 10000 FEET
COMPILED BY A.D. HELLMAN FROM
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1:24000 (1964). DIAGRAM SCALE APPROX.
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Figure 2

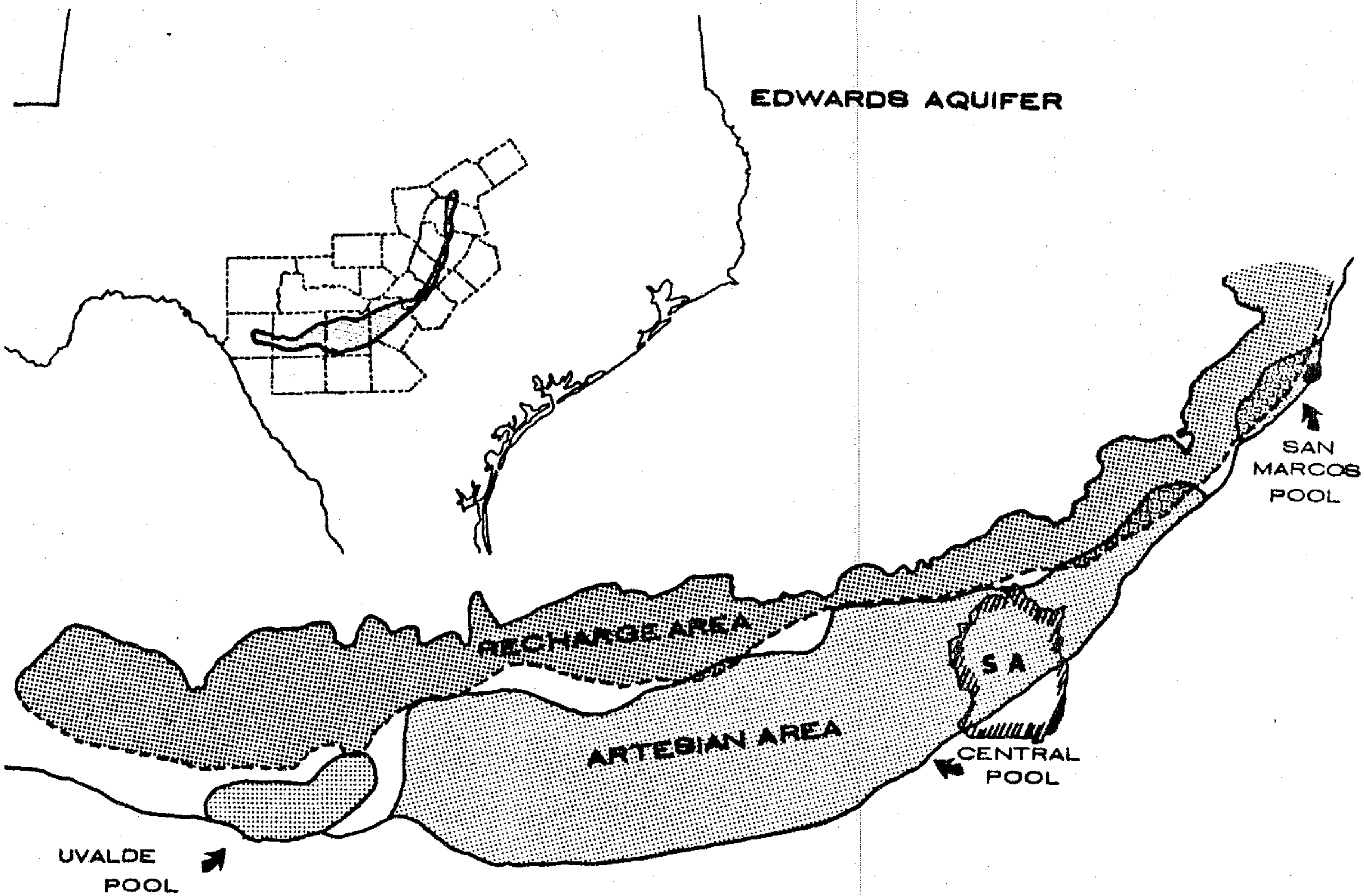

EDWARDS AQUIFER
RECHARGE AREA
ARTESIAN AREA
S A
SAN
MARCOS
POOL
CENTRAL
POOL
UVALDE
POOL

Figure 3

The thermally consistent water from the San Marcos has long been noted (Brown 1953) and generally varies by less than 1 or 2°C in the headwaters at any time during the year. The stability of this stream, both in terms of flow dependability and thermal characteristics, is thought to have provided the appropriate ecological conditions necessary to allow the extreme endemism of the San Marcos biota.

History

A brief sketch of the earliest inhabitants and visitors to the San Marcos Springs and surrounding vicinity is provided by Brune (1975):

> "When the Spanish explorers discovered these springs in 1743, they estimated there were 200 springs. From 1755 to 1756 a mission was located there. The springs were an important stop on El Camino Real from Nacogdoches to Mexico. In 1840 Bonnell described them as 'the most pleasant and delightful situation in the Republic (of Texas)'. Power plants, gins, corn mills, and an ice factory used the water power. The springs were a stop on the Chisholm Cattle Trail from 1867 to 1895."

In addition, the city of San Marcos developed (following early flooding and Indian attacks at the original site of the city several kilometers downstream from the headsprings) around the headsprings area. An early Federal fish hatchery was established near the springs (Jordan and Gilbert 1895). An amusement park (Aquarena Springs) has leased the headsprings area as a private user of the spring environment.

The population of San Marcos has risen from 741 in 1870 to nearly 19,000 in 1970 (U.S. Dept. Agriculture 1972) and no other county along the Balcones fault zone has had a greater relative growth than Hays County. Population projections predict that this accelerating growth of San Marcos and Hays County will continue. Currently, the expected population of San Marcos is approximately 40,000 people by 1990 (Clark and Holz 1971), foreseen to double in the two decades between 1970 and 1990.

Flooding

Information on flooding in the San Marcos area is available from 1913 to date (U.S. Army Corps of Engineers 1971) and the five largest floods of record are (in order or magnitude):

(1) 10 September 1921
(2) 15 May 1970
(3) September 1952
(4) 1929
(5) 1913

Other floods of lesser severity were also recorded in: 1957, 1958, 1959, 1960, and 1968.

During many of the floods occurring in the San Marcos area, water can be observed "flowing upstream" in the San Marcos River channel from flood waters delivered by the flooded Blanco River (U.S. Army Corps of Engineers 1971) especially when the basin of the San Marcos River proper has received minimal rainfall.

Although not the largest flood on record, the May 1970 flood was without question the most costly in terms of damages, due to price increases and greater flood plain occupancy (Longley 1975). It is expected that further growth in the San Marcos area will cause future floods of even moderate magnitudes to create damages similar to those caused by this large 1970 flood, in part due to the increased runoff rates resulting from increased urbanization since 1970.

KNOWN BIOLOGY OF GAMBUSIA GEORGEI

Taxonomy and Relationships With Other Species

The San Marcos gambusia, *G. georgei*, a member of the Poeciliidae, belongs to a genus of more than 30 species of livebearing freshwater fishes of central American origin. The genus *Gambusia* is rather well defined and members may be distinguished from related genera of this family by the thickened upper pectoral fin rays found in mature males (Rosen and Bailey 1963). Only a limited number of *Gambusia* species are native to the United States and of this subset, *G. georgei* is endemic to only a limited area of the San Marcos River in central Texas. This environment has long held the interest of ichthyologists due to the diversity and endemism of its fishes. Two other species of *Gambusia* are also inhabiting this system. One species, *G. geiseri*, is endemic to the San Marcos River and the nearby spring-fed Comal River in New Braunfels, Texas. The other species, *G. affinis*, is widespread in the southern United States, is the northernmost representative of the genus (and family) and has been widely introduced throughout the world to control the abundance of mosquito larvae.

The largespring gambusia (*G. geiseri*) is the most abundant vertebrate in the upper San Marcos River. This species was confused for a time with *G. affinis*, not so much due to difficulties in distinguishing forms, but rather due to problems surrounding a confusion of nomenclature (Hubbs 1926). During the interval of confused identity, *G. geiseri* was transported (as *G. patruelis* = *G. affinis*) throughout much of Texas (and elsewhere) as a means of mosquito control. Isolated remnant populations from these early stockings still are present today (Peden 1970; Hubbs et al. 1978).

Because of the relatively prominent role of *G. geiseri* in the San Marcos River and considering its endemic nature within this stream, scant attention was normally paid to G. affinis, which is commonly found throughout the southeastern United States. In the latter 1960's Hubbs and his students began an investigation to determine certain of the controlling ecological factors affecting the interaction of these two coexisting species in the San Marcos environment. During this time it was noted that certain morphological differences existed in the samples taken of G. affinis. One form appeared little different from other G. affinis from widely separated portions of its range. The other morph appeared significantly different from typical G. affinis. It was this form which was describle as G. georgei (Hubbs and Peden 1969).

Original Description of the San Marcos Gambusia

The San Marcos gambusia was described in 1969. The holotype is stored at the University of Michigan Museum of Zoology (UMMZ 187447) and is a mature male 29.3 mm standard length caught by Clark Hubbs and Michael M. Stevenson on 7 March 1968 in the San Marcos River beneath the Highway IH-35 bridge crossing. Table 1 summarizes certain of the morphological counts and measurements which characterize G. georgei. The gonopodial structure of Gambusia varies dramatically among species and has classically been used to classify the various members. Sam Marcos gambusia males have a unique gonopodium differing from all other known species. A description of this structure follows (from Hubbs and Peden 1969):

> "Gonopodial characters.--The gonopodium is broadly acute. The third ray is moderately bowed over elbow. Eight to ten antrorse slender moderately long spines. Distal spine usually extends to tip of gonopodium. Distal four or five spines with well developed bases. Ray 4a extends almost to distal tip if gonopodium or occasionally exceeds ray 3. Well developed elbow opposite level of proximal 3rd ray spines. This elbow composed of from five to six enlarged segments which are fused together on their anterior surfaces. Elbow greatly thickend so that there is little space between it and the enlarged bases of the spines on ray 3. Distal two or three segments of ray 4a slender and not fused to each other. Proximal segments of elbow opposite distal one or two serrae of ray 4p. Posterior and anterior branches of ray 4 diverge moderately at level near proximal serra and converge distally. Ray 4p a little shorter than ray 4a. Ray 4p with four or five retrorse long slightly curved serrae."
>
> "Small retrorse claw or hook on posterior branch of ray 4 with short pointed apex. Anterior branch of ray 5 moderately bowed over serrae and terminating in small J-shaped claw."
>
> "Usually two gonopophyses. Occasionally a weakly developed short third gonopophysis present (perhaps resulting from intro-gresion with G. affinis?). First gonopophysis without uncini, its shaft forming an angle of about 40° with vertebral column. Second gonopophysis with well developed uncini. Third caudal vertebra with normal haemal spine (except when it is modified into a short weakly developed gonopophysis)."

The San Marcos gambusia is unique morphologically from all other species in several known gonopodial characters, including the presence of more than five segments in ray 4a incorporated into the elbow and also by having a compound claw on the end of ray 4p. Figure 4 shows the gonopodial structures of a male G. georgei. A similar gonopodium from G. affinis is also included for comparison.

The rather plainly-marked color pattern of G. georgei is subtly different from G. affinis. Scales tend to be strongly crosshatched in contrast to the less distinct marking on scales of G. affinis. In addition, G. georgei tend to have a prominent dark pigment stripe across the distal edges of their dorsal fins. A diffuse mid-lateral stripe from the base of the pectoral fin extending posteriorly to the caudal peduncle is also often present, especially in dominant individuals. As in G. affinis, a dark subocular bar is visible and is easily elicited from frightened fish. Compared to G. affinis, G. georgei have many fewer spots and dusky pigmented regions on their caudal fins. The median fins of wild-caught specimens of the San Marcos gambusia tend to be colored lemon-yellow. In dominant or "high" males, this color can approach a bright yellowish-orange in appearance, especially around the gonopodium. A bluish-sheen is evident in more darkly pigmented individuals, especially near the anterior dorso-lateral surfaces of adult females.

Evolutionary Relationships With Other Species of Gambusia

Two similar views on the relationships of Gambusia appeared in 1963 (Rivas 1963; Rosen and Bailey 1963). Although these two works differed in certain details, such as how to divide this group into subunits, e.g., Rivas lists the species of Gambusia in five subgeneric groupings (and has 2 related genera), while Rosen and Bailey divided this group into 6 subunits, the affinities of G. georgei appear to lie with either the G. nobilis or the G. affinis subgroupings (Hubbs and Peden 1969). If the "senilis" and "nobilis" groups of Rivas are combined (following the evidence of Hubbs and Springer (1957) who showed a close relationship between these groups), then both his combined group and Rosen and Bailey's "nobilis" group are very similar. Because G. georgei shares an equal number of known attributes with both the "nobilis" and "affinis" groups, assignment to either group is extremely difficult.

Hubbs (1957) suggested that G. heterochir (a member of the widely fragmented G. nobilis complex) likely occupied a much larger geographic range than its presently very restricted distribution in the Clear Creek headsprings in Menard County, approximately 350 km northwest of San Marcos. It is considered possible for an ancestor of G. heterochir or G. nobilis to have repeatedly colonized the San Marcos area and to have been isolated in this system. By a series of repeated invasions of either "nobilis-like" or "affinis-like" fish, the present species composition of Gambusia could have evolved in the San Marcos area.

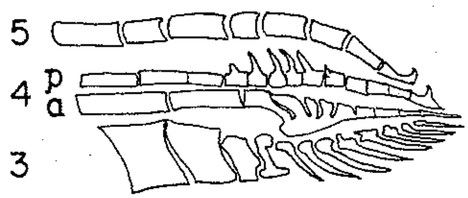
Table 1

Measurements (thousandths of standard length)

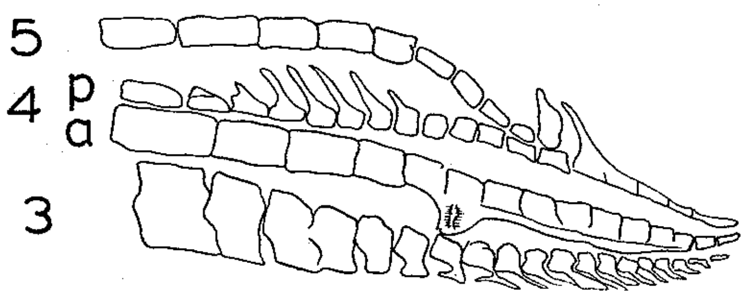
	Males	Females
number of specimens	14	31
standard length (range in mm)	21.3-29.3	25.6-39.2
Body depth	195-218	186-212
Dorsal origin to tip of lower jaw	577-606	620-642
Anal origin to tip of lower jaw	429-476	545-574
Dorsal origin to caudal base	403-431	354-406
Anal origin to caudal base	539-577	431-478
Caudal peduncle depth	139-158	134-150
Head length	245-281	237-296
Head width	134-164	165-179
Snout length	95-104	94-114
Orbit length	75-86	74-95
Interorbital width	90-112	114-133
Mouth width	81-98	82-119
Dorsal fin length	220-260	205-226
Anal fin (gonopodium) length	279-315	186-206
Caudal fin length	232-260	213-253
Pectoral fin length	184-207	184-204
Pelvic fin length	83-104	95-123

Counts

	Males (N)	Females (N)
Dorsal fin rays	7(43),8(1)	6(1),7(66),8(1)
Pectoral rays (total)	24(1),26(5),27(3),28(1)	26(9),27(1)
Lateral series scales	29(1),30(6),31(3)	30(8),31(2)
Scales rows around caudal peduncle	16(10)	16(10)
Anal fin rays	---	9(9),10(1)



(A) Gambusia georgei



(B) Gambusia affinis

Figure 4

Adapted from Hubbs and Peden (1969) and Hubbs (1957). Fin ray elements are indicated.

Because of these difficulties in the classification of G. georgei, Hubbs and Peden (1969) looked to other criteria for the placement of this species into one of the accepted species groups. Because hybridization among Gambusia tended to occur with greater frequency among members of the same subgrouping, Hubbs and Peden considered G. georgei to be a member of the G. affinis group since hybridization was known to occur from G. georgei x G. affinis crosses, but not from G. georgei x G. geiseri (a member of the G. nobilis group) crosses. The presence of G. georgei in the San Marcos River together with a member of either subgenus is unusual regardless of the group affinities of G. georgei, since Rosen and Bailey (1963) suggested that sympatry among Gambusia should only occur with members of different subgenera. The San Marcos River, however, is an environment with two species from one subgenus, in apparent violation of the "rule" of Rosen and Bailey. It is suggested that perhaps the "rule" is essentially valid, but that the unique San Marcos environment has allowed the coexistence of two members of the same subgenus, but one member (G. georgei) must be restricted to extremely low population densities.

Hybridization in the Gambusia at San Marcos

Hybridization between G. georgei and G. affinis has been ongoing since at least 1925 with little apparent problems in maintaining the genetic integrity of either species (Hubbs and Peden 1969). Hubbs and Peden suggested that as many as 10% of the "affinis" type individuals in the San Marcos area are intermediate with respect to G. affinis and G. georgei. The presence of three G. georgei x G. affinis hybrids in our present study indicates that this hybridization continues and probably remains similar to the situation found during the earlier study in 1968.

In the San Marcos River, we also found four individuals putatively identified as G. geiseri x G. affinis hybrids. Although this particular hybrid combination has not been reported from nature prior to this account, the extreme rarity of this hybrid cross, compared to the abundances of the parental species as well as their isolated occurrences, would seem to indicate that G. geiseri and G. affinis have a high degree of reproductive isolation. Similar findings have been reported for these species by Peden (1970) and Hubbs and Delco (1960).

Ecological Factors Influencing Abundance of Gambusia georgei

Habitats

In this study, we attempted to sample selected sites by seining on a year-round basis and to selectively sample as much of Gambusia habitats of the upper San Marcos as possible. We have examined all reasonable environments during float trips through the area. We have also sampled similar environments in the San Antonio River, Comal River and Barton Creek.

Given the previous geologic and hydrologic back ground the specific habitats available for San Marcos Gambusia and descriptions of our study sites follows (Figures 5 and 6).

The San Marcos River begins as a group of various sized spring openings from the depths of Spring Lake. The original site of these springs has been impounded and the water is maintained to approximately three meters above its natural level. Even with the additional height of water caused by the dam, spring outflows cause marked surface boils in the water in Spring Lake, more than 10 m above the spring outflows. The water flows from Spring Lake over the dam spillway and mill race by an abandoned ice manufacturing building.

Station 1 was located on the west bank, primarily, beginning approximately 30 m downstream from the outflow from dam spillway and extending downstream an additional 50 m. Poeciliid habitats at this station consist of heavily vegetated sides with slight to moderate currents. Few shallow, muddy backwaters were encountered; those habitats which were muddy were also heavily vegetated with *Ceratophyllum*, other aquatic macrophytes and brush. A large drainage pipe for urban runoff empties into the San Marcos River at this station and a small amount of relatively fine sand and gravel substrate is found in this area. In the shallow backwater areas surrounding this drainpipe, isolated *G. affinis* were taken. Following rains in this area, pockets of standing water were commonly found in the downstream portions of this station. In these small isolated pools, *Poecilia latipinna* and *P. formosa* were often collected. The relatively high proportion of vegetated shallow-water habitat along the sides of the San Marcos, along with consistent currents throughout this station, appeared to offer more suitable habitat for *G. gieseri* than for either of the two more quiet water inhabiting species. The predominance of *G. geiseri* in samples from Station 1 support this assessment.

Downstream from this station is Sewall Park, maintained by Southwest Texas State University. The streambanks on both sides of the river have been lined with concrete for about 150 m and the stream, in this portion, serves as a swimming area for university students. Because of the limited amount of edge habitat in this section, few *Gambusia* were observed; of those seen, all appeared to be *G. geiseri*.

Downstream from the Sewall Park area, the San Marcos flows through the urban San Marcos area. The stream banks appear relatively unmodified but the channel configuration produces swift riffle areas over a substrate of rocks and gravel interspersed with moderately shallow, flowing pools. The sides of the streambank are heavily vegetated in places and large quantities of aquatic plants are present throughout this section. The habitats in this stretch are essentially similar to those found at Station 1. Approximately 1 km below Sewall Park is a small dam (Roger's Dam) in Rio Vista Park, the major city park of San Marcos. The impounded area from this dam extends ca 300 m upstream. The west bank has been lined with concrete for most of its length in this impounded section while shallow water areas along the east

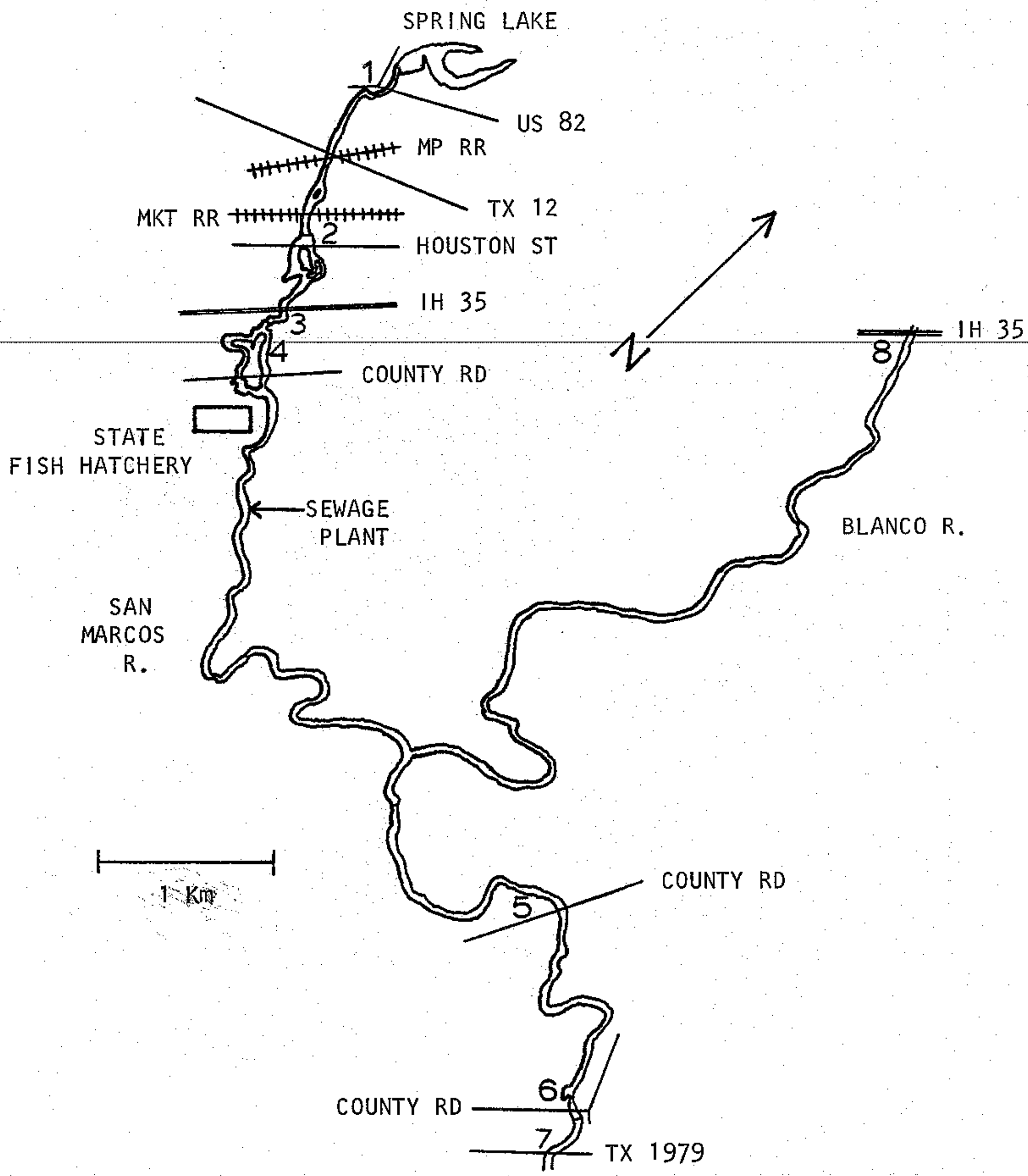

SPRING LAKE
1
US 82
MP RR
TX 12
MKT RR
2
HOUSTON ST
IH 35
3
4
COUNTY RD
STATE
FISH HATCHERY
SEWAGE
PLANT
SAN
MARCOS
R.
IH 35
8
N
BLANCO R.
1 Km
COUNTY RD
5
6
COUNTY RD
7
TX 1979

Figure 5

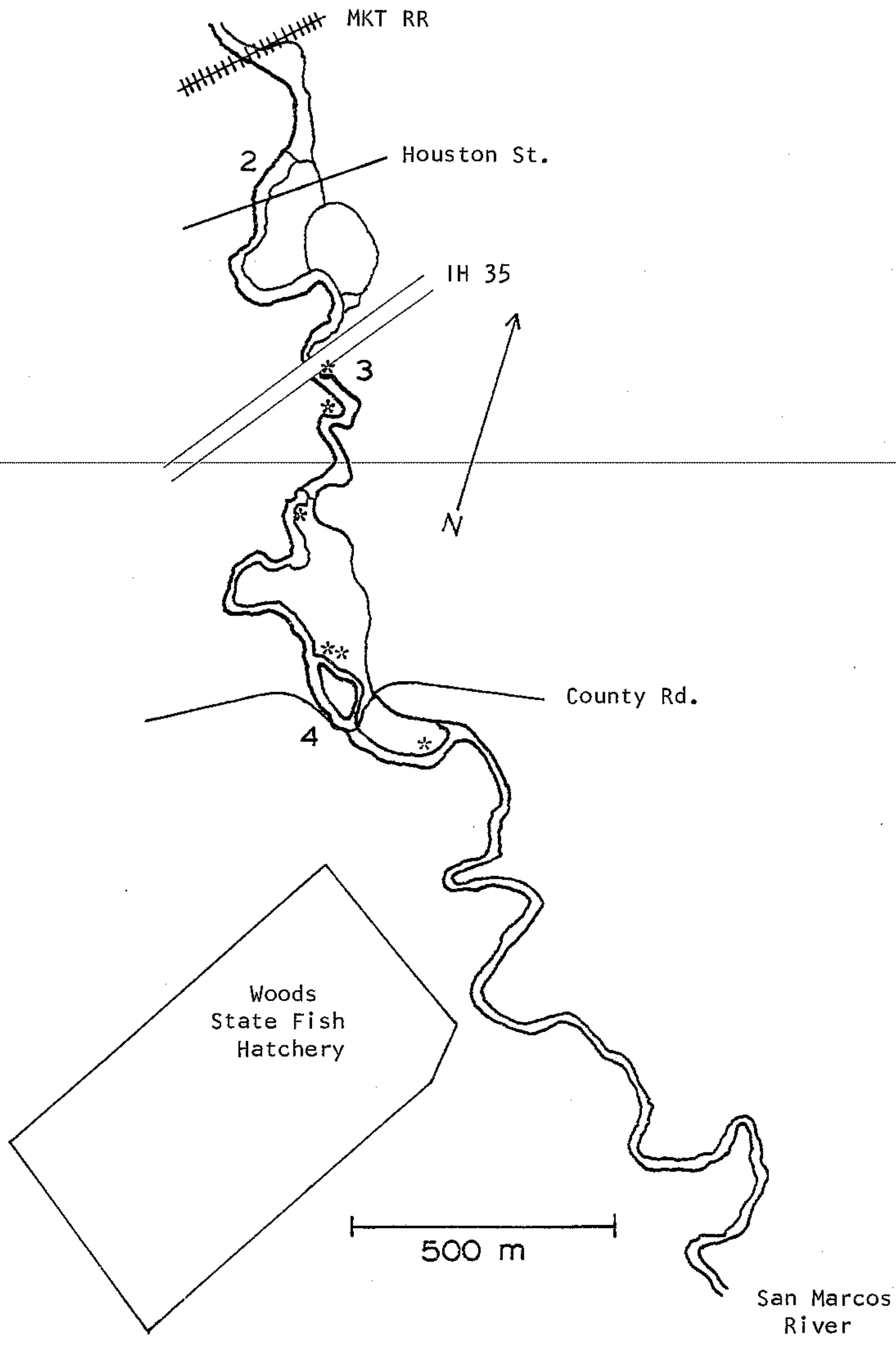

MKT RR
2
Houston St.
IH 35
3
N
County Rd.
4
Woods
State Fish
Hatchery
500 m
San Marcos
River

Figure 6

bank have extensive growths of vegetation. Gambusia geiseri were found in considerable numbers near the surface in and around the aquatic vegetation often at quite some distance offshore, while G. affinis were taken in more inshore, quiet water environments. Limited open, shallow water environments were found in the area along the east bank underneath the MKT railroad bridge spanning the river. Stands of Colocasia antiquorum (Elephant ears) were found associated with these areas as well as nearer to the downstream end of this impounded section in the vicinity of the small boat ramps which have been cut into the side of the streambank for the vehicles which periodically remove stream vegetation from this area. In both of these open areas, Poecilia were taken as well as limited numbers of G. affinis.

Downstream from the dam at Rio Vista Park, and extending downstream for approximately 100 m, is Station 2. Turbulence from the water flowing over the spillway of the dam has created a relatively deep, swiftly moving portion near the west bank and a relatively shallow, sand and gravel area toward the east bank. Little streambank vegetation was found near the east bank in the upper portion of this station, however, extensive stands of aquatic macrophytes were found in the shallow waters near the west bank in the lower portion of this station. An extensive riffle system near the mid-portion of this station separates the shallow quiet waters of the east bank upstream and the quiet waters of backwater environments, both upstream and downstream where varying amounts of silt had been deposited, G. affinis and Poecilia were encountered.

Downstream from Station 2 to the Interstate 35 crossing, the San Marcos River maintains a relatively deep, steep-sided channel with few Gambusia habitats. A diversion channel beginning near the dam at Rio Vista Park and extending downstream to an old mill removes a small portion of water from the main river. Gambusia affinis abound in these channels and also in the often stagnant side pools found in conjunction with this diversion. Two ephemeral stream channels extend from the mill and return water to the main river channel. Several spring seeps occur in the downstream of these diversion channels, bounding the southern side of a region known locally as Glover's Island, which is maintained as a children's park. In these areas, spring-adapted aquatic plants and G. geiseri are abundnt. In the shallow, eurythermal areas of this section, G. affinis and Poecilia are common.

The San Marcos River makes a series of sharp turns downstream from the entrance of the second diversion channel. Following a major riffle system immediately upstream from the IH-35 crossing, the San Marcos makes a sharp turn to the east and flows underneath the highway crossing. Under the north-bound (east) access road is a shallow, gradually sloping mud and clay substrate area which is where the type specimen of G. georgei was collected. Our Station 3 encompasses the area surrounding the IH-35 crossing extending both up and downstream for approximately 50 m. Immediately across the river from the type locality is a partially scoured area on the west bank in which has been created a shallow pocket of quiet water. The substrate is primarily muddy clays, but often considerable silt and brush were also found. Following another sharp bend in the river to the south, is another small backwater region, along the west bank, relatively cleared of plants, with mud and tree roots as the primary substrate. Elephant ears (Colocasia) are dense in this area and provide additional shade in addition to the shade provided by the large trees also found here. Three species of Gambusia and both species of Poecilia were found at this station. Heavily vegetated habitats near flowing water were occupied by dense populations of G. geiseri. Relatively open areas in quiet waters near both banks were occupied by G. affinis in sparse populations. Fourteen G. georgei were taken in the backwater environment found immediately downstream from the second bend of the river at this station (west bank locality). One G. georgei and one G. georgei x G. affinis hybrid were also taken at this station at the type locality. Considerable changes in the amount of suitable G. georgei habitat have apparently occurred since 1968, when G. georgei were first extensively collected. Continuing erosional activities in the vicinity of the bridge pilings at Station 3 have removed much of the shallow, mud-bottomed area at the type locality which has resulted in considerable losses of suitable habitat. Similarly, loss of habitat due to the erosional forces of the San Marcos River and extensive growths of streambank vegetation (expecially certain introduced species such as Colocasia) have reduced the available G. georgei habitat at the downstream collecting site of this station.

Downstream from Station 3, the San Marcos becomes progressively turbid, riffle areas become increasingly farther apart and the river begins to cut ever deeper into the river channel, creating high bluffs in some areas. Approximately 300 m downstream from Station 3, a small dam (Cape Dam) is encountered which backs up water nearly to Station 3. A side channel removes a portion of the water from the main river and carries it to an old cotton gin immediately downstream from Station 4 (described later). The dam is only partly successful in limiting upstream migrations of fishes as many cascades and openings are present which has been overgrown with Colocasia. In the muddy bottomed habitat near the margin of this locality, one G. georgei was taken.

Downstream from this location and following the entrance of a small ephermeral creek (Willow Springs Creek), the San Marcos River splits and continues around a small island, known locally as Thompson's Island. Most of the river's flow travels along the west side of the island; the river in this stretch is swift and clear. The substrate is composed of relatively large rocks and gravel with minimal vegetation in riffle areas. A small portion of the San Marcos flows along the east side of the island and in this area, water currents are slow to moderate. Heavy growths of Colocasia are found in the shallow backwater areas and a relatively dense stand of trees provides a heavy canopy and much shade. Station 4 consisted of the poeciliid habitats found from the upstream edge of Thompson's Island downstream along the north bank to near the county road crossing and also downstream from the road crossing approximately 75 m to the pumping area for the Woods State Fish Hatchery. The outflow of the diversion channel carrying water from near Station 3 to the old cotton gin operation empties its water across from the fish hatchery pumping area and these structures represented the downstream limit to our Station 4. As with Station 3, three species of Gambusia (and both species of Poecilia) were taken at

Station 4, in habitats with characteristics essentially identical to those where these species were taken at Station 3.

Immediately downstream from Station 4, the U.S. Geological Survey maintains a water quantity metering station. The San Marcos River, in this stretch between Station 4 and the confluence with the Blanco River, is deeply entrenched within its banks and bottom substrates are predominately hard clays and mud. Occasional log jams create partial blockage to river flows in several areas and a thick canopy of very large oaks and other trees provides considerable shading in this 4.5 km section. Few *Gambusia* habitats were found in this stretch; offshore *Gambusia* collected in more rapidly flowing water, shady environments were generally *G. affinis*. The San Marcos Secondary Sewage Treatment Plant has its outfall into the San Marcos River approximately 1.5 km above the confluence of the Blanco River. Some foam has been present on each of our periodic visits to this area and the suds from this sewage outfall emission are visible for about 100 m downstream. The quantity of effluent which causes this foam is not, at least at this time, having a noticeable effect on the *Gambusia* in this section.

Approximately 0.5 km downstream from the Blanco confluence is located an old mill dam (Alvord Dam) which impounds water upstream in both the Blanco and San Marcos rivers for about 1 km. In this slack water environment few *G. geiseri* were found, but many *G. affinis* were taken along the shallow edges. Below this impoundment, the river travels over a series of riffles located approximately 100 m upstream from a county road crossing. Sampling was conducted in this section above the road crossing along the south bank (Station 5) in the area where the original settlement of San Marcos was located during the early 1800's. Approximately 1 km downstream from Station 5, a small spring-fed creek enters from the north and periodic flooding of this stream has caused a moderately large backwater area to develop along the southern side of the San Marcos River, across from the stream mouth. This area has been futher cleared of underbrush and is used as a cattle watering area by the local landowners. A variety of *Gambusia* habitats are found in this section (Station 6). Flowing water habitats along the main river channel were found to have moderately dense populations of *G. geiseri*, while the quieter backwater areas contained, at times, extensive *G. affinsis* populations. In the quietest waters and in the sections with little aquatic vegetation, large numbers of *Poecilia* were taken.

Below this station is another dam at Martindale which causes slack water environments from the dam upstream nearly to Station 6 (ca 500 m). Below this impoundment, the river flows over an extensive riffle system and continues to flow moderately swiftly over a cobble and gravel substrate downstream for approximately 0.5 km to Station 7, immediately upstream from the state highway crossing (Hwy. 1979).

At Station 7, the amount of suitable *Gambusia* habitat appeared to depend upon local water conditions to a greater extent than at the upstream San Marcos stations. Variation in water temperatures and water levels were often considerable and a small sand and gravel bar which was present during the first half of the present collection period was submerged and partially washed downstream during spring flooding of this area. This temporarily depressed the numbers of *Gambusia* found at this station.

An additional station (Station 8) was established on the Blanco River approximately 5 km above its mouth at the Interstate 35 highway crossing, north of San Marcos. Blanco River water appeared moderately murky at all times and expecially muddy following periods of rainfall. Considerable variation in water temperatures and flows occurs in the Blanco River at this station, far more than was observed in the San Marcos River. Shallow habitats were seined at this station and only *G. affinis* were found. *Poecilia latipinna* and *P. formosa* were both taken at this station in the quietest water with sparsely vegetated substrates. This represents an extension of the introduced range of *P. formosa* which had not been found previously elsewhere in the Guadalupe River system outside of the San Marcos River.

Periodic collections in the Comal River in Landa Park, New Braunfels, San Antonio River in Brackenridge Park, San Antonio, and Barton Creek in Austin, were taken; however, no *G. georgei* were found in these samples. Among the poeciliids found, *G. geiseri*, *G. affinis* and *P. latipinna* were taken from the Comal River environs, *G. affinis*, *P. latipinna* and *P. reticulata* (guppies) were taken from the San Antonio River and only *G. affinis* were encountered in the Barton Springs area. It is likely that these areas do not include *G. georgei* among their aquatic representatives.

Habitat Preferences of San Marcos Gambusia

In general, the San Marcos gambusia prefers quiet waters adjacent to sections of moving, but seemingly of greatest importance, thermally consistent, waters. Substrates on which *G. georgei* were found were mostly muddy but generally not silted habitats, and shade from overhanging vegetation or bridge structures was one factor common to all stations where *G. georgei* were taken. Very few localities along the upper San Marcos River with habitats appearing suitable for *G. georgei* were found in our investigations, in concordance with previous findings (Hubbs and Peden 1969).

Compared to *G. georgei*, *G. affinis* tended to show similar preferences for shallow, still waters, but differed strikingly from *G. georgei* in their ability to colonize environments with greater temperature fluctuations, such as the partially isolated sloughs, intermittent creeks and drainage ditches found in the upper San Marcos River, and in the Blanco and lower San Marcos rivers, as well.

The most abundant vertebrate in the upper San Marcos River is G. geiseri. The largespring gambusia is often found in gently to moderately moving water, among submerged and emergent vegetation and in areas with thermal consistency. Dense schools of this species are commonly observed in much of the upper sections of this river. The distinct preferences of differing current velocities between G. geiseri and the other two Gambusia species is suggested as one factor likely influencing the abundance of hybrid individuals between the three Gambusia species. Because G. georgei and G. affinis share greater similarity in the habitats they occupy and G. geiseri appears to be ecologically segregated from these other two species to a greater degree, the former two species apparently have much more contact and, thus, have a greater probability of mismating than do either of these species with G. geiseri.

Abundance of Gambusia georgei

Our sampling of Gambusia in the San Marcos area yielded the data shown in Table 2. Of the 20,199 Gambusia collected, 18 G. georgei (0.09% of total), 4002 G. affinis (19.8% of total) and 16,172 (80.1% of total) G. geiseri were taken. In addition, 3 G. georgei x G. affinis hybrids (unlisted in Table 2) were taken at the following sampling periods and stations: one hybrid at Station 3 (24 November 1979), two hybrids at Station 4 (4 November 1978(1); 16 May 1979 (1)). Four putative G. geiseri x G. affinis hybrids (also unlisted in Table 2) were also taken during the course of this study at the following dates and stations: three hybrids at Station 3 (12 April 1979(2); 20 September 1979(1)) and one hybrid at Station 5 (12 October 1979).

The unique nature of the upper San Marcos River is clearly reflected in the relative proportion of G. geiseri compared to other Gambusia at the collection stations. Largespring gambusia in the upper San Marcos stations (Stations 1-4) comprise approximately 95% of all Gambusia with relatively little variation evident between stations or collection dates. The species composition of samples taken below the confluence of the Blanco River (Station 5-7) were also similar to each other and in these samples, G. geiseri accounted for only approximately 25% of all Gambusia taken. The variation in Gambusia species composition in these downstream areas was greatly increases relative to the more stenothermal upper San Marcos River environments and the variation in terms of absolute abundance of Gambusia in different seasons appeared also greater.

Only G. affinis were taken in the Blanco River Site (Station 8) and considerable seasonal variation in the abundance of this species at this station was noted.

Most G. georgei (83.3%) were taken at Station 3 and all were taken between Station 2 and the Blanco confluence (exclusive). This region of the San Marcos tends to have a higher degree of shade (due to an extensive tree canopy) and thermal stability compared to either areas upstream (less shade)

Table 2

COLLECTION DATE	1 geiseri	1 affinis	1 georgei	2 geiseri	2 affinis	2 georgei	3 geiseri	3 affinis	3 georgei	4 geiseri	4 affinis	4 georgei	5 geiseri	5 affinis	5 georgei	6 geiseri	6 affinis	6 georgei	7 geiseri	7 affinis	7 georgei	8 geiseri	8 affinis	8 georgei
	STATION																							
4 Nov '78	848			621	3		680	15		462	4		9	183		432	324		155	96			148	
22 Nov							373	13		316	48		75	14										
14 Dec	575	1		154	5		278	4		276	7		11	99		235	343		48	76			50	
9 Jan '79				525	28		166	4		277	4													
8 Feb	281	22		256	13		233	4	1	155	7					12	111		1	8			15	
25 Mar							250	8																
31 Mar				544	41		740	19		246	16													
12 Apr							748	205		421	3	1												
3 May				303	17		357	6	1	244	2													
16 May							318	7	6	330	157					17	219						191	
13 Jun	178	7		302	5		238	18	2	161	1		1	2					7	15				
28 Jun							243	14	1	241	2	1												
17 Jul							323	39	4	83	4													
20 Sep	452	61		298	2		211	20		118	1	1	1	68		11	398			47			222	
12 Oct				226	3		267	7		110	8			24		27	290							
24 Nov				235			184	2		224	2					59	200							
Totals	2334	91		3464	117		5609	385	15	3664	266	3	97	390		793	1885		211	242			626	
$\bar{x}$ % *G. geiseri* per collection	95.4%			97.1%			95.5%			94.8%			22.3%			21.3%			28.7%			0.0%		
(s.d.)	(5.04)			(2.46)			(3.06)			(8.25)			(32.7)			(20.4)			(24.2)			(0.0)		

or downstream (less thermal stability). The downstream areas below Station 4 seem to have, in addition, even more shading (perhaps excessive for G. georgie?) than habitats where G. georgei were found. It is interesting to note that another species, a caddisfly, Protoptila arca, endemic to the San Marcos River (Edwards and Arnold 1961; Espey et al. 1975), has a nearly identical range as G. georgei. This species of caddisfly is thought to be limited in its downstream distribution by the presence of Alvord Dam, located below the Blanco confulence. This structure has a known physicochemical influence on the San Marcos River and exerts a back water effect upon the San Marcos almost as far upstream as the U.S. Geological Survey gauging station immediately downstream from our Station 4 (Espey et al. 1975). This gauging station is also in close proximity to our farthest downstream capture point of G. georgei in this study.

Other Known Collections of Gambusia georgei

The historical sequence of known G. georgei (and G. georgei x G. affinis hybrids) collections prior to this study is presented in Table 3. Where possible, the location of capture and in which research museum the specimens are located are also given.

Unfortunately, early records of exact sampling localities are not available for the 1884 or 1925 collections. Localities were listed merely as "San Marcos Springs" (R. R. Miller, pers. comm.). It seems likely that these earliest collections were taken at or near the headsprings area near our present Station 1. If this is the case, then G. georgei appears to have significantly altered its distribution over time. Samples prior to 1950 from the San Marcos River downstream from Station 1 are extremely scarce, however.

This is further substantiated by the presence of G. georgei at Station 2 during 1953 but not subsequent to that time. The farthest downstream record of G. georgei is approximately 1 km below the outfall of the San Marcos Secondary Sewage Treatment Plant and was collected with an Ekman dredge (Whiteside, pers. comm.). As few G. georgei were found far downstream from Station 4 in our present study and because this species appeared largely restricted to the vicinity of Stations 3 and 4, the downstream record seems likely to be a migrant individual and not near the center of this species' greatest abundance. The capture of an active surface inhabiting fish in an Ekman dredge suggests a somewhat inactive fish in an untypical environment. Perhaps the individual found by Whiteside was a dying male that had drifted downstream in the current from its preferred habitat. The region of the San Marcos River between Rio Vista Dam and the downstream end of the State Fish Hatchery appear to include the critical habitat for G. georgei. The apparent decrease in abundance of G. georgei since 1968 seems a real phenomenon since many more G. georgei were taken at the critical stations (Station 3 and 4) in 1968 than collected in our study. In fact, a single sample from the earlier period had more of the San Marcos gambusia represented

Table 3

Station	Date Collected	N	Museum (Catalog No.)
"San Marcos Spring"	Summer 1884	2	UMMZ 65250
"	13 May 1925	1(hybrid)	UMMZ 72566
Station 2	11 January 1953	1	TNHC 7201
Between Station 4 and 5	14 August 1960	8	TNHC 7205
"	"	1(hybrid)	TNHC 7210
Station 4	18 September 1960	1	TNHC 7195
"	24 June 1961	8	TNHC 7202
"	22 July 1961	13	TNHC 7204
"	25 August 1961	21	TNHC 7206
"	"	1(hybrid)	TNHC 7217
Station 3	10 January 1968	21	TNHC 7196
"	7 March 1968	1(holotype)	UMMZ 187447
"	"	44(paratypes)	UMMZ 187448
"	"	5(hybrids)	UMMZ 187445
"	6 May 1968	5	TNHC 7214
"	8 May 1968	17	TNHC 7197
"	? May 1968	9	TNHC 7212
Station 4	"	7	TNHC 7207
Between Station 4 and 5	8 May 1968	2	TNHC 7199
"	9 May	13	TNHC 7203
"	"	1(hybrid)	TNHC 7208
"	1974	1	---
		173	

than all of our collections. The abundance of this species seems to have been much lower between 1970 and 1979 as Whiteside's samples had only the single male and many other collections in the vicinity of Station 3 were fruitless in obtaining G. georgei.

Possible and Potential Competitors

Competition for resources may be one factor which imposes extreme limits on the abundance of G. georgei. In addition to expected high levels of interspecific competition from other Gambusia, especially G. affinis, other, less closely related species, can also impact G. georgei populations. As studies have shown, many fishes (especially when small) have exceedingly similar food resource utilizations (Hubbs et at. 1978). If exotic or non-native species are added to aquatic systems, greater amounts of competition or overlap among species is possible. These exotic species may, in the absence of their normal control agents, be able to acquire resources with greater efficiency than native species. Also, during the exponential population growth phases of recently introduced species, even short-term extensive niche overlap with G. georgei is likely to negatively impact this species.

Table 4 shows, by station, species which are not native to the San Marcos River, but which were collected in Gambusia habitats. Although abundances of these potentially competing species are not shown, the densities of Poecilia (both species), Lepomis (especially L. auritus) and the cichlids, Cichlasoma cyanoguttatum and Sarotherodon mossambicus, appeared high in habitats where G. georgei were found. Unnatural interference from these species, especially, may be having a considerable influence on the ability of G. georgei to recolonize the San Marcos River following perturbations such as flooding.

Laboratory Culture of Gambusia georgei

Four individuals (2 males, 2 females) were kept alive from the 16 May 1979 collection at Station 3 and raised in 57 liter aquaria at the University of Texas at Austin. Aquaria were kept at a relatively constant 20°C with summertime photoperiods (14 L; 10D). Reproduction was first noted on 10 August 1979 when one female produced 12 young. A culture was initiated using aquaria and two shallow flow troughs. At present more than 40 G. georgei have been born in the laboratory although a bacterial infection has greatly affected a portion of the culture. A brood of more than 60 young were present in one female (third generation in the laboratory in the laboratory) but these young appeared to have been aborted prior to full development. This female had a second brood of approximately 30 young four weeks after the first brood was aborted. Outdoor culture of G. georgei began at the University of Texas Brackenridge Field Laboratory during April 1980.

Table 4

Species	STATION 1	2	3	4	5	6	7	8
Astyanax mexicanus	X	X	X	X	X	X	X	X
Cyprinus carpio	X							
Carassius auratus	X							
Notemigonus crysoleucas					X		X	X
Poecilia latipinna	X	X	X	X	X	X	X	X
P. formosa	X	X	X	X	X	X	X	X
Micropterus dolomieui				X	X			
Lepomis microlophus	X		X		X	X	X	X
L. auritus	X	X	X	X	X	X	X	X
Ambloplites rupestris	X	X	X	X				
Cichlasoma cyanoguttatum	X	X	X	X	X	X	X	X
Sarotherodon mossambicus		X	X		X	X		

DISCUSSION

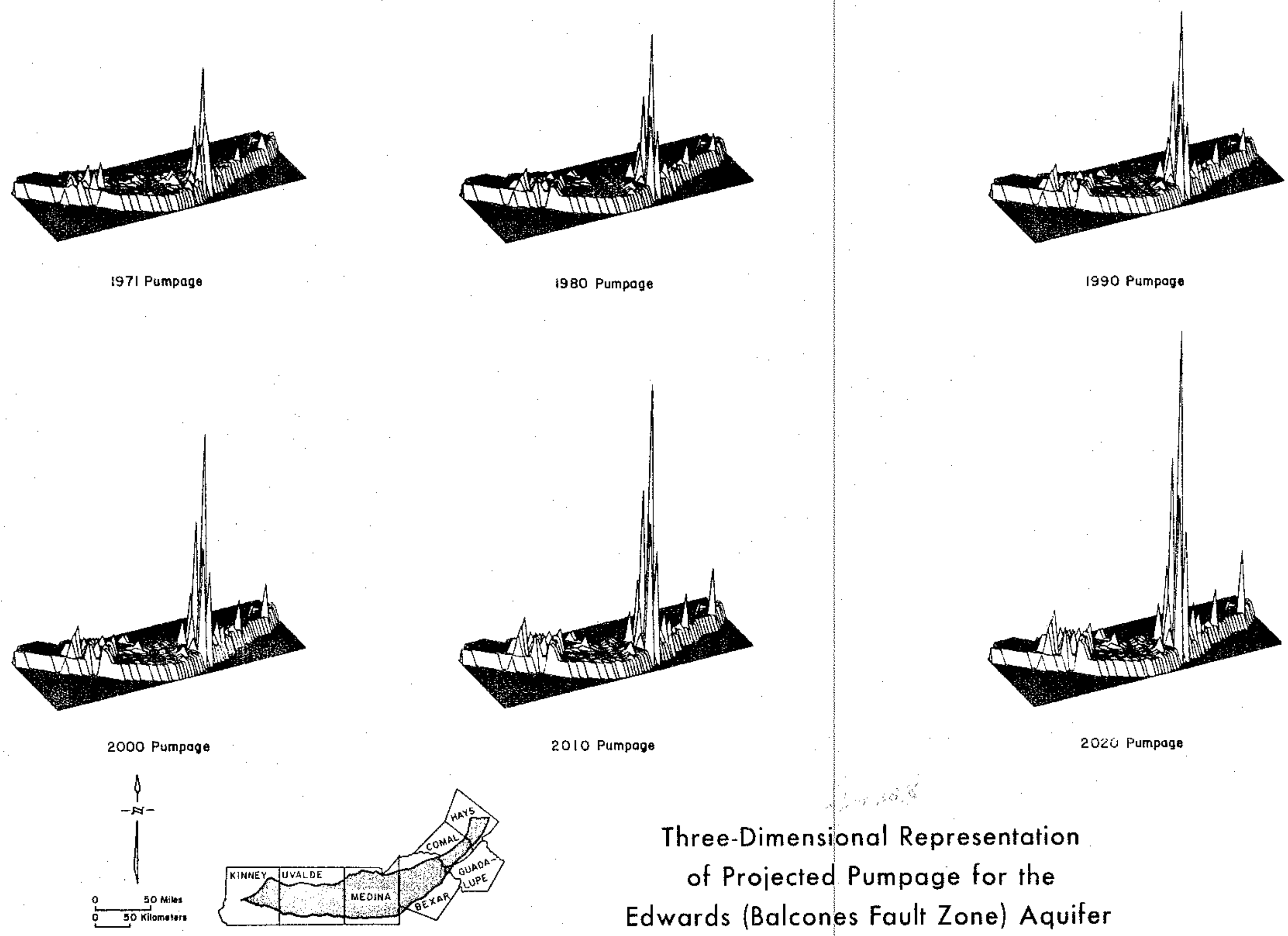
Threats to the Survival of *Gambusia georgei*

We consider that several major threats exist to the continued survival of *G. georgei* in the upper San Marcos system. Many factors have been noted in previous listings of *G. georgei* in various conservation organizations' lists of threatened and endangered species and our appraisal of these factors and estimates of future trends for these and other factors are herein discussed.

Projections For Water Use

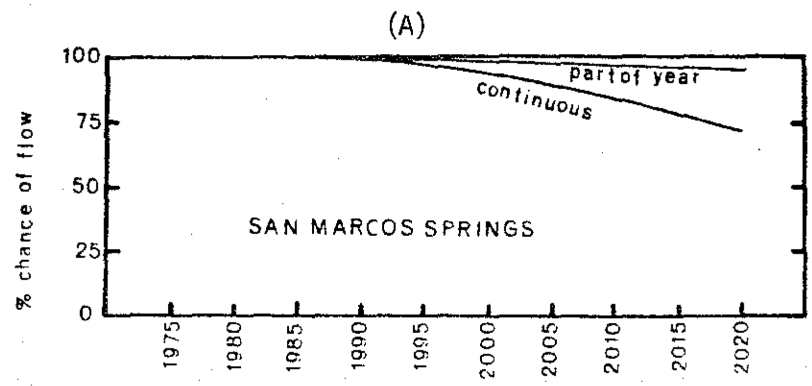
Because the San Marcos River's flow is intimately tied to water usage over the entire Edwards Aquifer, growth or increased utilization of underground water resources throughout the aquifer will depress the availability (and hence, flow) of the water from the San Marcos springs. Figure 7 shows diagrammatically the estimates for projected pumpages from the Edwards Aquifer through the year 2020 (Texas Water Development Board 1977). The tremendous increase in water usage in the San Antonio region is especially evident. Because of this anticipated growth in the central region of the Edwards Aquifer, several estimates have been made concerning the influence of the increasing pumpage of the spring flow at San Marcos. Data from the Bureau of Reclamation suggest that demands on the Edwards Aquifer, even considering a "low" (and unlikely) rate of growth for this region, will far exceed the recharge (Longley 1975). Given various schemes of water usage, the Bureau of Reclamation projects that the probability of continuous flow from the San Marcos Springs by the year 2020 is somewhere between only 50-75% certain (Figure 8). According to Texas Department of Water Resources data, assuming full projected development, the flow from the San Marcos Springs will reach zero around the year 2010 (Figure 9). It appears that there is some difference between methodologies for calculation projections of spring flow for this region, for example, varying degrees of recharge, drought and related water usage may cause the springs to dry up a few years earlier or later than than 2010. It is most significant that all projections show the San Marcos springs without any flow sometime after the year 2000. This is the most serious threat to the continued existence of *G. georgei*. It will also affect every other organism in the San Marcos environment.

Estimates of the required minimum flows from the San Marcos springs necessary to maintain the biota have been given by Espey *et al.* (1975). Given a historical minimum flow of 77.3 m^3/min, Espey *et al.* estimated that the critical flow rate of the San Marcos must be no less than 67.2m^3/min (instantaneous rate), 134.4 m^3/min (monthly average rate) and slightly greater than 168 m^3/min on a yearly average basis. Minimum flows, based upon these projections, would be sufficient to maintain not only water of the proper current velocities and temperature regimes, but also would allow



Three-Dimensional Representation of Projected Pumpage for the Edwards (Balcones Fault Zone) Aquifer

Figure 7


(A)
100
75
50
25
0
% chance of flow
part of year
continuous
SAN MARCOS SPRINGS
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020

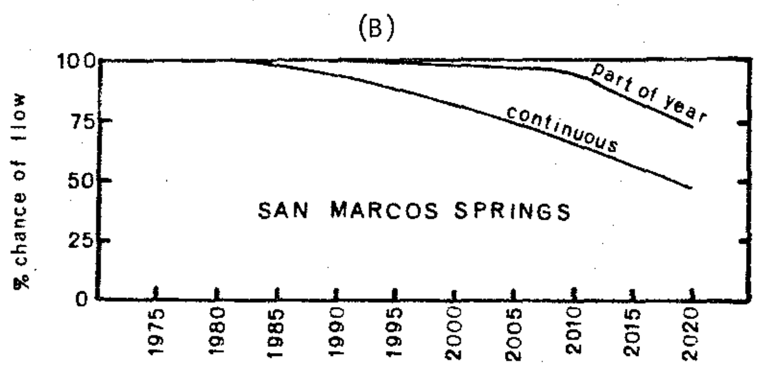

(B)
100
75
50
25
0
% chance of flow
part of year
continuous
SAN MARCOS SPRINGS
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020

Figure 8

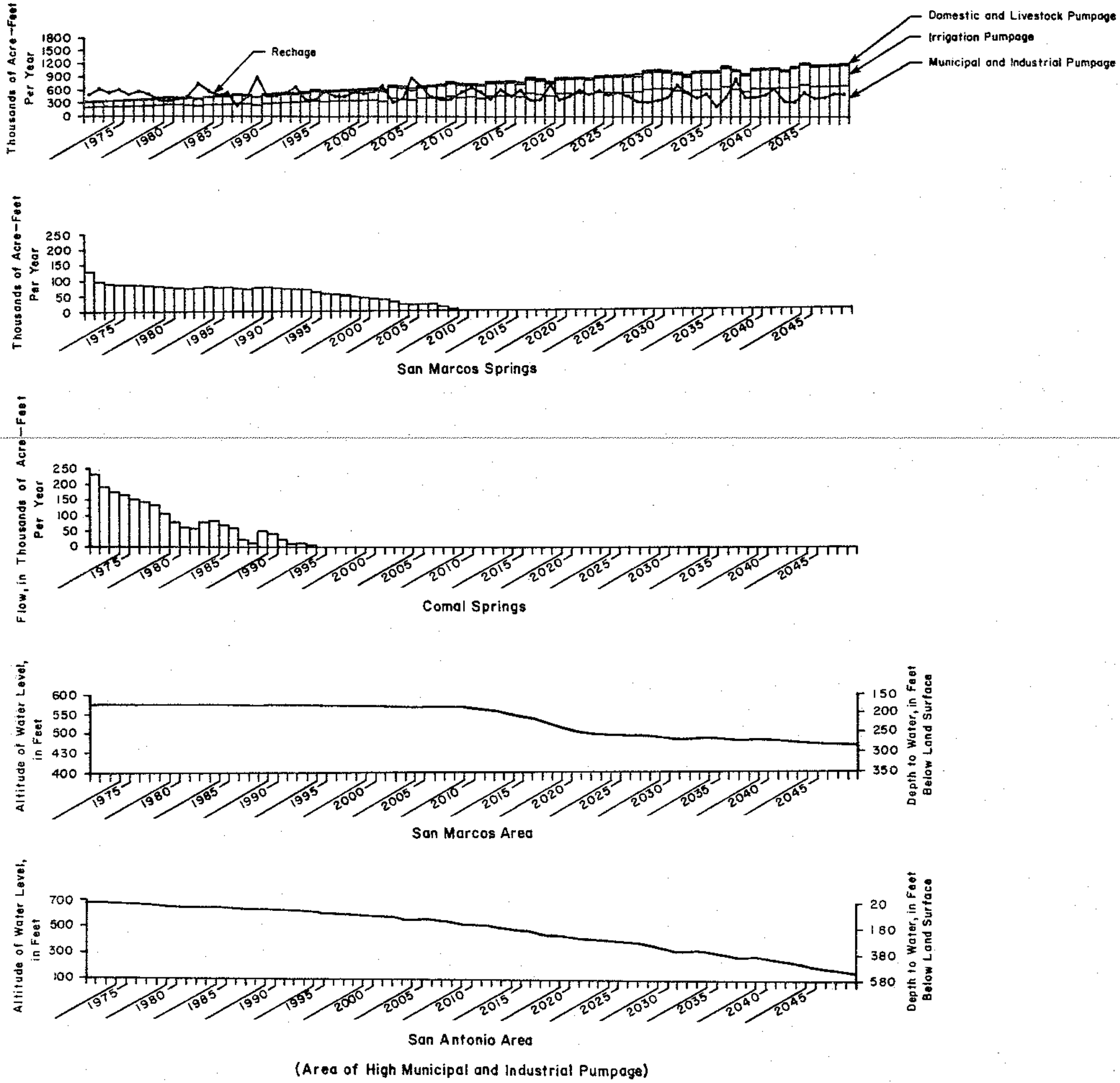

Thousands of Acre-Feet Per Year
Rechage
Domestic and Livestock Pumpage
Irrigation Pumpage
Municipal and Industrial Pumpage
Thousands of Acre-Feet Per Year
San Marcos Springs
Flow, in Thousands of Acre-Feet Per Year
Comal Springs
Altitude of Water Level, in Feet
Depth to Water, in Feet Below Land Surface
San Marcos Area
Altitude of Water Level, in Feet
Depth to Water, in Feet Below Land Surface
San Antonio Area
(Area of High Municipal and Industrial Pumpage)

Figure 9

sufficient water to maintain the river channel's edge and stream bank morphology necessary for the survival of many organisms.

On a more local scale, the city of San Marcos is, at present, undergoing expansive growth (Longley 1975). The effect of urbanization on watersheds is discussed by Edwards (1976) who found that increased urbanization caused increased flooding and erosion (due to uncontrolled runoff), pollution, siltation and a general decrease in species diversity and species numbers in impacted aquatic environments. Although the San Marcos is a larger system than was studied by Edwards, the resulting patterns appear applicable to other aquatic systems flowing through urban centers.

Changes to the upper San Marcos watershed must be approached with extreme caution to avoid degrading any habitat suitable for G. georgei populations. The series of five impoundments proposed by the Soil Conservation Service (U.S. Dept. Agriculture 1978) on tributary creeks feeding into the upper San Marcos River is expected to decrease the severity of flooding in the San Marcos River watershed. This is expected to have a slight benefit on the abundance of G. georgei. A secondary portion of the of the S.C.S. plan is to upgrade recreational facilities in the Rio Vista Park area. We foresee little impact from the upgrading of these facilities on the abundances of G. georgei after the project is completed. However, since the entire range of the fragile San Marcos gambusia is immediately downstream from these facilities, extreme care should be taken during the construction phases to insure the protection of this species.

Hybridization

The production of hybrid individuals between G. georgei and G. affinis has continued for many years without obvious introgression of genetic material into either of the parental species. Given the long history of hybridization between these two species, this factor is not thought to be of primary importance in considerations of the endangered status of G. georgei. Hybridization will undoubtedly continue, but so long as the proportion of hybrids remains relatively small compared to the abundance of "pure" G. georgei, few problems associated with genetic swamping or introgression should be present.

Exotic Species and Competition For Resources

Exotic species pose a significant threat to G. georgei, especially with individuals of Poecilia, which share many similarities in habitat use with G. georgei. Although Poecilia in the San Marcos River exhibit broad thermal tolerances (especially to high temperatures), overlap in habitat with G. georgei appears especially great during winter and spring when thermally moderated, quiet, shallow habitats are chosen. Juvenile centrarchids and cichlids, in the San Marcos River, also appear to share habitat similarities with *G. georgei* populations. In addition, the abundance of the predaceous characin (*A. mexicanus*) may have an additional adverse impact on the abundance of the San Marcos gambusia.

Current Status of *Gambusia georgei*

The San Marcos gambusia, in addition to the U.S. Department of Interior's proposed designation as an Endangered species, is also listed as Endangered by the International Union for the Conservation of Nature and Natural Resources (I.U.C.N. 1980), the Endangered Species Committee of the American Fisheries Society (Deacon et al. 1979) and the Texas Organization for Endangered Species (T.O.E.S. 1979). We concur with the assessment of *G. georgei* by these groups and consider the San Marcos gambusia to be endangered using all presently available information. *Gambusia georgei* is extremely rare and likely on the verge of extirpation.

The continued survival of *G. georgei* appears dependent upon the maintenance of a continual flow from the San Marcos Springs and the further presence of the appropriate ecological conditions (such as crucial, undisturbed habitats) in the San Marcos River. The projected increases in water usage and resulting losses of water in the streams on the Edwards Plateau region is a problem which will not easily be resolved. Human cultural demands on the water supply of this area exceed the amount of water available on a continued basis. This is expected to become an even greater problem in the future.

Stability within the San Marcos River system appears to be the key to the survival of the San Marcos gambusia. This stability will have the added benefit of not only insuring the protection of *G. georgei*, but also conserving the other unique elements of the Sam Marcos aquatic environment as well.

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