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Non-Native Suckermouth Armored Catfishes in Florida: Description of Nest Burrows and Burrow Colonies with Assessment of Shoreline Conditions

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Purpose

Non-native populations of the Neotropical family Loricariidae, the suckermouth armored catfishes, have been introduced and become established in many warm-climate regions of the world, including parts of the United States (e.g., Florida and Texas). In Florida, the most common loricariid catfishes are members of the genus *Pterygoplichthys* (Figure 1). Over the past 20 years these catfishes have invaded most inland drainages in the central and southern parts of the Florida peninsula. In certain rivers, canals, and lakes, they are widespread and abundant, accounting for a large proportion of the total fish biomass. Adult *Pterygoplichthys* attain sizes well over 40 cm long.

In both their native and introduced ranges, *Pterygoplichthys* and certain other loricariid catfishes excavate and maintain burrows in shoreline slopes for use as spawning and nesting sites (Figure 2). The burrows are reportedly excavated and maintained by adult males. In places where these catfish are abundant and the shore habitat suitable, burrows are common. Burrows typically occur in aggregates with individual colonies consisting of a few to perhaps dozens of burrows. In larger reaches of some waterways (e.g., Florida's St. Johns River) burrows created by *Pterygoplichthys* number in the hundreds or even thousands. The burrows are thought to cause or exacerbate bank erosion. Presumably, greater burrow densities increase the likelihood of bank failure. However, there are no quantitative data available to adequately evaluate possible

Figure 1. Adult male Pterygoplichthys *taken from Oklawaha River drainage, Florida on 4 June 2006. Fish measured 536 mm total length (415 mm standard length) and weighed 1.4 kg. At time of capture this catfish was stationed at the entrance of a nest burrow containing eggs. (Photograph by L. G. Nico)*

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Figure 2. Nest burrows of loricariid catfishes in their native range in South America: Cano Mavaquita, upper Orinoco River basin, Venezuela. Type locality for Leporacanthicus triactis *(Isbrücker et al. 1992). (Photograph by L. G. Nico)*

associations between presence and abundance of burrows and bank instability.

The goal of the present study was to obtain baseline information on the burrows of *Pterygoplichthys* in Florida and to provide a preliminary assessment of shoreline conditions, including factors associated with bank stability and erosion. Specific objectives included: 1) survey portions of selected rivers and canals in peninsular Florida to determine the number and location of loricariid catfish nest burrows; 2) measure and characterize burrow structures and surrounding habitats; 3) identify shoreline features correlated with the presence of burrows; and 4) categorize bank condition and erosion. To better understand the likely impacts associated with these catfish and their burrows, literature on the burrows of loricariid catfishes and other animals was also reviewed.

Introduction

The suckermouth armored catfishes (family Loricariidae) are an extremely large and diverse group of New World freshwater fishes. The family includes six subfamilies, an estimated 90 genera, and approximately 700 described species (Armbruster and Page 2006, Nelson 2006) with many more species remaining to be described (Reis et al. 2003, Birindelli et al. 2007). The natural distribution of this catfish family extends from the La Plata River of southern South America northward to Costa Rica of Central America, or from about 35° S to 12° N latitude (Berra 2001). Members of the family may be found from low elevations up to 3,000 m and, depending on species, adult loricariids range in body size from relatively small, less than one or a few centimeters long, to over 1 m total length (Fuller et al. 1999, Nelson 2006). Although there is dramatic variation in body shape and dentition, as a group loricariids are characterized by a depressed body covered by large bony plates, a unique pair of maxillary barbels, and a ventral suctorial mouth (Covain and Fisch-Muller 2007). The sucker mouth of loricariids enables adherence to the substrate even in fast-flowing water and, in combination with specialized teeth, is an adaptation for feeding by scraping submerged substrates to consume algae, small invertebrates, organic sediments (e.g., detritus and mud), and even wood (Schaefer and Stewart 1993, Nico and Taphorn 1994, Yossa and Araujo-Lima 1998, Delariva and Agostinho 2001). Many members of the family are popular aquarium fishes used for controlling algae in tanks.

Several members of three loricariid genera (*Hypostomus*, *Pterygoplichthys*, and *Ancistrus*), all belonging to the subfamily Hypostominae, have been introduced outside their native ranges. All or most introductions into the wild are likely linked to the ornamental fish trade (Fuller et al. 1999, Nico and Martin 2001, Vidthayanon 2005, Page and Robins 2006). Some of these non-native populations are firmly established in a number of warm-climate regions around the world. Among introduced loricariids, members of the genus *Pterygoplichthys* are the most widely introduced (Figure 1) with reproducing non-native populations now documented as occurring in North and Central America, Asia, the Caribbean, and Hawaii. *Pterygoplichthys* are one of the most abundant fish species

in certain habitats within their native range (Saint-Paul et al. 2000) and introduced populations are large and, in some places, they comprise a substantial proportion of the total fish biomass (personal observation. Leo G. Nico).

In North America *Pterygoplichthys* are particularly common in certain drainages in the southern United States in Florida and Texas (Fuller et al.1999, Nico and Martin 2001) and in Mexico (Mendoza et al. 2006, Wakida-Kusunoki et al. 2007). Reproducing populations are also known from the islands of Oahu in Hawaii (Sabaj and Englund 1999, Yamamoto and Tagawa 2000), Puerto Rico (Bunkley-Williams et al. 1994), and Jamaica (Jones 2008). In Asia, *Pterygoplichthys* species have become increasingly widespread. The earliest documented records are from Singapore (Lim and Ng 1990: misidentified as "*Hypostomus*;" also see Page and Robins (2006)) and Indonesia (Kottelat et al. 1993). More recently, members of the genus have been reported as established or possibly established in Japan (Nakabo 2002), Taiwan (Liang et al. 2005), Thailand (Vidthayanon 2005), the Philippines (Chavez et al. 2006), Malaysia (Page and Robins 2006), and Vietnam (Serov 2004, Levin et al. 2008). An unidentified *Pterygoplichthys* (= *Liposarcus*) was reported as occurring in a river in Costa Rica (Bussing 2002), but the situation is dynamic. In late 2008, William Bussing (personal communication) informed the authors that introduced loricariids were spreading rapidly in Atlantic slope drainages of Costa Rica, but the identity and number of species have not been determined. Collections or sightings of *Pterygoplichthys* or *Hypostomus* have also been reported from other locations outside their native ranges, although there is as yet little or no evidence of natural reproduction. For example, a specimen identified as *P. disjunctivus* was recently taken from the Asi River in Turkey (Ozdilek 2007).

Pterygoplichthys are medium to moderately large fishes (Figure 1). Captured adults from introduced populations generally measure 30 to 55 cm total length (TL) although maximum size probably exceeds 70 cm TL (Liang et al. 2005; unpublished data, Leo G. Nico). Over the past 15 years, *Pterygoplichthys* species in Florida have become increasingly widespread and abundant (Fuller et al. 1999, Nico 2005). The authors' fish surveys, together with reports and data from others (e.g., Shafland et al. 2008) indicate that these catfishes have rapidly expanded their ranges and one or more *Pterygoplichthys* taxa now occur in all major drainages and most minor drainages in the central and southern part of the Florida peninsula. In many waterways *Pterygoplichthys* have become a major component of the aquatic community in terms of both numbers of individuals and fish biomass (personal observation, Leo G. Nico). Environmental impacts are not fully understood, but where these introduced loricariids are abundant, their feeding behaviors and burrowing activities can cause considerable disturbance (Fuller et al. 1999, Yamamoto and Tagawa 2000, Hoover et al. 2004). Among introduced loricariid catfishes, both *Pterygoplichthys* and *Hypostomus* are known to excavate burrows along the sloped shorelines of lentic and lotic habitats. However, there is little information in the scientific literature on the burrows and nesting behaviors of these catfishes. This shortage of information is surprising, given the broad distribution and abundance of these catfishes within and outside their native ranges.

This bulletin describes the burrows and burrow colonies of *Pterygoplichthys* based on field observations on non-native populations inhabiting canal and river systems of peninsular Florida. Preliminary observations on active nests in clear-water stream habitats are included. A review of the literature on burrowing by loricariids, burrowing by other fishes, and on burrowing by other non-native aquatic species is also provided. The general goal of the research on introduced *Pterygoplichthys* was to gather information on invasive populations, especially with regard to their natural history and ecological effects.

Methods

Study Area

Field work was conducted in the central and south-central part of the Florida peninsula between latitudes 26° 59'N and 29° 13' N (Figure 3). Drainages surveyed for catfish burrows included parts of two artificial canals and four natural rivers: St. Lucie Canal, Okeechobee Rim Canal, Peace River, Withlacoochee River, Alafia River, and Oklawaha River. Tributaries of a few of these waterways were also investigated. Selection

of these waterways and reaches was based on several criteria: 1) drainages were known or strongly suspected of containing *Pterygoplichthys*; 2) waterways represented a diversity of habitat types, ranging from artificial canals to natural flowing systems; and 3) many of the waterways were already familiar and were accessible by small boat. Nest burrows in a few of the waterways chosen for the surveys had been observed during previous field work.

Field surveys and measurements

Field work was conducted in April and May 2006. During this period, selected reaches of the six waterways were surveyed and a range of exposed (above water line) and some submerged catfish burrows were located, measured, and assessed (Figure 3). To locate catfish burrows, waterways were surveyed by boat. The shoreline, including exposed bank and adjacent submerged shallows, was visually inspected. All surveys were conducted during good weather conditions and daylight hours. Field work was performed by two- or three-person crews traveling in a small watercraft, either non-motorized canoe (upper Withlacoochee River) or by motorized canoe or john-boat (all other sites). In general, the visual hunt was focused along a single bank during passage upstream and focused on the opposite bank during the return journey downstream. The search for burrows consisted of traveling slowly (less than about 10 km/h) within about 5 to 10 m from the targeted shore, documenting presence of burrows or other cavities in the bank. In most instances detection of one or a few burrows led to discovery of additional burrows nearby. Geographic coordinates of burrow sites were determined using a GPS device.

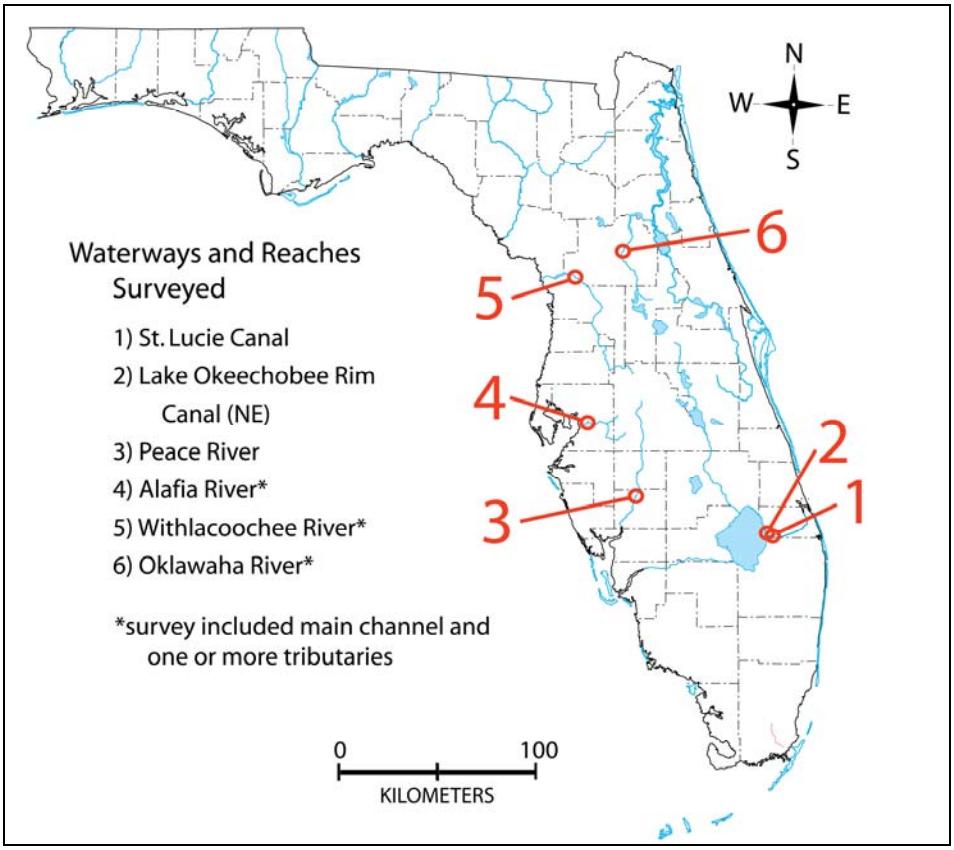

Figure 3. Map of Florida showing the waterways and location of reaches surveyed for nest burrows of loricariid catfish during spring 2006.

The probability of detecting burrows varied within and among sites due to local conditions (e.g., water levels, water clarity, type and extent of shoreline cover). The likelihood of detecting burrows visually, especially in turbid waters, is greatest when water levels are low and many burrows are fully exposed above the water line. During 2006 water levels of many rivers in peninsular Florida were low throughout much of the spring and early summer. However, even during low water some burrows are difficult to detect. In some reaches, large portions of the shore were obscured by dense vegetation (e.g., leafy shrubs, cypress stands). Some waterways had relatively clear water, facilitating the detection of submerged burrows. In contrast, it is likely that a higher proportion of submerged burrows went undetected in sites with turbid water. In addition, single burrows were more difficult to detect than groups of burrows and burrows below the water line or in root mats were also less likely to be observed than burrows in open areas.

Sighting of any bank hole was immediately followed by close inspection of the sighted cavity to judge whether it was a catfish burrow and to determine if there were additional burrows in the vicinity. Some bank holes were degraded to such an extent that it was not always possible to confirm whether

the "burrow-like" structure was created by *Pterygoplichthys*. These unconfirmed holes were noted but not included in subsequent burrow analyses. In the field, each burrow site was assigned a unique number and individual burrows of those sites chosen for close examination were also coded. To provide additional documentation, burrows, burrow colonies, and surrounding habitat were photographed with a digital camera. In a few cases, burrow counts were verified and augmented by later examination of photographs.

A wide variety of descriptive information and measurements were recorded for most sites where nest burrows were found. Data collected from *Pterygoplichthys* burrows included burrow length, maximum width at entrance, maximum height at entrance, vertical and horizontal distance to water edge (measured from bottom of burrow entrance), tunnel shape (e.g., single tunnel versus bifurcated), burrow volume, average slope of tunnel, horizontal angle of burrow entrance relative to shoreline (downstream = 0 degrees), compass bearing perpendicular to the shore, burrow condition, burrow moisture, and occupancy of burrow (i.e., active versus abandoned). Because the majority of burrow tunnels were somewhat triangular in cross section, burrow volumes were calculated by multiplying the average triangular area of the burrow entrances by burrow length.

Burrow moisture is an indication of the amount of standing water in burrows at the time of measurement, ranging from completely wet if fully submerged, to dry if completely above the water line. The horizontal angle of burrow entrance relative to water edge (i.e., shoreline) provided information on whether a burrow tunnel was angled downstream (e.g., 45 deg) and presumably away from direct current, oriented upstream (e.g., 135 deg), or perpendicular (90 deg). If a submerged burrow was occupied or guarded by an adult *Pterygoplichthys*, the burrow was designated as active. All other burrows, including dry burrows, were considered inactive or abandoned. To document structure, internal materials, and presence of eggs, the authors visually inspected the interior of many burrows, in some cases with the aid of lanterns. A few tunnels were probed or opened by hand.

In addition to measurements on individual burrows, quantitative and qualitative data were recorded for shoreline habitats where catfish burrows were discovered. These included slope of bank (at the entrance of each burrow), height of exposed bank, vegetative groundcover, and an estimate of bank stability/state of erosion. Soil compaction was measured on the bank adjacent to each burrow entrance (length of probe to achieve 300 psi). At selected colonies, a composite sample of soils was collected from all or most of the burrows of the colony (see below).

Individual nest burrows, burrow colonies, and shoreline habitats were measured by using a combination of meter sticks, surveying rods, and tape measures, supplemented whenever necessary with the use of an adjustable T-square and other measuring devices (e.g., rangefinders). The slopes of banks and burrows were determined using a Swanson® magnetic angle finder and a 60-cm-long Stabila® 86 electronic inclinometer and level (both instruments sealed in a plastic wrap to prevent moisture damage). Depending on local conditions, angle measurements were occasionally verified or determined in conjunction with other types of angle finder devices (e.g., Empire® angle finder and Sealey® stainless steel protractor). Soil compaction was estimated with a DICKEY-john® soil compaction tester (0 to 600 psi).

Soil composition analysis

Soil samples were collected from eight colonies. For each colony, a sample consisted of a composite taken from outside and adjacent to the burrow entrance of two or more nest burrows. All samples were from exposed colonies (above water line), except for two subsamples from a partly-active colony in the Oklawaha River. Soil samples from each site were saved in separate plastic bags prior to analysis. All resulting soil samples were provided to Universal Engineering Sciences, Inc., a full-service geotechnical engineering laboratory located in Gainesville, Florida, to determine soil composition, including soil description, natural moisture, and particle-size distribution. Particle size was determined by dry sieve analysis, using six sieves (mesh size numbers 4, 10, 40, 60, 100, and 200). Their procedures followed those of the American Society for Testing and Materials (ASTM): D422 Standard Test Method for Particle-Size Analysis of Soils; and D2216 Test Method

for Laboratory Determination of Water (Moisture) Content of Soil and Rock. Excess soils from each of the samples that were not needed for analysis were returned for possible future laboratory analyses.

Evaluation of the relationship between burrows and bank stability

To investigate relationships between loricariid catfish burrows and bank stability, the authors examined the distribution pattern and density of burrows and analyzed data on the shoreline habitats selected for colony sites by *Pterygoplichthys*. Attempts to quantify impacts were limited to evaluation of small portions of shoreline containing selected colonies and based on measurements taken during a single visit. According to Ott (2000), "…. a bank is stable if it does not change appreciably within a defined time frame." Because erosion is a dynamic and long-term process, occurring to varying degrees in all waterways, it is difficult to measure the contribution made by burrowing animals during a single season. According to Lawler (1986), even where bank retreat is monitored, it is seldom easy to pinpoint the significant features of a site that are apparently promoting or retarding bank erosion. The situation is especially complex in streams and canals where water levels and flows change considerably over the course of a year (see Couper (2004) and Duan (2005)). Although the existence of bank vegetation is considered a stabilizing factor, most colony sites are largely devoid of ground and leafy vegetation when the burrows are submerged and actively used by loricariid catfish. Consequently, a measurement of vegetative cover has only slight relevance in an evaluation of the effects of *Pterygoplichthys* burrowing.

The contributions of loricariid catfish burrowing to erosion and sedimentation may be thought of as having both immediate and long-term effects. Initial impacts from burrows are linked to the amount of sediment removed from shorelines during burrow excavation. Long-term impacts such as compromised ability of banks to persist through the next flood require periodic monitoring of individual sites and are beyond the scope of this study (refer to Couper (2004) and Duan (2005) for discussions on appropriate spatial and temporal measurement scales in the study of river bank erosion).

In their evaluation of the impacts of introduced Chinese mitten crab burrows, Rudnick et al. (2005) calculated erosion impact as the amount of sediment removed by the crabs per volume of stream bank. Based on a modification of the methods used by Rudnick et al. (2005), sediment removal was calculated as the percent of soil removed by *Pterygoplichthys* (the sum of all volumes of burrows present in a colony) per the rectangular-shaped portion of the bank occupied by a colony (Figure 4).

As part of the present study, the largest colony measured in each waterway surveyed was selected for analysis. Burrow volumes were calculated as described above and no adjustments were made for old or degraded burrows. Because the majority of burrows measured were either less than 1 m in length or were angled so that they did not head straight back into the bank, all or most burrowing was concentrated in the 1-m depth of the bank. Therefore, the available volume of soil for burrowing was the vertical and horizontal extent of the colony multiplied by 1-m depth. For

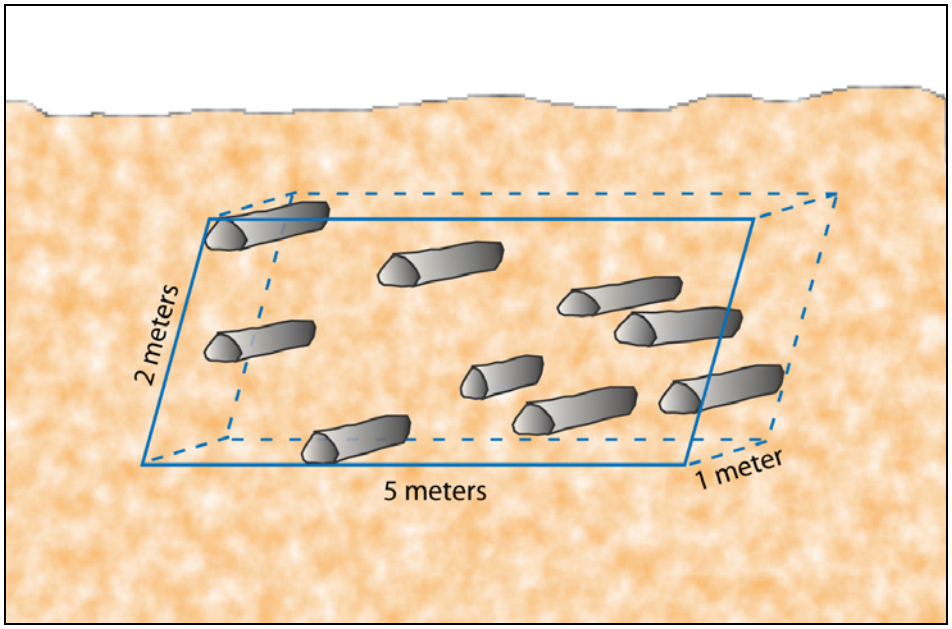

Figure 4. Diagram of a burrow colony showing the three-dimensional portion of the shoreline used to calculate the relative amount of sediment removed by Pterygoplichthys.

example, if the lowest and highest burrow openings were 2 m apart, and the most upstream and most downstream burrows in the colony were 5 m apart, then the rectangular area was 2 × 5 m and the total volume of the involved bank would equal 10 m^3 (Figure 4).

Analyses and statistics

Multivariate ordination, correlation, and paired variable plots were used to explore possible relationships among the recorded array of burrow and habitat characteristics. PRIMER 6 software (Clarke and Warwick 2001) was used to create principal components analysis (PCA) plots of burrow dimension and soil composition data. Because burrow data were collected in various units ranging from angles in degrees to inches of penetration to achieve soil compactions of 300 psi, these data were normalized prior to creating the complete burrow PCA. When only height, width, and length burrow parameters or soil composition proportions were analyzed, the PCAs were done on untransformed data.

Table 1
Summary of the 2006 Loricariid Burrow Field Surveys (Burrow counts do not include holes and other cavities if reasonable doubts existed concerning their creation. A burrow site is defined as a bank area within a single reach (<50 m shoreline) where all burrows were in relatively close proximity. Burrow sites with multiple burrows were considered colonies)

Drainage	Dates	Channel Length Surveyed (km)	Burrow Sites Detected [per km]	Number Burrows Detected [per km]
Withlacoochee River (South)[a]	April 24 & 27, May 5	27.5	4 [b] [0.1]	21 [b] [0.8]
St. Lucie Canal	May 15	4.4	2 [0.5]	10 [2.3]
Lake Okeechobee Rim Canal	May 15	4.6	0 [c]	0 [c]
Peace River	May 18	2	5 [d] [2.5]	41 [d] [20.5]
Alafia River [a]	May 19	11.25	2 [0.2]	21 [1.9]
Oklawaha River[a]	May 30	6.75	5 [0.7]	25 [3.7]
Totals		56.5	18 [0.3]	118 [2.1]

[a] Survey included main channel and one or more tributaries.
[b] Includes one colony site where individual burrows could not be counted because of extreme degradation.
[c] Numerous exposed bank holes and undercuts were found in the Lake Okeechobee Rim Canal but it could not be determined if these represented old and highly weathered catfish burrows or undercuts created by other processes.
[d] Peace River census resulted in detection of at least five burrow colonies; burrows from two of the five colonies were not measured.

Results

Numbers and distribution of burrows and burrow colonies

Sampling information on the six waterways surveyed is summarized in Table 1. During the study period, approximately 56 km of waterway were surveyed and 118 burrows considered to have been excavated by *Pterygoplichthys* were documented. In some waterways, holes above the water line could not be definitively attributed to the work of non-native catfish, although it is likely that at least some of these holes were *Pterygoplichthys* burrows from previous years. Generally, these holes appeared to be highly degraded because of erosion or wave wash. It is probable that additional burrows were present but went undetected. For example, although a large colony was found in the Withlacoochee River, it was suspected that there were additional burrows below water due to the geometry and composition of the site's bank. However, it was impossible to view any additional burrows in the deep and turbid water.

Burrows were detected in five of the six waterways surveyed (Figure 3, Table 1). The only exception was the Lake Okeechobee Rim Canal. Although that waterway had many exposed cavities along the upper edge of the canal's bank line, they were extremely degradated and it could not be concluded with any confidence that these undercuts had been created by *Pterygoplichthys*. Lake Okeechobee and its adjacent canals are known to contain large populations of *Pterygoplichthys* (Nico 2005).

The 118 observed catfish burrows were distributed among 18 sites, with the number of burrows per site ranging from 1 to 16 (mean = 6.6). Sites with multiple burrows, where nearest burrows were generally situated within a few meters of one another, were considered colonies. Among these, 15 burrow sites consisted of at least four burrows. In two other cases, sites consisted of only two burrows. Only one site held an isolated burrow considered to be

made by *Pterygoplichthys*. A few isolated cavities at other sites were either highly degraded or so irregular (e.g., odd-shaped cavity under a large stone) that they were not treated as *Pterygoplichthys* burrows nor were they included in the analyses.

All detected burrows were located along the river and canal banks. No burrows were observed in the bed of waterways, although some waterways were deep and turbid and any bottom burrows would have been obscured. Similarly, it is conceivable that burrows were present in stream bottoms where there were numerous limestone boulders and ledges. Of the burrows detected, 85 (72 percent) had entrances that were exposed above the water edge, either entirely or partially (>50 percent of burrow entrance above the water line). Some colonies included a combination of both submerged and exposed burrows.

Burrows were not distributed evenly within or among waterways (Table 1). The section of the Peace River that was sampled had the highest densities of burrow sites (2.5 per km) and burrows (20.5 per km). This area was mostly exposed banks that were suitable for burrowing and ideal for detecting burrows at the low water stage during the site visit. In natural rivers, all observed burrow colonies were located along the outer bends of channels, but in most surveyed reaches only a relatively small proportion of cutbanks contained burrows. Burrows were also absent from certain sites where the conditions, based on characteristics of sites with burrows, seemed suitable. Burrow colonies were much more evident in upstream portions of natural drainages where there were steeper banks and greater fluctuations in water levels. In downstream portions of rivers and other reaches where banks were low or almost nonexistent, burrows were either absent or went undetected.

Individual burrow colonies encompassed relatively small sections of bank. The horizontal extent (i.e., alignment parallel to shoreline) of colonies varied widely, ranging from one or a few meters for small colonies, to well over 15 m for colonies composed of many burrows. In contrast, the vertical layouts of most colonies were within a 1-m stratum of shoreline. In general, burrows within colonies were relatively contiguous, but in some cases dense masses of tree roots and other structures subdivided the colonies into subgroups. For example, in the Withlacoochee River, a series of burrows were present along a single sharp outer bend of the river. At this site docks and a boat ramp widely separated the burrows present into two main groups.

In most colonies, some burrows were grouped together. Among these clumped burrows, the distance between adjacent burrow openings was typically less than 1 m. In some cases only about 25 cm of soil separated adjacent burrow openings. In terms of vertical distribution, the lowest burrow opening was typically never less than about 1.5 m below the highest burrow within a colony. Due to the water level at the time sampled, exposed burrows were located up to 1.35 m above and 4.7 m horizontally out from the water's edge. These two parameters were positively correlated and largely described the overall bank slope at sampling sites (Figure 5).

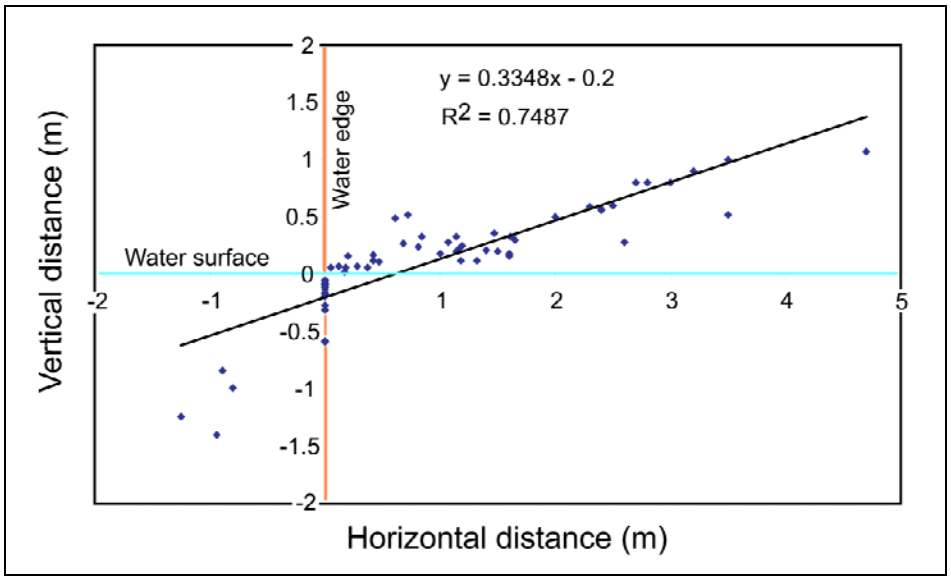

Figure 5. Relationship between vertical and horizontal distances from Pterygoplichthys *burrows to waterline (adjusted R^2 = 0.74, p<0.001). The 0-horizontal line represents the waterline. Burrow points above this line were those whose entrance was completely above the water. The 0-vertical represents the water's edge. As shown in this figure, most of the observed nest burrows were exposed because of low water and most of these were within 2 m out from the water's edge, but less than 0.5 m above water surface.*

Burrow characteristics

Complete measurements were taken for 63 burrows; 58 of these were considered to be in sufficient condition (e.g., tunnel had not completely collapsed) to be included in statistical analyses. Additional burrows were examined in the field, but only partial measurements or other information were recorded for these structures. Most burrows (61 of 63 burrows examined) were rather simple structures, consisting of a single opening and a relatively straight tunnel without marked bends or bifurcations. However, there were two exceptions. One burrow was bifurcated (Y-shaped), having a single entrance and then splitting near its midpoint into two separate, blind chambers. In contrast, another burrow structure had two openings, its two entrance tunnels converging into a single interior tunnel. Based on its geometry, the two entrances tunnels were probably excavated by different catfish that dug into a common end.

The interior slope of individual tunnels typically angled gently downwards, ranging from -18 to 11 degrees (mean = -8 degrees) (Table 2). Consequently, burrows with entrances slightly above the water surface tended to be dry at the opening but contain water toward the rear. Horizontal alignment of tunnels, relative to the shoreline edge, varied even within colonies, with some tunnels angled downstream, some upstream, and some approximately perpendicular. The average alignment was slightly downstream (81 deg). The proximity of tunnels in some colonies and the wide variation in tunnel horizontal alignment likely explain the two-mouthed tunnel described above.

Table 2
Dimensions of *Pterygoplichthys* Burrows Measured in Five River and Canal Systems, Florida

Dimension	n	Minimum	Maximum	Average	Standard Deviation
Bank slope (degrees)	61	30	92	64.4	17.5
Burrow vertical position (cm to water surface)	74	-140	135	28.7	56.2
Burrow horizontal position (cm to water edge)	63	-125	470	103.6	124.6
Burrow height - floor to roof (cm) at entrance	60	7	27	14.2	4.2
Burrow width (cm) at entrance	62	11	45	21.0	6.8
Burrow tunnel length (cm)	63	20	130	77.5	27.5
Burrow volume (cm^3)	60	1,960	58,630	12,911	10,476
Burrow slope (along tunnel) (degrees)	60	-18	11	-8.0	7.1
Burrow angle (degrees, downstream = 0)	60	15	160	81.7	24.6
Soil compaction – inches of rod to achieve 300 psi	55	0.5	28	10.1	8.3

The entrance and tunnels of most burrows were somewhat triangular in cross section, although some were arched and a few oval or rounded at the mouth. In some cases, the burrow geometry was partly determined by adjacent structures (e.g., tree roots). Burrow tunnels ranged from 20 to 130 cm (mean = 77 cm) in length, and the dimensions of the entrance ranged from 11 to 45 cm (mean = 21 cm) in width, and 7 to 27 cm (mean = 14 cm) in height (Table 2). Heights of burrow entrances were consistently less than entrance widths, with height averaging 66 percent of width. Burrow height and width were positively correlated (Figure 6).

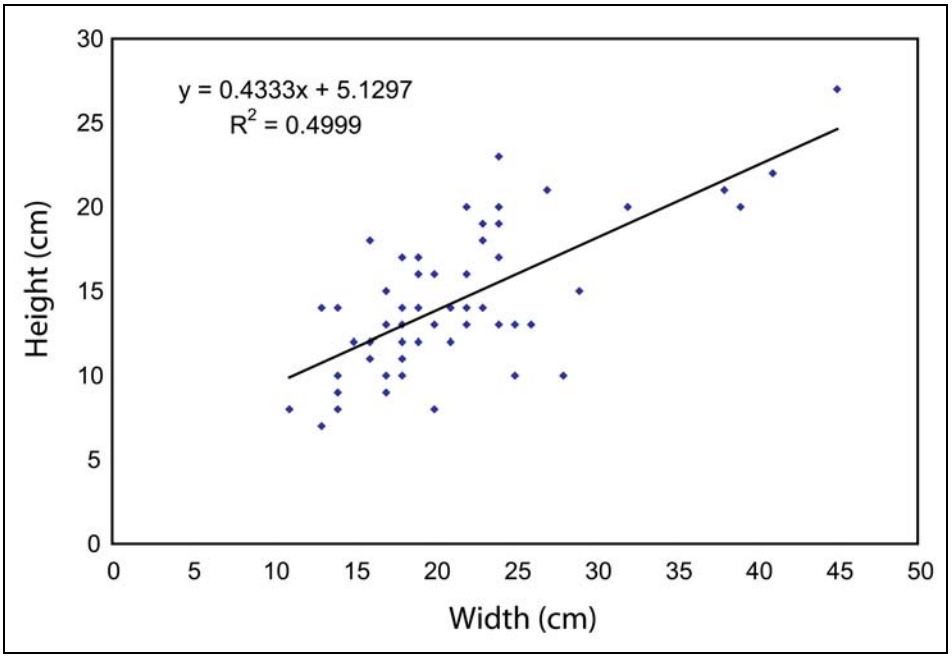

Figure 6. Relationship between Pterygoplichthys *burrow entrance height and width (adjusted R^2 = 0.49, $p < 0.001$).*

Variation in both tunnel length and volume was likely related, at least in part, to burrow age and condition (also see later section Evaluation of Bank Stability and Erosion). For example, some of the largest burrows were either active nests or considered to be only recently abandoned. The four Oklawaha River burrows had the largest interior volumes and also were the deepest below the water surface (Figure 7). Three of these were also the only active burrows measured. In contrast, exposed burrows located high on the bank tended to be smaller, presumably a result of bank erosion. In at least one case, it appeared that the catfish had begun excavating a burrow but after only a few centimeters of digging, abandoned the unfinished burrow.

The complete burrow dimension PCA plot (Figure 8) revealed that although burrows were sampled across the state, there was no distinct pattern of burrow dimension with sampling site. Only four Oklawaha River burrows clearly separated from the rest of the sites. Three of these four burrows were active, each occupied by an adult *Pterygoplichthys* guarding the burrow entrance. The first principal component axis (PC1) accounted for 33 percent of variation and was associated with height and width of burrows and vertical distance to water surface. PC2 was associated with burrow length, burrow slope, and angle relative to flowing water, but only accounted for an additional 22 percent of variation.

When the PCA was limited to burrow height, width, and length, the first two principal components accounted for 99 percent of the variation (Figure 9). PC1 was

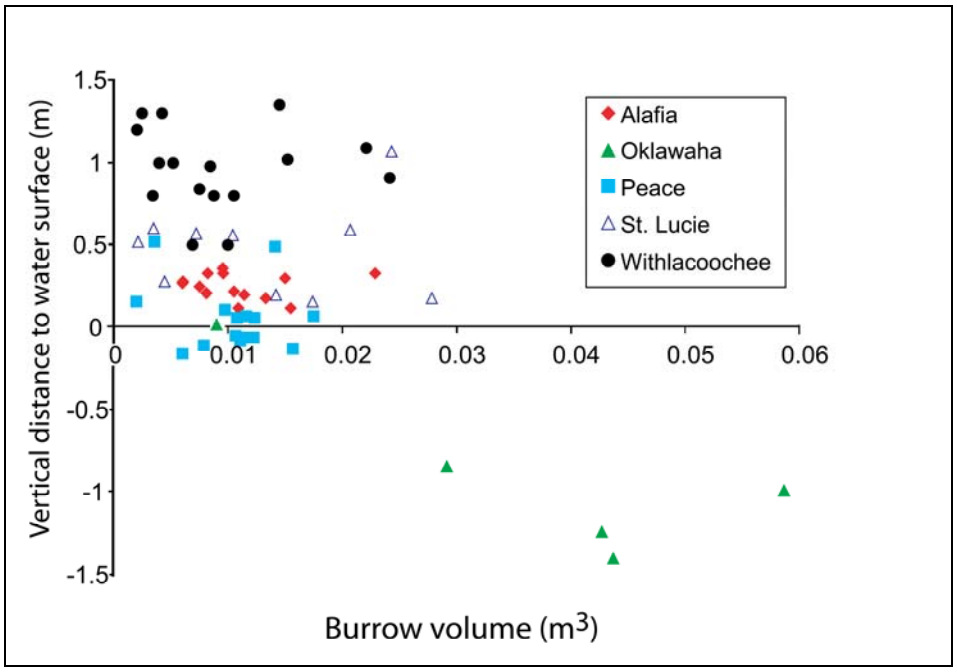

Figure 7. Relationship between burrow volume and vertical distance to water surface. Note that the three Oklawaha burrows with the largest volumes were active with catfish tending nests.

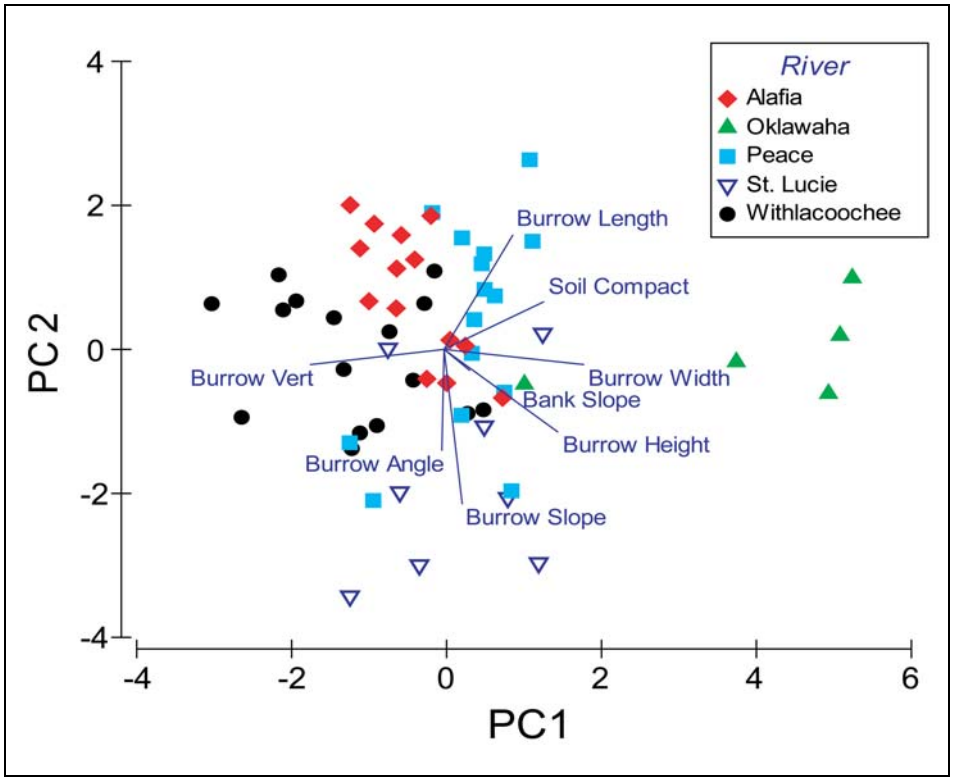

Figure 8. Principal component analysis plot of Pterygoplichthys *burrow dimensions from Table 2 (excluding volume) measured at 58 burrows in five river and canal systems in Florida with principal component vectors superimposed. PC1 is associated with height and width of burrows and vertical distance to water surface. PC2 was associated with burrow length, burrow slope, and angle relative to flowing water.*

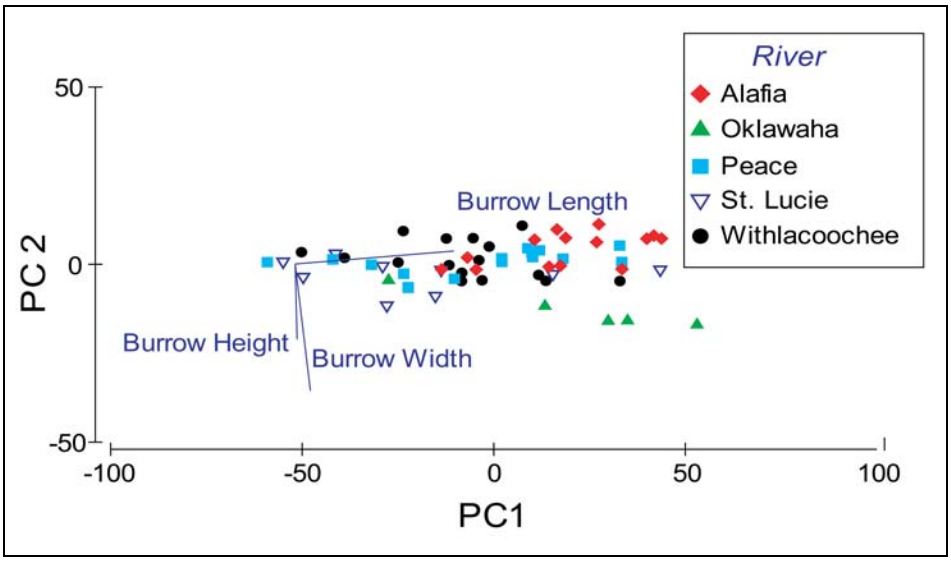

Figure 9. Principal components analysis of burrow height, width, and length among 58 burrows in five Florida river systems. PC1 is associated with increasing length, while PC2 is associated with increasing height and width.

associated with increasing length, while PC2 was associated with increasing height and width. Again, the active Oklawaha burrows separated from other sites.

Burrow colony habitats

Habitats with burrow colonies were fairly diverse, evidence that *Pterygoplichthys* are relatively flexible in their choice of sites for burrow construction, spawning, and nesting. Burrows were present in small streams (e.g., Alafia River), moderate-sized streams, and artificial canal habitats, representing an array of water types and flow regimes. In both canals and rivers, burrows were located on sloping channel banks and all appeared well within the "bankfull stage" limits of respective waterways. In natural rivers, all colonies were found along the outer bends of channels, although the geometry of bends selected varied from slight meanders to sharp. In canals, burrows were found along straight sections where much of the bank was exposed and steep.

The height, cross-sectional shape, and general slope of river and canal banks with colonies were also diverse. The cross-section morphology of most banks was not uniform, often irregularly shaped and with a rather stair-stepped profile at some sites. In stair-stepped banks, burrows were usually situated in one or more of the strata with the greatest incline. The height of exposed banks with burrows ranged from less than 1 m to over 3 m. In most sites the burrows were located well below the top of the bank. In contrast, a series of cavities—possibly created by *Pterygoplichthys*—along the shore of the Lake Okeechobee Rim Canal were found within the uppermost meter of the bank.

The portion of the banks with burrows typically contained few leafy or herbaceous plants. However, as is normal in riverine environments, herbaceous and some small woody plants were found sprouting within burrow colonies exposed by low water. As would be expected, the longer the exposure, the greater the plant coverage. However, even in exposed areas the vegetation was relatively sparse, probably due to a combination of periodic inundation and scour. Parts or all of some colonies were closely associated with the large roots of riverside trees (e.g., cypress). In these places, root mass was partially exposed along the bank and burrows had been excavated among the large roots. In the St. Lucie Canal, some of the burrows were along the uppermost edge of the rip rap rock.

Land habitat within or immediately adjacent to where burrow colonies were present varied. Habitat included narrow bands of gallery forest, cattle pasture, old fields, riverside clubhouses and other residences with boat docks, and a mix of other land uses. Most waterway reaches surveyed were located in rural or low-density residential areas. None of the sites was urban.

Soil characteristics of burrow colony sites

Analysis of particle sizes indicated that the soil composition among the eight colonies sampled was largely a mixture of fine and very fine sands and silts-clay (Figure 10). Based on the classification of the Soil Science Society of America, soil textures were sandy-clay-loams (four sites), clays (two), sandy-clay (one), and sand (one). Soil composition PCA showed that sites varied considerably (Figure 11). Alafia River and Peace River Site 4 both had large amounts of clay, Oklawaha River and Peace River Site 1 had medium and coarse sand, while the other sites had mostly fine and very fine sands. PC1 accounted for 76 percent of variation and was

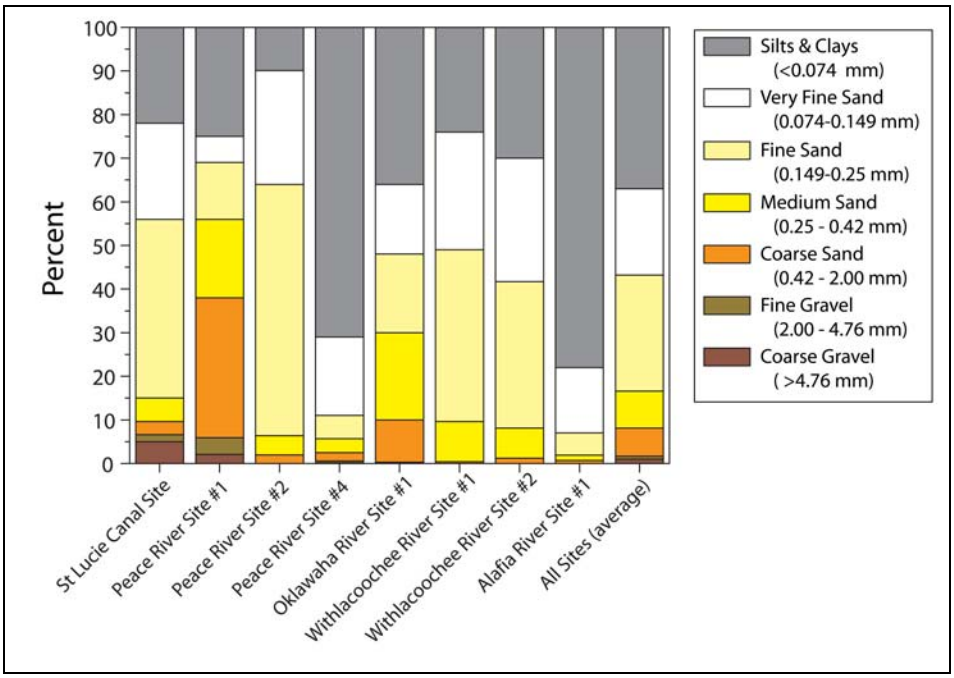

Figure 10. Soil composition of samples taken from eight different Pterygoplichthys *burrow sites in five river and canal systems in Florida.*

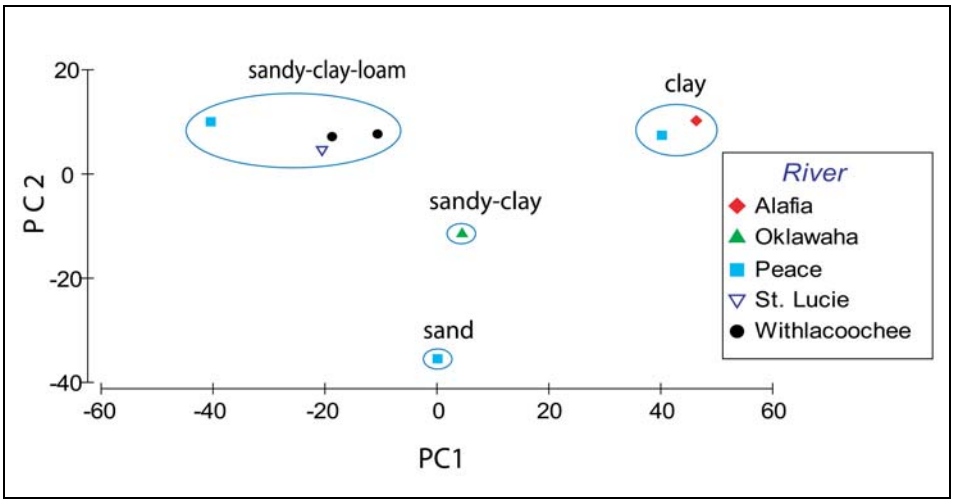

Figure 11. Principal component analysis plot of soil composition associated with Pterygoplichthys *burrows in five river and canal systems in Florida with component vectors superimposed. PC1 is associated with increasing silt/clay and decreasing fine sand proportions. PC2 is associated with decreasing proportions of coarse sand. Soil texture designations follow the classification of the Soil Science Society of America.*

associated with increasing silt-clay and decreasing fine sand proportions. PC2 was associated with decreasing proportions of coarse sand and accounted for an additional 22 percent of variation. Despite differences in soil composition among sites, there appeared to be little difference in the dimensions of burrows (Figure 9). Burrow volume was associated with degree of submergence and occupation by catfish.

Soil compaction measurements ranged from 0.5 to 28 (average 10.1) in. of probe penetration to achieve 300 psi (Table 2). Measuring of soil compaction was considered relevant to an analysis of *Pterygoplichthys* burrows for a variety of reasons. Minimum values may be indicative of sites where the soil density was such that burrows were unlikely to collapse. Low values were also thought to be indicative of soils more likely to erode. Maximum values were indicative of soil that was relatively dense, but not dense enough to prevent successful excavation by *Pterygoplichthys*. There are a few caveats associated with the results. Most measurements were made on dry bank surfaces, adjacent to burrows that were exposed. Upon hydration, the soil compaction properties would differ from exposed, dry banks. Some exposed banks had been baked in the sun, so that an outer crust was formed making it difficult to penetrate with the probe.

Evaluation of bank stability and erosion

General observations on the nest burrow sites indicate that *Pterygoplichthys* generally excavate their burrows in shoreline habitats of rivers and canals already prone to erosion (e.g., outer bends of meandering rivers, steep banks often composed of sandy-clay-loams with sparse vegetation cover). They typically select relatively steep portions of banks with soils friable enough to dig into, yet stable enough to not collapse easily. Such bank conditions make it easier for *Pterygoplichthys* to excavate, but also more likely to slump or erode.

Average burrow volume was calculated at 12,911 cm^3. Thus for a typical colony of 12 burrows, 154,932 cm^3 or about 0.15 m^3 of soil was removed. In evaluating

the amount of sediment removed from an area of bank, analysis was restricted to colonies with the highest number of burrows in each of the five waterways with burrows. Based on that data, *Pterygoplichthys* removed an estimated 1 to 4 percent of sediment per rectangular (1-m deep) volume of bank through their burrowing activities (Figure 4, Table 3). Because sites were not monitored over time, a distinction was not made between ages of burrows.

The relative amount of sediment removed would be greater if calculations are based on the average volume of active burrows. For example, the volumes of each of the three burrows in the Oklawaha River with guarding males present (presumably also maintaining the burrows), ranged from over 0.04 to nearly 0.06 m^3 (Figure 7). As suggested by this relationship between burrow volume and distance (vertical) to water surface, a possible explanation for differences in observed volumes of active versus abandoned or even exposed burrows is provided in Figure 12. The assumption is that burrows above the water and other abandoned burrows were, prior to erosion, as large as the active burrows discovered in the Oklawaha River.

Overview of waterways surveyed

Brief accounts for each of the six waterways surveyed are as follows (Figure 3):

- **St. Lucie Canal.** The St. Lucie Canal, 64 km long, connects Lake Okeechobee with the Atlantic Ocean. The water in the canal is relatively turbid. Burrow sites examined in the St. Lucie Canal were on or near the base of steep banks within or just above existing rip-rap revetment (Figure 13). The upper portions of much of the shoreline, unprotected by rip-rap, appeared highly unstable. Although the burrows probably were contributing to bank instability, their contribution almost certainly was low relative to erosion caused by wave action, in particular, the incredibly forceful waves that strike the shore whenever high-speed boats and yachts pass (a common event). Burrows in high-traffic waterways could act synergistically to increase erosion. Two burrow colonies were discovered during the survey. All detected burrows were exposed, although some of the burrows in the larger colony were near the water's edge and subject to waves.
- **Lake Okeechobee Rim Canal.** This artificial waterway, composed of a number of unconnected segments, extends along large sections of the outer border of the 230-km long, high earthen levee that surrounds Lake Okeechobee. Besides the occasional small-boat wake, these canals are very low-energy systems, more similar to lake habitats than riverine environments. In the area that was sampled, along a northeast side of the lake, the canal is separated from the toe of the levee by a wide and flat open shore area. Water levels at the time were moderately low, exposing undercuts and fissures along the upper part of the low bank on the levee side of the canal (Figure 14). However, the

Table 3
Data from Colonies with Highest Number of Burrows in Each of the Five Waterways Sampled (Vertical extent of colony is the distance between the highest and the lowest burrows relative to water surface (negative numbers indicate entrance floor of burrow was below water). Horizontal extent is the distance between the most upstream and most downstream burrow. Summed burrow volume is the total volume of all burrows at site (see Methods for calculation))

Waterway system	Withlacoochee	St. Lucie	Peace	Alafia	Oklawaha
Site field number	LGN 06-34	LGN06-42	LGN06-51	LGN06-55	LGN06-59
Maximum vertical distance (m)	1.35	0.6	0.24	0.36	0.02
Minimum vertical distance (m)	0.84	0.16	-0.59	0.12	-1.4
Vertical extent of colony (m)	0.51	0.44	0.83	0.24	1.42
Horizontal extent of colony (m)	14.5	11.7	4.9	18.3	7.28
Summed burrow volume (m^3)	0.11	0.11	0.17	0.15	0.18
Available bank volume (m^3)	7.40	5.15	4.07	4.39	10.34
Proportion of bank volume	0.01	0.02	0.04	0.04	0.02
Number of burrows in colony	11	8	16	14	5
Burrow density (#/m^2)	1.49	1.55	3.93	3.19	0.48

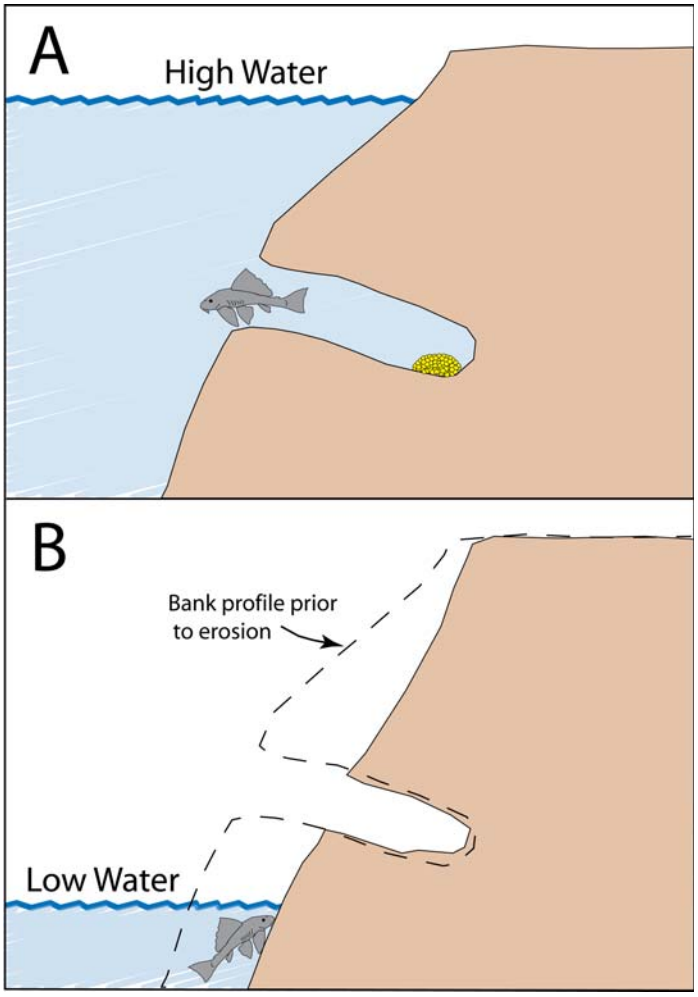

Figure 12. Bank profile and longitudinal section of a Pterygoplichthys *burrow. Drawing shows possible sequence of events over time as water levels drop and bank erodes: a) high water period showing active burrow with eggs being guarded and burrow structure maintained by adult catfish; and b) same site during low water, after nest has been abandoned and exposed to air. As a result of lack of maintenance by catfish and continued exposure of burrow to wave wash and other forces, the bank has eroded, causing the burrow structure to degrade and its length to become reduced.*

Figure 13. Portion of a burrow colony on the St. Lucie Canal showing three exposed burrows, indicated by red flags (Field # LGN 06-41). Here burrows are closely associated with rip-rap revetment and the rock apparently affords burrows protection from the heavy wave wash of passing boats. (Photograph by L. G. Nico)

Figure 14. Photograph of a portion of the west shore of the Lake Okeechobee Rim Canal just north of the St. Lucie Canal. Many highly eroded holes such as these were scattered above the waterline and could not be definitively attributed to the work of Pterygoplichthys*. A portion of the levee surrounding the lake is in the background. (Photograph by L. G. Nico)*

extreme degradation of these holes made it impossible to discern that these undercuts had been created by *Pterygoplichthys*. Lake Okeechobee and adjoining waters are known to contain large populations of *Pterygoplichthys* (Nico 2005) and dried carcasses of *Pterygoplichthys* were found along the canal's bank. In the reach surveyed, the distance between the eroding bank and the toe of the levee is considerable (probably much greater than 50 m). Consequently, even if some or all of these burrows were created by *Pterygoplichthys*, the associated erosion did not appear to be an immediate threat to levee integrity. The authors walked a small portion (<100 m) of the lake shore along the interior part of the levee. The lake shore was protected by rip-rap rock and a brief tour revealed no evidence of burrows along its margin.

- **Peace River.** The 171-km long Peace is a moderate-sized stream with tannin-stained water and moderate water clarity. Although fed by a few springs, most of its volume is from other sources. The river is characterized by sharp bends

and consists of moderately steep banks throughout most of the reaches surveyed. Fishes in the Peace River have been sampled on numerous occasions. *Pterygoplichthys* were first captured in the system in 1995 and were relatively common in subsequent fish collecting samples. During a 2006 survey for burrows, the river was at very low water stage and large numbers of *Pterygoplichthys* were seen in shallow portions of the river. The low water also enabled documentation that the nest burrows of this species are common in the system (Figure 15).

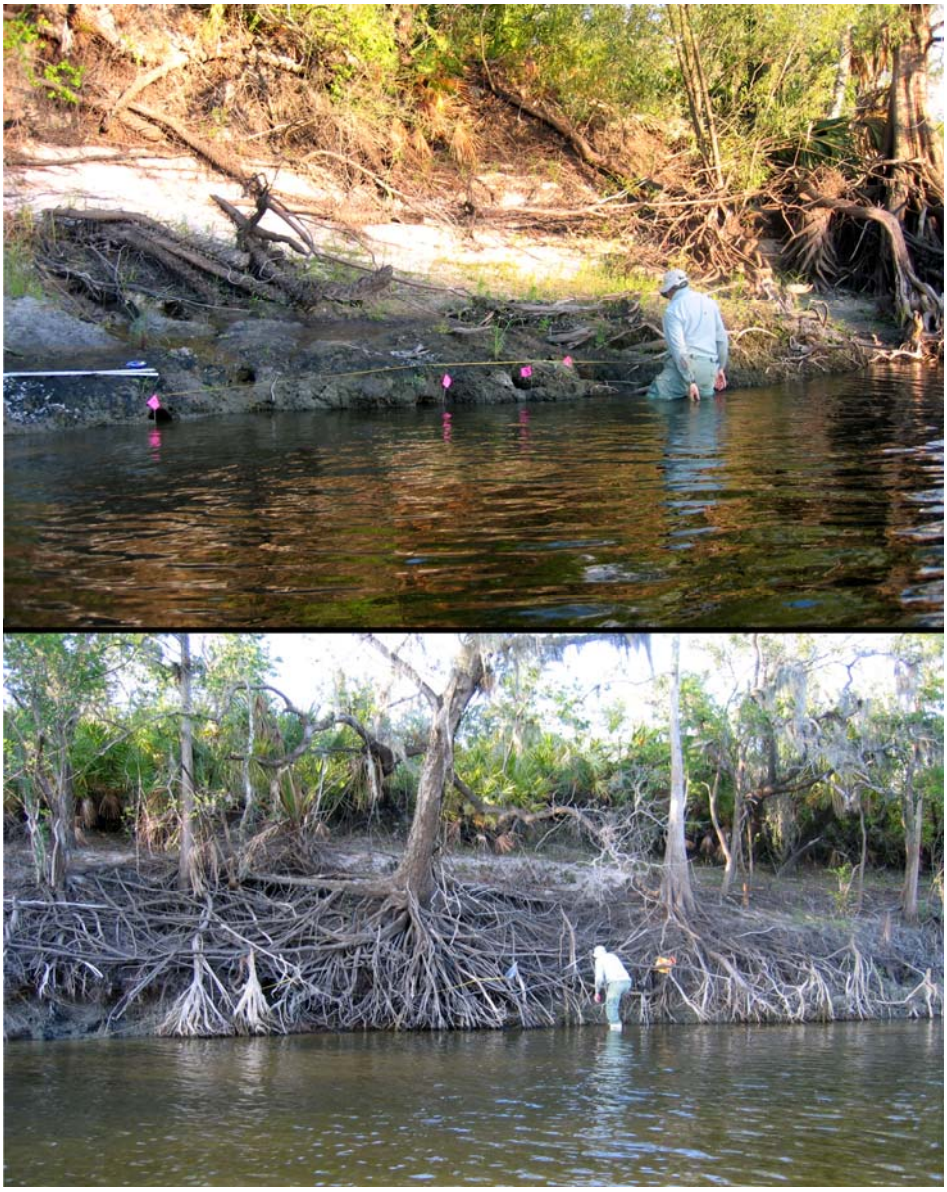

Figure 15. Burrow colonies on the Peace River. Upper photograph: Portion of colony showing four exposed burrows indicated by red flags. This colony includes exposed and submerged burrows, although the submerged burrows did not appear to be active nests. Lower photograph: Portion of this colony encompassed tree roots and some burrows were hidden among the large roots. Such burrows would likely pass undetected if the river was surveyed during higher water and the burrows were submerged. (Photographs by L. G. Nico)

- **Alafia River.** The 40-km long Alafia is a small meandering stream with tannin-stained water and moderate water clarity. Some tributaries, such as Buck Creek, are spring fed with clear water. During the survey, the Alafia was at low water stage. *Pterygoplichthys* were common and easily sighted in most shallow sections of the river. Interestingly, another herbivorous fish, the native striped mullet *Mugil cephalus* was also common. Although a few isolated cavities were observed, some possibly nest burrows of *Pterygoplichthys*, the first burrow colony was located upstream in an area with steep banks (Figure 16).
- **Withlacoochee (South) River.** The 252-km long Withlacoochee (South) is a natural meandering river of moderate size. Although the main channel is naturally tannin stained, over recent years water clarity in the main channel of the Withlacoochee River has declined considerably. One of its major tributaries, the Rainbow River, is a spring-fed stream with clear water running through low topography and flush with vegetation. The lower reaches of the Withlacoochee in the vicinity of Dunnellon, together with the lower Rainbow River, are impounded. Near the town of Dunnellon the elevation is low and there are few exposed banks. Although *Pterygoplichthys* are occasionally sighted in the Rainbow River, no evidence of burrows was found. In the main channel of the Withlacoochee no catfish burrows

were located until traveling much farther upstream, where exposed high ground was more common (Figures 17 and 18). Three of the burrow colonies were located along bends where there were residences. At two of these sites the burrows were situated around boat docks and there was clear evidence of erosion. One of the sites included in the 2006 survey contained active burrows in 1997, indicating that the same sites are used for spawning over multiple years (Figure 19). Although excavation of burrows among tree roots is not uncommon, in the Withlacoochee burrows were discovered among the roots of cypress (Figure 20). Another burrow colony was highly degraded, located along a shore within a pasture and much of the river bank apparently trampled by cattle.

- **Oklawaha River.** The 121-km long Oklawaha is a low-gradient, meandering stream. The main channel has tannin-stained waters with moderate clarity. Its tributary, the Silver River, is spring-fed and has clear water. Because the Oklawaha is primarily groundwater fed, it was not as low as other sampled rivers. The Oklawaha was the only drainage where submerged nests that were being actively guarded by adult *Pterygoplichthys* were observed (Figure 21). The authors were able to photograph and collect an adult male and also recover the guarded eggs at one colony site (Figures 1, 22, and 23).

Follow-up studies are currently underway in the Oklawaha and its tributaries, part of a more detailed investigation of burrow colonies and *Pterygoplichthys* behavior.

Figure 16. A portion of a large burrow colony on the Alafia River showing 10 exposed burrows indicated by red flags. This colony was constructed in soil of high clay content and the shore seemed to be relatively stable. (Photograph by L. G. Nico)

Figure 17. Burrow Site #1 on the Withlacoochee River (Field # LGN 06-34). This colony included exposed burrows, some located upstream and others downstream of the private boat dock. Eleven burrows were measured, but additional burrows were later seen immediately downstream and it was suspected that the colony also included a few burrows still submerged (Photograph by L. G. Nico)

Figure 18. A portion of Burrow Site #1 on the Withlacoochee River showing five of the 11 exposed burrows actually measured (Field # LGN 06-34). Typical of many Pterygoplichthys *colonies, the burrow openings are triangular and some burrows are closely grouped. (Photograph by L. G. Nico)*

Figure 19. Photograph showing upstream portion of Burrow Site #2 on the Withlacoochee River (Field # LGN 06-35). This burrow colony was situated on the outside of a sharp bend near decks and boat ramps of private residences. The eight burrows detected at this site were degraded, most had partially filled with silt and some had already collapsed (red arrows indicate location of two of the eight burrows). Two active burrows submerged and guarded by adult catfish were observed at this site by LGN during a visit in June 1997, indicating that the same colony sites are used over multiple years. (Photograph by L. G. Nico)

Discussion

Descriptions of suckermouth armored catfish burrows in the literature

Based on a review of the literature, the excavation and maintenance of burrows by certain loricariid catfish species is rather unique among primary freshwater fishes. The complex behavior of creating and maintaining burrows by *Pterygoplichthys* and certain other loricariids is most similar to that of several marine fishes. As with *Pterygoplichthys*, their burrows are also generally used for spawning and nesting habitat.

The reproductive behavior among loricariids, including the sites selected for spawning and nesting and the extent of parental care of eggs and young, is very diverse and rather complex (Covain and Fisch-Muller 2007). Use of natural cavities (e.g., hollow logs) for spawning and nesting is practiced by some loricariids, for example, *Ancistrus* and *Loricaria*, among others (Eric et al. 1982, Sabaj et al. 1999, Covain and Fisch-Muller 2007). However, the excavation of nesting burrows among loricariids appears restricted to certain genera and species within the subfamily Hypostominae and is typical of members of the genera *Hypostomus* and *Pterygoplichthys*. Nevertheless, the published literature is incomplete. For instance, it is not known with certainty if all species in these two genera excavate burrows. In addition, although some loricariids are considered cavity spawners, including some non-hypostomine taxa (Covain and Fisch-Muller

Figure 20. Small burrow colony, highly degraded, on the Withlacoochee River (Field # LGN 06-36). This site was within a reach of live and dead cypress. The site with burrows was one of the few areas in this part of the river with exposed bank. If any burrows were within the reaches with dense cypress roots, they would have been difficult or impossible to detect. (Photograph by L. G. Nico)

Figure 21. A portion of a small burrow colony in the Oklawaha River drainage consisting of one exposed burrow (see red flag, center right) and four submerged burrows containing eggs and guarding adults (Field # LGN06-59). (Photograph by L. G. Nico)

2007), it is not known how many other loricariid genera include burrow excavators. For example, at least one other hypostomine, *Leporacanthicus triactis*, has been found to occupy burrows (Figure 2; Isbrücker et al. 1992). Adults of this species are likely responsible for the actual excavation of the burrows. Although not observed, some have speculated that *L. triactis* might simply be using bank holes excavated by cavity-nesting birds, occupying already excavated holes after river levels rise during the rainy season and the burrows become submerged (see *http://www.scotcat.com/factsheets/leporacanthicus_triactis.htm*).

There is a fair amount of literature on the reproductive biology of loricariid-hypostomine catfishes (e.g., Sabaj et al. 1999, Suzuki et al. 2000, Liang et al. 2005), but relatively little information has been published on the burrows of these fishes. This is surprising given the fact that burrows are most likely an integral part of reproduction for many hypostomines. In their review of the modes of fish reproduction, Breder and Rosen (1966) referenced only two papers that mention loricariid burrows. The first was a publication by Carter and Beadle (1931) describing field investigations in the Paraguayan Chaco. In their account on "*Ancistrus anisitsi*" (now recognized as *Pterygoplichthys anisitsi*), the only mention of burrows is the statement: "The eggs are laid in holes in banks at the edge of the swamp …" [pg. 348]. In a subsequent paper, Azevedo (1938), based on discussions with local fishermen, reported that "*Plecostomus plecostomus*" [= *Hypostomus plecostomus*] deposits its eggs in holes. In neither of the cases mentioned above did the authors discuss the possibility that these catfishes were responsible for the actual excavation of the nest holes.

Figure 22. Adult Pterygoplichthys *stationed at the entrance of a burrow in the Oklawaha River drainage. Native* Lepomis *species, such as the Redbellied Sunfish (*Lepomis auritus*) seen here on right, have been observed in the vicinity of burrows, possibly nest robbers waiting for opportunity to prey on* Pterygoplichthys *eggs and young (Field # LGN06-64). The burrow in the photograph is part of a colony included in an ongoing study on* Pterygoplichthys *behavior and burrow activity. (Photograph by Travis Tuten)*

Figure 23. Egg mass recovered from Pterygoplichthys *burrow. The guarding adult from this nest is shown in Figure 1.*

One of the first widely-circulated articles that included data on the excavation of burrows by loricariids is that of Grier (1980). Publishing his findings in an aquarium magazine, Grier briefly described and provided a few photographs of the burrows of a species of *Hypostomus* (reported as *Hypostomus plecostomus*) inhabiting small ponds in Florida used to cultivate ornamental fish. He noted that, given suitable "turf," *Hypostomus* constructed burrows into the side of a pool. Grier reported that each burrow normally consisted of a single opening but interiorly the burrow subdivided into three or four different tunnels. The author noted that the burrows extended "3–4 feet" (0.9–1.2 m) and were parallel to the surface of the pond. According to Grier, these tunnels rarely extended upwards or downwards, over or below, the burrow opening (i.e., the burrows were generally horizontal). In a subsequent publication, Burgess (1989) also briefly described the burrows created by *Hypostomus* raised in Florida aquaculture ponds, reiterating much of the same information previously provided by Grier (1980) but without citing a source. In slight deviation from Grier, however, Burgess reported that tunnels were 1.2–1.5 m deep.

Garcia-Pinto et al. (1984) investigated the reproductive biology of a loricariid catfish inhabiting artificial ponds at an aquaculture station in Zulia State, northwestern Venezuela. The researchers reported that the species was native to the area, the Lake Maracaibo basin, and referred to it by the common name "Armadillo Pintado" and scientific name *Hypostomus watwata* (according to the loricariid expert Jon Armbruster, *Hypostomus villarsi* is probably the valid name for this species). Garcia-Pinto and his colleagues provided a brief description of the sites and morphology of burrows excavated by

this catfish and, of additional importance, included a photograph of a nest entrance and drawings showing dorsal and longitudinal views of different nests. Each of the ponds holding the catfish measured 0.25 ha, and the pond bottoms and surrounding dikes were composed of clay. It was noted that male catfish selected an area either on the pond bottom or bank and, after finding a suitable spot, used their pectoral fins to remove any debris and loose mud so as to expose the underlying surface of compact clay. According to the researchers, the catfish would then dig a burrow in the cleared area (unfortunately, the authors do not describe the actual excavation process, for example, whether or not fish used their pectoral fins, rasping teeth, or a combination, to dig the burrow).

Garcia-Pinto et al. (1984) stated that the completed burrow was almost cylindrical, with an average length of 81.5 cm and an opening entrance averaging between 17.3 and 21.9 cm in diameter. The interior tunnels varied, some consisting of only a single tunnel but others were bifurcate. Burrows excavated on the pond bottom were described as having a slight incline with respect to the horizontal pond bottom, whereas burrows excavated in the surrounding dike were reportedly perpendicular to bank edge and, presumably, horizontal. One diagram by the researchers shows as many as three nest burrows in very close proximity, with adjacent burrow openings within 10 cm or less of one another. In addition, all three burrow openings were situated within a circular area (about 1.5 to 2 m in diameter) on the pond bottom cleaned of debris. The inner part of the cleared area, nearest the burrow openings, consisted of excavated material and the outer part of the cleared area consisted of the clean or exposed hard clay bottom. Garcia-Pinto et al. (1984) further observed that male and female catfish entered or exited any one burrow by way of a single opening. They added that other members of the subfamily Hypostominae populating natural tributaries within the Lake Maracaibo basin exhibited reproductive behavior similar to that of the catfishes inhabiting the research station's artificial ponds.

Among the literature examined, the most detailed descriptions of loricariid catfish burrows are included in two unpublished reports produced by the Hawaii Department of Land and Natural Resources and are based on investigations of non-native loricariids present on the island of Oahu (Devick 1988, 1989). The most significant of these documents is Devick's 1988 report containing results of field studies on a large population of *Pterygoplichthys*, identified as *P. multiradiatus*, established in Wahiawa Reservoir (a 141.6-ha impoundment also known as Lake Wilson). The report includes a series of photographs and drawings of the catfish and their burrows. During late August 1987, when the water level was low, a survey revealed 3,746 exposed nests (above water line) in the reservoir. However, this number was considered to be a low estimate because many burrows hidden in grass or other cover went undetected. Devick (1988) stated that the burrows were present in a variety of clay and mud substrates along the reservoir shoreline. He noted that the basal edges of abandoned tilapia nests were favored, possibly because the relatively soft mud within these sites permitted easy burrowing. During the study, the entrance opening of 860 burrows were measured and 18 entire tunnels were excavated to obtain information on burrow dimensions. In contrast to what Grier (1980) had described for *Hypostomus* burrows in Florida, Devick (1988) reported that the burrows of *Pterygoplichthys* in the Hawaii reservoir were highly irregular and typically sloped downward. In some sites, crayfish burrows were connected to the catfish burrows. Devick assumed that the crayfish burrows were sometimes enlarged by the catfish when creating their own tunnels. In areas where catfish burrows were numerous, the shafts sometimes connected, although the connecting of two tunnels was thought by Devick to be inadvertent.

Devick described the tunnels as having basal grooves, apparently formed by the extended pectoral fins of the catfish. Consequently, in cross-section, the burrows were somewhat triangular in shape. The dimensions of 18 burrows examined ranged from 48 to 107 cm (mean = 80 cm) long and 10 to 26 cm (mean = 14 cm) wide. These were excavated by catfish ranging in size from 21 to 51 cm (mean = 28 cm) long. Devick (1988: Figure 10) presented a graph that provided information on the number of tunnels and tunnel width. Based on that graph, entrance width of 860 burrows ranged from about 3.5 to 27 cm and averaged about 13 cm. The

small size of some burrows (less than 4 cm wide) would indicate that even relatively small juvenile *Pterygoplichthys* excavate burrows, but Devick does not discuss this subject (based on Devick's own data on the relationship between burrow width and catfish length, a 4-cm-wide burrow would have been created by a catfish approximately 8 cm long).

Burrows of loricariid catfishes are mentioned briefly in other literature that was reviewed. For example, Suzuki et al. (2000, p. 802) stated that "…*Hypostomus ternetzi* … deposits its eggs in nests excavated in stream banks." Lucanus (2001) included a photograph of a large catfish burrow colony that he reportedly shot along the main channel of the Orinoco River in Venezuela. While collecting fish in an Orinoco River tributary in Venezuela, Leo Nico discovered a colony composed of about a dozen burrows along the shore of a small stream (Figure 2). During a brief investigation of the site, adult *Leporacanthicus* were pulled from two of the burrows and these specimens ultimately were preserved and used as type material for description of a new species, *Leporacanthicus triactis* (Isbrücker et al. 1992).

Other fishes that excavate burrows

Among fishes, active excavation and maintenance of burrows has been documented largely for certain marine taxa, including members of the families Anguillidae–freshwater eels (Aoyama et al. 2005); Cepolidae–bandfishes (Atkinson and Pullin 1996); Congridae–conger eels (Tyler and Smith 1992); Gobiidae–gobies (Ishimatsu et al. 1998, Itani and Uchino 2003, Gonzalez et al. 2008); Malacanthidae–tilefishes (Able et al. 1982, Twichell et al. 1985); Opistognathidae–jawfishes (Colin 1973); Pholidichthyidae–convict blenny (Clark et al. 2006); Stichaeidae–pricklebacks (Nash 1980); Serranidae–groupers (Jones et al. 1989); and others (Atkinson and Taylor 1991). Members of the marine family Malacanthidae are especially renowned for burrowing. For example, juveniles and adults of the tilefish *Lopholatilus chamaeleonticeps* dig burrows of various sizes and shapes in clay substrates in deep water on the sea floor, presumably as refuge from predators. The burrows of this species average 1.6 m in diameter and 1.7 m in depth, although the largest may extend several meters deep and are thought to be quite old (>30 years), conceivably spanning several generations if successively inhabited (Able et al. 1982, Twichell et al. 1985).

Compared to marine fishes, few freshwater fishes are known to excavate and maintain burrows (Atkinson and Taylor 1991). In addition to loricariids of the subfamily Hypostominae, there is evidence of burrowing among lungfishes of the Class Sarcopterygii (Atkinson and Taylor 1991) and some members of the family Synbranchidae–swamp eels (Lüling 1958; Personal Communication, Leo G. Nico). There are probably others. Admittedly, swamp eels and certain other freshwater fishes also simply burrow into soft substrates or loose soil without creating discrete tunnel systems.Among these fish, whether a discrete burrow is formed likely depends upon the consistency of the sediment (see Atkinson and Taylor 1991). In addition and in contrast to species that actively burrow, many other fishes use natural and artificial cavities (e.g., many ictalurid catfishes) or occupy burrows created by other organisms (e.g., Randall and Earle 2006).

Impacts associated with burrows

To date, the most detailed discussions on the possible effects of loricariid catfish burrows are based on studies and observations of introduced loricariids in Hawaii. In Hawaii, non-native *Pterygoplichthys* are common and these fish have excavated thousands of nesting tunnels in the earthen banks of reservoirs and streams. Their burrows have been reported as contributing to siltation problems and bank instability (Devick 1989, Yamamoto and Tagawa 2000). Devick (1989), assessing the impact of a large population of *Pterygoplichthys* in a Hawaiian reservoir (Wahiawa), concluded that the burrows of this catfish, over the long term, were having a significant impact on siltation. Devick noted that there were probably 30,000 or more catfish burrows dug in the reservoir in 1988, which he estimated as representing some 150 tons of additional silt accumulation in the reservoir bottom. Yamamoto and Tagawa (2000) noted a number of ecological effects associated with the introduction of *Hypostomus* sp. cf. *watwata* into Hawaii. In particular, they reported the nesting burrows of these catfish cause erosion problems and increase silt loads in Hawaiian streams.

However, no quantitative data were provided.

Pterygoplichthys burrows in Florida rivers and canals were found to be similar in size and structure to the burrows of non-native *Pterygoplichthys* studied in Hawaii (Devick 1988, 1989). While Devick's research in Hawaii focused on inhabitants of an impounded lake, the large number of burrows found demonstrated the potential amount of benthic habitat that these catfish can modify. Whether densities of *Pterygoplichthys* in Florida have achieved the levels experienced in Mexico or Hawaii is uncertain, although incredibly high numbers of *Pterygoplichthys* have been observed in some Florida rivers and springs. At very high densities, the number of burrows could significantly contribute to erosion of banks and modification of benthic habitats.

Survey results also indicate that *Pterygoplichthys* are relatively flexible in their choice of sites for burrow construction, spawning, and nesting. Habitats with burrows include small and large natural rivers and canals. Although the largest natural rivers in the survey were only moderate in size, the St. Johns River, the largest river in Florida, has a substantial *Pterygoplichthys* population. During low water conditions in 2007, large numbers of burrows were observed in exposed banks of the river's main channel. More recently, Dr. William Loftus (personal communication) boated on the upper St. Johns River in early 2009 during low water and observed thousands of exposed *Pterygoplichthys* burrows along the banks in areas between Lake Harney and Puzzle Lake and in the vicinity of Lake Jessup and Lemon Bluff. In these areas, Loftus also saw evidence of substantial sloughing of banks, which he attributed to the presence of the many burrows.

There are also unpublished reports of *Pterygoplichthys* burrows in Florida lakes. Moreover, although surveys were conducted in relatively rural areas, the presence of nesting *Pterygoplichthys* near human dwellings indicates that these fish are not readily disturbed by human activity. This behavioral plasticity in selection of sites for burrowing indicates that few freshwater habitats can be expected to be immune from effects associated with their burrows. According to Duan (2005), the rate of bank erosion is a function of the hydraulic forces, bank geometry, bank material cohesion, and frequency of bank failure. In response to a query about the possible association between catfish burrows and bank erosion, the hydrological engineer Jennifer Duan (personal communication) stated that the burrows will make banks more unstable, will facilitate bank erosion, and then make rivers more meandering.

Based on the present field assessment, *Pterygoplichthys* generally excavate their burrows in shoreline habitats of rivers and canals already prone to erosion (e.g., outer bends of meandering rivers, steep banks often composed of sandy-clay-loams with sparse vegetation cover). They typically select relatively steep banks with soils friable enough to dig into, yet stable enough to not collapse easily. Such bank conditions make it easier for *Pterygoplichthys* to excavate, but also more likely to slump or erode.

It is likely that the burrowing activities of these catfish exacerbate existing erosion problems but their overall contribution to bank instability and rate of erosion appears to vary among sites. For example, burrow sites examined in the St. Lucie Canal were on or near the base of steep banks within or just above existing rip-rap revetment. Although the burrows probably were contributing to bank instability above the rip-rap of this canal, their contribution almost certainly was low relative to erosion caused by wave action, in particular, the incredibly forceful waves that strike the shore whenever high-speed boats and yachts pass (a common event). *Pterygoplichthys* burrow colonies were discovered on outer bends of river meanders associated with small boat docks. The co-occurrence may simply be due to catfish and humans using similar criteria to select sites. For catfish it is the relatively steep, exposed bank, and relatively firm soil of outer bends. For humans it is the higher ground, which is less prone to flooding, and deep water. Property owners living on the river near colonized banks and some boaters will likely be aware of *Pterygoplichthys* activity.

In addition to *Pterygoplichthys* and various other fishes, a diverse array of aquatic and many terrestrial animals commonly excavate burrows. Negative effects associated with the burrows and burrowing activities of these animals vary, typically depending on the local setting (i.e., vulnerability of the site), the abundance of the burrowing species, and the number,

size, and configuration of the burrows. Negative effects may be economic or ecological, although neither is mutually exclusive (e.g., Williams and Corrigan 1994, Gabet et al. 2003).

In general, most impacts associated with burrows are attributed to their possible contribution to erosion and bank instability and, related to this, damage caused to existing man-made structures (e.g., dams, retention walls, and foundations) because of undermining. Animals that burrow in or near waterways may be particularly problematic because their activities may increase bank instability, erosion, and siltation. In the vicinity of earthen dams, burrows may dramatically alter hydraulics or flownet within the embankment, thereby damaging and leading to possible failure of the dam structure (Federal Emergency Management Agency (FEMA) 2005).

According to Meadows and Meadows (1991), the burrows of animals can alter the water content, permeability, shear strength, and other geotechnical properties of the sediment matrix. Greater stream flows increase the risk of bank failure, and undercutting tends to exacerbate the situation (Wynn 2004). Based on these relationships, the occurrence of *Pterygoplichthys* burrows along the outer bends of rivers where the force of the current is often greatest may very well further increase the probability of bank failure. In contrast, banks with woody and herbaceous root mats significantly increase bank slope stability over bare conditions (Wynn 2004), consequently, sites where *Pterygoplichthys* burrow among tree roots are more armored against erosion.

In addition to *Pterygoplicthys* and *Hypostomus*, a number of other non-native species introduced into North America excavate burrows and have been implicated in causing environmental harm to shoreline habitats due to their burrowing activities. Examples include the Chinese mitten crab (*Eriocheir sinensis*) in the San Francisco Bay-San Joaquin Delta of California (Rudnick et al. 2000, 2005), the Austral-Asian isopod (*Sphaeroma quoyanum*) in salt marshes of San Diego Bay and San Francisco Bay (Talley et al. 2001), and the green iguana (*Iguana iguana*) in southern Florida (Kern 2004, Ferriter et al. 2008).

The burrowing activities of non-native Chinese mitten crabs, especially where the species is abundant and burrows very dense, have been linked to bank weakening, erosion, loss of bank vegetation, and bank collapse (Herborg et al. 2003, Rudnick et al. 2000, 2005, and citations therein). Herborg et al. (2003) analyzed the history of these introduced crabs in Europe and noted that their burrow-digging habit can cause serious river bank erosion, usually observed in tidally-influenced areas or other stretches of rivers with fluctuations in water level. Burrows are made in river banks with steep gradients, sites having soil with the necessary structural strength to allow burrowing. The appearance of this non-native in California was a concern partly because of their potential impact to the integrity of the extensive levee system in the San Francisco Bay region as well as the natural stream banks of the Bay's tributaries (Rudnick et al. 2005).

In their recent assessment of crab burrow impacts in intertidal portions of tributaries in South San Francisco Bay, Rudnick et al. (2005) reported that Chinese mitten crabs removed an estimated 1 to 6 percent of sediment per 0.5 m^3 of stream bank through burrowing activities over the period of study (2000–2002). They noted localized bank slumping, particularly in spring following rain events. According to the researchers, sediment loss from burrowing activities may be substantial in the intertidal tributaries where the crabs occur. Sediment loss was reported to be influenced by multiple factors including crab population abundance, connectivity of the burrow systems, and sediment composition.

The burrowing isopod *Sphaeroma quoyanum* from Australia-New Zealand was first reported in California in the late 1800s. Wasson et al. (2001) stated that the burrows of this isopod riddled virtually every bank examined in one estuary, which they noted was perhaps exacerbating already high rates of tidal erosion. Talley et al. (2001) examined habitat alteration by this non-native isopod in California salt marshes. In these habitats, the isopod typically selected peat and mud walls of tidal creek and marsh edge banks for their burrows. Using enclosure experiments, the investigators were able to demonstrate that isopod activities enhanced sediment loss from banks and estimated that some losses exceeded 100 cm of marsh edge per year. Talley et al. concluded that the effects of habitat

alteration by this invading species are likely to increase in severity in the coastal zone as these ecosystems become degraded. According to Talley et al. (2001), others had noted that the intensive burrowing activities of this species weakened mud and clay banks of salt marsh edges, thus making them more susceptible to erosion by wave action or stream flow. However, the researchers stated that their study was the first to quantify impacts caused by the isopod's burrowing.

The green iguana (*Iguana iguana*) is another non-native in North America that digs burrows. Ferriter et al. (2008) reported that large numbers of non-native iguana burrows can be observed in the banks of many canals and levees in and around the Greater Everglades. They noted that these burrows present a maintenance liability, leading to bank instability and bank erosion. Ferriter et al. stated that further evaluations are needed to fully understand the impact of burrows on bank integrity and maintenance costs. However, the researchers concluded that even moderate densities of green iguanas have some impact on bank stability. In a separate analysis, Kern (2004) reported that the burrows of non-native populations in south Florida undermine seawalls, sidewalks, and foundations. Burrows next to seawalls allow erosion and eventual collapse of the structure.

The environmental effects caused by introduced loricariid catfishes remain inadequately documented and generally little understood. The substantial gap in knowledge is due to a variety of factors. Analysis of impacts in natural systems is a complex undertaking. Cause-effect relationships are difficult to establish because of many interacting biotic and abiotic variables. Non-native *Pterygoplichthys* populations in Florida and other regions are highly successful invaders and considered a threat to native aquatic communities and habitats (Figures 24 and 25). Their environmental threat is a combination of distinctive life history attributes, especially feeding and reproductive behaviors, coupled with their large size and high population densities (Fuller et al. 1999, Hoover et al. 2004).

Increasing numbers and distribution of *Pterygoplichthys* have

Figure 24. Pterygoplichthys *have become abundant in many Florida waterways but their impacts are difficult to quantify, especially in complex natural systems. In February 2007 a large number of these non-native catfish were observed massed in Alexander Spring, Florida. (Photograph by Brian MacGregor)*

Figure 25. Non-native Pterygoplichthys *gathering around an adult female manatee and her yearling calf at Blue Springs, Volusia County, Florida. The catfish often settle on manatees to possibly rest or graze on algae that commonly grows on their backs. (Photograph by James P. Reid, U.S. Geological Survey)*

undoubtedly been accompanied by an increase in the number and distribution of *Pterygoplichthys* burrows and burrow colonies. Future research into the durability of burrows and colonies through fluctuating water conditions should better inform about erosion impacts. Understanding *Pterygoplichthys* nesting behavior and burrow fidelity would also give some indications of burrow maintenance and persistence.

Summary

Non-native populations of the Neotropical family Loricariidae, the suckermouth armored catfishes (also referred to as loricariid catfishes), have been introduced and become established in many tropical and subtropical regions of the world. In Florida, members of the loricariid genus *Pterygoplichthys* are now common in most drainages in the central and southern parts of the peninsula. In certain rivers, canals, and lakes, these fishes are abundant.

Breeding adult *Pterygoplichthys* excavate and maintain burrows in shoreline soil. These burrows are used mostly as spawning and nesting sites. The burrows are thought to cause or exacerbate bankline erosion in canals and rivers. However, there is little published information on the burrows of loricariid catfishes and no quantitative data are available to adequately evaluate any association between presence and abundance of burrows and increased erosion.

The purpose of the present study was to provide baseline information on the burrows of *Pterygoplichthys* in Florida and to provide a preliminary assessment of shoreline conditions (e.g., bank stability and erosion). Waterways surveyed for catfish burrows included parts of six rivers and canals: St. Lucie Canal, Okeechobee Rim Canal, Peace River, Withlacoochee River, Alafia River, and Oklawaha River.

Field surveys were conducted during spring-early summer 2006 when water levels in peninsular Florida were low and the likelihood of detecting burrows, especially those exposed by low water, is greatest. During the study period, approximately 56 km of waterway were surveyed. Burrows were detected in five of the six waterways surveyed. The only exception was the Lake Okeechobee Rim Canal. That canal had many exposed cavities along the upper edge of banks; however, because of the extreme degradation of these holes, it could not be determined that these undercuts had been created by *Pterygoplichthys*.

In total, the presence of 118 burrows considered to have been excavated by *Pterygoplichthys* were documented. Of the burrows detected, 85 (72 percent) had entrances that were exposed above the water edge, either entirely or partially (>50 percent of burrow height). Some sites included a combination of both submerged and exposed burrows. All detected burrows were located along the river and canal banks. No burrows were observed in the beds of waterways, although some waterways were too deep and turbid to detect bottom burrows.

Findings indicated that burrows were not distributed evenly within or among waterways. Burrows were mostly aggregated into colonies. Among the six waterways surveyed, burrows were distributed among 18 sites, with the number of burrows per site ranging from 1 to 16 (mean = 6.6). The 2-km section of the Peace River that was sampled had the highest densities of burrow colonies (2.5 per km) and burrows (20.5 per km). In natural rivers, burrow colonies were much more evident in upstream portions of natural drainages where there were steeper banks and greater fluctuations in water levels. In these rivers, colonies were found along the outer bends of channels, although the geometry of bends selected varied from slight meanders to sharp. In canals, burrows were found along straight sections where much of the bank was exposed and steep.

The horizontal extent (i.e., alignment parallel to shoreline) of colonies varied widely, ranging from about one or a few meters for small colonies, to well over 15 m for colonies composed of many burrows. In contrast, the vertical layouts of most colonies were within a 1-m stratum of shoreline.

Complete measurements were taken for 63 burrows and 58 of these were considered to be in sufficient condition to be included in statistical analyses. Most burrows (61 of 63 burrows examined) were rather simple structures, consisting of a single opening and a relatively straight tunnel without marked bends or bifurcations. Burrow tunnels ranged from 20 to 130 cm (mean = 77 cm) in length, and the dimensions of the entrance ranged from 11 to 45 cm (mean = 21 cm) in width, and 7 to 27 cm (mean = 14 cm) in height.

Variation in both tunnel length and volume was likely related to burrow age and condition. The largest and longest burrows were active burrows, submerged and occupied by an adult *Pterygoplichthys*.

Habitats with burrow colonies were fairly diverse, evidence that *Pterygoplichthys* are relatively flexible in their choice of sites for burrow construction, spawning, and nesting. For example, the height, cross-sectional shape, and general slope of river and canal banks with colonies were also diverse. Soil was sampled at eight colonies and subsequent analysis of particle sizes indicated that soil composition was a mixture of fine and very fine sands and silts-clay, with the most common soil type being sandy-clay-loams.

In terms of bank stability and erosion, general observations on the nest burrow sites indicate that *Pterygoplichthys* generally excavate their burrows in shoreline habitats of rivers and canals already prone to erosion (e.g., outer bends of meandering rivers, steep banks often composed of sandy-clay-loams with sparse vegetation cover). They typically select relatively steep portions of banks with soils friable enough to dig into, yet stable enough to not collapse easily. Such bank conditions make it easier for *Pterygoplichthys* to excavate, but also more likely to slump or erode.

It is likely that the burrowing activities of these catfish exacerbate existing erosion problems but their overall contribution to bank instability and rate of erosion appeared to vary among sites. For example, burrow sites examined in the St. Lucie Canal were on or near the base of steep banks within or just above existing rip-rap revetment. Although the burrows probably were contributing to bank instability above the rip-rap of this canal, their contribution almost certainly was low relative to erosion caused by wave action, in particular the incredibly forceful waves that strike the shore when high-speed boats and yachts pass. Boat traffic on the St. Lucie Canal was high during the survey and may act synergistically with burrows to increase erosion in some sites.

Based on burrow volumes and numbers of burrows per site, *Pterygoplichthys* were estimated to remove 1 to 4 percent of sediment per rectangular (1 m deep) volume of bank through their burrowing activities. However, estimates may be low since many of the burrows measured in the study were abandoned and relatively small (presumably because of erosion). Abandoned and exposed burrows were about half the volume of the few active burrows encountered.

Some *Pterygoplichthys* burrow colonies on outer bends of river meanders were associated with small boat docks. The co-occurrence may simply be due to catfish and humans using similar criteria to select sites. For catfish it is the relatively steep, exposed bank, and relatively firm soil of outer bends. For humans it is the higher ground, less prone to flooding, and deep water. In any case, property owners living along waterways near colonized banks and some boaters will likely be aware of *Pterygoplichthys* activity.

We found that *Pterygoplichthys* burrows in Florida rivers and canals were similar in size and structure to burrows associated with introduced populations in Hawaii (Devick 1988, 1989). While Devick's research in Hawaii focused on an impounded lake situation, the large number of burrows found there demonstrated the potential amount of benthic habitat that these catfish can modify. It is uncertain whether densities of loricariid catfishes in Florida have reached the levels experienced in Mexico or Hawaii because of a shortage of field surveys. At very high densities, the number of burrows could significantly contribute to erosion of banks and modification of benthic habitats.

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