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Research Article

Asian swamp eels (Synbranchidae, *Monopterus*) in Florida: distribution, spread, and range of hydrologic tolerance over twenty-seven years (1997–2023)

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Abstract

Asian swamp eels (*Monopterus albus/javanensis*) were first reported as introduced to Florida waterbodies in 1997 near Tampa and Miami; a third population was recorded by 1999 in Homestead. Initial assessments, published soon after swamp eels in southern Florida were first recorded in wetlands beyond canals and ponds (in 2007), concluded there was little threat to Florida's aquatic ecosystems. Long-term data now suggest they precipitated population crashes of crayfishes and small fishes in the eastern Everglades. We used records from continuous long-term monitoring programs, sporadic monitoring studies, and online databases to reconstruct swamp eel presence across Florida. Monitoring studies provided wetland hydrologic variables to assess limits for swamp eels. From 1997–2007, populations in southern Florida remained restricted to canals; initial spread from 2007–2017 across southern Everglades National Park proceeded slowly and the two populations covered ~1500 km^2 of southern Florida. From 2017–2022, the rate of spread increased as they spread west and north (~5800 km^2 range). Through 2014, the Tampa population occurred only along southern/eastern Tampa Bay (~60 km^2) but has since spread south along the Gulf Coast, east into central Florida, and south along the Lake Wales Ridge (~11,000 km^2). We found evidence of two potentially new introductions, in Palm Beach County and Orlando. There was no clear evidence of limitation of wetland drying on swamp eel occurrence in the Everglades; they were captured in marshes that dried for 1–5 months during the previous dry season, but short-hydroperiod wetlands may have slowed spread. In the Everglades, evidence suggests swamp eels may have been inadvertently spread into marshes from canals used to deliver water for flood control and hydrologic restoration. Swamp eels are currently spreading unchecked across Florida, and there should be great concern about continued spread in this region and their establishment and spread elsewhere.

Key words: Ecosystem restoration, Everglades, invasive fish, invasion history, *Monopterus albus*, Synbranchiformes

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Introduction

Swamp eels (family Synbranchidae) are found primarily throughout tropical and subtropical ecosystems, but range into temperate areas in eastern Asia (Rosen and Greenwood 1976; Perdices et al. 2005; Fricke et al. 2022). Synbranchids have a long history of being introduced to new regions, which has been primarily associated with their use in Asian cuisine, Buddhist prayer rituals, and food markets (Nico et al. 2011, 2019). The first known introductions are from the 1800s (i.e., movements of swamp eels around east Asia), and the most recently introduced populations have been documented after 2010 in the south central United States; an overview of their global introduction history can be found in Nico et al. (2019).

Native synbranchids are found in southern Mexico and Cuba, but no species are native to the Nearctic, including subtropical Florida. The first introduced population of synbranchids in the Nearctic was established by a population belonging to the *Monopterus albus*/*javanensis* complex and was detected in 1994 in wetlands along the Chattahoochee River near Atlanta, Georgia, United States (Starnes et al. 1998; USGS 2023). Two other populations from this species complex were detected in 1997, one near Tampa, Florida and the other in northern Miami-Dade County, Florida ('North Miami' population); a fourth population was detected in 1999 in southern Miami-Dade County ('Homestead' population; Collins et al. 2002). Additionally, two established populations of *Ophichthys cuchia* (formerly *Monopterus cuchia*) have been recorded in the United States, one in New Orleans, Louisiana and the other in Houston, Texas (Jordan and Nico 2020; Best et al. 2022). The Atlanta population and all three Florida populations have generally been referred to as *M. albus*, but there are at least two species in Florida (some referred to as *M. javanensis*) and likely another in Georgia (Collins et al. 2002). Given the recent description of new synbranchid species (see Britz et al. 2018), taxonomic changes to the family and potential application of the name *M. albus* to the Neotropical species *Synbranchus marmoratus* (Britz et al. 2021), and the need for further taxonomic revision (Perdices et al. 2005) and subsequent determination of the phylogenetic position of introduced populations (Collins et al. 2002), we use the generic term 'swamp eels' to refer to any individuals/populations while maintaining the prevailing standard that the Florida introductions are represented by the *M. albus*/*javanensis* species complex.

The distribution of the Atlanta swamp eel population originally detected at the Chattahoochee Nature Center has apparently remained restricted to within a few kilometers of the introduction site, although monitoring efforts are limited and a potential second population was recently detected in a tributary ~18 km to the southwest (Johnson et al. 2021; USGS 2023). In contrast, the swamp eel populations in southern Florida spread rapidly through the canals of Miami-Dade and Broward counties (Shafland et al. 2010), but were not detected outside of canals until 2007, when they were reported from marshes of the C-111 Panhandle region of the southeastern Everglades (Kline et al. 2014). From 2006 to 2010, limited efforts were made to remove swamp eels from the canals along the border of the Everglades using boat electrofishing in an attempt to restrict their distribution, reduce their populations, and slow their spread to the wetlands of the Everglades (Galvez et al. 2011). Most recently (data through 2012) in an assessment focused on Everglades National Park, Kline et al. (2014) reported swamp eels from throughout the C-111 Panhandle region, as well as around the northern end of Taylor Slough near where the slough receives water from the L-31W Canal. However, it is recognized that swamp eels are cryptic invaders and can be difficult to detect (Taylor et al. 2021) and are not often captured by methods readily accessible to the public (Shafland et al. 2010; Ame and Mayor 2021). Many of the observations documented by the public are of various larger egrets or herons capturing swamp eels (Taylor et al. 2018).

Early studies on swamp eels in the United States mentioned some concern for their potential to disrupt native ecosystems (Starnes et al. 1998; Collins et al. 2002), while preliminary effects of swamp eels in Georgia (Starnes et al. 1998) were later repudiated (Straight et al. 2005). Although concerns for potential effects of swamp eels continued to be mentioned in the literature (e.g., Nico et al. 2019; Sakaris et al. 2019), the few studies looking at potential swamp eel effects did not provide evidence that they may noticeably damage aquatic communities. In Florida in particular, an initial dietary study in aquaculture ponds (Hill and Watson 2007) and overall assessment of swamp eels in the state (Shafland et al. 2010) concluded that swamp eels had minimal ability to disrupt aquatic communities. These conclusions were premature (Pintar et al. 2023a, b). At the time Shafland et al. (2010) published their study, swamp eels had only been documented outside of anthropogenic canals in southern Florida native wetlands on one occasion (Kline et al. 2014), and no studies had been conducted on effects in natural habitats in the region.

The shallow (typically 10–80 cm deep) subtropical wetlands of the Everglades include temporary (<12 months) and near-permanent (multi-annual) hydroperiods. The wetlands within Everglades National Park were invaded from the adjacent canals near Homestead, FL sometime between 2000, when first found in the C-111 Canal (a canal open to Everglades National Park) and 2007, when they were first collected in wetlands downstream of the canal. Pintar et al. (2023a) assessed the current state and potential effects of the 10+ year swamp eel establishment in Taylor Slough (400 km^2 drainage; Fig. 1) on the eastern side of Everglades National Park. In that drainage, swamp eels have not only persisted since they were first detected, but have become more common than all other large fishes (>8 cm standard length) combined (Pintar et al. 2023a). Their invasion has been associated with the near-complete loss (>99%) of both species of procambarid crayfish, and declines or crashes (46–99%) of four out of the six previously most common small fish species. These effects of swamp eels have been partly tied to their drought resistance (Pintar et al. 2023a), due to the physiological capacity to withstand surface water loss (Rosen and Greenwood 1976; Liem 1987; Tay et al. 2003; Chew et al. 2005), unlike any other large fishes in the Everglades. This characteristic enables them to prey on species like crayfish and small fishes that are reliant on the short predator-free time periods at the start of the wet season for breeding and population growth (Trexler et al. 2005; Dorn and Cook 2015). The drought tolerance of the species has not been explored directly, but swamp eel populations have recently expanded beyond Taylor Slough (Pintar et al. 2023a, b).

In this paper we collated all available data to document the current and historic distributions of swamp eels in Florida, examine the range of hydrologic conditions where they have been captured within the wetlands of southern Florida, examine the detection capacity of two coordinated sample methods, and then discuss their potential future spread and its potential consequences.

Materials and methods

List of location abbreviations

ENP Everglades National Park;
LOX Arthur R. Marshall Loxahatchee National Wildlife Refuge (WCA 1);

SRS Shark River Slough, ENP;
STA Stormwater Treatment Area;
TSL Taylor Slough, ENP;
WCA Water Conservation Area.

Data sources

To create sequential maps of the presence of swamp eels over time in Florida, we compiled as many records as possible of swamp eels in Florida from 1997 to 2022, though we may have missed some records as some of our inquiries went unanswered. Because processing of 2023 samples was incomplete at the time of publication, records from 2023 and January 2024 were only included when they extended the known range or filled in spatial gaps between previous records. We broadly classified data sources into three categories: (1) long-term (>5-year) monitoring projects aimed at assessing responses of aquatic animal populations in the Everglades ecosystem to restoration and hydro-management, (2) short-term (<5-year) projects in canals of southern Florida, and (3) miscellaneous records posted to online databases or provided to us personally. The long- and short-term datasets are focused on southern Florida and the Everglades ecosystem south of Lake Okeechobee (Fig. 1) and miscellaneous records cover all of Florida. Long-term sampling efforts were focused on ENP and WCA 3, with additional projects in WCA 2, LOX, and the STAs. Among short- and long-term datasets, sampling methods primarily used 1×1 m^2 throw traps (water depth <1m; Jordan et al. 1997) or airboat electrofishing in wetlands and deeper (mostly <2.2 m) alligator holes (Chick et al. 1999), along with minnow traps and drift fence arrays (set at depths from 0.2–1.1 m in wetlands). Throw traps are active samplers that give density estimates (point estimates) by using seines and dip nets to clear a 1-m^2 area of all animals captured by a 1-mm mesh box (open on top and bottom) that is thrown into the marsh. This process is repeated multiple times in a wetland to create density estimates of small animals (e.g., Dorn and Trexler 2007). Electrofishing followed methods described in Chick et al. (1999) and has been detailed in other studies (e.g., Parkos et al. 2011; Pintar et al. 2023a). The datasets are described in brief below. We contacted/explored additional data sources including the Conservancy of Southwest Florida, Flickr, the Florida Fish and Wildlife Conservation Commission (FWC), and ecologists at Tribes and federal agencies (see Suppl. material 1).

Long-term datasets

Swamp eel records from long-term (>5-year) datasets across the Everglades provided the largest portion of records located outside of canals, representing 1,917 swamp eels captured from 2008 to 2023. These datasets are the most spatially expansive across the Everglades (Suppl. material 2: figs S1, S2), have consistent methodology for the duration of each project, and most have long periods of sampling prior to swamp eel detection (Table 1).

CERP-MAP: This dataset consists of throw trap data collected as part of the Comprehensive Everglades Restoration Plan (CERP) Monitoring and Assessment Project (MAP) from 2005–2022 (South Florida Ecosystem Restoration Task Force 2022). Sampling occurred in 146 'principal sampling units' (PSU) in wetlands across the Everglades ecosystem, from southern ENP north through LOX. Three throw trap samples (Jordan et al. 1997) were collected once per year in each PSU during the wet season (typically late September through early November). Data were collected by the Dorn/Trexler Aquatic Ecology Lab at Florida International University (FIU).

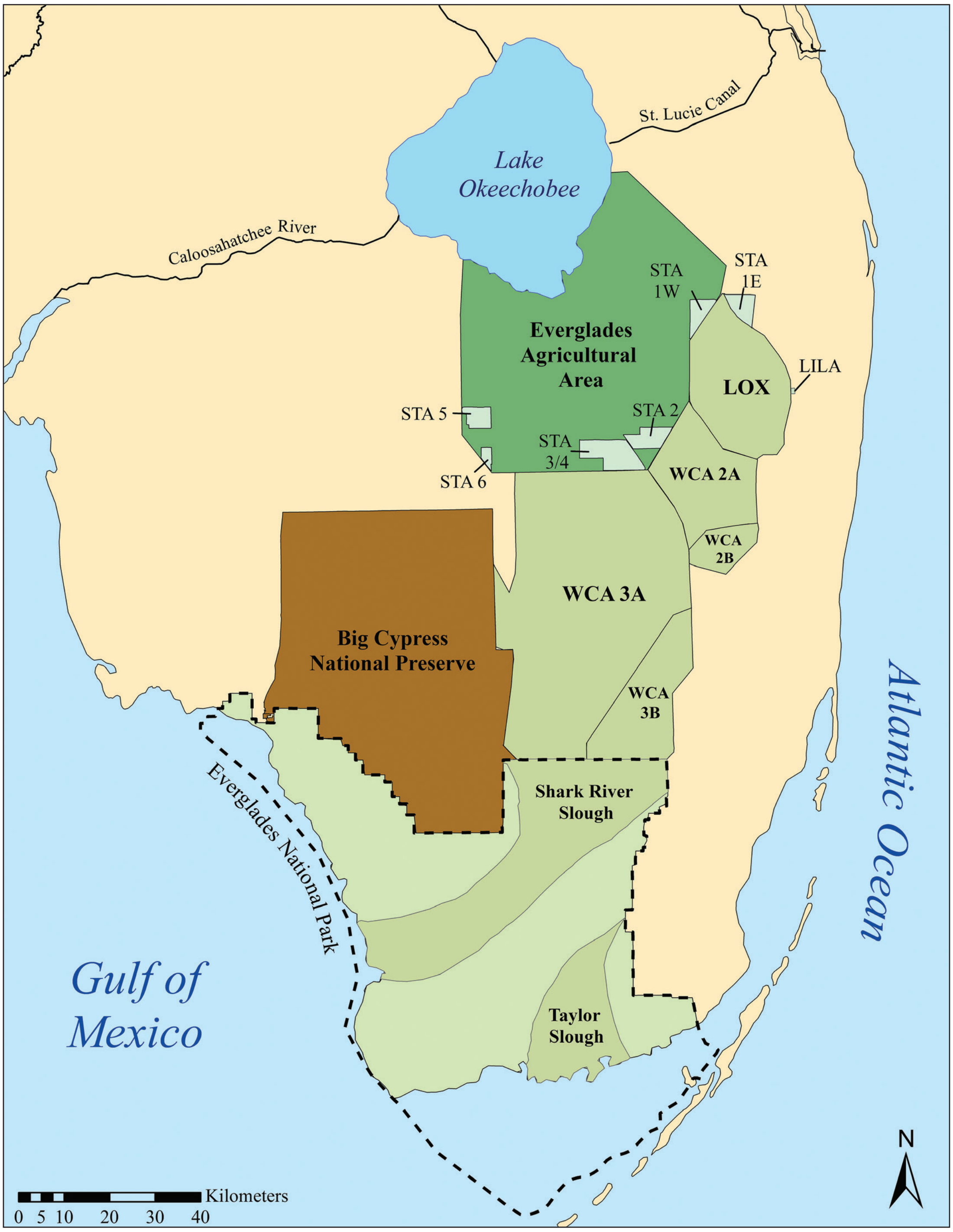

Figure 1. Map of southern Florida showing major regions of the Everglades ecosystem, including Everglades National Park (ENP), Big Cypress National Preserve, Loxahatchee Impoundment Landscape Assessment (LILA), Loxahatchee National Wildlife Refuge (LOX), the Water Conservation Areas (WCA; WCA 1 = LOX), Stormwater Treatment Areas (STA), and the Everglades Agricultural Area.

DECOMP: This dataset consists of throw traps (3 replicates per site), drift fences (3 replicates per site from 2019 until April 2020, then 1 replicate per site until March 2021), and airboat electrofishing (1–3 five-minute transects per site) of wetlands between the L-67A and L-67C canals of WCA 3B. Samples were taken twice per year from 2010–2017 and 2019–2022. Extensive sampling of sloughs began in 2019, with prior sampling primarily in the L-67C Canal. Data were collected by the Dorn/Trexler Aquatic Ecology Lab at FIU.

Table 1. Summary table of long-term datasets, their spatial and temporal scopes, the methods used to capture swamp eels, and the total number of individual swamp eels included in the dataset. All electrofishing is airboat-mounted.

Dataset	Spatial Scope	Temporal Scope	Methods	# swamp eels
CERP-MAP	All wetlands of ENP, WCA 2 & 3, LOX	2005–2022 1×/yr	Throw trap	29
DECOMP	WCA 3B near L-67 Canal	2010–2017, 2019–2022 2×/yr	Throw trap, Minnow trap fence arrays, Electrofishing	18 (throw trap), 3 (minnow trap), 273 (electrofishing)
IOP	ENP eastern boundary & SRS	2004–2022 3–5×/yr	Minnow trap fence arrays	21
LILA	Loxahatchee Impoundment Landscape Assessment	2008–2013, 2018–2022, 2×/yr	Throw trap and Fyke nets	0
MWD	Sloughs & alligator ponds of SRS, TSL, C-111 PHD, WCA 3	1996–2023 5×/yr (throw trap), 4×/yr (electrofishing)	Throw trap, Electrofishing	316 (throw trap), 1167 (electrofishing)
Misc. WCA	WCA 2 & 3, LOX	2007–2023 1–4×/yr	Electrofishing	2
Parkwide	All wetlands of ENP	2002–2019 1×/yr	Minnow trap	14
Rocky Glades	ENP Rocky Glades	1999–2019 monthly	Minnow trap	47
STA	STAs 1E, 1W, 2, 3/4	2016–2021 1–2×/yr	Throw trap in STA 2, Electrofishing in all four	3 (electrofishing)
UTS	Upper Taylor Slough	2017–2021 6×/yr	Throw trap	24

IOP: This dataset consists of un-baited minnow traps (3-mm mesh) set within larger fence arrays/funnels (4 traps per array) soaked for 24-hour periods at 12 sites (50 total drift fences) along the eastern border of ENP near the C-111, L-31W, and Aerojet canals; 5 sites (2 drift fences per site) in SRS of ENP; and at 3 sites (4 total drift fences) in ENP between SRS and the C-111 Canal. Samples were taken 3–5 times per year from 2004–2022. Data were collected by the Dorn/Trexler Aquatic Ecology Lab at FIU.

LILA: The impounded wetlands (Loxahatchee Impoundment Landscape Assessment; LILA) on the eastern edge of LOX were sampled with throw traps (14 random samples collected per sample season per 8-ha wetland) and fyke nets (and hoop nets) multiple sizes soaked for 24 hours for three consecutive nights twice a year for a series of 9 years spanning 2008–2022. Data were collected by the Dorn Aquatic Ecology lab at Florida Atlantic University until 2021 and then by FIU in 2022.

MWD: This dataset consists of throw trap and airboat electrofishing collected as part of the Modified Water Deliveries (MWD) to ENP project and ENP long-term monitoring efforts (Jordan et al. 1997). Throw trap data (5 or 7 throw trap samples per plot; 3 or 5 plots per site) were collected at 3 sites in TSL, 6 sites in SRS, 2 sites in WCA 3B, and 8 sites in WCA 3A from 1996–2023. An additional site in WCA 3A was sampled from 1996–2006; four sites in the C-111 Panhandle were sampled from 2008–2023. Airboat electrofishing was conducted at 18 of these marsh sites (three 5-minute transects per plot) and at nearly 50 alligator ponds over the course of the study (Chick et al. 1999; Pintar et al. 2023a). Data were taken four (electrofishing) or five (throw trap) times per year to monitor populations of small fishes, invertebrates, and large fishes in response to changing water management to ENP. Data were collected by the Dorn/Trexler Aquatic Ecology Lab at FIU and ENP.

Misc. WCA 2A, 3A, & LOX: This dataset consists of airboat electrofishing (Chick et al. 1999) conducted at three marsh sites in the middle of LOX and at three sites in central/southern WCA 2A. There were two plots per site with three transects per plot; three alligator ponds were also sampled in LOX. Data were typically collected four times per year from 2006–2020 to monitor populations of large fishes in these regions. Additional sampling efforts were performed in southern WCA 2A during the dry season of 2022 and at two of the MWD project sites north of Interstate 75 during January and November 2023. Data were collected by the Dorn/Trexler Aquatic Ecology Lab at FIU.

Parkwide: Distribution study of aquatic animals across ENP from 2002–2019 using un-baited minnow traps once per year during the end of the wet season (October–November). Data were collected at 104 total sites across the park (59–87 sites sampled per year); there were six un-baited galvanized wire mesh minnow traps (three 3.0 mm and three 6.4 mm with 2.2 cm openings) set for approximately 24 hours at each site. Data were collected by ENP.

Rocky Glades: Monthly distribution study using minnow traps at 17 sites in the Rocky Glades of ENP from 1999–2019. From June 1999 to September 2000, 9 sites were sampled monthly in the Rocky Glades using six 6.4 mm galvanized wire mesh minnow traps with 2.2 cm openings set for approximately 24 hours. Collected individuals were identified, measured, and released alive; traps were reset for a subsequent 24-hour sample and pulled the next day (~48 hours total effort). From April 2001 to April 2019 this study was expanded to 17 sites sampled with six un-baited galvanized wire mesh minnow traps (three 3.0 mm and three 6.4 mm with 2.2 cm openings). Minnow traps were each baited with a 1.25 to 2.5 cm piece of frozen bait shrimp. Data were collected by ENP.

STA: Throw trap and electrofishing sampling collected one or two times per year from 2016–2021. Throw trapping was only performed in STA 2 but electrofishing occurred in multiple cells/regions of all four STAs (1E, 1W, 2, and 3/4; STA 5/6 was not sampled). Data were collected by the Dorn/Trexler Aquatic Ecology Lab at FIU.

UTS: This was a subproject of the MWD project from 2017–2021 with throw trap sampling occurring bimonthly. Sampling covered 12 sites in the northern (upper) portions of TSL near the L-31W Canal. Data were collected by the Dorn/Trexler Aquatic Ecology Lab at FIU.

Short-term datasets

Swamp eel records from short-term datasets of canal electrofishing totaled 11,188 swamp eels (Table 2).

Aerojet Boat: Electrofishing project on the Aerojet Canal from 2012–2014. Structural changes to the canal in 2014 made it impossible to access most areas and the project stopped. Data were collected by ENP.

CESI Canals: Data collected and used by Gandy and Rehage (2017) using boat electrofishing of canals along the borders of ENP and WCA 3 from 2010–2013.

ECISMA: A 'fish slam' type project (collections by multiple teams over a short period of time to try and detect non-natives) organized by ENP and the Florida Fish and Wildlife Commission with boat electrofishing of canals in Miami-Dade County near ENP in 2014. Duplicate data from the Aerojet Boat project were removed.

Galvez et al.: Swamp eel removal efforts from 2006 to 2010 in the canals east of ENP collected by Galvez et al. (2011). It includes swamp eels captured and removed (N = 5,915) from canals, as well as those observed but not caught (N = 4,458), which could have been captured during subsequent sampling efforts. Some swamp eels captured were used by Sakaris et al. (2019).

Table 2. Summary table of short-term datasets, their spatial and temporal scopes, the methods used to capture swamp eels, and the total number of individual swamp eels collected. All electrofishing is boat-mounted.

Dataset	Spatial Scope	Temporal Scope	Methods	# swamp eels
Aerojet Boat	Aerojet Canal	2012–2014	Electrofishing	39
CESI Canals	L-31, C-111, L-29, and L-67A canals	2010–2013	Electrofishing	627
ECISMA	L-5, L-30, L-102, L-103, L-113, L-28INT canals	2014	Electrofishing	71
Galvez et al. 2011	C-102, C-103, C-111, C-111E, C-113, L-31N, L-31W canals	2006–2010	Electrofishing	10,451

Miscellaneous datasets

These datasets provided 798 additional records, not necessarily individual swamp eels as some records may have had multiple individuals (Table 3).

Audubon: Records of swamp eels caught in the coastal Everglades mostly south and east of the C-111 Panhandle region and Taylor Slough by Audubon's Everglades Science Center with associated salinity data. Data were provided by Alexander Blochel and Jerry Lorenz

EDDMaps: Online reporting platform for detecting invasive species run by the University of Georgia. We only used records that were verifiable with photos and clearly distinct from other records in other databases (cross-posting often occurs).

FWC: Swamp eels caught electrofishing primarily from canals in southeast Florida and rivers in southwest Florida by the Florida Fish and Wildlife Conservation Commission from 2014 to 2022. Data were provided by Daniel Nelson.

iNaturalist: All observations of swamp eels (or of birds with swamp eels) posted to iNaturalist.org from the state of Florida. We used "Synbranchidae" as the filtering term for initial searches and all records were posted as *Monopterus* sp., *M. albus*, or *M. javanensis*; we maintain the species complex as the lowest level of identification. Permission was obtained from users whose observations had restrictive licensing (all rights reserved) for inclusion in this project.

Miscellaneous: Records of swamp eels sent to us as personal communication. Two records were from Hunter Howell (University of Miami), three from Jennifer Rehage's lab (FIU), and one each Mark Pepper (ENP), Jeff Kline (ENP), Nathan Dorn (FIU), and Jenn Miller (Fort Myers). We also include the original North Miami detection site as a miscellaneous point as it was not included in other datasets.

USGS-NAS: Records of swamp eels from the USGS-NAS (USGS 2023) database. All records of *Monopterus* sp. and *M. albus* were collected and identified as the species complex for our purposes. We filtered out all iNaturalist observations and other potential duplicates that were part of other datasets here.

Table 3. Summary list of miscellaneous datasets, their spatial and temporal scopes and the total number of swamp eel records they encompass (not necessarily individual swamp eels).

Dataset	Spatial Scope	Temporal Scope	# records
Audubon	Coastal Everglades	2007–2021	40
EDDMaps	Florida	1997–2022	4
FWC	Florida	2014–2022	541
iNaturalist	Florida	2012–2024	87
Miscellaneous	southern Florida	1997, 2022–2024	10
USGS-NAS	Florida	1997–2021	116

Rate of spread

Using all of the locations of swamp eels we obtained from 1997–2022, we created five estimates of the rate of swamp eel spread in wetlands of southern Florida. These estimates were generated based on the distance and timing of occurrences between most distant points in those regions and the number of years between those most distant observations. These five estimates were (1) from southeastern ENP from the C-111 Canal to the park road near Nine Mile Pond, (2) from Royal Palm to southern SRS, (3) from the Tamiami Canal to southern SRS, (4) across WCA 3B, and (5) across WCA 3A.

Range of hydrologic conditions, swamp eel sizes, and detection methods

We used data on marsh-caught swamp eels using both electrofishing and traps (predominantly throw traps) from the CERP-MAP, DECOMP, MWD (excluding alligator ponds), and UTS datasets through May 2022. The primary methods for sampling fishes in wetlands had depth limitations. When trails were not accessible by airboats, throw trapping continued in some areas when we had access by helicopter, but only five samples (versus seven) were collected from MWD and UTS sites in ENP when accessed by helicopter. Additionally, marshes were not sampled with throw traps if the field-measured water depth was <5 cm or >100 cm. Electrofishing was not typically performed if water depths were <20 cm, but a few depth measurements indicated electrofishing may have been rarely conducted in shallower conditions. Therefore, while we expect swamp eels were present in the marshes when the water depth was <5 cm (throw traps) or <20 cm (electrofishing), we do not have the ability to assess that potential occurrence with these datasets. Instead, we focus our analysis of their presence on the antecedent water depths experienced in the fluctuating semi-permanent wetlands. Some locations reach annual lows of 10–20 cm during the dry season while other wetlands are seasonal and have annual dry conditions (water surface below soil surface).

Total lengths (TL, mm) of individuals caught by electrofishing were measured in the field, and lengths of individuals caught in traps were measured in the lab. Some smaller swamp eel lengths, particularly for electrofishing, were noted as <100 or <200 mm, all of which we have excluded from our length assessments. Each swamp eel individual was counted as a unique occurrence; if multiple swamp eels were captured in one sample such as one throw trap sample or one electrofishing transect, they were counted separately. Using the date and location of each swamp eel occurrence in our datasets through May 2022, hydrologic conditions were estimated from the Everglades Depth Estimation Network (EDEN; Telis 2006; Liu et al. 2009). Daily depth records in cm for the sample sites were based on EDEN values corrected by our *in situ* measurements of depth. Three primary variables were obtained or calculated: (1) the depth (cm) at the time of collection, (2) the number of days since a site was dry (DSD; depth <5 cm; Trexler et al. 2005), and (3) the length of the previous dry season (LDS; days the depth was <5 cm during the previous dry season; ranging from 0 to 160 days; Pintar et al. 2023a). These variables have been used as indicators of current and past hydrologic conditions and have been used to model relationships between hydrology and populations of aquatic animals in the Everglades (Trexler et al. 2005; Dorn and Trexler 2007; Pintar et al. 2023a). We then explored the variation in hydrologic conditions at locations where swamp eels occurred by sampling methods and over time. To consider the evidence for recruitment and establishment in different locations, the variation in captured swamp eel sizes was assessed across time (seasonally and across the entire time series), along with examination of sizes found in the driest years/sites.

Using MWD data, we compared the detection of swamp eels at a site using electrofishing versus throw traps. We determined which method first detected swamp eels at each plot in TSL, SRS, and WCA 3 and compared the number of sampling periods during which swamp eels were detected at a plot by each sampling method. Sampling locations (e.g., the C-111 Panhandle) and time periods (e.g., December) with limited or no electrofishing were excluded from analyses. Lastly, we summarize ecosystem salinity associated with swamp eel occurrences in the Audubon dataset because these captures were from estuarine wetlands.

Results and discussion

We found 13,882 swamp eel records with both dates and locations in Florida from 1997 to 2022; on maps we include 21 additional range-extending records from 2023 and January 2024. All occurrence data and full resolution maps are archived on Figshare (Pintar et al. 2024).

Historical distributions and spread

For more than a decade after their first introductions (estimated mid-1990s), populations of swamp eels were mostly confined to the canals in eastern Miami-Dade County and a few water bodies near Tampa Bay. As of 2024, swamp eels can be found through a large and expanding portion of Florida from Orlando southward (Figs 2, 3). The three originally detected populations (Tampa, North Miami, Homestead) all appear to have undergone rapid expansion, mostly after 2015 (Suppl. materials 3, 4: figs S4–S11), while we have also detected what appear to be new introductions at two other locations, in Palm Beach County and Orlando. Detailed distribution histories are discussed below.

Tampa Bay and Central Florida

Our understanding of the distribution and spread of the population originally detected near Tampa has not had the benefit of extensive monitoring programs like those in the Everglades of southern Florida. The distribution of the Tampa population was largely determined based on USGS-NAS, iNaturalist, and some FWC observations and does not necessarily indicate clear spread via any specific waterways. The Tampa population was apparently restricted to the southern/eastern sides of Tampa Bay and north of Sarasota until after 2014 (Fig. 2, Suppl. material 3: figs S4–S7) at which time the distribution of occurrences covered only ~60 km^2. This population has since spread throughout the region roughly bounded by the Lake Wales Ridge to the east, the Caloosahatchee River to the south, the Gulf of Mexico to the west, and to the north by a 2022 record indicating spread northward into the Hillsborough River; this population now covers ~11,000 km^2. In 2015, swamp eels appeared in the upper Peace River watershed and were found in the southern portion of the Peace River watershed near Charlotte Harbor in 2018, the same year swamp eels started being documented throughout the lakes and wetlands along the Lake Wales Ridge (Fig. 2).

During 2021, several iNaturalist observers began documenting swamp eels in Myakka River State Park (also in the Charlotte Harbor watershed). The observations of swamp eels in the area of Myakka River State Park highlight the value of citizen science observations for illustrating the spread of swamp eels in this area, since it is

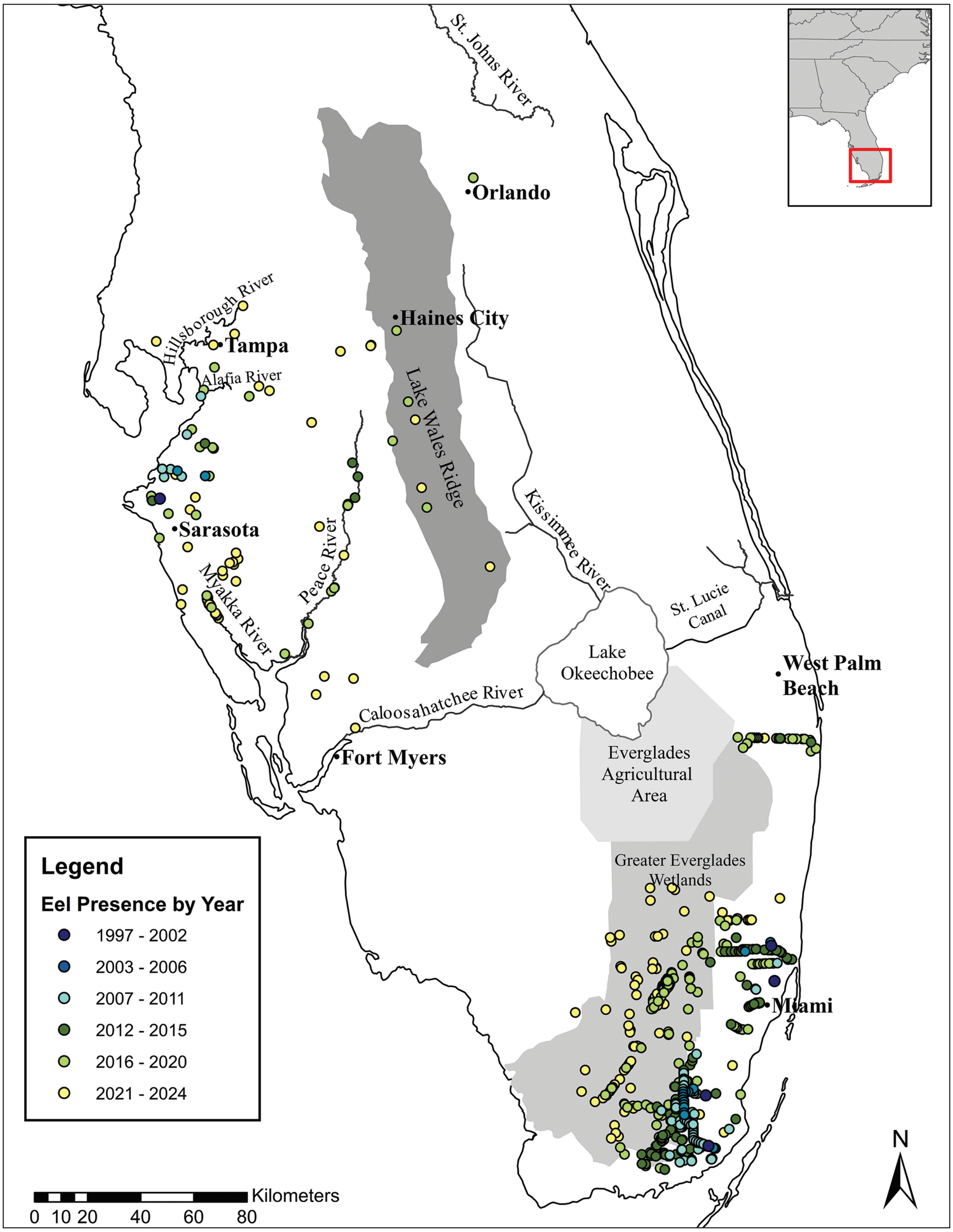

Figure 2. Map of all swamp eel records across Florida from 1997–2024. Points are colored by year of record.

an area heavily visited by the public and with many wading birds that have been observed catching swamp eels. The sparsely populated areas, and perhaps fewer parks, between the Gulf Coast and the Lake Wales Ridge lack citizen observations and have only a few records from USGS-NAS on the Peace River (Fig. 2).

The exact dispersal pathway of swamp eels in central Florida and how they spread from the area around Tampa Bay to the Charlotte Harbor watershed

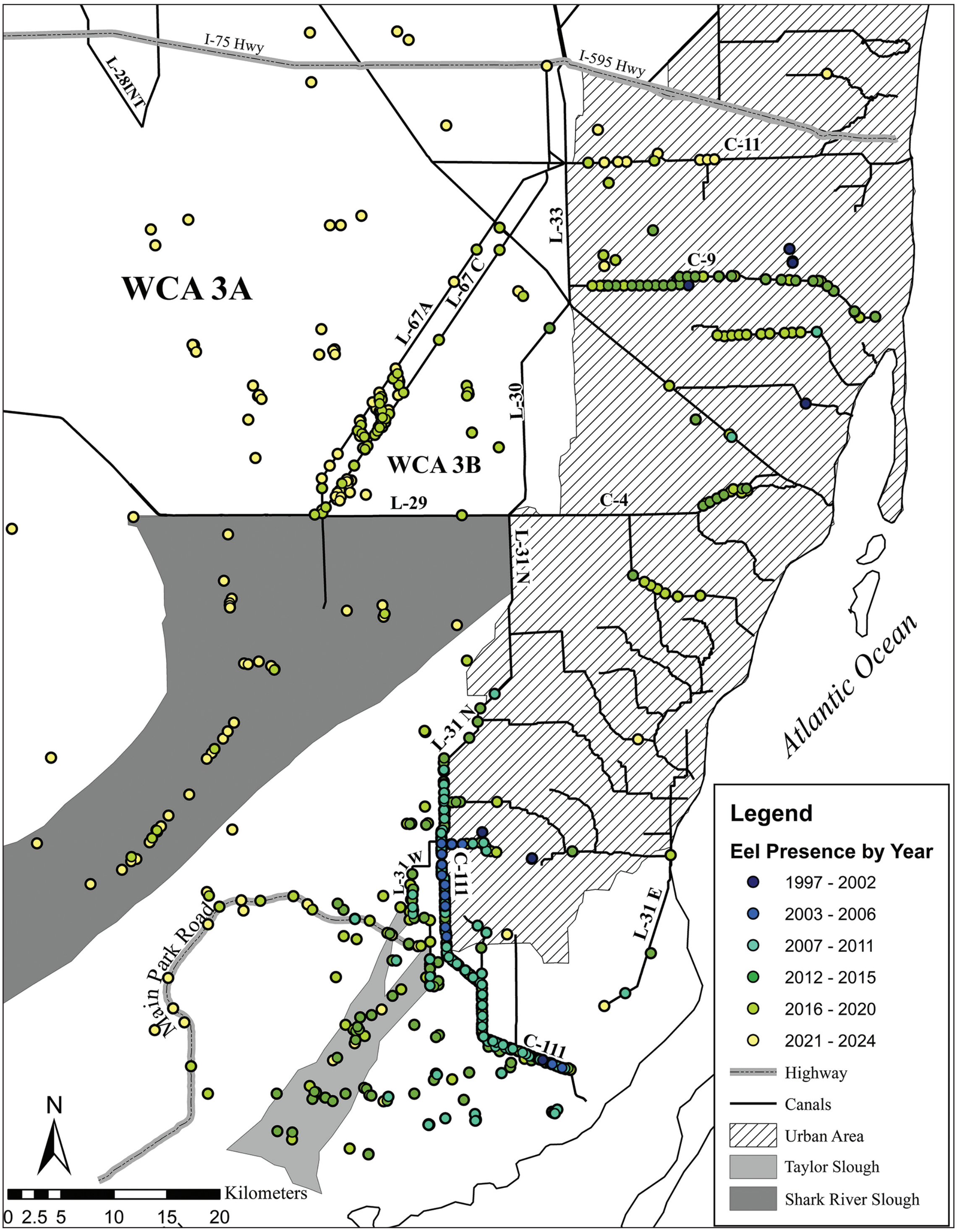

Figure 3. Map of all swamp eel records across southern Florida (WCA 3 southward) from 1997–2024. Points are colored by year. Hashed areas are developed and agricultural regions.

could not be discerned. Given the relative proximity of our few data points, the ability of the species to tolerate drought, and the topographic flatness of the state it is possible these new points represent movement eastward to the headwaters of the coastal drainages around Tampa and then a jump into the Peace River Watershed, which drains to Charlotte Harbor, during a particular high-water point in a year.

Orlando

A more distinct occurrence of swamp eels was documented in 2020 and 2022 at the Mead Botanical Garden in Winter Park near Orlando (Fig. 2). These occurrences were 64 km northeast of the next closest swamp eel occurrence in Middle Hamilton Lake near Haines City, making it the most spatially isolated known swamp eel occurrence in Florida. Whether the Orlando occurrence represents spread from the Tampa population or an isolated population is unknown due to a lack of data in the region. There are likely routes of spread between Haines City and Winter Park, but they are not as direct as movement through a riverway or across a large open wetland. Additionally, the continued occurrence of swamp eels at the Mead Botanical Garden, but not at other sites in the region, is peculiar and supportive of a distinct population. Importantly, the Winter Park records are in the St. Johns River watershed and potentially represent a new avenue of spread both northward and southward through the largest river watershed in the state.

Palm Beach County

In 2015, swamp eels were first recorded from the Palm Beach Canal near Palm Beach International Airport (Fig. 2), and then in 2016 they were found in STA 1E to the west along the same canal just north of LOX. Swamp eels have continued to be documented in the canal with FWC monitoring efforts. This potentially represents another introduction of swamp eels as the next closet records were 60 km to the south. Sampling in LOX, WCA 2, and the LILA impoundment wetlands have yet to detect swamp eels in or around LOX or WCA 2, and no USGS-NAS or iNaturalist observations have been reported nearby. However, limited electrofishing in LOX was performed until 2020 and no projects in the developed areas of Palm Beach County are known that might detect swamp eels. It is perhaps possible the Palm Beach population was a result of the spread of swamp eels from the populations to the south, but repeated observations along this canal and a lack of observations anywhere in the heavily populated 60 km between this population and those in Miami-Dade and Broward counties suggests a unique introduction. Further assessment of the distribution of swamp eels in Palm Beach County is needed, along with their potential relation to other populations. The occurrence of swamp eels on the upstream side of LOX in the constructed nutrient remediation wetlands (STAs) suggests they may soon colonize and spread into that large wetland.

Southern Florida – North Miami and Homestead

As of January 2024, swamp eels were known to occur in southeastern Florida from just north of Interstate highways 75 (Alligator Alley) and 595 southward (Fig. 3, Suppl. material 4: fig. S11). This includes the developed and agricultural areas of Broward and Miami-Dade Counties, nearly all of WCA 3A, all of WCA 3B, and much of ENP. In ENP, regions with swamp eels include the C-111 Canal and Panhandle wetlands, TSL, SRS, and the Rocky Glades. As of 2017 the two populations in southern Florida were potentially still spatially separated and covered a total area of ~1500 km^2 (North Miami: 700 km^2; Homestead: 800 km^2). We expect that the two populations (likely different species or subspecies; Collins et al. 2002) of swamp eels originally detected in North Miami and Homestead are now mixed in the region, covering a total area of at least 5,800 km^2, and their separate contribution to the overall spread and distribution cannot be delineated with these records. Additional study of the genetic composition of swamp eel populations across the current distribution in Florida may help better determine the spread of the North Miami and the Homestead variants and their relatedness to newly detected populations in Palm Beach County and Orlando.

Our findings in the southern portion of Miami-Dade County and ENP support those of Kline et al. (2014), with the first appearance of swamp eels outside of canals occurring in the C-111 Panhandle region in 2007 and then in 2009 at Royal Palm (Fig. 3, Suppl. material 4: figs S8, S9), both in areas downstream of canals. From 2009 through 2014 (Suppl. material 4: figs S9, S10), there was a proliferation of swamp eel occurrences from control and monitoring efforts in canals on the eastern boundary of ENP. There was limited sampling effort in the C-111 Panhandle marshes until sampling was expanded in 2008 in response to collections of swamp eels south of the canal in 2007. When marsh electrofishing began in 2009 in the C-111 Panhandle region, swamp eels were already established in the marsh. Electrofishing in TSL was consistent since 1996, but swamp eels were not detected in the center of the sloughs until 2012. Following their first detection at the Royal Palm visitor center near the main park road in 2009, swamp eels invaded and established throughout TSL (established everywhere by 2014) while they were also beginning to be documented in the Rocky Glades and spreading west along the park road in ENP. Cold events and severe droughts during subsequent dry seasons in 2010/2011 (Boucek and Rehage 2014; Rehage et al. 2016) may have played some role in limiting initial spread into Taylor Slough, but limited data from Panhandle marshes in close proximity to the C-111 Canal suggest swamp eels there either recolonized quickly following those events or may not have been impacted to the extent other non-native fishes were (Pintar et al. 2023a, b).

Although water management along the eastern boundary of TSL experienced a shift in infrastructure and operations during the early 2000s that altered water flows to Taylor Slough through the L-31W Canal (Kline et al. 2014; Kotun and Renshaw 2014), the management and infrastructure remained relatively consistent until about 2012 when a series of new water management actions began. These included new pump stations and seepage management structures that increased connectivity of water flows from the C-111 and L-31N canals. By 2017, these structures were actively delivering water through sections of the L-31W Canal into ENP. Our findings suggest that it is possible that changes to water deliveries from structures bordering the C-111 and L-31 canals unintentionally encouraged the westward colonization and movement across the short hydroperiod prairies and into the deeper sloughs of TSL between 2012 and 2017.

At the same time (2010–2014) as swamp eels were spreading through southeastern ENP, records continued to document swamp eels in the area around the C-9 Canal in northern Miami-Dade and Broward counties (Suppl. material 4: figs S9, S10). Swamp eels were not found in the L-30 Canal until 2014, suggesting what was likely the North Miami population of swamp eels was spreading west and then south; the L-30 Canal is on the east/urban side of the protective levee outside of WCA 3B. Beginning in 2015, a new pump station (S-356) on the L-29 Canal changed the historic west to east gravity fed flow direction out of the Everglades (via S-334) to capture seepage in the L-30 and L-31N canals and pump water to the west into northeast SRS of ENP. From 2015 to 2018 FWC canal electrofishing continued to document the occurrence of swamp eels in urban canals before the beginning of a rapid westward range expansion in 2017 and 2018 (Suppl. material 3: fig. S7).

In 2017, swamp eels were first recorded within WCA 3B, and in 2018 they were found at the northeastern end of the L-67A Canal on the border of WCA 3A (Suppl. material 4: figs S10, S11); these areas are downstream of the S-9 pump station that moves water from the C-11 Canal from the eastern side of the protective levee into the WCA canals and marshes. In 2019, swamp eels were further documented in

WCA 3B and the Tamiami Canal, while the start of electrofishing in sloughs between the L-67A and L-67C canals (on the border of WCAs 3A and 3B) documented the widespread occurrence of swamp eels in that area. Sampling that occurred from 2010 to 2017 in the L-67C Canal notably did not detect swamp eels, suggesting a rapid invasion of WCA 3B up to the border of WCA 3A adjacent to the L-67A Canal in 2018. Simultaneously, downstream of the Tamiami Canal, the first two swamp eels in SRS were found in 2018 and 2019, before being found throughout most of the slough in 2020. Whether swamp eels in SRS spread south (downstream) from the Tamiami Canal and/or westward across shallower areas of Everglades National Park is not clear due to a lack of electrofishing in the marshes on the east side of SRS. A series of iNaturalist observations along the park road suggest a likely westward spread toward southern SRS, while the known occurrences of swamp eels upstream of SRS (WCA 3 and adjacent canals) indicate swamp eels may have arrived in SRS from both the north (upstream) and east (across the Rocky Glades). Since 2020, we have seen the continued occurrence and establishment of swamp eels throughout SRS and their initial spread westward towards the southwestern Everglades. In 2021, swamp eels were first detected in WCA 3A and have since been found across most of the region with the first records north of Interstate 75 during fall 2023. A November 2023 iNaturalist observation along the loop road in Big Cypress National Preserve is the westernmost record of the southern Florida populations.

In southern Florida, the total distance spread from the first detection site in the C-111 canal has been >40 km westward, while that from the North Miami site appears to be >60 km to the northwest. Two estimates of the rate of spread in the southeastern Everglades indicated swamp eels spread at 2.5–3.1 km/yr for their movement across seasonal wetlands from the C-111 Canal across TSL to the park road near Nine Mile Pond, and from Royal Palm across the Rocky Glades to southern SRS. Assuming swamp eels entered SRS from the Tamiami Canal, their spread southward through contiguous longer hydroperiod wetlands could be estimated at 13 km/yr. This rapid spread observed since 2017 is also supported by the rates observed in other longer hydroperiod slough habitats in WCA 3B (13.5 km /yr) and WCA 3A (20–25 km/yr).

Range of hydrologic conditions

From our four datasets used for this assessment, a total of 1,557 swamp eels were caught in marshes; 1,510 of those swamp eels had recorded lengths. There were 1,202 swamp eels caught electrofishing (1,157 with lengths), and 354 individuals (352 with lengths) caught in throw traps (excluding drift fences).

Projecting the future distribution and effects of swamp eels requires us to evaluate how much hydrologic disturbance they can withstand across the wetland hydrologic gradient. Other large-bodied fish populations in the Everglades are limited by past drying and take years to recover because the landscape is topographically flat (Chick et al. 2004; Parkos et al. 2011). Our review of the data indicated swamp eels were captured in wetland habitats spanning much of the hydroperiod gradient in the Everglades. The minimum number of days since drying (DSD) associated with a capture was less than one month (24 days) – a value likely limited by the timing of sampling at the start of the wet season, wherein the wet season begins in June and sampling for our monitoring studies often starts in July. The maximum DSD was over 11,300 days (31 years continuous hydroperiod) from swamp eels collected in 2021 and 2022 from sites in WCA 3 (DPM project and one MWD record) that have not dried since before the MWD project began and before swamp eels were detected in Florida (Suppl. material 5: fig. S12).

The range of depths associated with swamp eel captures in wetlands varied similarly for electrofishing and trap captures, with depths ranging from 10–100 cm (Table 4). As noted in the methods, the lower limit of depths is based on sampling limitations with throw trap samples not collected when depths are <5 cm and electrofishing samples typically not collected when depths are <20 cm. The range of depths in which swamp eels have occurred since 2009 have also shown some general trends towards being higher in more recent years (Suppl. material 5: fig. S13), which is likely a combination of the spread of swamp eels to deeper regions and a recent increase in the hydroperiod of southern Everglades regions (associated with increased connectivity across the Tamiami Trail) with higher captures, like TSL (Kotun and Renshaw 2014) or a recent string of high rainfall/highwater events observed since 2015.

The most interesting hydrologic condition is perhaps the length of the previous dry season (LDS), which provides an indication of the severity of the drying that occurred at a site over the most recent dry season. The minimum, mean, and median LDS values were all quite low (Table 4; Suppl. material 5: fig. S14), which should be expected since few sites have dried in recent years as swamp eels have spread and become more common across the Everglades. Indeed, many sample sites where they are present have never dried during the history of swamp eels in Florida and so the minimum LDS is zero days. However, the maximum LDS for sites where swamp eels have been observed is 140 days for electrofishing and 142 for throw traps – indicating swamp eels have occurred at sites that have recently been dry for nearly 5 months. Dry seasons that lasted for 140 and 142 days were near the maximum (160 days) observed in the entire history of our longest datasets from sloughs. All LDS values >142 days occurred in SRS and WCA 3 long before (2012 and earlier) the arrival of swamp eels in those regions.

All of the >130-day LDS swamp eel occurrences (N = 9) were in the C-111 Panhandle region during 2011 (Suppl. material 5: fig. S14), but occurrences of swamp eels at sites with LDS values of 90–129 days (N = 19) occurred in the C-111 Panhandle during 2009 and 2011 and northern TSL during 2019 and 2020 as part of sampling for the MWD and UTS projects. Most of the >90-day LDS swamp eel occurrences were during sampling that occurred during October and December sampling periods, which gave swamp eels 3+ months to recover or colonize, but the severity of the drought in 2011 precluded collection of any July samples, so it is difficult to assess exactly how soon after re-flooding that swamp eels can be found. Furthermore, many of these occurrences were at sites in the C-111 Panhandle close (<1 km) to a canal (the entirety of the UTS region is <5 km from canals). Nevertheless there were occurrences of swamp eels found with >90-day LDS values at sites 6–10 km from a canal and >2 km from coastal creek habitats. Swamp eels found at sites >2 km from canals and creeks included both adults and juveniles, and the juveniles (~60 mm) seem unlikely to migrate long distances to/from deeper refuges compared to adults, suggesting they probably aestivated in place during the previous 3–4-month dry period. In SRS and TSL, swamp eels have been found throughout the sloughs during July sampling following dry seasons that lasted between 30 and 70 days; a few of these individuals were juveniles, but most captures were of larger individuals caught during electrofishing (electrofishing targets larger size classes).

Records documented here suggest that swamp eels can withstand droughts perhaps as long as many of the good crayfish-producing (*Procambarus alleni*-inhabited) short hydroperiod wetlands in marl prairies of southern Florida. This means the western Everglades could experience *P. alleni* population reductions if swamp eels become established in those wetlands (Pintar et al. 2023a), which have 7–11-month hydroperiods. Direct experimental demonstrations of the effects of drying on swamp

Table 4. Summary statistics of swamp eel occurrences: days since a site was last dry (depth <5 cm; DSD), depth, length of the previous dry season (days depth <5 cm; LDS), and total length of swamp eels for data on individuals caught electrofishing and traps (throw traps and drift fences).

	Min	Max	Mean	Median
DSD (days)				
Electrofishing	34	11,385	1,304	278
Traps	24	11,399	913	429
Depth (cm)				
Electrofishing	11.3	116.4	38.9	37.3
Traps	10.4	91.5	40.7	39.9
LDS (days)				
Electrofishing	0	140	10.7	1
Traps	0	142	13.8	0
Length (mm)				
Electrofishing	114	1000	425	395
Traps	19	423	76	64

eels, comparing their resistance to that of burrowing crayfish (Dorn and Volin 2009), along with monitoring of shorter hydroperiod prairie habitats should help develop stronger expectations about the future of swamp eels and their effects.

In the coastal Everglades, the range of salinities from the Audubon dataset was 0.3–22.3 PSU. Excluding 15 occurrences in freshwater (<1 PSU), the mean salinity was 8.5 PSU. Seven occurrences were in slightly saline water (1–3 PSU), eight in moderately saline water (3–10 PSU), and ten were in highly saline water (10–35 PSU). Only two occurrences were in water with salinity >20 PSU, both in 2008, soon after swamp eels were first recorded in the C-111 Panhandle region. Schofield and Nico (2009) documented that swamp eels from all three original populations can withstand salinities as high as 18 PSU for several days, but mortality rates do vary among populations. In the Schofield and Nico (2009) results, the Homestead population of swamp eels, which is almost certainly the same population documented by the Audubon dataset, had 100% survival up to 40 days in all salinities they were exposed to. Together, these results suggest some populations (or species) of swamp eels are able to survive for extended periods of times in saline conditions (at least as high as 20 PSU) and could potentially use shallow coastal marshes as dispersal pathways.

Swamp eel sizes

The mean sizes of swamp eels caught varied as expected by method, with electrofishing capturing larger individuals (mean = 425 mm TL) and throw traps catching mostly juveniles (mean = 76 mm), with overall sizes ranging from 19 mm to 1000 mm (Table 4). There was no clear seasonal variation in the sizes of swamp eels caught electrofishing (Suppl. material 5: fig. S15), which may suggest no potential size-based (and inherently sex-based since they are hermaphroditic and all become males as they grow; Liem 1963; Yang and Xiong 2010; Matsumoto et al. 2011) mortality related to seasonal variation in hydrologic conditions. There was a clear trend of increasing sizes of swamp eels caught in traps from the start of the wet season (June) through the end of the dry season (April; Fig. 4). This suggests that most swamp eel breeding occurs at the start of the wet season and the growth of these new recruits progresses consistently throughout the water year from the start of the wet season in June through the end of the following dry season in May (Long and LaFleur 2011).

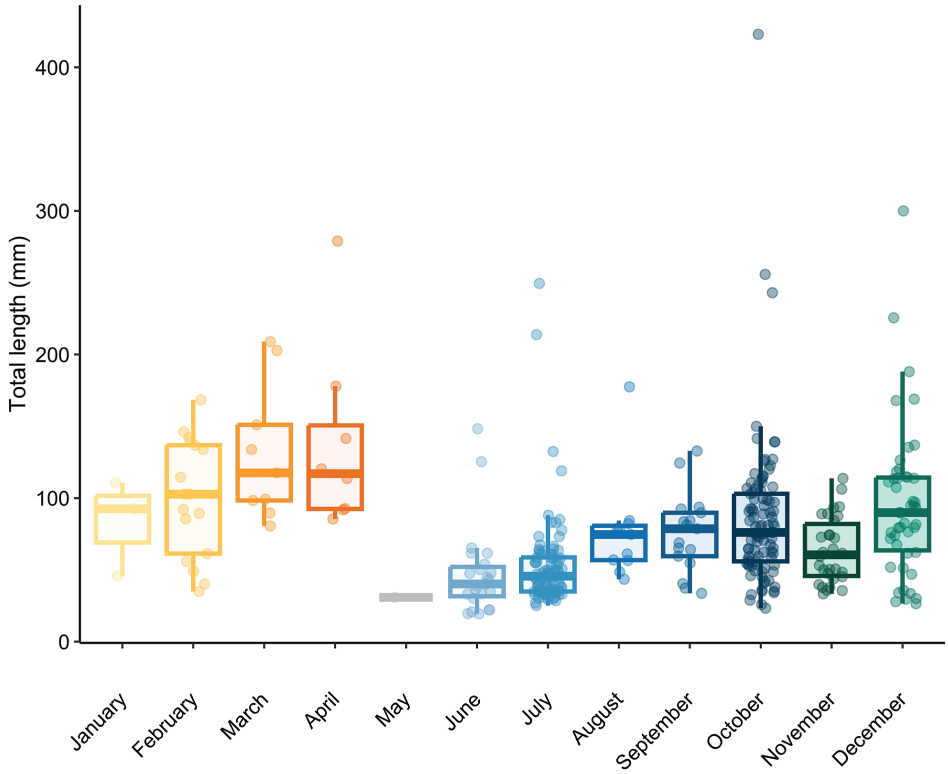

Figure 4. Boxplot of swamp eel lengths (mm) caught in throw traps in marshes by month of capture.

Detection methods

Across the 34 plots of MWD sampling where swamp eels were found, the first detection was by electrofishing in 25 plots (74%), with first detection by throw trapping in 7 plots (21%), and in 2 cases both methods detected swamp eels during the same sampling period (6%). Among all sampling periods when swamp eels were detected at a site, 65% of the time they were captured only by electrofishing, 15% only by throw trap, and 20% by both methods.

Electrofishing was the method by which swamp eels were most often first and most regularly detected in all sites where electrofishing and throw trapping were both performed. However, our personal observations and what was reported by Shafland et al. (2010) indicate fewer than half of swamp eels observed electrofishing are actually caught and recorded, potentially underestimating their abundance relative to other large fishes. The limitations to detecting swamp eels by throw trapping (or other methods that are not electrofishing) seems likely to limit our ability to document the spread of swamp eels at fine scales across the Everglades. Ongoing projects like CERP-MAP that cover large areas of the Everglades (Suppl. material 2: figs S1, S2) only sample with throw traps (and only take three throws per 64 ha PSU) once per year. In contrast, the MWD sampling included repeated (4–5× per year) sampling over ~6 ha total area (throw trap plots are each 0.3–1 ha) by both throw traps and electrofishing passes. The sampling intensity builds upon the evidence in Pintar et al. (2023a, b) demonstrating the importance of long-term monitoring programs that are able to assess the presence and densities of multiple taxa along with their seasonal trends, which are critical for assessing population biology and ecological interactions in ecosystems. In addition, using a diversity of sampling methods in a long-term monitoring program may improve the ability to detect rare and low density invasive species as they spread since the species present are sometimes rare and at low density, particularly early in their spread (e.g., Parkos et al. 2019). Swamp eels are also not effectively caught with hook and line or in traps used by fishermen or trappers (Ame and Mayor 2021), which further limits the ability to detect swamp eel spread in areas without such intensive biological monitoring programs. Some wading birds, on the other hand, do appear to be effective at catching at least some swamp eels and the public observation records have proven useful for detecting new populations and range expansions (Taylor et al. 2018; iNaturalist records here, particularly those from Orlando).

Continued spread, future distribution, and effects

The rapid spread after an initial lag may suggest that swamp eels in Florida are an example of a sleeper population (Spear et al. 2021): an established population that was initially limited to canals, and apparently innocuous (based on very limited data), that suddenly became invasive. The challenge is to identify the environmental factor(s) that triggered the rapid spread after 2009 because the populations remained in canals for what appears to be 12–13 years after first detection and perhaps >15 years after introduction. No obvious food web changes occurred in adjacent Everglades sloughs and no mutualisms would seem necessary to encourage an irruptive range expansion (Spear et al. 2021). It is possible that this rapid population spread was not triggered by an environmental factor (i.e., was not a sleeper population), but perhaps more likely that the species was simply building a population in the canals for 15 years and that the lag was a natural population growth phenomenon or related to changes in water management and infrastructure that promoted their spread. The sequential hermaphroditic lifestyle may make reproductive potential for a newly establishing swamp eel population limited until large individuals, which are mostly male, become prevalent, which occurs at around 3 years (42 cm total length) in some populations (Liem 1963). However, we expect that a population introduced in the mid-1990s would have individuals exceeding that threshold by the time the first swamp eels were detected in Florida during the late 1990s. Of course, the amount of sampling effort and reporting may have also increased, giving the impression of more rapid spread when new sampling initiatives and reporting came into existence around 2014 (e.g., fish slams). However, within the Everglades itself where there was an established long-term monitoring program this does not seem to be a likely cause. The swamp eel removal efforts that occurred from 2006 to 2010 (Galvez et al. 2011) may have helped to reduce populations in canals and rates of colonization of marshes, but these control efforts covered only a few canals near ENP. It is unknown what the overall population size within individual canals and across southern Florida was at the time, so we do not know what percent of the population was actually removed, although for Galvez et al.'s (2011) effort catch efficiency was 54%, similar to the 48% estimated by Shafland et al. (2010).

Past efforts to predict the spread of invasive species have been met with wildly varying degrees of success (Gallien et al. 2010). Although we do not attempt to model the future distribution of swamp eels in the Everglades or Florida, results of climate-matching by Nico et al. (2019) for the *M. albus/javanensis* complex indicated highly suitable conditions across Florida and the coastal plain north to North Carolina. As a largely tropical and subtropical species complex, cold weather across much of the continent may limit its persistence, although some members of the *M. albus/javanensis* complex are found further north in eastern Asia and may be more cold tolerant, hence the persistence of the population near Atlanta (Johnson et al. 2021; Saylor et al. 2021). With our current understanding of the occurrence of swamp eels across the various hydrologic conditions observed in the Everglades, there does not appear to be any clear limit to the severity of previous dry seasons that would restrict swamp eel occurrence among the current or historic hydrologic conditions documented as part of the MWD project.

Most of the data from the southern Everglades points to changes in water management and associated structures to increase flows to ENP and Florida Bay as playing some role in limiting and/or promoting swamp eel spread, but whether any of those water control structures can be used at this point in the invasion to limit their spread is unknown. For instance, the lack of swamp eels in WCA 2 and LOX may in part be due to their relative isolation, but at the same time those areas are not as extensively sampled, especially by electrofishing, and thus may not have adequate early detection capabilities.

From 2000 to 2011, the marshes of TSL dried every year or two, while the regions between TSL and the C-111 Panhandle were likely even drier. These dry years may have played an important role in limiting the spread of swamp eels from the C-111 Panhandle region and from Royal Palm to southern TSL. In the years following 2011, water was deeper and hydroperiod longer in TSL. Therefore, while swamp eels may be adapted to survive dry periods in marshes, these dry periods may not be conducive to the rapid spread of swamp eels. This does not mean that if conditions were dry swamp eels would not continue to spread, but that their rate of spread may be slowed. Taken together the results of the spread estimates from our assumed invasion routes suggest that swamp eels may spread faster in longer hydroperiod wetlands (11–12 months) than short hydroperiod wetlands in the southern Everglades (~5–10-month hydroperiods). Regardless, intentionally drying regions of the Everglades to inhibit the spread of swamp eels seems unlikely as it would be directly counter to one of the main goals of restoration – increasing the flow and hydroperiods in much of ENP (Sklar et al. 2005; National Academies of Sciences, Engineering, and Medicine 2023).

During the past decade (2012–2022), construction projects installed pumps and culverts, removed levees and roadways, and altered flow pathways to improve the quantity, timing, and distribution of water flows to Everglades marshes, which in turn has increased surface water connectivity of wetlands and canals. Our understanding of the historic rate of spread means that we should expect the continued spread of swamp eels northward and westward through the Everglades, especially since the potential removal of such a difficult to capture species from a large wetland seems unlikely (Loftus 1988). The newfound presence of swamp eels in the St. Johns watershed is concerning because if that population establishes and grows it has a pathway for rapid dispersal and range expansion through eastern Florida to Jacksonville and potentially further north.

Starnes et al. (1998) wrote that there should be concern for swamp eel establishment and spread "…throughout our coastal lowlands from Texas to Chesapeake Bay." We are at a point now where this is more of a possibility than ever before. The premature conclusions that stated swamp eels posed little risk (Hill and Watson 2007; Shafland et al. 2010), lack of understanding regarding the uniqueness of the traits posed by swamp eels (Lawson and Hill 2021), limited to complete lack of efforts to control their spread soon after detection, inaction by the U.S. Fish and Wildlife Service to ban imports under the Lacey Act, and limited prohibitions by individual states have led to the continued introduction of swamp eels across the United States (Nico et al. 2019; Jordan and Nico 2020; Best et al. 2022). The decimation of critical wading bird prey populations that was observed in TSL could counteract some of the goals of the multi-billion-dollar effort to restore the Everglades if observed impacts spread throughout the Everglades with the expanding population (Pintar et al. 2023a). If swamp eels continue to spread, establish, and persist in wetlands, the expected trophic functions of freshwater ecosystems across Florida may be threatened. Furthermore, species such as the geographically restricted crayfish endemic to small areas of the Florida Panhandle (Franz and Franz 1990) and elsewhere in the southeastern United States may become threatened if swamp eels spread to those regions and have effects similar to those seen in the Everglades. Swamp eels flew under the radar for over two decades and now they perhaps present themselves as future contenders for the title of one of the most destructive aquatic animals ever introduced to the United States.

Author Contributions

MRP: research conceptualization, sample design and methodology, data analysis and interpretation, writing – original draft; NDS: data analysis and interpretation; JLK: investigation and data collection, writing; MIC: funding provision, writing; NJD: research conceptualization, sample design and methodology, data analysis and interpretation, writing - review & editing.

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Ethics and Permits

All projects received the appropriate permits and approvals. The projects that accounted for the bulk of our samples collected (MWD and CERP) received approval from Florida International University's IACUC committee (most recently IACUC-22-047 and IACUC-20-029-CR02) and collections were made under a series of permits, with the most recent being EVER-2022-SCI-0045 and EVER-2022-SCI-0046 from Everglades National Park, B14-011 from Loxahatchee National Wildlife Refuge, and S-22-01 from the Florida Fish and Wildlife Conservation Commission.

Data Accessibility

Data and full resolution figures are available on Figshare (Pintar et al. 2024).

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Supplementary material 1

List of other data sources and sites and first swamp eel occurrences in the MWD dataset (table S1)

Authors: Matthew R. Pintar, Nicole D. Strickland, Jeffrey L. Kline, Mark I. Cook, Nathan J. Dorn
Data type: docx

Link: https://doi.org/10.3391/ai.2024.19.2.124660.suppl1

Supplementary material 2

Maps of sites by project and sampling method (figs S1–S3)

Authors: Matthew R. Pintar, Nicole D. Strickland, Jeffrey L. Kline, Mark I. Cook, Nathan J. Dorn
Data type: docx

Link: https://doi.org/10.3391/ai.2024.19.2.124660.suppl2

Supplementary material 3

Annual maps of swamp eel occurrences across Florida from 1997–2024 (figs S4–S7)

Authors: Matthew R. Pintar, Nicole D. Strickland, Jeffrey L. Kline, Mark I. Cook, Nathan J. Dorn
Data type: docx

Link: https://doi.org/10.3391/ai.2024.19.2.124660.suppl3

Supplementary material 4

Annual maps of swamp eel occurrences in southern Florida from 1997–2024 (figs S8–S11)

Authors: Matthew R. Pintar, Nicole D. Strickland, Jeffrey L. Kline, Mark I. Cook, Nathan J. Dorn
Data type: docx

Link: https://doi.org/10.3391/ai.2024.19.2.124660.suppl4

Supplementary material 5

Figures of the hydrological conditions swamp eels were documented in and swamp eel lengths (figs S12–S15)

Authors: Matthew R. Pintar, Nicole D. Strickland, Jeffrey L. Kline, Mark I. Cook, Nathan J. Dorn
Data type: docx

Link: https://doi.org/10.3391/ai.2024.19.2.124660.suppl5