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Research Article

Asian swamp eels in North America linked to the live-food trade and prayer-release rituals

Leo G. Nico[1,*], Andrew J. Ropicki[2], Jay V. Kilian[3] and Matthew Harper[4]

[1]*U.S. Geological Survey, 7920 NW 71st Street, Gainesville, Florida 32653, USA*
[2]*University of Florida, 1095 McCarty Hall B, Gainesville, Florida 32611, USA*
[3]*Maryland Department of Natural Resources, Resource Assessment Service, 580 Taylor Avenue, Annapolis, Maryland 21401, USA*
[4]*Maryland National Capital Park and Planning Commission, Montgomery County Parks, Silver Spring, Maryland 20901, USA*

Author e-mails: *LNico@usgs.gov (LGN), aropicki@ufl.edu (AJR), jay.kilian@maryland.gov (JVK), Matthew.Harper@montgomeryparks.org (MH)*

**Corresponding author*

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Abstract

We provide a history of swamp eel (family Synbranchidae) introductions around the globe and report the first confirmed nonindigenous records of *Amphipnous cuchia* in the wild. The species, native to Asia, is documented from five sites in the USA: the Passaic River, New Jersey (2007), Lake Needwood, Maryland (2014), a stream in Pennsylvania (2015), the Tittabawassee River, Michigan (2017), and Meadow Lake, New York (2017). The international live-food trade constitutes the major introduction pathway, a conclusion based on: (1) United States Fish and Wildlife Service's Law Enforcement Management Information System (LEMIS) database records revealing regular swamp eel imports from Asia since at least the mid-1990s; (2) surveys (2001–2018) documenting widespread distribution of live *A. cuchia* among ethnic food markets in the USA and Canada; (3) indications that food markets are the only source of live *A. cuchia* in North America; and (4) presence of live *A. cuchia* in markets close to introduction sites. Prayer release appears to be an important pathway component, whereby religious practitioners purchase live *A. cuchia* from markets and set them free. Prevalence of *A. cuchia* in US markets since 2001 indicates the species is the principal swamp eel imported, largely replacing members of the Asian complex *Monopterus albus/javanensis*. LEMIS records (July 1996–January 2017) document 972 shipments containing an estimated 832,897 live swamp eels entering the USA, although these data underestimate actual numbers due to undeclared and false reporting. LEMIS data reveal most imports originate in Bangladesh, Vietnam, and China. However, LEMIS wrongly identifies many imported swamp eels as "*Monopterus albus*"; none are identified as *A. cuchia* although specimens from Bangladesh and India are almost certainly this species. Some imported *A. cuchia* are erroneously declared on import forms as *Anguilla bengalensis*. To date, there is no evidence of *A. cuchia* reproduction in open waters of North America, presumably because it is a tropical-subtropical species and all introductions thus far have been in latitudes where winter water temperatures regularly fall near or below freezing.

Key words: fang sheng, introduction pathways, invasive fish, life release, live-food markets, merit release, Synbranchidae

Introduction

Swamp eels (family Synbranchidae) are a group of eel-like percomorph fishes naturally distributed in the Old and New Worlds, including parts of

Asia, Australia, Africa, and South and Middle America (Rosen and Greenwood 1976; Berra 2007). They are secretive animals, difficult to study, and their taxonomy is poorly understood. Most members of the family are restricted to tropical and subtropical zones (Kullander 2003), although a few occur in temperate regions where temperatures seasonally fall to near or below freezing (Fan 1990; LG Nico, *pers. obs.*). Swamp eels typically inhabit fresh waters, although some species are regularly found in both fresh and brackish waters, and a few are entirely or mostly known from estuarine or coastal environments (Day 1875; Rangarajan and Jacob 1960; Daget 1992). Indicative of their adaptability, one member of the family, previously known only from freshwater systems, has been reported from hypersaline waters of a mangrove island (Tyler and Feller 1996).

Swamp eels are elusive, predatory fishes that are frequently nocturnal and generally highly fossorial (Nayar 1951; Rosen and Greenwood 1976; Gorzula and Señaris 1998; Favorito et al. 2005; Matsumoto et al. 2011; Britz et al. 2018). Species most frequently observed are those that are somewhat epigean. These surface-water dwellers are usually encountered in shallow or near-shore sites among vegetation or debris, although they also spend substantial parts of their time (daily or seasonally) underground in burrows or buried in mud. Swamp eels occur in a wide variety of habitats, including rivers, ephemeral streams, canals, ditches, lakes, reservoirs, small ponds, rice paddies, marshes, and swamps, as well as caves and wet soil (Rosen and Greenwood 1976; Beamish et al. 2003; Miller et al. 2005; Mol 2012; Montenegro et al. 2012). They display an array of unusual behavioral and physiological adaptations. Many (perhaps all) are capable of air breathing and several species are known to be amphibious, periodically crawling on land (Das 1927; Carr and Giovannoli 1950; Lüling 1958; Johansen 1966; Munshi and Hughes 1992; Graham 1997; Vincent 2012). Among certain well-studied taxa, sex reversal seems to be the norm, and, in such cases, all or some proportion of the adult females in a population transform to functional males (Liem 1968; Lo Nostro and Guerrero 1996; Barros et al. 2017).

Exploitation of swamp eels as food by humans has a long history in both the Old and New Worlds (Prestes-Carneiro and Béarez 2017; Yin et al. 2018), although in modern times the practice is largely associated with peoples from eastern and southeastern Asia (Hasan et al. 2012; Liang et al. 2016; Yin et al. 2018). In Asia, live swamp eels are commonly on display in food markets (Yin et al. 2018). Over recent decades, large numbers of live swamp eels from Asia have been regularly imported and distributed among ethnic food markets in the USA and Canada (Nico et al. 2011; this paper). The trend is presumably associated with the growth of Asian communities in North America in combination with expanded international trade and modernization of long-distance, live animal transport. Market customers who purchase swamp eels often have them butchered on site, but some buyers

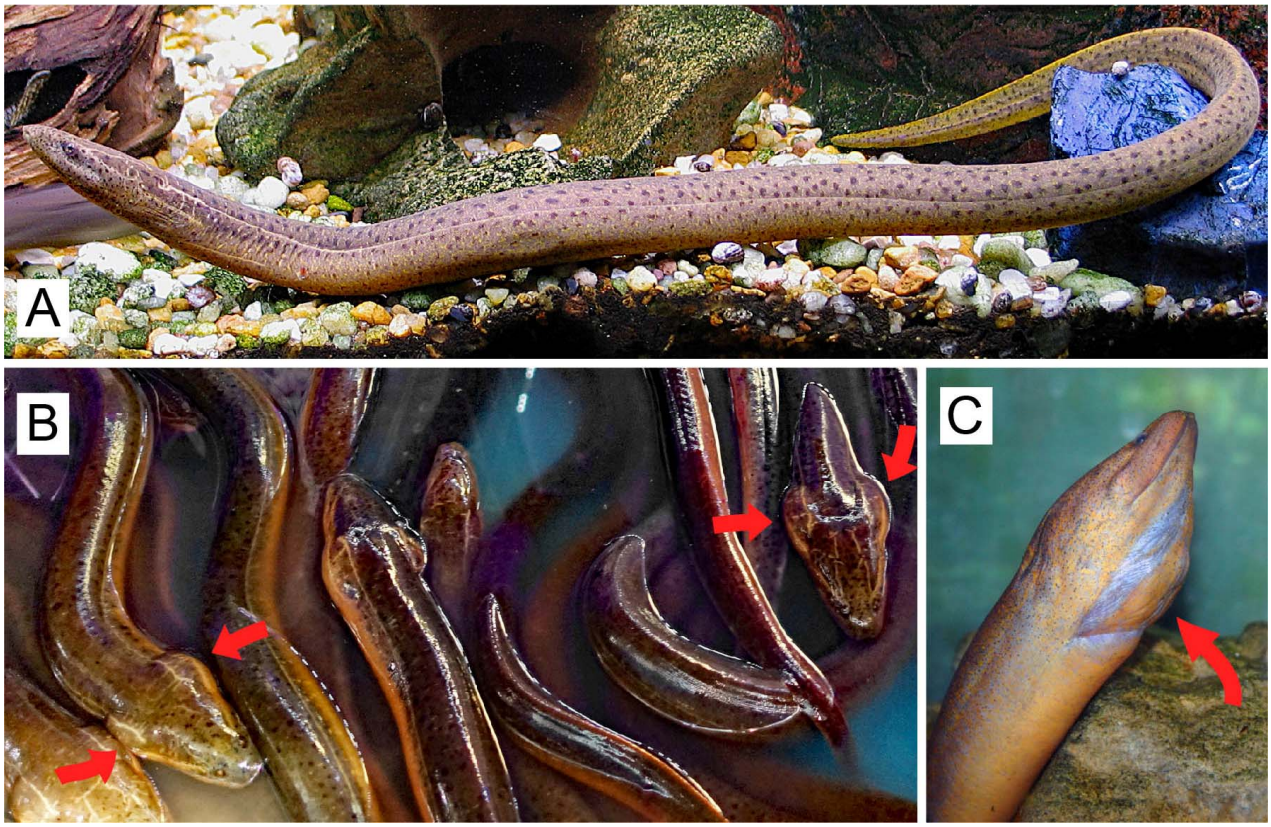

Figure 1. (a) An adult *Amphipnous cuchia*—live in aquaria—obtained from a Florida food market (field# LGN 02-51); (b) dorsal view of cluster of live *A. cuchia* in an Atlanta market, some with their lateral air sacs inflated—as indicated by arrows (field# LGN 15-92); and (c) lateral head view of head of a swamp eel belonging to the *M. albus/javanensis* species complex taken from a Florida canal, with ventral throat region partially inflated with air (field# LGN 08-75). Swamp eels of the *M. albus/javanensis* group lack paired air sacs and when actively air breathing can be readily distinguished from *A. cuchia*. Photographs by Leo G. Nico.

walk away with specimens alive in plastic bags or buckets and a portion of these fish may be introduced into the wild (Nico et al. 2011; this study).

Swamp eels are well suited for the live-food trade due to their advanced air-breathing capabilities, tolerance of a broad range of environmental conditions, and ability to survive long periods without food. For example, two captive *Amphipnous cuchia* (Hamilton, 1822) survived nearly an entire year without food (McClelland 1845). Similarly, "*Monopterus albus*" is also known to survive months of starvation, even when held outside standing water (when kept moist) (Liem 1963, 1967; LG Nico, *pers. obs.*). Such feats of endurance ensure high survival rates during long-distance transport, even when the fish are tightly packed together in small containers. The physiological and behavioral traits that make swamp eels ideal for international shipping and market survival, doubtless also increase their chances of survival when introduced into the wild.

In this paper, we provide a brief history of swamp eel introductions across the globe and document the first confirmed nonindigenous occurrences of the Asian swamp eel *Amphipnous cuchia*, a species commonly referred to as the cuchia (kuchia) or mud eel (Figure 1). Records are provided from five widely separated sites among five states in the USA. Records from three sites are captures supported by voucher specimens; records from the other

two sites are corroborated by photographic evidence and eyewitness accounts. An assessment of the introduction pathway is presented, with evidence linking North American introductions to the international live-food trade and live-food markets, and religious prayer-release rituals. We also briefly review swamp eel taxonomy and compare external characteristics for distinguishing imported taxa.

Taxonomy

The history of swamp eel taxonomy and identification is long and complicated (Rosen and Greenwood 1976; Collins et al. 2002; Favorito et al. 2005; Perdices et al. 2005; Cai et al. 2013). Much of the confusion and persistent taxonomic instability stems from absence of distinct or reliable external features among the different genera and species, poorly known geographic ranges, superficial original descriptions of many nominal species, and numerous synonymies. Synbranchidae, according to current taxonomy, is composed of four genera and 26 valid species (Fricke et al. 2019). Although the family is widely distributed around the world, no species is native to the USA or Canada.

In this paper, we follow the recommendation of Tyson Roberts (Smithsonian Tropical Research Institute, *pers. comm.*, September 2017) in recognizing *Amphipnous* as valid and in assigning *cuchia* to this genus (contrary to Eschmeyer's Catalog of Fishes, which uses the binomial *Monopterus cuchia*). The native geographic distribution of *A. cuchia* is broad, consisting of a large portion of southern and southeastern Asia, including parts of India, Pakistan, Bangladesh, Myanmar and Nepal (Silas and Dawson 1961, Figure 2). We refer to the widespread *Monopterus* species complex of eastern and southeastern Asia as *Monopterus albus/javanensis*. Such a designation is based primarily on genetic research revealing that the swamp eel commonly referred to as either *Monopterus albus* (Zuiew, 1793) or *Monopterus javanensis* Lacepede, 1800 is actually composed of multiple (perhaps five or more), genetically-distinct, cryptic forms (Collins et al. 2002; Matsumoto et al. 2010; Cai et al. 2013; Arisuryanti 2016).

History of introductions

The history of swamp eel introductions on a global scale has not been summarized previously. Records include a mix of confirmed and alleged introductions within both the Old and New Worlds. In some cases where species identification appears reliable, doubts persist as to whether the record represents a natural rather than non-native occurrence. Although current taxonomy of Synbranchidae makes it difficult or impossible to assign many to species, it appears that most confirmed and many suspected introductions involve members of the *M. albus/javanensis* complex (e.g., clades A, B, and C of Collins et al. 2002). In contrast, only a few reported

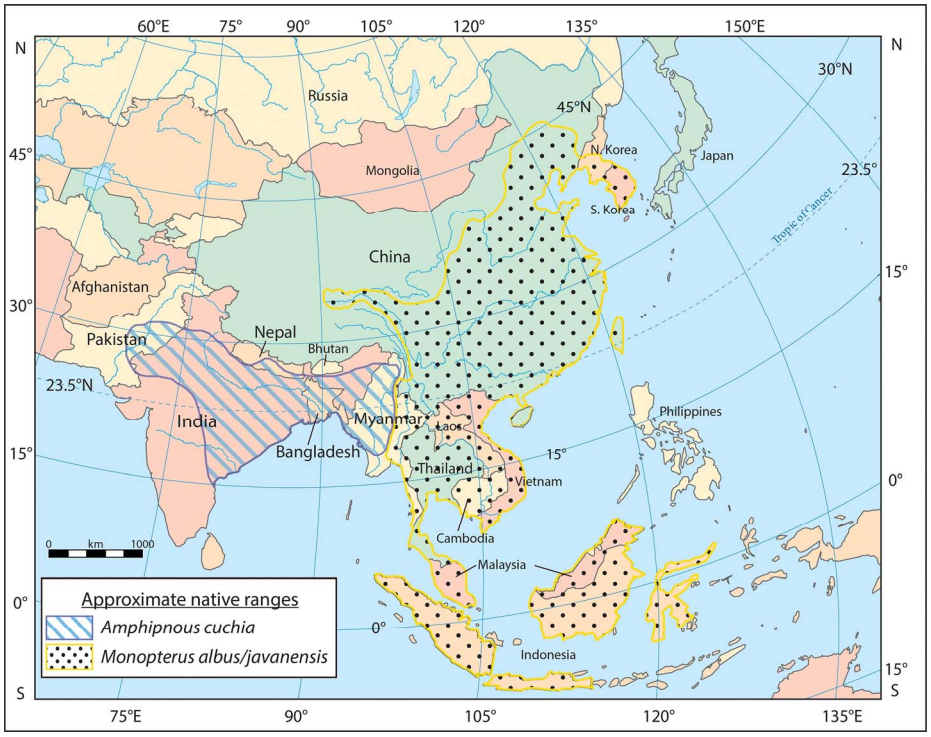

Figure 2. Approximate native geographic ranges of *Amphipnous cuchia* (Hamilton, 1822) and the *Monopterus albus/javanensis* species complex. Distribution of *A. cuchia* derived from Silas and Dawson (1961) and that of *M. albus/javanensis* from Fan (1990) supplemented by other sources.

introductions involve two New World species complexes, *Synbranchus marmoratus* Bloch, 1795 and *Ophisternon aenigmaticum* Rosen and Greenwood, 1976. In this paper we report on confirmed cases of introduction of another swamp eel native to the Old World, the Asian species *Amphipnous cuchia* (Figure 1a, b). Following is a summary of what is known about the introduction history of the above four taxa.

Monopterus albus/javanensis species complex

Most records pertaining to introductions of this complex refer to "*Monopterus albus*". Non-native occurrences have been reported for sites in Asia (China, Japan, Philippines), Australia, Hawaii, and North America, some dating to the 1800s (e.g., Wang et al. 1994) and others quite recent (e.g., Collins et al. 2002). In addition, genetic studies suggest certain *M. albus/javanensis* clades present in Taiwan and Indonesia may not be native (Matsumoto et al. 2010; Arisuryanti 2016). Although only a few introductions have been documented within eastern and southeastern Asia, their importance as a food fish suggest transplants and introductions have occurred multiple times over past centuries.

China. The "*Monopterus albus*" population present in northwest China's Xinjiang Province (Hami Prefecture) is considered descended from an introduction in 1875 or 1876 during the Qing dynasty; the fish were purportedly transported from Hunan Province (Yangtze River Basin) by members of General Zuo Zongtang's army (Li 1985; Wang et al. 1994).

Although Xinjiang Province is a much colder environment than Hunan, the karyotypes of the two populations are nearly identical (except for some differences in chromosome length), evidence researchers argue support Hunan as the probable source (Wang et al. 1994).

Japan. Swamp eels of the *M. albus/javanensis* complex found in southwestern regions of the islands of Honshu and Kyushu are considered introduced (Okada 1966; Matsumoto et al. 1998, 2010). Non-native status is supported by genetic analyses indicating a close relationship to populations inhabiting Asia's northeastern mainland (Matsumoto et al. 2010). The source of populations in Honshu's Nara region are purported to be descended from some 10 fish that a missionary brought from the Korean Peninsula around 1900 and released into a pond near the Uda River (Okada 1966, citing Imatani 1958). Other populations found in Japan's main islands may be offspring of separate introductions (Okada 1966). The Nara population has expanded its range since initial introduction and is now widespread in the Kizu, Yamata, and Yoshino river systems (Matsumoto et al. 1998). In Japan, introduced swamp eels are common in rice paddies and ditches. Their burrowing activities damage rice field dikes causing water loss; they also invade aquaculture ponds and prey on fishes (Matsumoto 1997, 1998). Swamp eels belonging to the *M. albus/javanensis* complex are also found on the Ryuku Islands, but analysis of their genetics and geographic distribution (continuous from the islands of Amami to Iriomote) suggests the form is endemic to southern Japan (Matsumoto et al. 2010). However, Ishikawa and Tachihara (2014) speculate that both native and non-native swamp eel lineages may be present in the Ryuku Islands.

Philippines. Swamp eels identified as "*M. albus*" and brought to the Philippines from Malaysia for aquaculture purposes are known to be reproducing and dispersing in the wild (Guerrero 2014). Although dates and number of separate introductions are unknown, all presumably occurred after about 2000. In northern Luzon Island, residents believe the invaders—known locally as "kiwit"—were introduced into Nagadacan rivers by a US Peace Corps volunteer in 2008, supposedly to serve as a food source for local people (Gascon 2011). Rice farmers in northern Luzon attest swamp eels to be common and a pest largely because their burrowing activities damage dikes and terraces, leading to water, soil, and nutrient loss. Some impacted areas are within the Rice Terraces of the Philippine Cordilleras, a UNESCO World Heritage Site (Gascon 2011; Roque 2011; Abella et al. 2014). In recent years, swamp eels have become so common in the Philippines that they are now a commodity and exported to other Asian countries for human consumption (Guerrero 2014; Cortez 2015). Most information on introduced swamp eels in the Philippines are based on media accounts (Gascon 2011; Roque 2011; Abella et al. 2014). Fowler (1918) reported "*M. albus*" in the Philippines over 100 years ago, but his record was likely a misidentification of *Ophisternon bengalense* McClelland,

1844, the only swamp eel recognized as native to the country (Herre 1934, page 16; Umali 1950, page 5 ; Rosen and Greenwood 1976, page 157).

Taiwan. Swamp eels referred to as "*M. albus*" inhabit Taiwan but their status and origin are unclear, with some arguing it to be native and others the result of introduction (perhaps post-1940) (Matsumoto et al. 2010). A genetic analysis of "*M. albus*" populations from multiples sites in Japan (Taipei, Puli, and Hengchun), China, and Indonesia revealed that the Taiwan samples were composed of at least two lineages within the "*M. albus* complex" (Matsumoto et al. 2010). Specimens from Taipei belonged to a China-Japan clade and those from Puli and Hengchun grouped within a Southeast Asia clade. Matsumoto et al. (2010) remained uncertain as to whether either clade was native or introduced to Taiwan but ventured that further phylogeographic analysis might resolve the issue. Cai et al. (2013) speculated that drops in sea level over the past 800,000 years may have allowed for the natural exchange of swamp eels between Taiwan and mainland China; however, they could not rule out possible past human-mediated transfers between the two regions. A genetic study by Arisuryanti (2016) detected an apparent third cryptic "*M. albus*" clade in Taiwan, a form also found in China.

Indonesia. The situation in Indonesia is similar to Taiwan. Arisuryanti (2016) conducted a genetic analysis of members of the *M. albus/javanensis* complex and found that Indonesia included two cryptic species, referred to as clade A and B. It was speculated that "clade B" may not be native to Indonesia but introduced from countries to the north. Alternatively, Arisuryanti (2016) posited that the "clade B" swamp eels could be native to Indonesia and possibly the source of introduction to other countries, perhaps via fish trading and marketing. The researcher commented that verification of native versus non-native status was difficult because all samples were obtained from farmers, fishermen, and markets. To resolve the situation, Arisuryanti (2016) concluded that future genetic analysis requires wild-caught specimens from natural habitats.

Australia. There are a few, scattered reports of fish identified as "*M. albus*" from Australia, all from the coastal region of Queensland. Several authors treat these "records" as introductions (Whitley 1960; Lake 1971; Merrick and Schmida 1984). Without providing sources, Whitley (1960) commented: "Some Oriental ricefield eels were introduced into Australia by Chinese in the early days but evidently died out." Similarly, Pusey et al. (2004) speculated that *M. albus* may have been imported into Australia by the Chinese during the goldrushes that took place in northern Queensland during the late 1800s. In contrast, Rosen and Greenwood (1976) suggested its occurrence in Australia may be natural. Recent ichthyologists still express uncertainty as to whether "*M. albus*" is of native or non-native status in Australia (Allen et al. 2002; Pusey et al. 2004). Some Australian records reported as *Monopterus albus*—particularly those unsupported by vouchers—are suspected of being misidentifications of swamp eels of the

genus *Ophisternon*, which are generally considered to be native to the country (Pusey et al. 2004).

USA. Wild *M. albus/javanensis* are firmly established in several places in the USA (Collins et al. 2002). Included are populations in the states of Hawaii (Island of Oahu, present since before 1900), Georgia (Chattahoochee River drainage, since the early 1990s), Florida (multiple drainages in the Tampa, Miami, and Homestead areas, all since the late 1990s), and New Jersey (Silver Lake area, since about 2008) (Starnes et al. 1998; Yamamoto and Tagawa 2000; Collins et al. 2002; Nico et al. 2011). Molecular data indicate the six different introduced populations represent as many as three cryptic species, with each geographically-separated population being composed of one of the three identified clades (Collins et al. 2002).

Synbranchus marmoratus and *Ophisternon aenigmaticum* complexes

The few reported or suspected cases of introductions involving New World swamp eels pertain to two widespread species complexes, *Synbranchus marmoratus* and *Ophisternon aenigmaticum*. Prior to its description in 1976, most *O. aenigmaticum* specimens were identified as *S. marmoratus*; consequently, some fish identified in older literature as *S. marmoratus*, were actually dealing with those of the *O. aenigmaticum* complex. The unstable taxonomy leads to confusion in attempting to determine if records represent natural versus non-native occurrences.

West Indies. Existence of *O. aenigmaticum* on the Caribbean islands of Saint Lucia and Grenada may be due to introductions by pre-Colombian Amerindians (Burgess and Franz 1989; Kenny 1995; Kullander 2003). This conclusion is presumably based on the belief that swamp eels are incapable of swimming broad expanses of open sea. Both *O. aenigmaticum* and *S. marmoratus* are thought to naturally occur on Trinidad (perhaps also Tobago) (Rosen and Greenwood 1976; Phillip et al. 2013). Some seem to consider presence of *Ophisternon* on all of the above islands, including Cuba, to be natural (Rosen 1975; Rosen and Greenwood 1976).

Brazil. Occurrence of swamp eels referred to as *Synbranchus marmoratus* (or *S.* cf. *marmoratus*) in the Iguaçu River system of Brazil is thought to represent transplants from other parts of the Paraná River Basin (Garavello et al. 1997; Larentis et al. 2016). Reasoning behind this conclusion is unknown.

Amphipnous cuchia

Except for records newly documented in this current paper, the only other published report of *A. cuchia* outside its supposed native range is that of Ogilby (1907), a record based on a single swamp eel specimen purportedly taken in northeastern Australia. In his report, Ogilby (1907) stated that the *A. cuchia* specimen he examined was part of a group of eels and catfishes sent to him some time prior by trustees of the South Australian Museum of

Adelaide. The capture date was not reported but a label accompanying the fish indicated the collection site was Edcombe (or Edgecombe) Bay, Queensland. The eel measured 300 mm total length (TL). Although Ogilby did not definitively assert that the specimen represented an introduction, that seems to have been his opinion. Some later authors considered the Queensland specimen as a non-native record (Lake 1971; Merrick and Schmida 1984). Paxton et al. (1989) tried to locate Ogilby's *A. cuchia* but declared "… no specimens found to substantiate the record". In their book on the Freshwater Fishes of North-Eastern Australia, Pusey et al. (2004) make no mention of *A. cuchia*, presumably dismissing the record, although they acknowledge that the identification of swamp eels to be highly problematic. We tentatively treat the Australia record of *A. cuchia* to be unconfirmed. Still, Ogilby's (1907) writings suggest that he was familiar with the existing literature and knew that *A. cuchia*—apparently unlike other swamp eels found in Australia—possessed scales. He also expressed confidence that the collection locality information received with the specimen was trustworthy.

Materials and methods

Field observations and collections

Nonindigenous records reported in this paper are based on captures of swamp eels by the authors and others at three sites, and a combination of photographic evidence and eyewitness accounts documenting releases at two additional sites. Wild-caught specimens were taken by various means, including spear or gig, hand nets, and in some cases with electrofishing gear. Some specimens collected were retained, and most of these were preserved and cataloged as vouchers in the Florida Museum of Natural History Ichthyology Collection (UF), Gainesville, Florida.

Surveys of live-food markets

Over the period 2001–2018, we surveyed ethnic food markets in the USA, Canada, and elsewhere to document occurrence of live swamp eels as part of an assessment of the live-food trade as an introduction pathway. Many of the markets were located via Internet searches using city names and such terms as "Asian market" and "live fish". In this way, it was sometimes possible to prioritize markets using such criteria as the numbers and kinds of live animals appearing in photographs on market websites. Any live swamp eels encountered were photographed on site and, in some instances, one or a few specimens were purchased and preserved as vouchers. In addition, various colleagues across North America shared their observations from personal visits to markets, with a few also providing photographs and specimens. Some market specimens referenced in the current paper were used in studies on swamp eel parasites (Nico et al. 2011; Cole et al. 2014).

Overall, 216 different markets in the USA and Canada were visited and, due to repeat visits, 295 separate surveys conducted. We surveyed markets within 22 metropolitan areas: Atlanta (15 markets), Baltimore (1), Chicago (14), Corpus Christi (2), Dallas (5), Detroit/Ypsilanti (6), Gainesville-Florida (2), Houston (17), Jacksonville-Florida (1), Little Rock-Arkansas (1), Nashville (3), New Orleans/Baton Rouge (5), New York City (>20), Oakland (4), Orlando (5), Salt Lake City (3), San Francisco (12), Seattle (7), St. Louis (2), Tampa (11), Toronto (7), and Washington D.C. (5). In addition, colleagues provided information or specimens from one or more markets in Boston, Los Angeles, Miami, and Vancouver. We visited some markets on multiple occasions and others only once. Markets ranged from small, independent grocery stores to large supermarkets, some belonging to chains. Most were retailers except for a few that appeared to operate as wholesalers. In some urban areas, multiple small markets or stalls were clustered together within a single large facility. When feasible, each stall was treated as a separate market. Some markets visited were devoted almost entirely to seafood, typically a mix of live animals held in tanks or tubs, interspersed with fresh-dead fish and other seafood on ice. In most markets with live swamp eels, the eels were in clear view of customers, but in some stores they were behind counters and not readily visible. Swamp eels encountered in markets were consistently adult-sized individuals, about 55 to 85 cm TL (Nico et al. 2011; Cole et al. 2014).

USFWS-LEMIS import data

The U.S. Fish and Wildlife Service (USFWS) is the main agency of the US government monitoring wildlife trade and maintaining Law Enforcement Management Information System (LEMIS) records. The records are derived from customs declaration forms pertaining to fish and wildlife imported into the USA and its territories (see USFWS Form 3-177 available at https://www.fws.gov/le/declaration-form-3-177.html). For each animal shipment—either declared or detected through inspection—a LEMIS record is created and assigned a unique control number along with coded entries indicating the animal's scientific and common names, quantity (number or weight), countries of origin and export, source (e.g., wild-caught versus captive-reared), port of entry, purpose, shipping date, exporter, importer, and other details.

Ideally the USFWS monitors the wildlife trade by physical inspections of shipments declared to contain or are thought to contain wildlife or wildlife products (GAO 1994). However, because of the enormous numbers and diversity of live animals entering the USA, monitoring imports and documenting the information completely and accurately is a challenge (GAO 1994; Smith et al. 2017). As a result, the LEMIS database may contain inaccuracies (Telecky 2000; Smith et al. 2008, 2017; Rhyne et al. 2012). For instance, if inspectors are unfamiliar with the animal taxa, there

Table 1. Traits useful in distinguishing *Amphipnous cuchia* from members of the *M. albus/javanensis* complex, the two taxa known to occur in live-food markets of North America. Information is based on published sources* and personal observations.

Character	*Amphipnouos cuchia*	*M. albus/javanensis* complex
Paired, laterally-positioned, suprapharyngeal air-chambers	Present	Absent
Shape of head region during aerial respiration	Laterally expands on both sides near head	Throat greatly expands ventrally
Scales on body	Present, but very small, usually limited to tail region	Absent
Palatine teeth	Moderately large, uniserial	Small, in two series or rows
Body coloration	Upper body brown, with numerous circular or oval black spots measuring 2-3 mm diameter or more	Variable among different members of the complex. Form found in most markets is brown or olive, peppered with irregular, small dark flecks (< 1 mm diameter)

* References: Das (1927), Silas and Dawson (1961), Rosen and Greenwood (1976), Munshi and Singh (1968), Munshi and Srivastava (1988), Talwar and Jhingran (1992), Munshi and Hughes (1992), Bailey and Gans (1998).

is potential for the acceptance of erroneous or false identifications provided by the shipper, exporter, or importer. Data entry errors also can occur.

According to USFWS agents contacted, live fish shipments are usually only spot checked and some shipments may go undeclared or unrecorded, leading to under-reporting of actual import quantities. For instance, those shipped by air from outside North America into Canada could subsequently be trucked to the USA without inspection. Presence of live fish would only be recorded by customs if the transporter revealed the cargo contents or if customs discovered the items during inspection. Similarly, items arriving by air to the USA could later be trucked to Canada. Although importers are supposed to provide destination, final destinations are not always provided.

We obtained LEMIS import data on three occasions covering July 1996–January 2017 and totaling 972 swamp eel shipments (earlier paper records no longer exist). Forty-one percent (i.e., 403) of the records only report weight (kilograms) rather than numbers of individuals. Weights represent fish (excluding container and water) and we estimated numbers of swamp eels by dividing the weight by 0.386. This conversion ratio is derived from data in Cole et al. (2014) who reported the average weight of 47 imported swamp eels was 386 g (range 174–850 g).

Identification of specimens

Swamp eels are snake-like fish distinguished from anguillid eels (also common in North American food markets) by various external characters: absence of pelvic fins, lack of pectoral fins (except in larval forms), reduction of anal and dorsal fins to rayless ridges, absence or substantial reduction of the caudal fin, and a gill opening consisting of a single slit or pore that opens ventrally. The only live swamp eels that we have observed in US food markets are Asian taxa: *Amphipnous cuchia* and certain members of the *M. albus/javanensis* complex. The two taxa can be readily distinguished by external traits (Figure 1, Table 1). Most notable, the air-breathing apparatus of *A. cuchia* consists of a pair of laterally-positioned

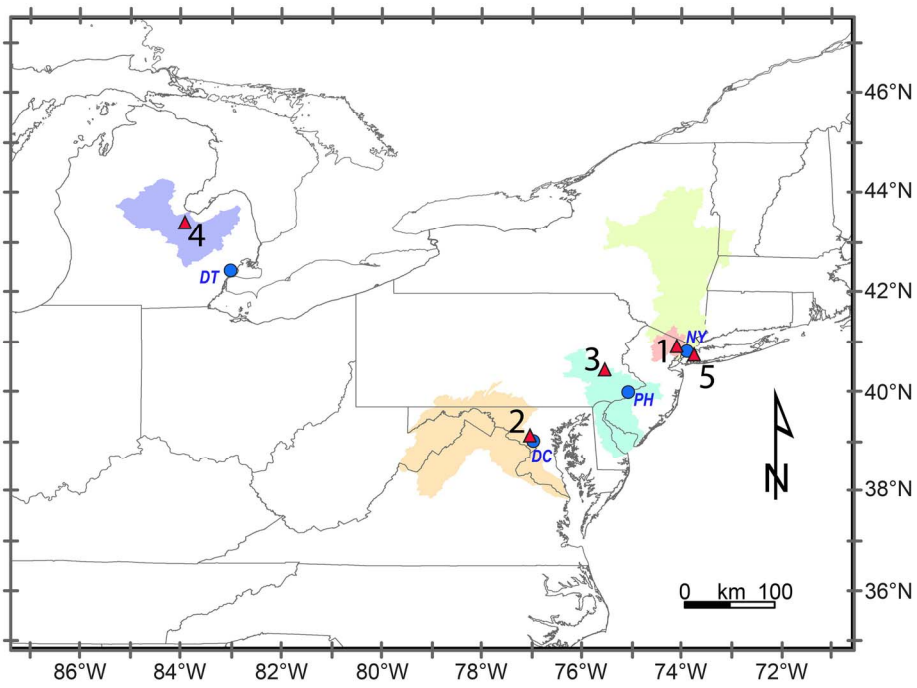

Figure 3. Locations of the five open-water sites (red triangles) in USA with records of the Asian swamp eel *Amphipnous cuchia*: 1) Passaic River, New Jersey; 2) Lake Needwood, Maryland; 3) Mensch Mill Pond, Pennsylvania; 4) Tittabawassee River, Michigan, and 5) Meadow Lake, New York. Shaded areas depict approximate drainage areas of associated river basins. Blue circles represent the nearest major metropolitan areas known to have food markets carrying live *A. cuchia*: New York City (NY), Washington, DC (DC), Philadelphia (PH), and Detroit (DT).

suprapharyngeal pouches, lung-like sacs connected to the pharynx and located slightly behind the head (Taylor 1831; Das 1927). During aerial respiration, air is taken in via the mouth and held in one or both pouches, causing the area behind the head to outwardly bulge laterally, noticeable when the eel is viewed from above (Figure 1b). In contrast, *M. albus/ javanensis* lack paired air chambers. Instead, air taken in during respiration is held in the buccopharyngeal cavity (i.e., orobranchial chamber), causing the throat to expand ventrally when inflated, evident when the eel is viewed from the side (Wu and Kung 1940; Figure 1c).

Results

Nonindigenous, open-water records

We document the occurrence of the Asian swamp eel *Amphipnous cuchia* in the wild from five sites in the continental USA, ranging in latitude from 39.1°N for the Maryland site to 43.4°N for the Michigan location (Figure 3, Table 2). Records span the period 2007–2017. All captures and sightings involved swamp eels at or near adult size. Information on the records follow in chronological order.

1) Passaic River (New Jersey)

The earliest US record of *A. cuchia* in the wild is associated with a Buddhist prayer-release ritual conducted 12 August 2007 at West Side Park in Paterson,

Table 2. Nonindigenous open-water records of the Asian swamp eel *Amphipnous cuchia* in USA, arranged chronologically. Date(s) may include, if known, day of release (R) and/or day(s) of capture. Distance to nearest live-food market is straight-line measurement between introduction site and the closest market(s) known to carry live *A. cuchia*. Supporting documentation includes catalog numbers of voucher specimens housed at Florida Museum of Natural History (UF) and corresponding LGN field number codes.

Location [Lat/Long]	Dates of release (R) and/or capture (C)	Introduction details	Distance to nearest markets with live *A. cuchia*	Supporting documentation
Passaic River at West Side Park, Paterson, New Jersey [40.9131°N, 74.1886°W]	R: 12 Aug 2007 C: not applicable	Prayer release ritual involving 33+ specimens	27 km	Photo documentation and news stories. Field# LGN07-59.
Lake Needwood near Rockville, Maryland (Potomac drainage) [39.1221°N, 77.1271°W]	R: unknown C: 4 & 7 Aug 2014	2 specimens collected with dip net and gig, others observed	2.8, 3.2, and 10.5 km	Field#'s LGN14-31 and 32; Voucher specimen: UF 242917 (n = 1)
Camp Mensch Mill pond, W Branch Perkiomen Creek, Pennsylvania (Schuylkill River drainage) [40.4403°N, 75.6270°W]	R: 1 June 2015 (?) C: 3 June 2015	Multiple specimens observed, only one live; likely prayer release ritual	70 km	Photo documentation, 3 specimens collected but not retained. Field# LGN15-99
Tittabawassee River near Saginaw, Michigan (Saginaw River/Lake Huron Basin) [43.3945°N, 84.0177°W]	R: unknown C: 17 May 2017	Single fish taken by angler, another observed	120 km	Field# LGN17-19; Voucher specimen: UF 242918 (n = 1)
Meadow Lake, Queens, New York City (Hudson River drainage) [40.7383°N, 73.8390°W]	R: 10 Aug 2017 (?) C: 10 Aug 2017	5 specimens collected with dip nets followed reported release	1.4 km	Field# LGN17-21; Voucher specimens: UF 242919 (n=5)

Note: In late 2018, 6 dead *A. cuchia* adult-sized specimens were found in Toogood Pond, Markham, Greater Toronto Area, Ontario, Canada (a voucher specimen is deposited and cataloged at ROM). Previously, in August and September 2005, live *A. cuchia* were obtained from a live-food market in Scarborough, Canada, approximately 10 km away from Toogood Pond (vouchers ROM 78528, n = 2 (624–730 mm TL)).

Passaic County, New Jersey, about 27 km west of New York City's Manhattan Chinatown (Henry 2007a, b). The release occurred on the north shore of the Passaic River near its junction with Molly Ann Brook. According to a news reporter who witnessed and photographed the ceremony, hundreds of "eels"—along with live turtles and frogs—were set free. Photographs of the eels allowed us to positively identify them as *A. cuchia* (Figure 4). The released animals had been purchased earlier in the day from markets in Manhattan's Chinatown. Ceremony participants consisted of several dozen devotees led by robed monks. The group performed a similar ritual in the park the previous year (Henry 2007a, b).

The Passaic River drains northern New Jersey and southern New York State. It flows into Newark Bay near the New York-New Jersey Harbor estuary. None of the swamp eels were recovered within the weeks after their release (T. Cussen, New Jersey Department of Environmental Protection, *pers. comm.*, 2007). Swamp eels of the *M. albus/javanensis* complex are established in southern New Jersey in Silver Lake (Nico et al. 2011; Cole et al. 2014), approximately 120 km south of the Passaic River site. That population, discovered in 2008 (shortly after the Passaic River release), is considered a separate introduction whose origin is unknown.

2) Lake Needwood (Maryland)

During July–September 2014, there were two collections and multiple sightings of live swamp eels at Lake Needwood, a 30-hectare, freshwater

Figure 4. Asian swamp eels and other live animals released into the Passaic River during a Buddhist prayer release ritual conducted at Westside Park in Paterson, Passaic County, New Jersey on 13 August 2007. Recent reexamination of the image by authors led to determination that the released eels were *Amphipnous cuchia*. Photograph by Samantha Henry with permission of USA TODAY Sports Images.

reservoir in Rock Creek Regional Park, Montgomery County, Maryland. Collected specimens were later identified as *A. cuchia*. All sightings occurred near and within the mouth of a tributary streamlet on the east side of the lake. The first sightings were by entomologist Tim Friedlander who reported seeing a few "eel-like fish" on 5–6 July 2014. One specimen, estimated to be 60 cm long, was photographed *in situ* (Figure 5a). County and state biologists visited the lake on 11 July 2014 and observed two live eels. On 15 July 2014, they sampled the lake with a backpack electrofishing gear, but only encountered a single specimen, dead on the shore. Baited traps deployed in shallow water over six nights (1–7 August 2014) yielded no eels. On 4 August 2014, biologist Ian Garvie and a co-worker collected the first live specimen, a fish measuring 687 mm TL swimming in open water and taken with a small net. Another specimen was speared with a frog gig on 7 August. Except for a specimen sighted (not collected) on 6 September

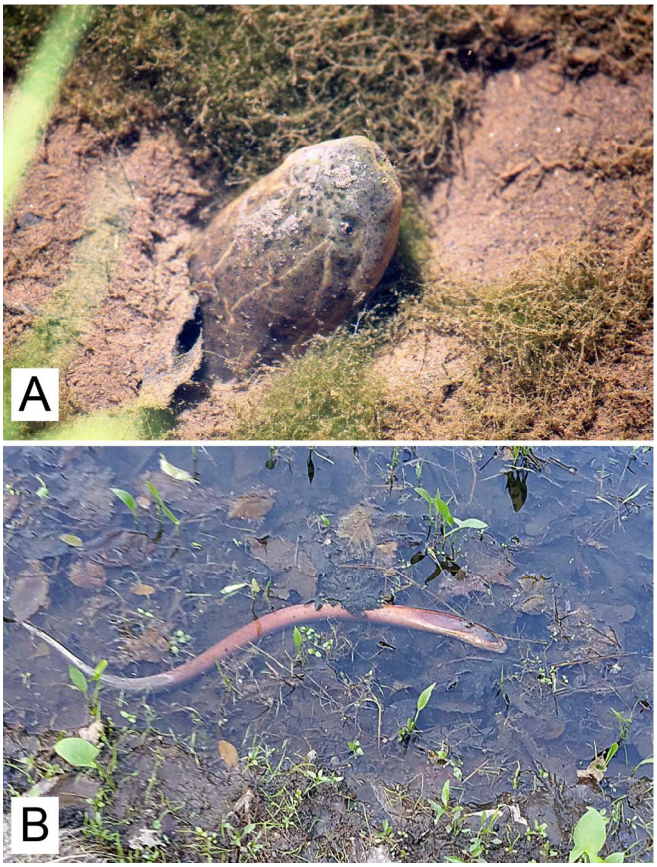

Figure 5. *Amphipnous cuchia* observed at two open-water sites: (A) live individual buried in soft substrate with head protruding, Lake Needwood, Maryland, 5 July 2014 (Field# LGN 14-33); and (B) recently dead specimen encountered in shallows of Camp Mensch Mill Pond, Pennsylvania, early June 2015 (Field# LGN 15-99). Photographs by Tim Friedlander and Erick Ammon.

2014, no additional swamp eels have been observed despite follow-up sampling of the lake and connected waterways with backpack electrofishing gear on 3 October 2014 and 26 May 2015.

Lake Needwood is in the Rock Creek watershed, Potomac River Basin, about 25 km north of Washington, DC. In 2015 and 2016, Maryland Natural Resource Police visited three food markets near Lake Needwood and confiscated live *A. cuchia*. Included was a 30 July 2015 seizure of 61 specimens from two stores near Lake Needwood, and a 7 March 2016 confiscation of 19 swamp eels from a market only 2.8 km from the lake (Table 2). Documents from one market indicated the swamp eels had come from a wholesaler in Brooklyn, New York, over 300 km away. The wholesaler's import declaration form revealed the original air cargo shipment, dated 18 February 2016, originated in Bangladesh and contained 5,600 live, wild-caught eels. The form wrongly identified the fish as *Anguilla bengalensis* (Gray, 1831).

3) Mensch Mill Pond (Pennsylvania)

On 1 June 2015, a local resident contacted authorities after seeing multiple dead "snakes" in Mensch Mill Pond, a pooled area on the West Branch Perkiomen Creek in rural Berks County, southeastern Pennsylvania. In

response and on the same day, Erick Ammon of the Pennsylvania Department of Environmental Protection (*pers. comm.* 2018) visited the pond site and concluded the animals were a type of "eel". He documented the finding with photographs (Figure 5b) and noted that the eels, about 25 individuals, were scattered throughout the pond and all appeared to be freshly dead. Ammon returned to the site 3 June 2015 and observed a free-swimming eel but was unable to capture or photograph it. A few of the less decomposed specimens were collected (later discarded). These were estimated to range from 50 to 80 cm TL. The uncaptured, live individual appeared to be over 25 cm TL. Based on photographs, we identified the eels as *Amphipnous cuchia*.

Mensch Mill Pond is a 0.5-hectare, shallow impounded reach of a small creek in the Schuylkill River drainage, Delaware River Basin. In 2014, the property bordering the pond was purchased by a Buddhist group purportedly from the Philadelphia area. Their ownership led to speculation that the fish release could have been part of a religious ceremony. The source of the swamp eels was never determined, although their numbers and size indicated the animals may have been from a live-food market.

4) Tittabawassee River (Michigan)

The Michigan *A. cuchia* record is based on a single specimen (743 mm TL) taken from the lower Tittabawassee River near the town of Saginaw on 17 May 2017 (S Herbst, Michigan Department of Natural Resources, *pers. comm.* 2018). The eel was recovered by an angler who reported seeing the barely alive fish lying along the shoreline near the Center Road boat launch. The angler observed a second live eel in the water near where the first was encountered on the same day. The captured specimen was provided to us and identified. Within a week of its discovery, state biologists surveyed the collection area and interviewed local anglers, but no additional swamp eels were observed or reported.

The Tittabawassee River, 116-km long, is a tributary of the Saginaw River within the Lake Huron-Great Lakes Basin. The lower reaches of the Tittabawassee where the swamp eel was collected is low gradient, about 100-m wide, and runs through forest and farmland. Winters in the region regularly reach freezing temperatures.

5) Meadow Lake (New York)

On 10 August 2017, state biologists captured five *A. cuchia* (540–779 mm TL) in Meadow Lake within Flushing Meadows Corona Park, Queens County, New York City (MK Cohen, New York State Department of Environmental Conservation, *pers. comm.* 2017). Biologists were responding to a report of a fish kill and upon arrival observed live swamp eels in shallows along the lake's northeast shore. The fish, alive but appearing stressed, were captured by dip net. A local man informed the collecting crew

Table 3. Live Asian swamp eels documented in food markets in the USA and Canada during period 2001–2017. Cities listed as location may include markets within surrounding metropolitan area. Most voucher material is in the form of whole preserved specimens cataloged and housed at the Florida Museum of Natural History (UF) and Royal Ontario Museum (ROM) [associated field number provided in brackets].

Taxa	Market location (number of different markets with live swamp eels)	Year (number of markets with live swamp eels)	Voucher material [field numbers]
Amphipnous cuchia	Boston/MA (1)	2001 (1)	UF 172315 [LGN 01-24]
	Orlando/FL (2)	2001 (1), 2002 (1), 2011 (1), 2012 (1), 2014 (1), 2015 (1)	UF 172316 [LGN 01-25], UF 242531 [LGN 02-51-OR], UF 242534 [LGN 12-01]
	Miami/FL (1)	2017 (1), 2018 (2)	UF 242535 [LGN 17-23]
	St. Louis/MO (1)	2002 (1)	UF 172322 [LGN 02-35]
	Atlanta/GA (2)	2010 (1), 2015 (1)	vouchers not catalogued
	Chicago/IL (1)	2015 (1)	no voucher
	Detroit/MI (2)	2014 (1); 2017 (1)	no voucher
	New Orleans/LA (1)	2016 (1), 2017 (1)	no voucher
	Houston/TX (1)	2015 (1)	no voucher
	New York, NY	2001 (3), 2011 (4), 2014 (4)	UF 172314 [LGN 01-18], UF 242533 [LGN 11-28]
	Washington DC (3)	2015 (2), 2016 (1)	UF 242487 [LGN 15-47], UF 242488 [LGN 15-48]
	*Toronto (1)	2005 (1)	ROM 78528 [LGN 05-17]
M. albus/javanensis complex	Atlanta/GA (1)	2003 (1), 2004 (1)	UF 172325 [LGN 03-35b]
	*Vancouver (1)	2006 (1)	ROM 84342 [LGN 06-85b]
Species undetermined	*Vancouver (1)	2006 (1)	no voucher [LGN 06-85a]

* Records associated with live-food food markets in Toronto and Vancouver, Canada are based on museum vouchers deposited at ROM and/or information provided as personal communications from E Holm (Royal Ontario Museum, 2019), N Mandrak (University of Toronto Scarborough, 2019), B Cudmore (Fisheries and Oceans Canada, 2007, 2018), and EB Taylor (University of British Columbia, 2019).

that several hours earlier he witnessed a group releasing large numbers of fishes and frogs, supposedly many more than what the biologists recovered. No additional swamp eels were sighted during follow-up boat-electrofishing surveys of Meadow Lake conducted on 12 September 2017 and of nearby Willow Lake on 1 May 2018. The five captured specimens were preserved and subsequently identified by us as *A. cuchia*.

Meadow Lake (38.4 hectares) is a shallow, slightly-brackish body connected to the more saline waters of Flushing Bay in the Hudson River Basin (Cohen and MacDonald 2016). Some released swamp eels may have gone undetected because the lake is difficult to survey by electrofishing due to high conductivity, low water clarity, and dense vegetation. The group involved in the release was never identified, but the sizes and types of animals freed cause us to suspect the source was one of the many nearby live-food markets, possibly liberated as part of a prayer release ritual.

Food market surveys

We documented live swamp eels in markets in 11 (50%) of the 22 metropolitan areas (Table 3, Figures 6–8). Of the approximately 190 different food markets visited, live swamp eels were found in 22 (11%). Among markets visited on multiple occasions and over multiple years, some consistently carried live swamp eels. In several markets without swamp eels,

Figure 6. Asian swamp eels for sale in ethnic live-food markets in the USA and Canada: (A) members of the *M. albus/javanensis* complex at a market in Atlanta on 7 August 2003 (Field# LGN03-35b) and (B) same taxa at same market on 1 June 2004 (Field# LGN04-07); (C) unidentified swamp eels, possibly *Amphipnous cuchia*, in market in Vancouver, 1 June 2006 (Field# LGN06-85a); (D) *A. cuchia* in market in Orlando, 2 November 2001 (Field# LGN01-25); and (E) *A. cuchia* in market in New York Chinatown, 28 July 2001 (Field# LGN 01-18). Photograph of the Vancouver market specimens by Becky Cudmore, all others by Leo G. Nico.

vendors admitted that they sometimes carried them live, but stocks temporarily sold out. A few markets advertised live swamp eels, but labeled tubs were empty. *Amphipnous cuchia* was by far the most common swamp eel, found in 21 different markets distributed among 11 different US metropolitan areas and its presence documented in multiple years (2001, 2002, 2006, 2010, 2011, 2012, 2014, 2015, 2016, 2017, and 2018). Live *M. albus/javanensis* were only found in one market, a large grocery store in Atlanta where it was observed in both 2003 and 2004. Air cargo labels on containers indicated the 2003 stock had been shipped from Vietnam to Atlanta (Supplementary material Figure S1) and, based on genetic analysis, corresponded to *Monopterus* "clade B" of Collins et al. (2002) (TM Collins, Florida International University, *pers. comm.*). A St. Louis market surveyed in 2002 was unique in that it had live *A. cuchia* in tanks and a few freshly-dead *M. albus/javanensis* on ice which the vendor revealed had been previously alive in the store. On a few occasions we witnessed customers purchasing swamp eels, and twice saw customers carry eels away live.

Food markets with live swamp eels ranged from small to large stores, a mix of ethnic and multicultural independent businesses and chain supermarkets.

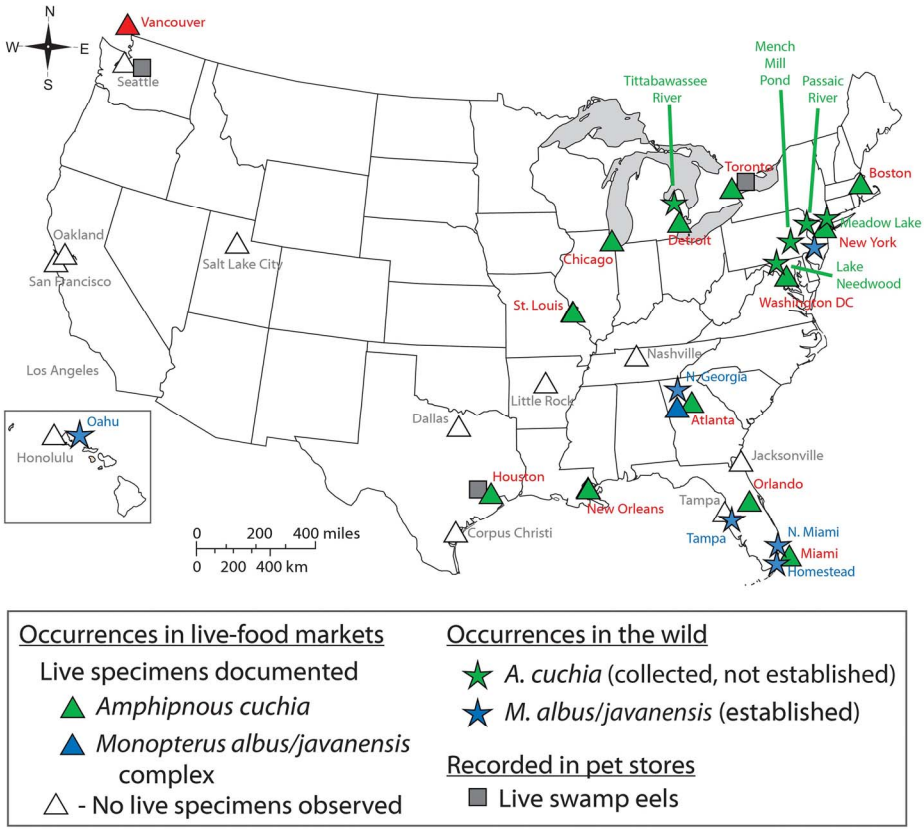

Figure 7. USA and two Canadian cities showing metropolitan areas included in live-food market surveys and locations of records from the wild. Most market information depicted is based on surveys conducted by authors over period 2000 to 2018. Documentation of live swamp eels in markets in Boston, Toronto, and Vancouver, and in three pet stores were provided by colleagues.

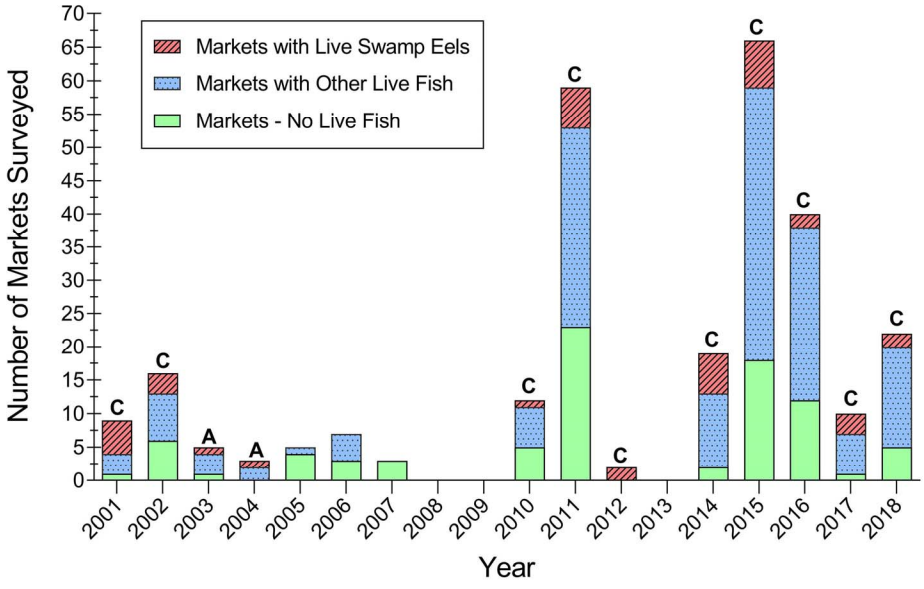

Figure 8. Summary data from survey of US live-food markets (2001 to 2018) showing number of markets surveyed within given year, number of markets in which live swamp eels were encountered, and number of markets with other live fish. Identity of market swamp eels are indicated by letter above bar, C = *Amphipnous cuchia* and A = member of the *M. albus/javanensis* species complex. Most markets surveyed were in the continental USA, although data from markets in Toronto (Canada), Honolulu, and Guam are included. Each visit to a market is treated independently, although a few markets were visited more than once over the course of study.

The live fish were held in tubs, tanks, or polystyrene boxes with identifying labels in East Asian script (sometimes with approximate English-language equivalent). Among markets assigning English names, at least ten markets advertised *A. cuchia* simply as "yellow eel" and one market consistently referred to them as "Chinese yellow eel". An Atlanta market promoted *M. albus/javanensis* as "Vietnam eel" or "Vietnamese eel", although another vendor labeled *A. cuchia* as "yellow eel (Vietnam)". Anguillid eels were normally labeled as "white eel".

Markets observed holding live *A. cuchia* are close to three of the five introduction sites (Table 2). For instance, live *A. cuchia* are common in multiple markets in New York's Manhattan Chinatown (i.e., 2001, 2011, 2014, and 2017), within 27 km of the Passaic River site and approximately 13 km from Meadow Lake. Numerous ethnic food markets also exist in Queens itself and an Internet search yielded photographic evidence that a market within 1.4 km of Meadow Lake held live *A. cuchia* as recently as October 2018.

Three Maryland markets surveyed in 2015–2016 with live *A. cuchia* were within a few kilometers (2.8, 3.2, and 10.5 km) of the Lake Needwood introduction site. In contrast, markets in Pennsylvania and Michigan holding live *A. cuchia* were relatively distant from the introduction sites in those states. Photographs on the Internet indicate at least one market in Philadelphia consistently had live *A. cuchia* for sale, a store approximately 70 km from Pennsylvania's Mensch Mill Pond. The only markets in Michigan where we documented live *A. cuchia* was in Detroit, approximately 120 km from the Tittabawassee River site. Admittedly, there may be markets with live swamp eels near introduction sites, markets unknown to us or not surveyed.

USFWS-LEMIS records

LEMIS swamp eel data are summarized graphically (Figures 9 and 10) and described below. All shipments identified in LEMIS as swamp eels were categorized in the database as live.

Taxonomic entries

Of the 972 entries for swamp eels in LEMIS, 966 (99.4%) were reported as either *M. albus* or its junior synonym, *Fluta alba*. Five filed entries identified shipments as "*Monopterus* species". A single shipment was reported as containing *Synbranchus marmoratus*. There were no entries identifying cargo as *Amphipnous cuchia* (or *Monopterus cuchia*) (Figures 9 and 10), but we concluded those imported from Bangladesh and India to be *A. cuchia*, not *M. albus* (i.e., *M. albus/javanensis* complex). This decision was based on: 1) *A. cuchia* is native and widespread in those two countries, whereas *M. albus/javanensis* purportedly is not (Silas and Dawson 1961); 2) *A. cuchia* is a commercial species in both countries, especially

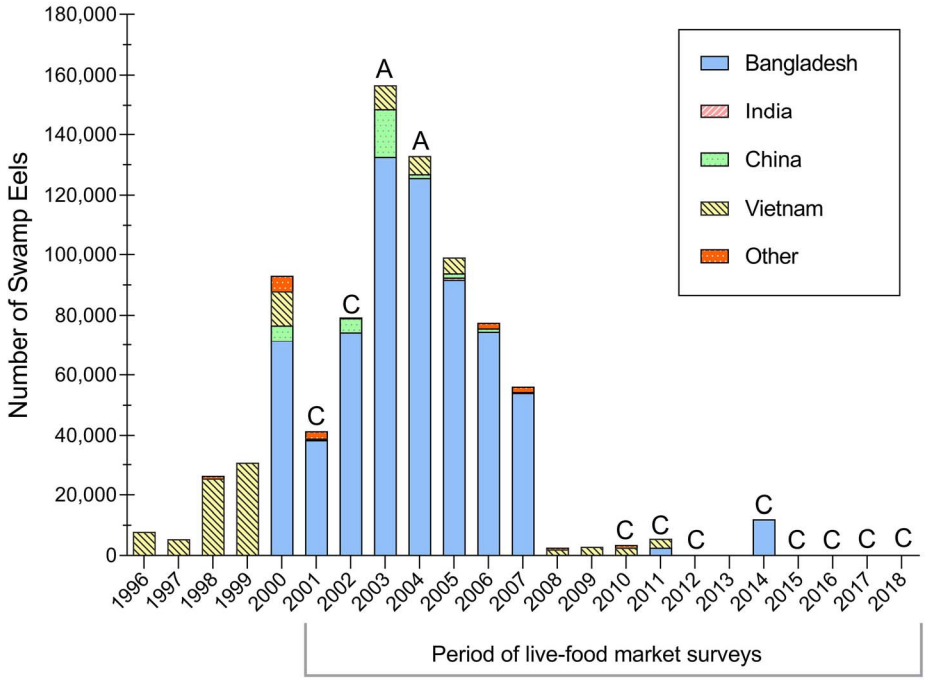

Figure 9. Summary of LEMIS data for the period July 1996–January 2017 showing the number of live swamp eels (family Synbranchidae) (n = 832,897) imported into USA and its territories by year and country of origin. The identity of live swamp eels documented during surveys of US food markets conducted intermittently over period 2000–2016 are indicated by letter above bar, C = *Amphipnous cuchia* and A = member of the *M. albus/javanensis* complex. Note: although most imported swamp eels in the LEMIS database are identified as *M. albus*, it is likely that swamp eels originating in Bangladesh and India are *Amphipnous cuchia* and those from other Asian countries are members of the *M. albus/javanensis* complex.

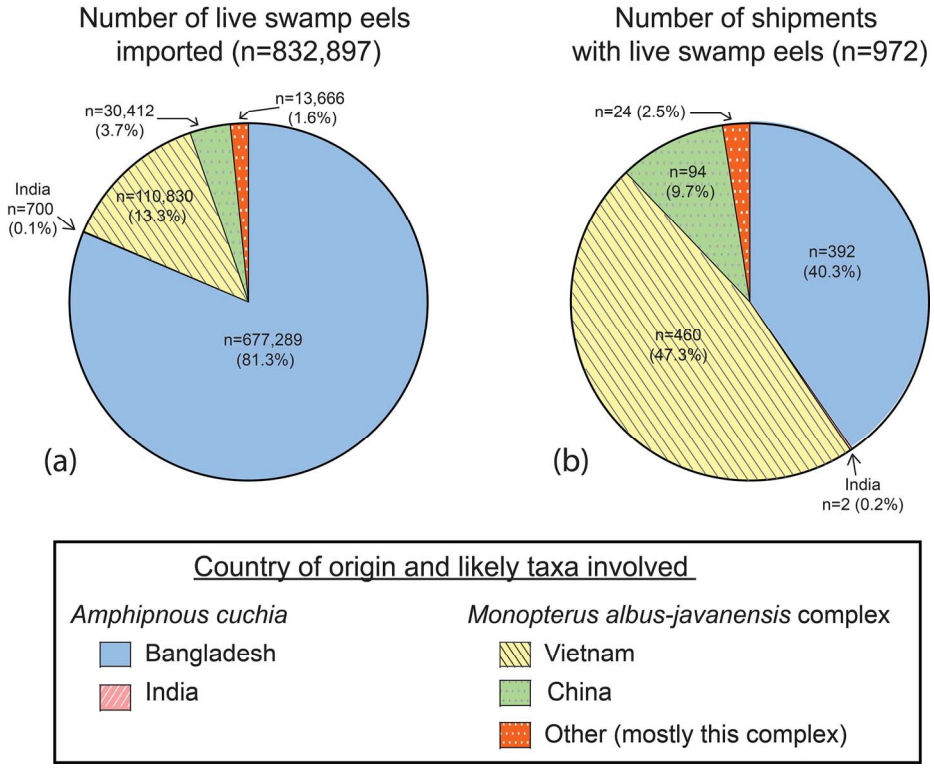

Figure 10. Summary of LEMIS shipment records for period July 1996 to January 2017 depicting: (a) Relative numbers of live swamp eels imported into USA and its territories by country of origin; and (b) numbers of imported shipments (n = 972) containing live swamp eels. Swamp eels originating in Bangladesh and India are presumed to be *Amphipnous cuchia*.

important in Bangladesh (Hasan et al. 2012; Miah et al. 2015); and 3) our own surveys documenting that *A. cuchia* is the predominant swamp eel imported to US markets.

Among markets found to have live swamp eels, we obtained USFWS import declaration documents from two stores, one in Maryland and another in Florida. In both cases, the species for sale was *Amphipnous cuchia*, but forms wrongly identified them as *Anguilla bengalensis*. Both are native to Bangladesh, the country listed as the origin on declaration forms. There are no LEMIS records of swamp eels being imported into the USA during 2016 and 2018 when the above stores held *A. cuchia*.

Quantity

Based on LEMIS records, we estimated that 832,897 live swamp eels were imported into the USA and its territories during July1996–January 2017. Most, 829,601 (99.6%), were filed as *Monopterus albus* (or *Fluta alba*). Remaining entries included an estimated 3,206 individuals recorded as *Monopterus* species and 90 individuals filed as *Synbranchus marmoratus*. Numbers per shipment ranged from two specimens up to an estimated 6,540 individuals. Four LEMIS records—all reported as shipments from Bangladesh—had entries for swamp eel numbers that seemed much too high and likely erroneous. The most blatant was an entry for a shipment dated 13 September 2004 purportedly containing 4,400,000 live specimens—a number greater than all other shipments combined. Following advice of a USFWS-LEMIS analyst contacted, we adjusted quantity values downward for four shipments: 4,400,000 live specimens (changed to 4,400), 19,000 (changed to 1,900), 12,340 (changed to 1,234) and 8,222 (changed to 822).

LEMIS data indicate the numbers of live swamp eels imported was greatest during the years 2000 to 2007, followed by a substantial drop (Figure 9). However, we still regularly encountered swamp eels for sale in US food markets even after 2007 (Figures 8 and 9). Although the LEMIS filings recorded almost all imported swamp eels imported over the period 1996–2017 as "*M. albus*", our 2001–2017 market surveys revealed that almost all imports were *A. cuchia*. Predominance of *A. cuchia* in US markets corresponds to LEMIS records indicating that most imports originated in Bangladesh.

Wildlife source

Filings indicate an estimated 815,478 (97.9%) of imported swamp eels originally came from the wild; whereas only about 15,756 (1.9%) swamp eels were listed as being from captive or aquaculture sources (i.e., either bred or born in captivity, or from aquaculture). Remaining filings, 1,663 (less than 1%) swamp eels, were entered as source unknown. Only two of the 387 shipments from Bangladesh were reported as coming from aquaculture sources. Both shipments from India were reported as being swamp eels bred in captivity.

Purpose of import

All live swamp eel shipments for which the purpose was entered (582 shipments) were coded as commercial, a broad category that does not differentiate between animals intended for the food trade versus the pet trade. A purpose was not entered for the remaining 390 filed shipments. However, filed names of the export/import businesses typically indicate human consumption was the main purpose. An exception was a shipment of 90 *Synbranchus marmoratus* imported by an aquarium fish business.

Transport method

We did not obtain transport data for the LEMIS filings, but a USFWS-LEMIS data analyst agent informed us that all or most shipments were likely via air cargo. Some live *A. cuchia* encountered by us in food markets were in their original shipping containers, typically polystyrene boxes, some with airline flight labels (Figure S1).

Country of origin or export

The LEMIS data indicated swamp eels were imported from 15 different countries, with most coming from Bangladesh (81.3%), Vietnam (13.3%), and China (3.7%) (Figure 10). Other Asian origins included Thailand (0.5%), Indonesia (0.2%), India (0.1%), Macao (0.1%), Taiwan (0.1%), and Philippines (< 0.01%). Several countries listed as origin were possible trans-shipment locations (e.g., Australia, Canada, perhaps Tonga). Asian swamp eels filed in the LEMIS system as coming from British Virgin Islands (VG), Bolivia (BO), and Bulgaria (BG) were likely the result of a wrong country code being reported or entered in place of Vietnam (VN) and Bangladesh (BD). The single shipment containing *Synbranchus marmoratus* originated in Peru.

Based on LEMIS data for swamp eels from Bangladesh and India, we estimated that approximately 83% of all live specimens imported into the USA over the period July1996–January 2017 were *A. cuchia*. This included 677,289 swamp eels in 392 shipments from Bangladesh and 700 swamp eels in two shipments from India. Based on 1996–2017 data, the earliest swamp eel shipments from Bangladesh occurred in 2000. The greatest numbers were imported over the years 2000–2007. The LEMIS data documents few imports after 2007, but some swamp eels are misidentified as anguillid eels (see later discussion regarding *Anguilla bengalensis*.)

Ports of entry

LEMIS filings document swamp eel shipments as entering the USA and its territories through 11 different ports. New York City predominated, accounting for 533 (54.8%) of the 972 swamp eel shipments entering the country over July1996–January 2017. That city also accounted for 736,609

(88.4%) of the total estimated number of live swamp eel specimens imported, with most, about 677,289 swamp eels, originating in Bangladesh. Other frequently used ports of entry included Newark, New Jersey (223 swamp eel shipments [24.0%]), Atlanta (86 [8.8%]), the Saipan (60 [6.2%]), Los Angeles (37 [3.8%]), and San Francisco (26 [2.7%]). Minor ports included Blaine, Washington (3), Dallas/Fort Worth (1), Baltimore (1), Miami (1), and Guam (1) accounted for only 0.7% of all shipments.

Voucher material

UF museum catalog numbers and LGN field collection numbers pertaining to preserved vouchers of wild-caught and market swamp eel specimens are provided in Tables 2 and 3.

Discussion

Amphipnous cuchia, a swamp eel species from southern and southeastern Asia, has been introduced to at least five open-water sites in the continental USA over the past decade. Although there is no evidence of reproduction in the wild, their appearance in US waters represents the first confirmed nonindigenous records of this species in the New World and perhaps the only confirmed open-water records of *A. cuchia* outside its known native range.

Occurrence of *A. cuchia* in North America is linked to the international live-food trade, a conclusion based on several lines of evidence: (1) LEMIS database records revealing regular swamp eel imports from Asia since at least the mid-1990s; (2) long-term surveys (2001–2018) documenting widespread distribution of live *A. cuchia* among food markets in USA and Canada; (3) indications that the live-food trade is the main or only source of live *A. cuchia* in North America and that species is not in US pet trade; (4) discovery of live *A. cuchia* in food markets close to some introduction sites; and (5) evidence (e.g., specimen numbers and large sizes, eyewitness account) that the swamp eels were obtained from food markets.

Although the LEMIS database does not record any imported swamp eels under the name *A. cuchia* or its synonyms, it is reasonable to conclude that swamp eels documented as originating in Bangladesh and India—where *A. cuchia* is native and commercially harvested—are this species (see earlier section on USFWS-LEMIS Records: Taxonomic Entries). Moreover, our market surveys indicate that *A. cuchia* has been the predominant imported swamp eel since about 2001, largely replacing *M. albus/javanensis*. *Amphipnous cuchia* has continued to appear regularly in US markets over recent years, even though LEMIS import records seem to indicate swamp eel imports have dramatically declined since about 2007. Indeed, according the LEMIS data, no swamp eels were imported into the USA in the years 2012, 2015, and 2016, even though during those same years our market surveys showed that large numbers of live *A. cuchia* were present in

various stores in or near the cities of Atlanta, Chicago, Houston, New Orleans, Orlando, and Washington DC (Figures 7 and 8, Table 3).

One explanation is that some swamp eels are being imported under different names. Support for this hypothesis comes from USFWS import declaration forms that accompanied live *A. cuchia* found in stores in Maryland and Florida that wrongly identified the animals as *Anguilla bengalensis* (family Anguillidae). *Anguilla bengalensis* is native to Bangladesh, but quite distinct from the two native swamp eels, *A. cuchia* and *Ophisternon bengalense*. If such misidentifications are a common occurrence, then the numbers of swamp eels being imported into North America might be severely underestimated.

Reasons for misidentification of imported swamp eels as anguillid eels in declaration forms is unclear. Likelihood that one swamp eel species may be mistaken for another is high, but anguillid eels and swamp eels are easily distinguished. Moreover, *A. cuchia* is a widespread and well known commercial fish in Bangladesh and widely recognized as an important export (Miah et al. 2015; Khatun et al. 2017; Sharmin et al. 2017). Conceivably, declaration of swamp eels as anguillid eels may be intentional in certain instances, perhaps to avoid regulations that limit the possession or sale of live swamp eels.

LEMIS data indicate there have been 1,024 shipments of anguillid eel from Bangladesh over the period January1999 to November 2018. The port of entry for all the imports was given as New York City. Most, 547 (53%) shipments, were reported as *Anguilla bengalensis*. Other anguillid shipments from Bangladesh identified included *A. australis*, *A. bicolor*, *A. japonica*, and *A. nebulosa*. Among these, only *A. bengalensis* (possibly also *A. bicolor*) are generally considered to be native to Bangladesh. The proportion of imported "Anguilla" that were actually swamp eels (i.e., *A. cuchia*) cannot be determined. However, during our 2000–2018 surveys of US markets, we never knowingly encountered live *A. bengalensis* even though the species' appearance is distinct from swamp eels and most other anguillids.

The introduction pathway

The introduction pathway of *A. cuchia* can be pieced together based on analysis and interpretation of LEMIS import records, results of our live-food market surveys, and recently published literature from Bangladesh detailing eel harvest and market channels. To date, all non-native swamp eels recorded from open waters of the USA are Asian taxa. Included are three members of the *M. albus/javanensis* complex and the newest addition, *A. cuchia*. These taxa are desirable food fish in many countries of eastern and southeastern Asia and evidence indicates that the live-food trade is the main—perhaps only—pathway responsible for the presence of *A. cuchia* in North America over the past few decades. There is no evidence that swamp

eels have ever been cultured as a food fish in North America, consequently live individuals observed in US food markets are almost certainly imported and their appearance in open waters likely tied to the live-food trade.

Over recent decades there has been increased global demand for swamp eels (and other eels) as human food. In response, several countries in Asia have attempted to develop commercial-level, aquaculture production of swamp eels, but with little success. Culturing of *M. albus/javanensis* is known in some Asian countries, such as Vietnam (Khanh and Ngan 2010) and Malaysia (Yin et al. 2018), but the operations are small scale and localized. Moreover, swamp eel pisciculture apparently is entirely or largely dependent on the harvesting of small, juveniles from the wild and growing them out in captivity. A few farmers in northeastern India are known to carry out similar activities with *A. cuchia*, taking young from the wild and stocking them in cement cisterns (Barman et al. 2013). Researchers in Bangladesh have also expressed interest in culturing *A. cuchia* but admit that there is still no commercial fry production or substantial commercial-level culture of the fish; consequently, Bangladesh exports depend entirely on wild captures (Miah et al. 2015; Roy et al. 2016; Khatun et al. 2017). The lack of aquaculture production aligns with information detailed in the LEMIS database which indicates at least 99% of all swamp eels imported into the USA are wild-caught.

In Bangladesh, wild *A. cuchia* are harvested year-round, with peak period being the low-water season (October to December) when the fish are easier to find and collect (Khatun et al. 2017; Sharmin et al. 2017). Collectors—referred to as "Kuchia catchers"—are mostly poor, young men, and the activity is their main source of income (Rahmatullah et al. 2015). Capture gear and methods used are largely traditional or low-tech, such as baited traps, hand lines, various handmade devices, as well as capture by hand (Hossain et al. 2007; Rahmatullah et al. 2015; Sharmin et al. 2017). In Bangladesh, collectors sell their catch directly to local markets or to middlemen who are part of the market-export channel. The market channel is a complex web involving anywhere from a few to many middlemen and wholesalers (e.g., traders, auctioneers), with the swamp eels ultimately transferred to export agents, foreign buyers, retailers, and customers (Hossain et al. 2007; Khatun et al. 2017; Sharmin et al. 2017).

Based on an analysis of data from 40 different traders, Sharmin et al. (2017) estimated that Bangladesh exports 35.9 metric tons of *A. cuchia* each month, with most exports going to China (75%), South Korea (10%), Thailand (8%), Japan (5%), and Malaysia (4%). Bangladesh reportedly also ships *A. cuchia* to South Korea, Thailand, Malaysia, Singapore, Indonesia, and Taiwan, Australia, New Zealand, Europe, and the Middle East (Hasan et al. 2012; Miah et al. 2015; Khatun et al. 2017; Sharmin et al. 2017). Only Hasan et al. (2012) mentions the USA as one of the countries with high demand for *A. cuchia*, reporting that as much as 3% of Bangladesh's

swamp eel exports go to the USA. Large numbers reportedly also ship to Canada (Miah et al. 2015).

Why *A. cuchia* is the major swamp eel imported into North America is not clear. Perhaps countries that traditionally export *M. albus/javanensis* now only sell to other Asian countries. Under this scenario, Bangladesh has seemingly responded by filling the void created in North American markets. Whether Bangladesh offers swamp eels at a lower cost is not known. According to the literature, Bangladesh does not appear to have developed more cost-effective or efficient methods in the wild-harvest or culture of swamp eels, relative to any of the other Asian countries known to export these fish.

Live-food markets in the USA

Swamp eels from Asia are transported to the USA as air cargo and we assume that all or most go to wholesalers/distributors who then distribute the live animals to retailers. For instance, a market in Maryland and another in Florida both obtained their stocks from a distributor in the New York City area, 300 km and 1,700 km away, respectively. It is unclear if large chain supermarkets differ in how they procure live swamp eels compared to small stores. Wholesalers in North America presumably use both ground and air transport to distribute live swamp eels to their network of retailers.

From market to open-water introduction

The final segment in the introduction pathway for swamp eels involves the way in which live specimens are transferred from food markets to open waters. Several possibilities exist. Religious prayer-release is documented as the reason for one *A. cuchia* open-water introduction and, to varying degree, implicated in some of the others. Admittedly, some customers visiting ethnic food markets in the USA purchase live swamp eels and other market animals for use as bait, opening the possibility of accidental or purposeful live releases by anglers, but evidence discussed below suggests this vector is unimportant regarding the freshwater releases documented in this study. The aquarium fish trade may be a separate pathway or, similar to prayer release, a final segment in the live-food trade pathway (if the fish purchased from food markets are initially kept as pets before release).

Prayer release

Prayer release—also known as merit, life, mercy, and ceremonial-animal release and by the Chinese term "fangsheng"—is a widespread and complex religious practice that has largely gone unnoticed and underappreciated as an introduction pathway (Everard et al. 2019). We consider prayer release an important segment in the live-food trade pathway,

Figure 11. Live swamp eels—members of the *M. albus/javanensis* complex—along with other live fish and animal species displayed in plastic bags outside a Buddhist temple (Wat Phra That Phanom) in Mukdahan, Nakhon Phanom Province, Thailand, on 29 January 2006 (Field# LGN06-26). The local venders sell live animals to temple visitors. Devotees of Buddhism purchase and then release live animals to gain merit, with some believing the eel release leads to monetary benefit. (Photograph by Leo G. Nico).

explaining how at least some market swamp eels enter the wild. Among the *A. cuchia* records reported in the present paper, the Passaic River introduction provides the strongest evidence of a link between live-food markets, prayer release, and wild introduction. Based on various lines of evidence (e.g., proximity of release sites to live-food markets and Buddhist temples), prayer release may be involved in the species' introduction to other US sites examined. It may also explain some *M. albus/javanensis* introductions (Nico et al. 2011). We have yet to uncover cases of *A. cuchia* being used in such rituals in Bangladesh or India, two countries where the species is most widespread. However, in China, Thailand, and other countries, prayer release is common and "eels" (all or mostly *M. albus/javanensis*) are frequently used in the ritual (Barrow 2011; Edmunds 2011; Liu et al. 2013; Basha and Dunlea 2017; Cooper 2018; Figure 11).

Prayer release takes multiple forms, differences likely linked to such factors as the Buddhist sect involved, region or country, the temple where rituals are held, local and individual belief systems, as well as types and numbers of animals locally available (Smith 1999; Holler 2002; Edmunds

2011; Yang 2015). History of the practice is long and complex, dating back more than a thousand years (Smith 1999; Shiu and Stokes 2008; Yang 2015). Followers of Buddhism are taught that prayer release expresses compassion and is a powerful way to accrue spiritual merit (Ahmed 1997; Smith 1999; Shiu and Stokes 2008; Gilbert et al. 2012; Liu et al. 2012; Yang 2015). Certain practitioners also believe the type and number of animals liberated determines the reward, for example, some imagine the release of eels yields financial benefit (Anonymous 2018). Admittedly, animal release is also performed by adherents of Daoism (Taoism), Jainism, Zoroastrianism (Parsi), some devotees of Catholicism and Protestantism, and by non-religious, animal rights advocates (Ahmed 1997; Holler 2002; Iliff 2002; Cohen 2012). However, the large number of Buddhists worldwide and the religion's emphasis on prayer release results in higher probability of this introduction pathway.

Prayer release is especially prevalent in eastern, southeastern, and southern Asia (Severinghaus and Chi 1999; Holler 2002; Gilbert et al. 2012; Liu et al. 2012), a pattern seemingly linked to large Buddhist populations. About 98% of the world's 495 million Buddhist adherents reside in Asia, mostly in China, Japan, Thailand, Vietnam, and Myanmar although substantial numbers are also present in other Asian countries (Johnson and Grim 2013). Over recent decades prayer release has seemingly become more common, even in non-Asian countries (West 1997; Shiu and Stokes 2008). Its proliferation presumably related to the growth of Buddhist communities (Johnson and Grim 2013; Yang 2015). For instance, between 1910 and 2010 estimated numbers of Buddhists have increased in North America from 47,200 to 4,454,000, in Europe (excluding eastern Europe) from 100 to 1,211,400, and in Australia/New Zealand from 7,500 to 562,000 (Johnson and Grim 2013).

The numbers and types of animals introduced globally into the wild through prayer-release is impossible to quantify, but may be substantial, perhaps hundreds of millions of animals annually (Humane Society International 2013). In Taiwan alone, it is estimated that practitioners spend USD 6 million to liberate 200 million animals each year (Agoramoorthy and Hsu 2007). A 2010 study in China indicated prayer-release organizations exist in every municipality (Zhuang 2019). The Beijing Fangsheng Association alone released an estimated 15 million animals in 2014 (Shuyin 2015). In parts of Asia, prayer release is so prevalent that a flourishing industry has developed around the farming, trapping, import, and sale of live animals for use in such rituals (Falconer 2009; Hong 2014; Fan 2016), a supply chain that includes poachers who harvest animals from the wild (Hong 2014; Fan 2016).

Animals released include an assortment of native and non-native fishes, frogs, turtles, birds, mammals, and invertebrates (e.g., crabs, insects). Included are wild-caught and captive-bred stocks, some reared specifically

for prayer release (Severinghaus and Chi 1999; Holler 2002; Agoramoorthy and Hsu 2005, 2007; Gilbert et al. 2012; Cooper 2018). In Asia and elsewhere, practitioners obtain their animals from pet shops (Severinghaus and Chi 1999), live-food markets (Liu et al. 2013), slaughter houses, and direct from fishermen (Everard et al. 2019). Vendors commonly station near temples hawking live animals to both visiting Buddhists and tourists, anyone interested in performing a prayer-release offering (Cooper 2018; LG Nico, *pers. obs.*; Figure 11).

In North America, live-food markets are a source of aquatic animals used in prayer-release (Henry 2007a; Cohen 2012; present study). Such markets are common in certain metropolitan areas, especially those with large Asian populations, and many offer a variety of aquatic animals, often at relatively low prices (LG Nico, *pers. obs.*). To what extent these "food markets" target prayer-release customers is unknown. Similar to the situation in Asia, practitioners of prayer release in the USA also take advantage of other live-animal sources. For instance, one Buddhist group in California is known to regularly visit a bait shop, spending thousands of US dollars to purchase the business's entire fish stocks (Lopez 2004); another group buys live seafood dockside direct from incoming commercial fishers (Woudenberg 2017). Similar events take place in other non-Asian countries. For instance, in England prayer-release practitioners purchased hundreds of live, non-native lobsters and crabs from a wholesale supplier then illegally released them into coastal waters (Sawer 2017). In New Zealand, religious adherents released "eels" and other fish, purportedly purchased from live-food markets and restaurants (Tan 2019).

Prayer-release activities take place almost any time of the year (Edmunds 2011). For example, in China's Guangdon Province, organized prayer release occurs almost daily (Zhuang 2019). The freeing of large numbers of animals typically happen during Buddhist festivals and holiday periods (e.g., Vesak Day), but also during important family events, such as weddings, birthdays, illnesses, and funerals (Severinghaus and Chi 1999; Holler 2002; Yeo and Chia 2010; Liu et al. 2013; Shuyin 2015; Yang 2015). Large groups may participate, but individuals acting alone may spontaneously free animals at any time (Severinghaus and Chi 1999). Releases of aquatic animals occur in a range of aquatic and wetland environments. Some temples have ponds designated for the purpose (Shiu and Stokes 2008; Fernquest and Techawongtham 2017). Rivers near temples are also convenient release sites (Basha and Dunlea 2017). Because prayer release is common in urban areas (Yang 2015), waterbodies near cities are regularly used (Li 2018).

Use as bait

In their native range, swamp eels are sometimes used as bait (Baldwin et al. 1996; López et al. 2002; Perdices et al. 2005; LG Nico, *pers. obs.*). We are

unaware of any North American bait shops that sell swamp eels for that purpose. However, a customer we encountered in a Florida food market was observed purchasing about a dozen *A. cuchia*, admitting that he regularly used live eels as bait during Cobia (*Rachycentron canadum* (Linnaeus, 1766)) fishing tournaments held in marine waters of the Gulf of Mexico. We do not believe bait release of swamp eels occurred at documented inland, freshwater, introduction sites. The typical, adult swamp eels sold in US food markets would be much too large a bait for most freshwater game fishes and a costly alternative (17 to 28 US$ per kg).

Aquarium pet trade

There is no evidence that *A. cuchia* is in the US aquarium trade. Sterba (1983) includes an account of the species in his Aquarium Encyclopedia, but makes no mention of it being in the trade. The species is listed—without details—as part of the ornamental fish trade of India and even apparently exported on occasion (Jayalal and Ramachandran 2012). Members of the *M. albus/javanensis* complex and "*Synbranchus marmoratus*" intermittently appear in the pet trade, sometimes within the USA (Fenner 1998; Howells and Rao 2003; Moreau and Coomes 2007; Jayalal and Ramachandran 2012). The origin of certain wild *M. albus/javanensis* populations in Florida are conceivably related to the aquarium industry, a suspicion based on existence of ornamental fish farms in the state as well as on observations that two of the three wild populations in Florida include highly colorful phenotypes. RB Socolof (ornamental-fish farmer, *pers. comm*. 2003) operated in the Tampa area and briefly handled imported *Monopterus* during the early 1970s, a stock that included color varieties the aquarium trade at the time called "psychedelic eels", but no market developed. The first wild *M. albus/javanensis* specimens collected in Florida were taken by one of us (LGN) in 1997 near Socolof's then abandoned farm. In Texas, swamp eels have long been illegal and on two occasions in 2003, state authorities seized *M. albus/javanensis* specimens from a Houston pet store (Howells and Rao 2003). One was a large (750 mm TL) albino (vouchered as UF 242532). The confiscated normal-colored specimens had come from a Florida dealer and were labeled as "yellow eels". Occasionally Internet pet-fish sources advertise *Synbranchus* and *Monopterus* for sale (e.g., http://www.modernpetcentre.in/golden-eel.html). Colleagues have provided documentation of *M. albus/javanensis* in a pet store in Oregon in 2001 (G Kovalchuk, The Dalles-Oregon, *pers. comm*. 2001) and of a species of undetermined identity from a Toronto aquarium shop in 2007 (B Cudmore, Fisheries and Oceans Canada, *pers. comm*. 2011).

Predicting invasion and potential negative consequences

Many of the traits displayed by certain members of the *M. albus/javanensis* complex, a taxa already proven to be invasive in Japan (Matsumoto et al.

1998) and Florida (LG Nico, *pers. obs.*), are also shared by *A. cuchia*. Both taxa are highly secretive, burrowing, predatory fishes that attain a size of about 90 cm TL or more (Das 1946; Narejo et al. 2002). In its native range, *A. cuchia* is found in both fresh and brackish environments (Hughes and Munshi 1979; Talwar and Jhingran 1992), although its upper salinity tolerance has never been experimentally determined. The species occurs over elevations ranging from near sea level to approximately 1,500-m (Shrestha 2008). *Amphipnous cuchia* is an obligate air-breather that is semi-terrestrial and able to survive extreme drought periods residing in mud burrows (Das 1946; Hughes and Munshi 1979; Banerji et al. 1981). Like *M. albus/javanensis*, *A. cuchia* is reputed to survive many months without food (McClelland 1845; Miah et al. 2015) and exhibits parental care of eggs and young (Das 1946; Munshi and Hughes 1992). However, sex reversal has thus far not been documented in *A. cuchia* (Liem 1968).

In Asia, *A. cuchia* is naturally found in tropical and subtropical regions (Silas and Dawson 1961; Figure 2). Its native range does extend north into lowlands areas of Nepal where it reportedly survives cold periods by burrowing in the mud (Shrestha 2008). One or more members of the *M. albus/javanensis* complex are known to survive in temperate climatic zones where winter air temperatures fall to or below freezing, as evidenced by their natural occurrence in China north to about 45.2°N latitude (Fan 1990) and the persistence of introduced populations in Japan north to about 34.8°N latitude (Matsumoto et al. 1998) and in New Jersey (USA) in a lake situated at 39.8°N latitude (LG Nico, *pers. obs.*). As reported for *A. cuchia*, *M. albus/javanensis* burrows underground to survive drought or cold periods (Matsumoto 1997). A coarse-scale climate-matching analysis suggests *A. cuchia* has the potential to establish in the southern USA, a more restricted range than that of *M. albus/javanensis* (Figure 12).

The introduction of swamp eels into the waters of North America poses several potential risks. Swamp eels are predators that prey on a variety of vertebrates and invertebrates, and their ability to move overland and invade waters where other predatory fish normally do not occur is a concern. Furthermore, swamp eels in North American food markets have been found to carry a variety of parasites (Nico et al. 2011; Cole et al. 2014). Most worrisome is the discovery that a relatively high proportion (28%) of samples of market *A. cuchia* imported from Asia were infected with *Gnathostoma spinigerum* Levinsen, 1889, a nematode known to cause the disease gnathostomiasis in humans (Cole et al. 2014). Although there is no evidence that *A. cuchia* is reproducing in the wild, certain foreign parasites that these introduced swamp eels carry have the potential to enter the receiving ecosystem. Even if swamp eels die shortly after release, fish-eating birds or other animals consuming the eel carcasses might become infected with some of the parasites present.

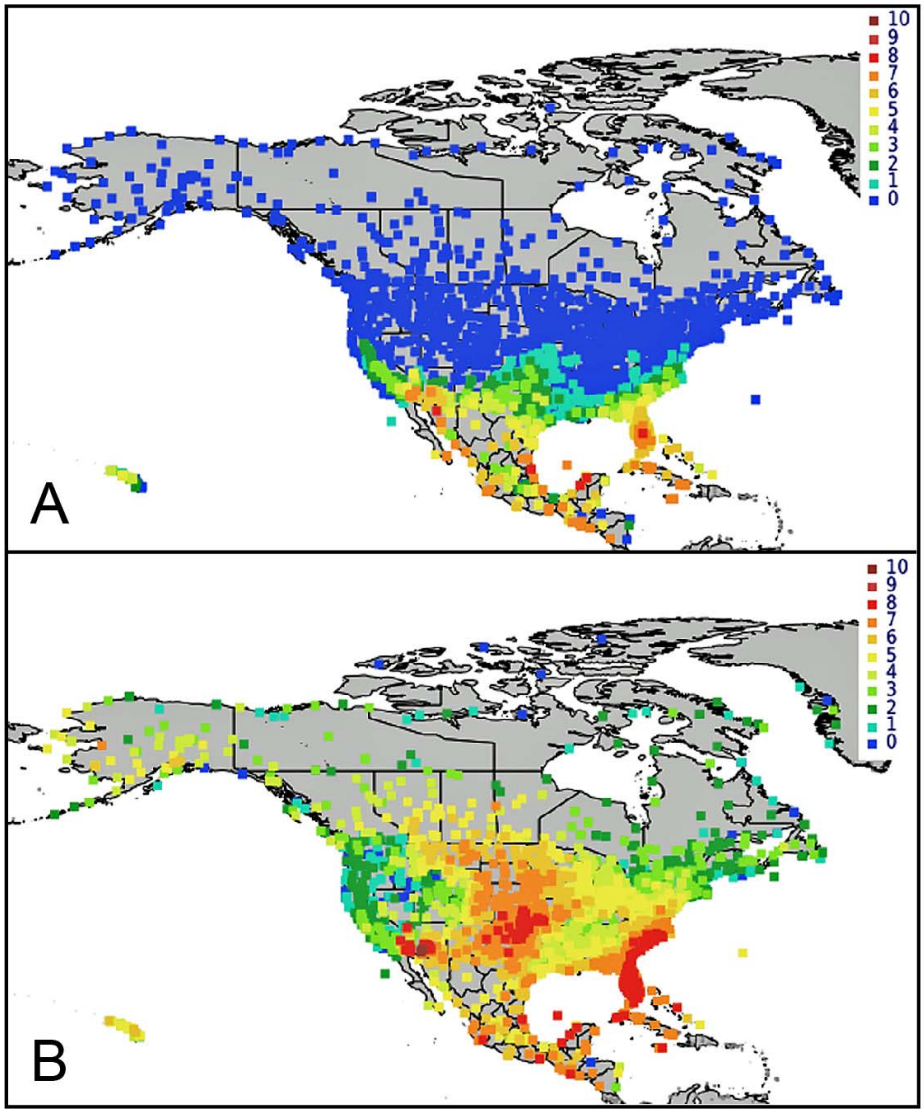

Figure 12. Potential North American ranges of (A) *Amphipnous cuchia* and (B) the *Monopterus albus/javanensis* species complex as predicted by climate-matching software Climatch using the approximated geographic native ranges delineated in Figure 2. High scores (warmer colors) indicate areas climate similar to that of native range (Australian Bureau of Rural Sciences 2010, 16 climate variables; Euclidean Distance). The greater potential for *M. albus/javanensis* to invade temperate regions presumably corresponds to natural occurrence of one or more members of this complex within Korea and northern China.

Current regulations in the United States

Currently, no member of the family Synbranchidae is listed under the injurious wildlife provisions of the Lacey Act, a federal conservation law of the USA (see https://www.fws.gov/injuriouswildlife/pdf_files/current_listed_iw.pdf). Consequently, the USFWS does not prohibit their importation or interstate transport. The other federal agency charged with regulating the entry of fishes into the USA is the Animal and Plant Health Inspection Service (APHIS) within the U.S. Department of Agriculture, but we are unaware of any special attention directed at swamp eels.

US states differ widely in their regulation of swamp eels, ranging from little or no specific restrictions to strict prohibition of certain species or the

entire family. Such differences in regulatory control are also reflected among the five states for which we document open-water records of *A. cuchia*. For instance, swamp eels are not specifically prohibited or restricted in Pennsylvania or Michigan (although these and other states typically ban or regulate the use or release of all or most nonnative aquatic animals). The other three states, New Jersey, New York, and Maryland, specifically prohibit or regulate the "Asian swamp eel *M. albus*" without reference to other members of the swamp eel family. For instance, New Jersey prohibits the possession or release of *M. albus,* and as of 2006 Maryland law includes *M. albus* in their list of non-native species that a person may not import, transport, purchase, possess, propagate, sell, or release into state waters. New York lists *M. albus* as a "regulated" invasive animal, making it illegal for anyone to knowingly introduce the fish into the wild, but—unlike the state's more restrictive "prohibited" category—it is not illegal to possess, sell, buy, propagate, or transport the species. In contrast, Texas and Louisiana, two states where we encountered live *A. cuchia* for sale in food markets, strictly prohibit possession, sale, or transport of any member of the family Synbranchidae without state authorization.

Conclusions

1. We document the first confirmed nonindigenous records of *Amphipnous cuchia*, an Asian member of the swamp eel family Synbranchidae. The species is documented from five open-water sites across five states in the USA.
2. The international live-food trade constitutes the major pathway for *A. cuchia* introductions. In addition, prayer release appears to be an important pathway component, whereby religious practitioners obtain live *A. cuchia* from sellers and subsequently set them free in open waters.
3. Ethnic food markets are considered the main source of live swamp eels in the USA. Our food market surveys document that *A. cuchia* has been the principal swamp eel imported into the USA since at least 2001, replacing swamp eels of the *M. albus/javanensis* species complex.
4. Our analysis of LEMIS data indicate most imports of live swamp eels are from Bangladesh (81.3%), Vietnam (13.3%), and China (3.7%) with the majority (97.9%) reportedly coming from the wild. The database labels most (> 99%) imported swamp eels as "*M. albus*" (or its synonyms); none are identified as *A. cuchia*, although specimens from Bangladesh (and India) are almost certainly this species.
5. An unknown proportion of live *A. cuchia* entering the USA are mistakenly or deceptively identified as *Anguilla bengalensis* on declaration import documents, a possible explanation as to why recent LEMIS records show few or no swamp eels being imported since 2007 even though we still regularly observe these fish live in food markets.

6. As yet, there is no evidence that *A. cuchia* is reproducing in any of the five US sites where introduced, likely because the species is native to tropical/sub-tropical regions of Asia and the introduction sites reported in the current paper are all in latitudes (39.1°N to 43.4°N) with cold winters. However, continued appearance of live *A. cuchia* in US food markets in southern states with more suitable climates, increases the risk of its introduction and establishment in the wild.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Polystyrene boxes (60 x 45 x 30 cm) containing live swamp eels—*M. albus/javanensis* complex—stored in rear area of an ethnic food market in Atlanta, Georgia, 7 August 2003 (Field# LGN03-35b).

This material is available as part of online article from:
http://www.reabic.net/aquaticinvasions/2019/Supplements/AI_2019_Nico_etal_SupplementaryFigure.pdf