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Salinity tolerance of non-native Asian swamp eels (Teleostei: Synbranchidae) in Florida, USA: comparison of three populations and implications for dispersal

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Abstract Three populations of non-native Asian swamp eels are established in peninsular Florida (USA), and comprise two different genetic lineages. To assess potential for these fish to penetrate estuarine habitats or use coastal waters as dispersal routes, we determined their salinity tolerances. Swamp eels from the three Florida populations were tested by gradual (chronic) salinity increases; additionally, individuals from the Miami population were tested by abrupt (acute) salinity increases. Results showed significant tolerance by all populations to mesohaline waters: Mean survival time at 14 ppt was 63 days. The Homestead population, a genetically distinct lineage, exhibited greater tolerance to higher salinity than Tampa and Miami populations. Acute experiments indicated that swamp eels were capable of tolerating abrupt shifts from 0 to 16 ppt, with little mortality over 10 days. The broad salinity tolerance demonstrated by these experiments provides evidence that swamp eels are physiologically capable of infiltrating estuarine environments and using coastal waters to invade new freshwater systems.

Keywords Ecophysiology · *Monopterus* · Nonindigenous species · Osmoregulation · Synbranchidae

Introduction

Swamp eels (family Synbranchidae) are teleost fishes widely distributed in tropical and subtropical regions of the Old and New Worlds (Rosen and Greenwood 1976; Berra 2001). Members of the family occupy a wide variety of shallow-water habitats, including inland and some coastal environments (Rosen and Greenwood 1976; Pusey et al. 2004). Rosen and Greenwood (1976) revised the family and recognized four genera: *Monopterus*, *Ophisternon*, *Synbranchus* and *Macrotrema*. However, because of minimal morphological differentiation, the taxonomy and phylogenetic relationships remain unclear (Bailey and Gans 1998; Collins et al. 2002; Favorito et al. 2005; Perdices et al. 2005). At least 18 synbranchid species are currently recognized (Favorito et al. 2005), and that number will undoubtedly increase as additional species are described and species complexes elucidated. Difficulty associated with identification of some species and uncertainty concerning the actual number and relationships of different swamp eel genera have implications for adequately assessing non-native populations. In particular, recorded observations on swamp eels in their native range may not

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necessarily apply to introduced populations because different, possibly unrecognized cryptic taxa with differing ecologies and life-history attributes may be involved.

Synbranchids are not native to the USA. During the 1990s, three separate, established populations were discovered in inland waters of peninsular Florida (Collins et al. 2002). Upon initial discoveries, it was thought that all introduced populations constituted a single species, the Asian swamp eel, *Monopterus albus*. This species (likely a species complex) has a broad geographic distribution in eastern and southeastern Asia (Collins et al. 2002; T. Roberts, personal communication). In an attempt to positively identify and determine possible sources of non-native swamp eels found in the USA, Collins et al. (2002) analyzed mitochondrial DNA sequences of multiple synbranchid taxa, including samples representing a broad range of introduced and native populations. They concluded that populations in Florida represented two different species or distinct taxa, each corresponding genetically with populations in different parts of Asia. The Homestead fish, from canals near Everglades National Park, were genetically distinct from populations present in systems in North Miami and the Tampa area. Collins et al. (2002) hypothesized that, regardless of taxonomic status, the genetically distinct lineages would be expected to vary in ecological or life-history traits, have different potential geographic ranges and potentially pose different threats to invaded ecosystems.

Survival and dispersal of introduced swamp eels is enhanced by an array of diverse adaptations. Swamps eels are largely fossorial and tend to be opportunistic predators. Many are able to breathe atmospheric air and, if the skin is kept moist, can persist multiple days out of water (Liem 1987; Nico, personal observation). A few species conduct brief terrestrial excursions, and there is considerable evidence that they survive extended dry periods by burrowing deep in mud (Liem 1987; Tay et al. 2003; Pusey et al. 2004; Favorito et al. 2005). Sex reversal has also been documented for some species (Liem 1963). In addition to life-history traits that most likely increase invasion success, swamp eels have an advantage because the climatic and habitat conditions in Florida and other parts of the southeastern USA are quite similar to conditions in their native range. Field surveys conducted over the past several years in Florida have shown that each of the three populations in the state is substantial, and that ranges are probably expanding (Nico, unpublished data). However, it is still uncertain how much of the Everglades ecosystem, Florida, and the southeastern USA will ultimately be colonized.

Salinity is an environmental factor determining expansion and ultimate geographic range of swamp eels. Ichthyologists classify the family Synbranchidae as secondarily freshwater, defined as freshwater species that tolerate varying degrees of salinity (Myers 1949; Miller 1966). However, the scientific literature contains few details on the salinity tolerance of swamp eels except for information that briefly describes distribution and general habitats. Considering the range of habitats where swamp eels have been collected, there is wide variation in salinity tolerance among different members of the family (Rosen and Greenwood 1976; Allen 1991; Lundberg 1993; Tyler and Feller 1996), but we are unaware of any published studies that used experiments to quantify tolerance limits.

The highest recorded salinity reported for the family involved *Ophisternon aenigmaticum*, a Neotropical species (or species complex) otherwise known only from fresh water (Tyler and Feller 1996). Although based on the collection of a single specimen, the record is noteworthy because the swamp eel was taken in hypersaline (39 ppt) waters within island mangrove habitat some 15 km off the coast of Belize. *Monopterus* is an Old World (Asia and Africa) genus currently represented by eight species (Nelson 2006). Certain species with extremely restricted distributions (e.g., cave forms) are known only from fresh water. More widespread taxa (e.g., *Monopterus cuchia*) typically inhabit fresh water although they are also occasionally found in brackish waters (Bhuiyan 1964; Talwar and Jhingran 1991).

Most published reports on “*Monopterus albus*” list it as occurring only in freshwater habitats (e.g., ditches, rice fields, marshes, swamps, ponds, lakes, streams, canals) (Smith 1945; Cheng and Zhou 1997; Serov et al. 2003), but there are exceptions. Talwar and Jhingran (1991) noted that *M. albus* inhabits “streamlets, canals and estuaries” in India. Likewise, in their publication on Singapore fishes Lim and Ng (1990) stated that *M. albus* is “able to tolerate polluted and even brackish water conditions.” However, past reports on the salinity tolerance of select native populations of

"*Monopterus albus*" should not be extrapolated to non-native populations because of the possibility that the taxon is a species complex composed of individual species with different physiologies.

Here we report the results of laboratory tests designed to determine the upper salinity tolerance of non-native swamp eels established in Florida. Our objectives were to assess the potential for introduced populations to penetrate Florida's estuarine habitats or use coastal waters (potentially as dispersal routes) and to determine if there were differences in salinity tolerance between the two genetic lineages. To our knowledge, this study is the first attempt to experimentally ascertain salinity tolerance of members of the family Synbranchidae.

Materials and methods

Two sets of experiments were conducted on non-native swamp eels collected in Florida: (1) chronic toxicity tests to compare salinity tolerances of the three Florida populations (Miami, Tampa, and Homestead), and (2) acute toxicity tests of the Miami population.

Chronic salinity tolerance

Swamp eels were collected from each of the three Florida populations (Homestead, Miami, Tampa) in late September/early October 2002 with a boat electrofisher. All collection sites are fresh water with salinities typically <0.4 ppt year-round. Individuals were transported to the laboratory (U.S. Geological Survey, Gainesville, FL) where they were weighed (±0.1 g) and placed in experimental aquaria with dechlorinated tap water (0.2 ppt). Swamp eels from the Homestead and Miami populations were held 13 days in experimental aquaria before the experiment began; individuals from the Tampa population were held 5 days.

Experimental aquaria consisted of Rubbermaid© clear plastic bins that held one swamp eel each. We used two sizes of bins; small bins (30l × 19 w × 9.5 h cm) for small swamp eels (generally <10 g), and large bins (34 l × 25 w × 15 h cm) for large specimens. Bins had locking lids (to avert escape) and small holes above the water line for air flow. Water depth was 3–4 cm. Synthetic aquarium sea salts (Forty Fathoms©, Aquatic Ecosystems, Inc.) were added to deionized water for salinity treatments. Dechlorinated tap water was used as a control (0.2 ppt). All salinity measurements were within 0.1 ppt as measured with a YSI model 556 MPS meter.

Tolerance to chronic changes in salinity was evaluated by initially holding the swamp eels in fresh water (0.2 ppt) and then exposing individuals to progressively increasing salinity (a change of 2.0 ppt every 2–3 days) until each treatment had reached its target salinity (12, 14, 16, 18 and 0.2 ppt [control]). We tested 169 adult and juvenile swamp eels, ranging in mass from 0.3 to 692.5 g (mean=113.5 g±9.6 SE). Based on weight–length relationships provided by Schofield and Nico (2007), mass measurements correspond to swamp eels ranging from 75 to 859 mm total length (TL), with a mean of 486 mm TL. Roughly equivalent numbers of individuals from the three Florida populations were used in each treatment (total: Homestead $n=52$, Miami $n=63$, Tampa $n=54$). Total sample sizes for treatments were: 0.2 ppt ($n=31$), 12 ppt ($n=34$), 14 ppt ($n=34$), 16 ppt ($n=36$) and 18 ppt ($n=34$).

Swamp eels in the various salinity treatments did not differ in mass (ANOVA, $df=4$, $P=0.853$), and variances were homogeneous (Levene's test, $df=4$, 164, $P=0.585$). Swamp eels reached their target salinities in a staggered (time-wise) fashion; however, each time we changed the salinity in one or more of the treatments, the water was changed for all fish (including controls) to maintain similarity of handling across treatments. We checked the eels once per day, 4 to 5 days per week. Water temperature was measured in ten randomly selected aquaria each time the swamp eels were checked and ranged from 18.5°C to 27.0°C (mean=22.4±0.6 SE; $n=880$). Variation among individual aquaria (within days) never exceeded a range of 1.7°C and was usually less than 0.5°C. Swamp eels were fed live, commercially-raised worms (earthworms, *Lumbricus terrestris* and blackworms, *Lumbriculus variegatus*) once per week. Swamp eels were maintained for at least 80 days at their target salinities (0.2 ppt=102 days; 12 ppt=88 days; 14 ppt=86 days; 16 ppt=84 days; 18 ppt=81 days).

Acute salinity tolerance

Individuals used in the acute salinity-tolerance experiment were collected from Snake Creek Canal in north Miami (salinity 0.3 ppt) with a boat electrofisher. They were transported to the laboratory where they were held in water from the collection site for 3 days, then weighed (±0.1 g) and placed in experimental aquaria with dechlorinated tap water (0.2 ppt). Experimental aquaria were the same as used in the chronic study.

Plunge-type acute-tolerance tests were performed by transferring swamp eels from their holding conditions (0.2 ppt) to one of six treatments (14, 16, 18, 20, 22 and 0.2 ppt [control]; $n=11$ for each treatment). Swamp eels in the various salinity treatments did not differ in mass (ANOVA, $df=5$, $P=0.999$), and variances were homogeneous (Levene's test, $df=5$, 60, $P=0.983$). They ranged in mass from 3.4 to 412.7 g (mean=68.13±12.85 SE; $n=66$), corresponding to a TL range of 161 to 730 mm and mean of 413 mm TL. Salinity was maintained at constant levels throughout the 10-day experiment. Swamp eels were checked at 2, 4, 6, 8 and 12 h elapsed time post-acute transfer on the first day, and then once each morning (between 08:00 and 10:00 h) for the next 10 days. Water temperature was measured in at least ten aquaria each day and ranged from 17.3°C to 22.6°C (mean=20.3±0.14 SE; $n=102$). Variation among individual aquaria (within days) never exceeded a range of 1.5°C. Swamp eels were not fed during the acute salinity-tolerance experiment.

Data analysis

Survival was estimated with a Kaplan–Meier product limit estimator (Kaplan and Meier 1958) and the log-rank test was used to compare survivorship curves (Savage 1956; Cox and Oakes 1984). Kaplan–Meier product limit estimators were computed slightly differently for acute and chronic salinity-tolerance experiments. For the acute salinity-tolerance experiment, the time at which swamp eels were transferred from their holding salinity (0.2 ppt) to their experimental salinities was designated as time=0. End time was scored as either (a) the time at which we discovered a test subject had expired, or (b) 240 h if the swamp eel was still alive at the conclusion of the experiment. For the chronic salinity-tolerance experiment, swamp eels reached their target salinities at different times (i.e., swamp eels in lower-salinity treatments reached their target salinities before higher-salinity treatments). Thus, the day the swamp eels were transferred to their target salinity was designated as time=0. Swamp eels were then maintained in their experimental salinities for at least 80 days after they had reached the target salinities. To determine whether size was related to survival time, we compared swamp eel mass to survival time (i.e., latency to death) with linear regression within salinity treatments.

Results

Chronic salinity tolerance

For all populations combined, survival was 93% at the control salinity (0.2 ppt), 53% at 12 ppt, 26% at 14 ppt, 31% at 16 ppt and 9% at 18 ppt. Swamp eels from Tampa and Miami began to die earlier in the experiment than those from Homestead (Fig. 1). Survival of swamp eels from Homestead in treatments from 12 to 18 ppt were not statistically different (Table 1). However, swamp eels from Tampa and Miami showed more variation among treatments, with deaths occurring more quickly in the more saline treatments (Table 1, Fig. 1).

There were no differences within populations (Homestead, Miami, and Tampa) for the control, 12 and 14 ppt treatments. Mean estimated survival time at 14 ppt was 63 days (95% Confidence Interval [CI]=55–70 days; all three populations combined). Swamp eels from Homestead were able to tolerate the higher salinity levels (16 and 18 ppt) for longer periods of time than swamp eels from Miami and Tampa (Table 2). For example, in the 18 ppt treatment, swamp eels from Miami and Tampa began to die within the first few days after reaching their target salinity (days 4 and 6, respectively). The last swamp eel from Miami at 18 ppt died on day 33. Similarly, the second-to-last swamp eel from Tampa at 18 ppt died on day 36, while the last remaining swamp eel in that treatment remained alive until the end of the experiment. This pattern was markedly different from the swamp eels from Homestead. Individuals from that population did not exhibit their first mortality at 18 ppt until day 44. Mean estimated survival time (for 50% mortality) for the Miami swamp eels at 16 ppt was 48 days (95% CI=35–61 days), significantly lower than Homestead (mean=72 days; 95% CI=64–80)

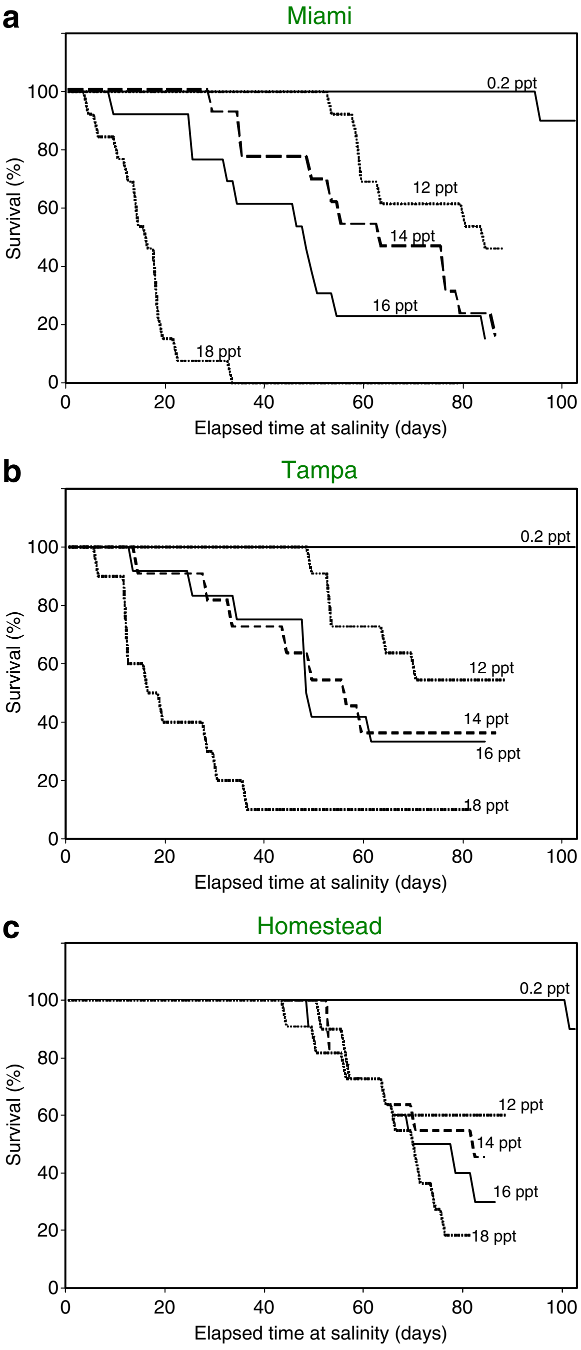

Fig. 1 Survival of swamp eels in the chronic salinity-tolerance experiments: **a** Miami (n=63), **b** Tampa (n=54) and **c** Homestead (n=52). Test results compare survival of swamp eels subjected to five different salinity concentrations: 0.2 (control), 12, 14, 16, and 18 ppt

Table 1 Within-population comparisons of survival curves of swamp eels from three Florida populations (Homestead, Miami and Tampa) to chronic changes in salinity

	0.2 ppt	12 ppt	14 ppt	16 ppt
Homestead				
12 ppt	*0.0291*			
14 ppt	*0.0011*	0.2194		
16 ppt	*0.0068*	0.6460	0.4089	
18 ppt	*0.0002*	0.1336	0.4278	0.1705
Miami				
12 ppt	*0.0048*			
14 ppt	*<0.0001*	0.0633		
16 ppt	*0.0002*	*0.0182*	0.3138	
18 ppt	*<0.0001*	*<0.0001*	*<0.0001*	*0.0081*
Tampa				
12 ppt	*0.0173*			
14 ppt	*0.0025*	0.2072		
16 ppt	*0.0017*	0.1159	0.9065	
18 ppt	*<0.0001*	*0.0004*	*0.0109*	*0.0081*

Probability values ($P<0.05$ in italics) for log-rank tests used for comparison among survivorship curves generated by the Kaplan–Meier estimator for five groups of swamp eels: four exposed to various salinities (12–18 ppt) and a group that was retained in well-water that served as control

and Tampa (mean=55 days; 95% CI=42–69). At 18 ppt, estimated survival times for the Homestead population (mean=67 days; 95% CI=60–74) was significantly greater than Miami (mean=16; 95% CI=12–20) and Tampa (mean=25; 95% CI=12–38).

Table 2 Within-salinity treatment comparisons of survival curves of swamp eels from three Florida populations (Homestead, Miami and Tampa) to chronic changes in salinity

	Homestead	Miami
Control (0.2 ppt)		
Miami	0.9731	
Tampa	0.3173	0.3404
12 ppt		
Miami	0.8006	
Tampa	0.8350	0.8443
14 ppt		
Miami	0.4089	
Tampa	0.7121	0.7199
16 ppt		
Miami	*0.0337*	
Tampa	0.1957	0.4821
18 ppt		
Miami	*<0.0001*	
Tampa	*0.0070*	0.1697

Probability values ($P<0.05$ in italics) for log-rank tests used for comparison among survivorship curves generated by the Kaplan–Meier estimator for five groups of swamp eels: four exposed to various salinities (12–18 ppt) and a group that was retained in well-water that served as control

Table 3 Output from linear regression analysis comparing swamp eel mass to survival times (i.e., latency to death)

	12 ppt	14 ppt	16 ppt	18 ppt	20 ppt	22 ppt
Chronic						
Homestead	0.383	0.022 (R^2=0.684)	0.016 (R^2=0.803)	0.851		
Miami	<0.001 (R^2=0.951)	0.002 (R^2=0.675)	0.871	0.022 (R^2=0.393)		
Tampa	0.204	0.286	0.321	0.161		
Acute						
Miami				0.029 (R^2=0.467)	0.003 (R^2=0.697)	<0.001 (R^2=0.789)

P values (and R^2 values, when $P<0.05$) are given for each population tested in the chronic salinity challenge and for the Miami population that was tested in the acute salinity tolerance experiment

Linear regression analysis showed that mass was related to survival time (i.e., small swamp eels were more likely to die sooner than larger ones) for the Homestead and Miami populations in several treatments (Table 3). However, there was no size effect on survival time for Tampa swamp eels (Table 3).

Acute salinity tolerance

Survival varied significantly among salinity treatments in the acute salinity-tolerance challenge (log-rank test, *df*=5, $P<0.001$; Fig. 2). Swamp eels in salinities of 0.2, 14 and 16 ppt exhibited high survival (80–100%), and those treatment results were not significantly different from each other (Table 4). Survival was low (9%) for swamp eels in the 18 ppt treatment. All swamp eels were dead by 24 h at 22 ppt and by 48 h at 20 ppt. Mean survival estimates (for 50% mortality) decreased as salinity increased; for swamp eels at 18 ppt, the mean survival estimate was 105 h (95% CI=75–135 h), 24 h at 20 ppt (95% CI=16–32 h) and only 13 h at 22 ppt (95% CI=9–16 h). Swamp eel size was significantly related to survival time; small swamp eels died sooner than large individuals (Table 3).

Discussion

The Homestead swamp eel population differed in salinity tolerance from Tampa and Miami populations, and this finding correlates with the molecular research of Collins et al. (2002) who concluded that the Homestead population is genetically distinct, possibly representing a different, but cryptic species. Overall, levels of tolerance to salinity exhibited by non-native swamp eels inhabiting Florida inland waters were greater than many freshwater species native to the

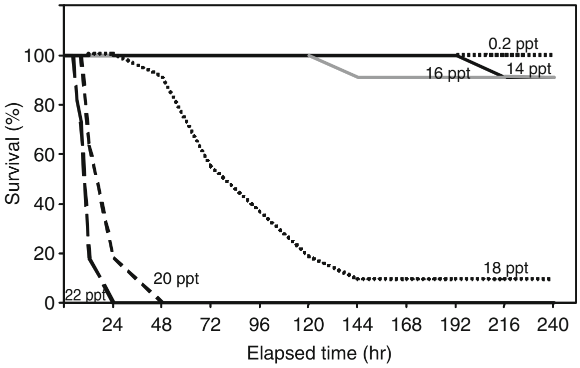

Fig. 2 Survival of swamp eels from the Miami population in the acute salinity-tolerance experiment. Test results compare survival response of swamp eels (*n*=66) subjected to six different salinity concentration treatments: 0.2 (control), 14, 16, 18, 20, and 22 ppt; *n*=11 for each treatment

Table 4 Comparison of survival curves of swamp eels from Miami to acute changes in salinity

ppt	0.2 ppt	14 pt	16 ppt	18 ppt	20 ppt
14	0.3173				
16	0.3173	0.9731			
18	*<0.0001*	*<0.0001*	*<0.0001*		
20	*<0.0001*	*<0.0001*	*<0.0001*	*<0.0001*	
22	*<0.0001*	*<0.0001*	*<0.0001*	*<0.0001*	*<0.0001*

Probability values ($P<0.05$ in italics) for log-rank tests used for comparison among survivorship curves generated by the Kaplan–Meier estimator for six groups of swamp eels: five exposed to various salinities (14–22 ppt) and a group that was retained in well-water that served as control. Endpoint of experimental exposure was 10 days.

southeastern USA. For example, largemouth bass (*Micropterus salmoides*) is only able to survive in waters up to 8 ppt for extended periods (Meador and Kelso 1990), above 8 ppt, it encounters osmoregulatory dysfunction (Susanto and Peterson 1996).

Many native and introduced fresh-water fish species occasionally use estuarine or brackish areas for feeding or dispersal (Schwartz 1964; Moyle and Cech 1988; Peterson 1988; Peterson and Meador 1994; Brown et al. 2001). However, use of brackish waters even for short periods provides an opportunity for fish species to disperse between and among drainages via coastal routes (e.g., Myers 1949; Bailey et al. 1954; Cross 1970; Rosen 1974; Swift et al. 1977; Loftus 1988; Brown et al. 2001). In addition, some predators normally found in fresh water (e.g., largemouth bass *Micropterus salmoides*, longnose gar *Lepisosteus osseus*) occasionally enter brackish or saline waters to forage (Carver 1966; Hackney and de la Cruz 1981; Rozas and Hackney 1984; McIvor and Odum 1988; Meador and Kelso 1990; Rehage and Loftus 2007). Other non-native fishes introduced to peninsular Florida are known to inhabit both fresh and, at least on occasion, estuarine waters. Among these are many cichlids (*Cichlasoma urophthalmus*, *C. bimaculatum*, *Sarotherodon melanotheron*, *Oreochromis aureus*, *Tilapia mariae*), a clariid catfish (*Clarias batrachus*) and a poeciliid (*Belonesox belizanus*) (Loftus and Kushlan 1987; Faunce and Paperno 1999; Faunce and Lorenz 2000; Trexler et al. 2000; Faunce et al. 2001; Serafy et al. 2003; Lorenz and Serafy 2006).

Swamp eels in peninsular Florida have mainly been collected from freshwater habitats, including canal and drainage ditch systems, small streams, ponds and lakes (Nico, unpublished data). However, all aquatic systems occupied by Florida swamp eels have connections to coastal environments, including some of Florida's more ecologically sensitive estuarine environments. For example, Homestead swamp eels occupy the C-111 canal network that drains portions of Everglades National Park, including coastal mangrove wetlands that ultimately flow into Florida Bay. Recently, three swamp eel specimens presumably dispersing from the Homestead population were collected in those mangrove habitats at salinities from 2 to 16 ppt (Robinson, Lorenz and Loftus, personal communication). Swamp eels may be able to access and persist several months or more in these low-salinity habitats, especially during the wet season, when salinity levels are generally less than 15 ppt (Hittle et al. 2001).

From a natural-resource management perspective, introduced swamp eels remain a perplexing problem. In a previous paper, we concluded that eradication of non-native populations in Florida is unlikely, and that control will be difficult (Schofield and Nico 2007). Considering the findings reported in this paper, broad salinity tolerance can be added to the long list of advantageous life-history traits (e.g., air breathing, sex reversal, pollution tolerance) associated with the nominal species "*Monopterus albus*". In combination, the diverse suite of characters pre-adapts swamp eels for survival and dispersal in peninsular Florida and perhaps other regions of North America. That situation may worsen in the future with global climate change. Increased salinity associated with sea-level rise is a recognised environmental problem amongst lowland coastal areas world-wide, and parts of Florida are at high risk to saltwater intrusion (Hoffmeister 1974; Davis et al. 2005).

Under any scenario involving increased salinity of inland waters, introduced swamp eels may have a competitive advantage over native freshwater fishes found in the southeastern USA. Still, most teleosts are able to reproduce only under narrowly-restricted salinity ranges (Nordlie et al. 1992). Because we are uncertain whether swamp eels in Florida are capable of spawning successfully in brackish waters, more research is needed to test this. Regardless, short-term tolerance of saline waters indicates these fish have the capability to use coastal and other brackish-water habitats as dispersal routes, potentially using estuarine environments as "saline bridges" to reach contiguous freshwater systems (sensu Brown et al. 2001, 2007).

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