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Occurrence and persistence of non-native *Cichlasoma urophthalmus* (family Cichlidae) in estuarine habitats of south-west Florida (USA): environmental controls and movement patterns

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Abstract. The geographic scope of species introductions has increased dramatically in the last 200 years. One of the greatest challenges to understanding the ecological consequences of non-native species is that it has been difficult to identify the attributes that allow them to become established outside their native range. This challenge is compounded by anthropogenic habitat alteration that often enhances the establishment and expansion of non-native species. Fishes in the family Cichlidae are notoriously adaptive, and contribute more non-native species to North America than any other fish family. This is especially true in Florida (USA), where 18 cichlid species have become established. The Mayan cichlid (*Cichlasoma urophthalmus*) was first documented in south Florida in 1983, and is present in many freshwater and estuarine habitats. This study reports a northward range expansion by *C. urophthalmus*, demonstrates the connectivity between altered freshwater habitats and tidal estuarine habitats, and suggests that the estuarine populations are ephemeral and dependent upon colonisation from populations in altered freshwater habitats.

Additional keywords: estuary, Gulf of Mexico, invasive fish.

Introduction

The geographic scope of introductions for some species groups has increased dramatically in the last 200 years (Ruiz *et al*. 2000), with consequences ranging from benign to catastrophic (reviewed in Mack *et al*. 2000). One of the greatest challenges to understanding the ecological consequences of non-native species is that it has been difficult to identify the attributes that allow them to become established outside their native range (Mack *et al*. 2000). Moreover, data on the ecological impacts of establishment by non-native species are lacking, frequently because there are insufficient data on the ecosystems in question to make a quantitative comparison (Courtenay and Williams 1992).

Documenting and predicting the establishment and rate of spread of a non-native species can be challenging. Many non-native species that become established and flourish in new regions do so after a lag. For example, the invasive terrestrial plant *Schinus terebinthifolius* was present in Florida (USA) for nearly 60 years before it became conspicuous, and has now increased dramatically in abundance and geographic coverage causing extreme ecological impacts (Schmitz *et al*. 1997). In addition, evolutionary adaptations may allow non-native species to survive in environmental conditions well outside those found in their native range (Mack *et al*. 2000), making range expansion less predictable.

Compounding these challenges is that habitat alteration often enhances the establishment and expansion of non-native species (Courtenay and Williams 1992). Habitat alterations may act as disturbance events, giving non-native species an advantage over native species, or an alteration may provide a new habitat in which the non-native species has an advantage over native species (Mack *et al*. 2000). Therefore, we can expect that, as human population increases and urban development spreads, the ecological and economic impacts of non-native species will also increase. Thus far, the rate of invasions by non-native species has increased concurrent with development, heightening the threat to native species and native fishery resources.

Within the United States, Florida ranks second only to California for the number of non-native fishes reported in its waters (Fuller *et al*. 1999). The high number of non-native fishes is probably a combination of the mild climate, high occurrence of altered habitats, and the large number of aquaculture operations (Fuller *et al*. 1999). Fishes in the family Cichlidae contribute more non-native species to North America than any other fish family: a result, in part, of their adaptability (Kornfield and Smith 2000). This is especially true in Florida, where 13 of 18 fishes classified as having reproductively active populations in the 1990s were cichlids (Shafland 1996). This number has grown, with 72 non-native fishes now recorded in Florida, 32 of which are documented as reproductively active, and 18 of these are cichlids (P. Shafland, unpubl. data: http://www.floridafisheries.com/fishes/exotic%20List.html). Non-native cichlids are also becoming established regionally, and species now occur across the Gulf of Mexico (Loftus 1987; Faunce *et al*. 2002; O'Connell

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et al. 2002; Bergmann and Motta 2005). The present paper reports on the recent range expansion in Florida of the non-native Mayan cichlid, *Cichlasoma urophthalmus*, its persistence and movement patterns in tidal estuarine mangrove creeks, and estimates of size structure.

Materials and methods

Study area

Charlotte Harbor is a sub-tropical coastal plain estuary on the south-west coast of Florida (USA) (Fig. 1), and is one of the largest estuaries in the state. Three rivers and numerous small creeks transport large amounts of freshwater into the estuary, primarily during the wet season (June–September), when, on average, 62% of annual rainfall occurs. By the end of dry season salinity in the upper reaches of estuarine mangrove creeks is $30\,g\,kg^{-1}$ or higher, and drops to $<5\,g\,kg^{-1}$ throughout the creeks during the wet season. The estuary is connected to the Gulf of Mexico through numerous natural passes. The climate is subtropical, mean water temperature ranges from 12°C to 36°C, and freezes are infrequent (Poulakis *et al*. 2003). Approximately 80% of Charlotte Harbor's mangrove fringe shoreline (red mangrove, *Rhizophora mangle*; black mangrove, *Avicennia germinans*) remains under protection from development (R. Repenning, Punta Gorda, FL, Florida State Department of Environmental Protection, pers. comm.; Hammett 1990).

Despite shoreline protections, Charlotte Harbor's drainage has been drastically altered for development, similar to much of Florida's southern coastline. The historical hydrologic conditions were characteristic of coastal uplands surrounding south-west Florida estuarine systems: gentle, low, flat slopes provided for slow overland sheet flow of surface waters, which were retained for extended periods in open palustrine wetland depressions within wet and mesic slash pine flatwoods during the wet season, but were dry during the dry season. These isolated wetlands were connected during periods of high water by wet prairies, hydric hammocks, and sloughs that conveyed surficial flows to oligohaline and mesohaline marshes at the upper reaches of the tidal estuarine system. In areas with upstream drainage basins, these surficial flows were concentrated into tidal creek systems that provided an important salinity and water chemistry gradient to the estuary. These conditions were significantly altered in the early 1950s by agriculture and mosquito ditches, and even more so by recent increases in residential development and water management control structures.

Focal species

Cichlasoma urophthalmus is native to the Atlantic continental slope of Central America (Miller 1966). The species is euryhaline ($0–37\,g\,kg^{-1}$), omnivorous (fishes, invertebrates, algae, detritus), tolerant of temperatures of 15–37°C, and capable of spawning in low and high salinities (Loftus 1987; Faunce *et al*. 2002; Bergmann and Motta 2005). Like many cichlids, *C. urophthalmus* shows considerable plasticity in ecological, biological, and physiological characteristics, allowing non-native populations to depart from characteristics considered standard in the native range (e.g. Loftus 1987; Martínez-Palacios *et al*. 1990; Martínez-Palacios and Ross 1992; Faunce *et al*. 2002; Bergmann and Motta 2005), thus increasing their invasive potential. In Florida, *C. urophthalmus* was first documented in 1983, in Everglades National Park (Loftus 1987) (Fig. 1), and is now considered established in freshwater and some estuarine habitats of South Florida (Shafland 1996).

Field methods

Seine sampling

As part of a multi-year project to study fish assemblages of estuarine mangrove creeks, four mangrove-fringed estuarine creeks, each ~2 km long, on the eastern shoreline of Charlotte Harbor (Fig. 1), were sampled with a 21×1.2 m centre bag seine ($1.2 \times 1.2 \times 1.2$ m bag dimensions) with 3.2 mm mesh. From February 2003 through October 2004, creeks were sampled every other month. Sampling was less frequent from October 2004 through December 2005 (October 2004; April, July, October, and December 2005). Each creek was divided into three equal-length strata (upper, middle, lower: ~0.7 km each; Fig. 2*a*, *b*), with five samples per stratum per sample period. Sample locations within each creek stratum were selected haphazardly in each sample month. For each sample, the net was set in a semi-circle against a mangrove shoreline and pursed to force fish into the bag. Seine sampling occurred near low tide, because this forced fish out of the flooded mangrove prop-roots, making them more susceptible to capture. Fish were measured (standard length, SL) and released at the site of capture. Temperature, salinity, and dissolved oxygen were recorded with a handheld meter (YSI 556 MPS, YSI Inc., Yellow Springs, OH). These data allowed estimates of occurrence and environmental requirements of *C. urophthalmus*.

For the purposes of this study, the creeks were categorised based on the degree of altered habitat within their upland drainages. The upland drainages of North Silcox and South Silcox Creeks (Fig. 2*a*, *b*) are within a State-owned buffer area that is managed as a natural area. However, within the South Silcox Creek drainage are three abandoned quarry ponds (mean depth of all ponds = 1.5 m; pond 1 = 152 m length × 15 m width; pond 2 = 212 × 15 m; pond 3 = 121 × 15 m) that are filled with water throughout the year and are connected to South Silcox Creek by remnant mosquito ditches during medium through high tides. Although Silcox Creek is connected to the ponds via shallow mosquito ditches, these ponds are considered other water bodies (i.e. not part of Silcox Creek). Irregular seine sampling occurred in these ponds during the study period. In contrast, Yucca Pen Creek and Culvert Creek upland drainages are severely altered by development, creating impervious surfaces and altering freshwater flow regimes. The altered flow regimes cause short, pulsing hydroperiods limited to the immediate creek with little overland sheet flow. In addition, Culvert Creek now begins at a culvert that passes under a road and connects to a large and deep (1.3 km length × 100 m width, >6 m depth) artificial pond (this pond was previously part of the creek channel). Culvert Creek is connected to the pond only during rainy season, when the pond overflows into the creek, so the pond and creek are considered separate water bodies.

Tag–recapture

Beginning July 2005, *C. urophthalmus* >65 mm SL were tagged with sub-dermal HDX Passive Integrated Transponder

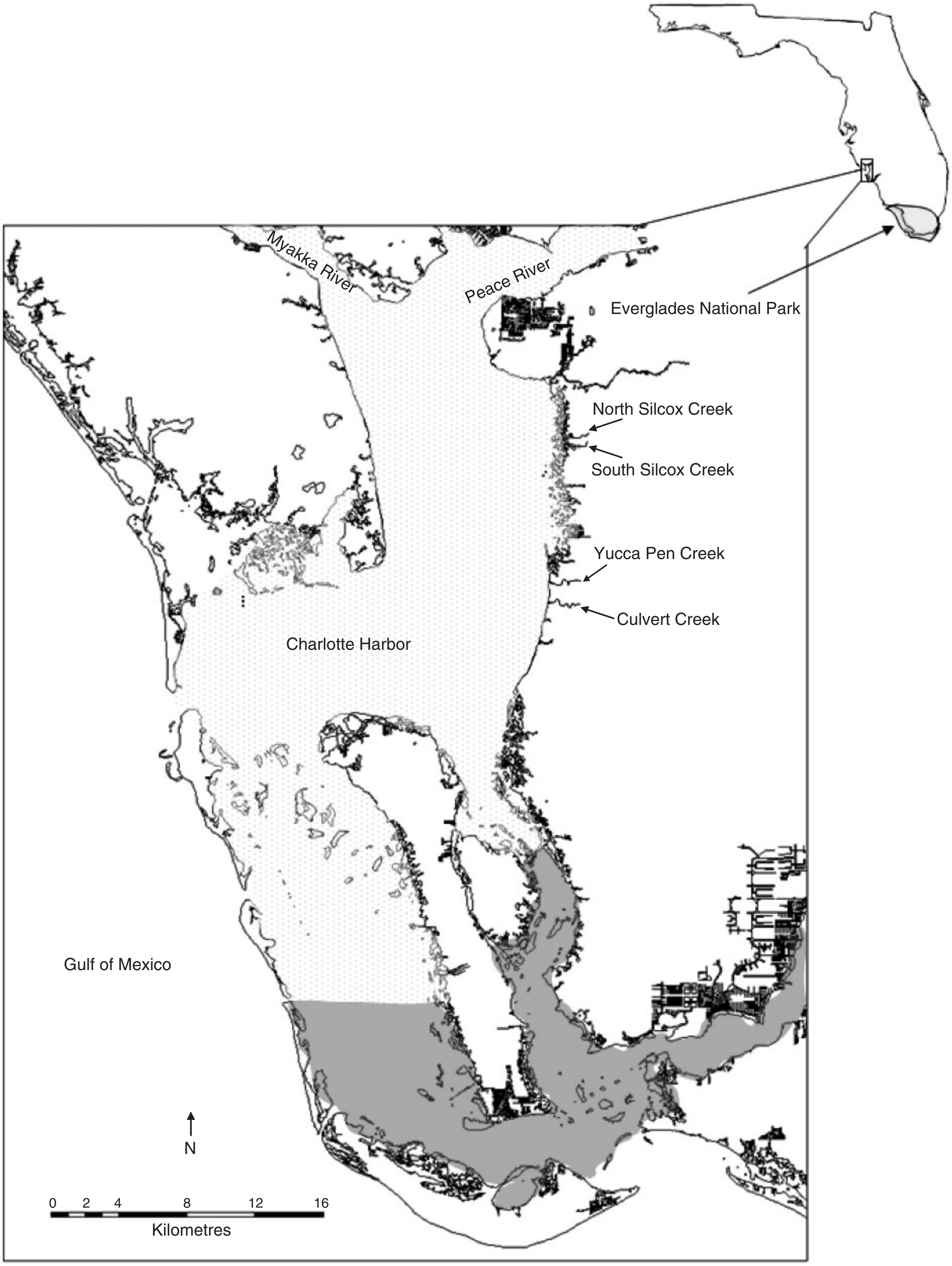

Fig. 1. Locations of Everglades National Park, where *Cichlasoma urophthalmus* were first documented in 1983, and Charlotte Harbor, FL and the study creeks. For Charlotte Harbor sampling by Florida Fish and Wildlife Research Institute, Fisheries Independent Monitoring Program, stippling denotes area sampled 2001–2005, dark grey denotes area sampled 2005–2006.

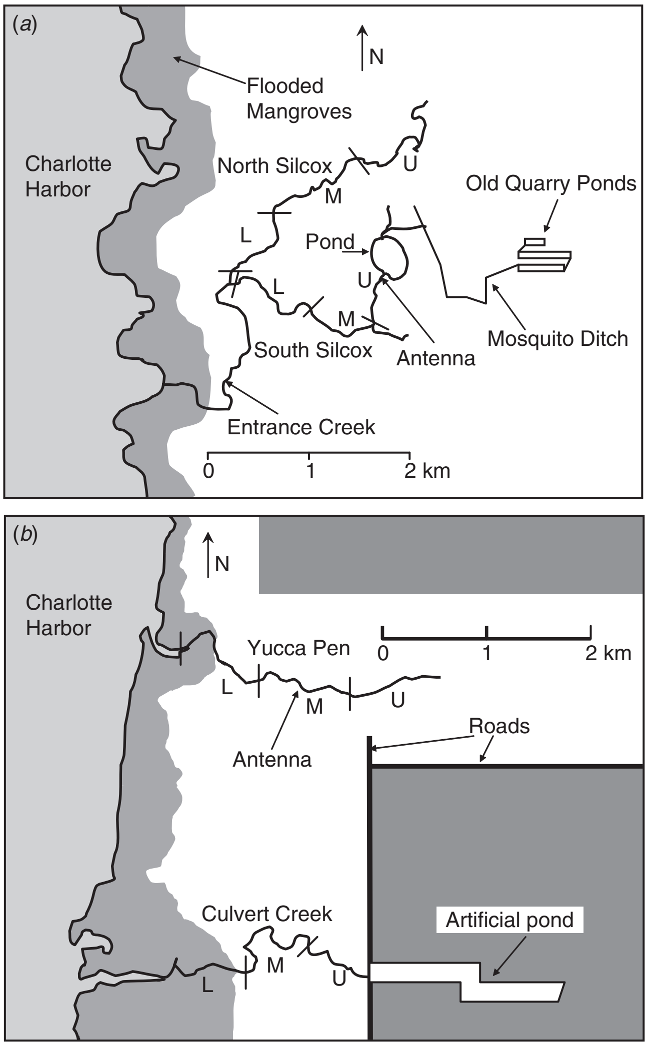

Fig. 2. Diagrams of study creeks: (*a*) North Silcox and South Silcox; (*b*) Yucca Pen, Culvert Creek, showing locations of antennae, upper (U), middle (M), and lower (L) zones, and artificial ponds and altered portions of upland drainages. Heavy stippling in (*b*) denotes land altered by development.

(PIT) tags (Texas Instruments Inc., Dallas, TX) to provide estimates of fish occurrence in creeks. Each PIT tag has a unique 10 digit number that allows individual fish identification. Fish were captured with the abovementioned seine during normal seine sampling and with a 30.3 m long × 1.2 m high centre bag seine (1.2 × 1.2 × 1.2 m bag, 19-mm mesh). Individuals captured during irregular seine sampling of the quarry ponds above South Silcox creek were also tagged. After capture, *C. urophthalmus* >65 mm SL were retained in floating mesh bags (25-mm mesh, 1-m^3 volume) until tagging. Pre-tagging retention time was a maximum of 30 min. All tagging occurred near the site of capture, with latitude and longitude recorded at the release location. Salinity, dissolved oxygen, and water temperature were also recorded for each tagging event. Fish were tagged by inserting a half-duplex PIT tag (23 × 3.4 mm) into the abdominal cavity through a 3 mm incision made with a surgical scalpel. Tag retention rates in this study and findings on other species (Baras *et al*. 2000; Jepsen *et al*. 2002; Adams *et al*. 2006) indicated that post-tagging sutures were not necessary.

Presence of *C. urophthalmus* in creeks was estimated from 'recaptures' by a remote PIT-tag antenna system that detected ~67% of tagged fish that swam through it (see Adams *et al*. (2006) for a detailed description of the PIT-tag antenna system). One antenna each was constructed in the upper section of one lightly degraded creek (South Silcox) and one highly degraded creek (Yucca Pen) (Fig. 2*a*, *b*). Tagging occurred in the creeks containing antennae as well as in adjacent creeks and the quarry ponds in the South Silcox drainage. Attempts to capture and tag fish in the artificial pond in the Culvert Creek drainage were unsuccessful because *C. urophthalmus* were resistant to electroshock at a level that was non-lethal to native species within the pond.

To determine tag retention, seven *C. urophthalmus* were captured and held in captivity in a tank >2000 L. After acclimation to captivity (i.e. regular feeding after two weeks), the fish were measured, tagged, and released back into the tank. Fish were fed, and after two weeks were recaptured and examined for tag retention and any deleterious tagging effects.

Data analyses

To determine whether the occurrence of *C. urophthalmus* was related to temperature or salinity (*sensu* Chavez-Lopez *et al*. 2005), catch data were classified as presence (1) or absence (0), and salinity and temperature data for all samples combined were examined with a non-parametric Mann–Whitney U-test. Abundance data were not used in this analysis because of the preponderance of zero *C. urophthalmus* in seine samples. A non-parametric test was used because transformed salinity and temperature data distributions would not approximate normality because of bimodal distributions that reflected the strong and distinct seasonal switch from wet to dry season (salinity) and contrasts between summer and winter (temperature). Backward stepwise regression was used to examine effects of salinity and temperature on log-transformed standard length (SL), with an $\alpha = 0.15$ to enter or remove. Backward stepwise regression was used because the model contained only two independent variables, and backward stepwise regression is better for simple models (Neter *et al*. 1990). To test the hypothesis that *C. urophthalmus* undergo ontogenetic shifts in salinity preference (Chavez-Lopez *et al*. 2005), salinity at time of capture was examined with a one-way ANOVA by size class, with Tukey *post-hoc* comparisons of means. Size classes were defined by Faunce *et al*. (2002) for *C. urophthalmus* in south Florida, and are used here as a best approximation for local ontogeny. Tagging dates and locations and dates of recapture by the antennae were examined qualitatively to estimate general movements and site fidelity of *C. urophthalmus* in estuarine creeks.

Results

Most *C. urophthalmus* were captured in conditions similar to those of their native range. The first *C. urophthalmus* was captured in the study creeks in June 2003, with 295 individuals captured since: 163 in Culvert Creek, 25 in Yucca Pen, 93 in South Silcox, and 14 in North Silcox. With the exception of Yucca Pen, the majority of *C. urophthalmus* were captured

Table 1. Number of *Cichlasoma urophthalmus* captured by Creek and Zone during sampling with the 21-m seine
See text for explanation of zones

Creek	Zone			
	Lower	Middle	Upper	Total
North Silcox	1	8	5	14
South Silcox[1]	7	18	68	93
Yucca Pen[2]	17	8	0	25
Culvert Creek[1,2]	13	61	89	163
Total	38	95	162	295

[1]Creeks with artificial pond habitats in their upland drainages.
[2]Creeks with anthropogenic impervious surface in their drainages, which alters freshwater flows.

Table 2. Salinity and temperature at time of capture for *Cichlasoma urophthalmus* in this study, and salinity and temperature ranges of occurrence in their native range in Central America

Variable	Native range[1]	This study	Range sampled[2]
Salinity ($g\,kg^{-1}$)	0–37	0–27	0–33
Temperature (°C)	15–37	18–32	9–33

[1]Martinez-Palacios *et al.* (1990).
[2]Range of abiotic variables sampled during this study.

in the upper zones of the study creeks (Table 1), which were closest to upland habitats. The relationship between salinity and *C. urophthalmus* occurrence was significant (U = 30 078, $P < 0.001$, $\chi^2_1 = 24.2$), with salinity lower when *C. urophthalmus* were present (mean = 11.96, s.e. = 1.13) than when they were absent (mean = 18.04, s.e. = 0.32). In contrast, temperature was not a significant factor in *C. urophthalmus* occurrence (U = 17 250, $P > 0.01$, $\chi^2_1 = 6.32$). Although the *C. urophthalmus* captured in creeks were present in environmental conditions similar to those of their native geographical range (Table 2), they are apparently tolerant of considerably lower temperatures. During the tag-retention experiment, a fish remaining in the outdoor holding tank during a cold front survived a water temperature of 10°C, far below the presumed 15°C minimum lethal temperature, with no obvious ill effects.

The overall relationship between salinity and *C. urophthalmus* life history stage was similar to that in its native range and in the Florida Everglades. Backward stepwise regression, however, revealed that standard length (SL) was somewhat dependent upon salinity and temperature ($R^2 = 0.25$, $F_{2,267} = 56.98$, $P < 0.001$), with both independent variables contributing to the relationship ($P < 0.001$ for each) (Fig. 3). The relationship between length and salinity was further supported by a significant difference in salinity at time of capture between juvenile (<40 mm SL, <1 year) and larger (>41 mm SL, >1 year) individuals (Table 3).

Within each year, two distinct cohorts were captured early in the year, with the cohort of smaller fish persisting and growing through the year (Fig. 4). The length–frequency distribution of Culvert Creek was the largest (Fig. 5), possibly indicating an older or more established population in this area.

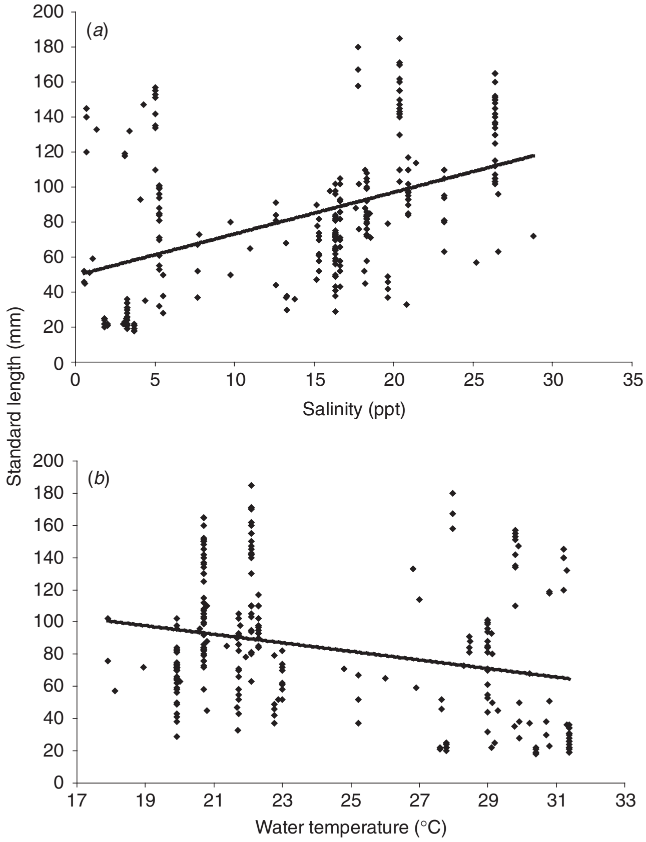

Fig. 3. Relationships between standard length of *Cichlasoma urophthalmus* captured with the 21-m seine and salinity (*a*) and water temperature (*b*). Backward stepwise regression (both dependent variables significant at α to enter or remove <0.001): Standard Length = −63.41 + 4.02(Salinity) + 3.68(Temperature); $R^2 = 0.25$; $F_{2,67} = 45.868$; $P < 0.001$.

Table 3. Salinity at time and place of capture of *Cichlasoma urophthalmus* by size (age) class
*Size (age) classes based on predicted lengths at age for males from Faunce *et al.* (2002) for Florida *C. urophthalmus*

(*a*) Results of one-way ANOVA on salinity at time of capture by size (age) class*

Source	d.f.	SS	MS	*F*	*P*
Size (age) class	6	5406.93	901.16	20.73	<0.001
Error	263	11433.24	43.47		

(*b*) Size (age) classes and mean salinity at time of capture. Size classes that share a letter (Tukey results) were not significantly different

Size class (mm SL)	Age*	Mean	Standard error	Tukey results
0–40	1	5.49	0.75	a
41–74	2	13.84	0.86	b
75–103	3	16.27	0.55	c
104–128	4	19.12	1.31	d
129–149	5	16.57	1.97	c
150–166	6	16.2	2.81	b, c
>166	≥7	21.68	1.08	d

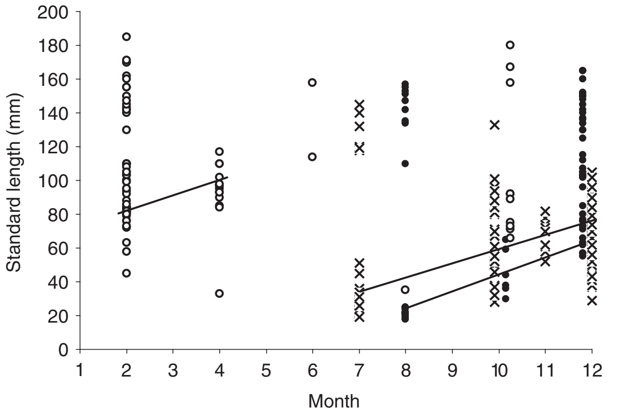

Fig. 4. Standard length of *Cichlasoma urophthalmus* captured with the 21-m seine by year and month. ○ = 2003, ● = 2004, × = 2005. Lines connecting months were drawn by hand to approximate growth of cohorts.

One hundred and sixty-one *C. urophthalmus* were tagged with PIT tags: three in North Silcox, 104 in South Silcox, 20 in ponds upland of South Silcox, 29 in Yucca Pen, and 5 in Culvert Creek (Table 4). Tagged *C. urophthalmus* were at large in the creek systems from 25 July 2005 (South and North Silcox Creeks) and 9 September 2005 (Yucca Pen and Culvert Creek) through November 2006. No tagged *C. urophthalmus* were recaptured by seine.

Although overall PIT tag antenna recapture rates were higher at Yucca Pen than South Silcox, average days at large were higher for South Silcox: 35.3% of fish tagged in Yucca Pen and Culvert Creek were recaptured at the Yucca Pen antenna *v*. 27.6% of fish tagged in North Silcox, South Silcox, and three upland ponds at the South Silcox antenna; average number of days at large between date of tagging and date of most recent recapture at South Silcox (mean = 40.9, s.e. = 1.1, median = 39, min = 0 (recaptured same day tagged), max = 116) *v*. Yucca Pen (mean = 28.4, s.e. = 4.8, median = 13, min = 1, max = 123).

Among-creek differences were also seen in tagging locations of antenna recaptures and in fish size. The greatest percentage of recaptures in South Silcox was from fish tagged in the middle zone and upper zones, whereas the highest recapture rates in Yucca Pen were from fish tagged the middle and lower zones. These patterns most likely reflected differences in freshwater flow – salinity throughout the length of Yucca Pen is lower during the wet season owing to greater freshwater input. The mean size of fish tagged was larger in Yucca Pen (151.9 mm SL, s.e. = 4.2) than South Silcox (114.4 mm SL, s.e. = 6.7).

Five instances of inter-water-body movement were detected, all involving altered habitats. Four fish tagged in two artificial upland ponds (old quarry ponds) were recaptured by the South Silcox antenna numerous times in the following months (Table 5), and then none since. One fish that was tagged in Culvert Creek on 26 July 2006 crossed the antenna in Yucca Pen 13 times between 30 July and 9 September 2006 (Table 5). None of the three fish tagged in North Silcox were recaptured.

Tag retention and survival were 100% ($n = 7$) for *C. urophthalmus* that were fitted with PIT tags and kept in large tanks for two weeks, with no observed ill effects.

Discussion

This study documents a notable northward range expansion by *Cichlasoma urophthalmus* in the Florida peninsula, links presence of *C. urophthalmus* in tidal estuarine creeks to altered upland habitats, and confirms the general environmental characteristics of the species, but also suggests the species is able to adapt to new conditions.

Building upon previous documentation of the establishment of *C. urophthalmus* in south Florida freshwater and estuarine habitats (Shafland 1996; Trexler *et al*. 2000), this study demonstrates the year-round occurrence of *C. urophthalmus* in estuarine habitats of Charlotte Harbor, thus expanding the documented geographic range of this non-native species. As in previous studies, *C. urophthalmus* show tolerance for a wide range of salinities, especially among large fish which were most frequently captured in mesohaline waters. *Cichlasoma urophthalmus* are able to tolerate a wide range of temperature and salinity (Stauffer and Boltz 1994), and can tolerate rapid changes in salinity (Martínez-Palacios *et al*. 1990). In portions of their native range, large individuals appear to prefer lower salinities (Martínez-Palacios *et al*. 1990), but in other areas they are most abundant in higher-salinity locations with submerged aquatic vegetation (Chavez-Lopez *et al*. 2005).

Findings also indicate, however, that *C. urophthalmus* are not likely to be permanent residents of Charlotte Harbor estuarine creeks, but instead are primarily seasonal invaders from altered habitats in the upland drainages of these creeks. Total abundance of *C. urophthalmus* was highest in the two creeks with altered habitats that provided deep basins of oligohaline water (ponds in the South Silcox drainage) or fresh water (pond in Culvert Creek drainage). Deep creek habitats are important dry-season habitats for adults in the Florida Everglades (Faunce and Lorenz 2000), and artificial canals in south Florida host high numbers of *C. urophthalmus* and other non-native species (Trexler *et al*. 2000). Interestingly, although the creeks in this study do have deep habitats, *C. urophthalmus* individuals were observed taking refuge in these deep areas only in Yucca Pen, which has a permanent connection to upland freshwater areas.

Habitat alteration and evolution may be combining to allow a range expansion of *C. urophthalmus* in Florida. Altered habitats can provide advantages to non-native species, allowing them to increase in abundance and geographic range (Mack *et al*. 2000). In south Florida, freshwater canals have provided habitats unlike any native habitats, and thus provide refuge for *C. urophthalmus* and other invasive species (Trexler *et al*. 2000). For *C. urophthalmus*, we hypothesise that the canals provide refuge from winter low temperatures that would otherwise limit their geographic range to areas farther south. The deep waters of many of these canals and ponds (e.g. >6 m for the Culvert Creek upland pond) probably stay warmer than surface waters during cold fronts that temporarily drop surface water temperatures below the assumed minimum (15°C) for *C. urophthalmus*. It is also possible, however, that in conjunction with these refuges, *C. urophthalmus* are evolving to be more tolerant of colder temperatures, as illustrated by a fish in an outdoor tank for the tag retention experiment that tolerated multiple days of water below 15°C (to 10°C).

The freshwater canal systems of south Florida and normal seasonal flooding provided avenues for movement beyond

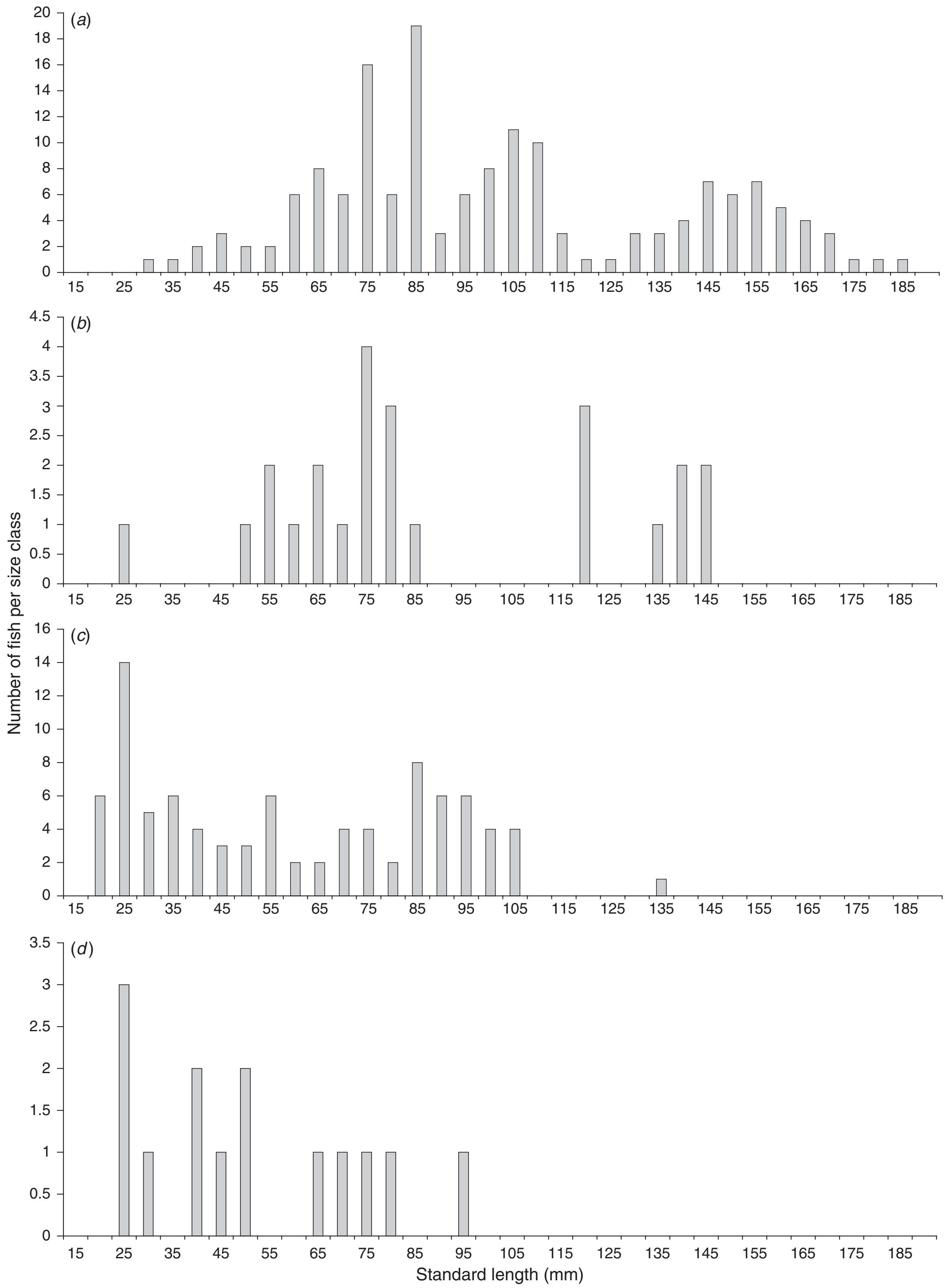

Fig. 5. Standard length of *Cichlasoma urophthalmus* captured with the 21-m seine by creek, all samples combined. (*a*) Culvert Creek, (*b*) Yucca Pen, (*c*) South Silcox, (*d*) North Silcox.

the original range in the Florida Everglades, and from upland freshwater to estuarine creek habitats. During wet season, when ephemeral wetland areas in the Florida Everglades are flooded, *C. urophthalmus* temporarily occupy these habitats (Faunce and Lorenz 2000). Although Faunce and Lorenz (2000) documented this pattern as local and ontogenetic, this is also a valid avenue for range expansion. During dry season, fish that are able to find artificial canals or ponds have refuge until next wet season when flooding might provide opportunities for additional movement. This pattern of habitat invasion is shown by the temporal and spatial patterns of *C. urophthalmus* occurrence in the present study: overall catches and presence of juveniles were greatest during wet season, when freshwater runoff provided connections between upland freshwater areas (primarily artificial ponds) and the tidal estuarine creeks. Seasonal changes in water level are also important drivers of habitat use patterns of *C. urophthalmus* and other species in the Everglades (Faunce *et al*. 2004).

Table 4. Number of *Cichlasoma urophthalmus* tagged by location, and number and percentage recaptured by remote antennae in the Upper Zones of Yucca Pen and South Silcox

See Fig. 5*a*, *b* for antenna locations. See text for description of zones

Creek/Zone	Number tagged	Number recaptured	Percentage recaptured
Yucca Pen	29	11	37.9
Lower	19	5	26.3
Middle	10	6	60
Upper	0	0	0
Culvert Creek	5	1	20
Lower	4	1	25
Middle	1	0	0
Upper	0	0	0
South Silcox	104	29	27.9
Lower	13	2	15.4
Middle	8	3	37.5
Upper	83	24	28.9
North Silcox	3	0	0
Lower	1	0	0
Middle	1	0	0
Upper	1	0	0
Upland Ponds (South Silcox drainage)	20	6	30
Total	161	47	29.2

Although spawning was observed in creeks of the Everglades (Faunce and Lorenz 2000), it is unlikely that spawning is occurring in the tidal creeks of Charlotte Harbor, further suggesting a connection to altered upland habitats. *C. urophthalmus* are able to spawn in the range of salinities encountered during the present study (Martínez-Palacios *et al*. 1990), but during four years of sampling no spawning beds or spawning activity was observed in the study creeks. Spawning beds of *C. urophthalmus* are conspicuous (Faunce and Lorenz 2000) and would have been noticed during sampling. Moreover, the low salinities which juveniles preferred were generally not present in the creeks until after the likely spring spawning season. In Yucca Pen and Culvert Creek, the currents associated with altered freshwater flows, and the resulting channelisation of much of the creek beds, probably prevent building of spawning beds. Therefore, we suggest that spawning occurs within the upland drainages of the creeks (artificial ponds), with colonisation downstream during wet season freshwater flows.

The size structure of *C. urophthalmus* in creeks also indicates connectivity to upland habitats, and the dependence on these habitats as sources of individuals. The occurrence of small (<40 mm SL) *C. urophthalmus* during wet season probably reflects their preference for meso- and oligohaline habitats. For example, juveniles can tolerate salinities $>37\ \mathrm{g\,kg^{-1}}$, but are usually found in low-salinity waters (Martínez-Palacios *et al*. 1990). In locations where *C. urophthalmus* was captured in Mexico, the mean salinity was $7.13\ \mathrm{g\,kg^{-1}}$ (Chavez-Lopez *et al*. 2005). In this study, small fish were most common in low salinity waters (mean $= 5\ \mathrm{g\,kg^{-1}}$) during the wet season (June through September), or unseasonably wet periods during the dry season.

This pattern was also observed within native habitats in Mexico, where bimodal size distribution was observed in all seasons (Chavez-Lopez *et al*. 2005). In Mexico, reproduction occurs in the rainy season (May–July), with a small secondary peak in gonadal activity in December (Chavez-Lopez *et al*. 2005). In this study, bimodal size distribution was also observed throughout the year, with the smallest fish occurring in July through October during the rainy season, after inland rainfall drains into the creeks and lowers salinities. In 2003, the smallest fish occurred in February, which coincided with an unusually rainy period during the dry season, and would correspond to spawning activity in December. Moreover, the creek with the largest upland freshwater refuge (Culvert Creek) had the greatest range of size classes of

Table 5. Summary of inter-waterbody movement of *Cichlasoma urophthalmus*, as compared with within-creek average recaptures and days-at-large

See Fig. 5*a*, *b* for antenna locations and zones

Tagging location	Standard length	Tagging date	Recapture location	Number of recaptures	Days at large*
Upland Pond 2	156	19 June 2006	South Silcox	2	29
	167	19 June 2006	South Silcox	96	116
Upland Pond 3	188	19 June 2006	South Silcox	8	100
	212	20 July 2005	South Silcox	98	99
Average for fish tagged within South Silcox				15.86	40.87
Culvert Creek Lower zone	186	27 July 2006	Yucca Peninsula	13	44
Average for fish tagged within Yucca Peninsula				3.92	28.43

*Days at large = the number of days between tagging date and last antenna recapture.

all creeks, suggesting multiple generations. And although fewer fish were captured in Yucca Pen, they were dominated by larger mature fish. In contrast, South Silcox was dominated by two size classes of smaller fish (most fish <100 mm SL), suggesting a more recent establishment or a population overflowing from elsewhere. The creek (North Silcox) with the least connection to altered upland habitats also had the fewest fish.

Data from PIT tag antenna recaptures also suggest movements were mostly limited to meso- and oligohaline habitats. The fish that was tagged in Culvert Creek, for example, and later recaptured by the Yucca Pen antenna, was tagged during the wet season when freshwater flows connecting the pond and creek allowed the fish to migrate downstream. Later in the year, when flows were reduced, travel upstream to the pond was not possible, so Yucca Pen was the only avenue by which fish could return to oligohaline upland habitats.

Other research efforts also suggest a connection between altered habitats and occurrence of *C. urophthalmus*, and indicate that the findings of this study are not a result of bias (Ruiz *et al*. 2000). The Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Fisheries Independent Monitoring Program (FIM), which completes ~918 samples (seine and trawl) per year in non-creek Charlotte Harbor estuarine habitats, captured only one *C. urophthalmus* between 2000 and 2005. In 2004, FIM began sampling in the Caloosahatchee River estuarine system (Fig. 1), which is heavily impacted by altered (managed) freshwater flows and urban development, and captured 166 *C. urophthalmus* in 160 seine samples in 2004 and 2005 (Patrick Casey, FWRI, Port Charlotte, FL, pers. comm.). Finally, the relatively short days-at-large (number of days between tagging and last recapture) for PIT-tagged *C. urophthalmus* suggests an ephemeral estuarine population. The maximum number of days at large for a PIT-tagged *C. urophthalmus* in this study was 123 (of a 280-day tagging period), even though *C. urophthalmus* in Florida may live seven years (Faunce *et al*. 2002). In contrast, a study in the same creeks as in this study found that PIT-tagged common snook (*Centropomus undecimalis*), which also lives seven years or more, were recaptured after four years at large. Because snook, a very mobile species, are recaptured after so many days at large, and overall antenna recapture rates are similar for snook (35%) and *C. urophthalmus* (30%), one would expect somewhat similar trends in days at large if *C. urophthalmus* populations were resident in estuarine creek habitats.

Combined, the data presented in the current study suggest that *C. urophthalmus* are established in altered upland freshwater or oligohaline habitats, and colonise estuarine creek habitats seasonally, with colonisation usually associated with increased freshwater flows from upland drainage areas during wet season. The presence of drainage ditches and artificial ponds that retain oligo- and meso-haline water year-round (before anthropogenic alteration these areas were dry during the dry season), may provide sources of recruitment into Charlotte Harbor's estuarine habitats. Thus, even if *C. urophthalmus* is unable to tolerate the high salinities of the dry season ($>30\ \mathrm{g\ kg^{-1}}$) in the estuary, recruitment sources within altered upland drainages may sustain this species in estuarine habitats, making it a *de facto* estuarine invader. This concurs with previous correlations between habitat alteration and exotic species invasions (Courtenay and Williams 1992), and underscores the challenges of understanding of managing biological invasions (Mack *et al*. 2000).

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