Gulf and Caribbean Research

Volume 23 | Issue 1

2011

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DOI: 10.18785/gcr.2301.02

Gulf and Caribbean Research Vol 23, 13-22, 2011 Manuscript received, January 26, 2010; accepted, August 16, 2010

DISTRIBUTION AND ABUNDANCE OF INTRODUCED FISHES IN FLORIDA'S CHARLOTTE HARBOR ESTUARY

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Abstract: A growing number of non-native fishes have been introduced into Florida waters in recent years, yet little information has been available on their distribution and abundance in southwest Florida. The ichthyofauna of the Charlotte Harbor estuary, Florida, was intensively sampled from 1989 through 2007. We collected eight introduced fish taxa: African jewelfish (*Hemichromis letourneuxi*), blue tilapia (*Oreochromis aureus*), brown hoplo (*Hoplosternum littorale*), grass carp (*Ctenopharyngodon idella*), Mayan cichlid (*Cichlasoma urophthalmus*), sailfin catfishes (*Pterygoplichthys* spp.), spotted tilapia (*Tilapia mariae*), and walking catfish (*Clarias batrachus*). These fishes were found principally in tidal rivers, especially the Caloosahatchee River. Other introduced species, such as Asian swamp eel (*Monopterus albus*), blackchin tilapia (*Sarotherodon melanotheron*), and pike killifish (*Belonesox belizanus*), are known to occur in neighboring bay systems but have yet to be reported in the Charlotte Harbor estuary. Continued monitoring will help us detect additional species that are introduced to the estuary, expansions in the ranges of documented species, and assemblage-level changes.

Key Words: Charlotte Harbor, Caloosahatchee River, Florida, cichlids, exotic fishes

Introduction

As human activity continues to expand in Florida, a growing number of non-native plants and animals, including fishes, are being introduced to the state. To date, more than 100 species of introduced fishes have been collected in Florida waters. Of these, 23 are considered to be "established" (i.e., appear to have permanent populations), and another nine are considered to be "possibly established" (Shafland et al. 2008).

Introduced fishes can affect native ichthyofauna by competing for resources such as food or habitat, introducing diseases or parasites, and through predation (Hill 2002, AFS 2008, FWC 2008). Fish introductions have affected native ichthyofaunas (e.g., Hedrick et al. 1998, Utah Division of Wildlife Resources 2002, Balirwa et al. 2003, Pilger et al. 2008) or ecosystems (e.g., Courtenay and Robins 1975, Leslie et al. 1987, Baxter et al. 2004, Reissig et al. 2006) in a variety of locations. Often, however, the effects that introduced fish species have on the native fauna are not known (Hill 2006). Detailed environmental data, especially baseline data collected before a species is introduced, are usually lacking, making it hard to detect impacts or to separate them from normal biological variability. For example, Trexler et al. (2000) found "little evidence of ecological effects of introduced fishes on the native freshwater communities in southern Florida" but concluded that "cryptic or delayed effects may have been overlooked." Nevertheless, fish introductions are usually considered undesirable due to their potential for causing unwanted changes in native populations and ecosystems (AFS 2008, FWC 2008, Leprieur et al. 2008, 2009, Vitule et al. 2009).

Knowing the distribution and abundance of an introduced species is an important step in understanding its potential impacts on an ecosystem. Trends in population size and distribution over time can be used to project a species' long-term status. Focusing subsequent research on the areas where an introduced species is most abundant may improve understanding of that species' habitat requirements and effects on native fauna. This information would help those charged with making management decisions, including those prohibiting future introductions or limiting the spread of a species that has been introduced.

Although the status and distribution of fishes introduced in many areas of Florida have been described (FWC 2008, FMNH 2008, Shafland et al. 2008), little information has been available on fishes introduced into the Charlotte Harbor area. Wang and Raney (1971) conducted the first extensive ichthyological survey of the Charlotte Harbor estuary in 1968—1969 and collected no introduced fishes. Poulakis et al. (2004) compiled all available data to produce a comprehensive list of fishes collected in the Charlotte Harbor estuarine system; five introduced species were included. Much of the information in the Poulakis et al. (2004) synthesis was derived from data collected by the Florida Fish and Wildlife Conservation Commission's Fisheries—Independent Monitoring (FIM) Program from 1989 through 2002. We used FIM Program data collected from 1989 to 2007 to update and describe in detail the occurrences and distributions of fishes introduced into the Charlotte Harbor estuary, including information on additional areas sampled in recent years (Caloosahatchee River, southern Matlacha Pass, and southern Pine Island Sound).

Materials and Methods

Study location

Charlotte Harbor is a relatively large (ca. 700 km^2; Hammett 1990), shallow estuary on the southwest coast of Florida (Figure 1a). The region is subtropical, with air temperatures averaging 16°C in winter (December–January) and 27°C in summer (July–August) (Hammett 1990). Yearly rainfall averages 134 cm, as much as 70% of it typically falling in summer (Taylor 1974). Occasional freezes and tropical cyclones can have considerable effects on the system (Hammett 1990, Stevens et al. 2006).

Three major rivers provide fresh water to the estuary: the Peace and Myakka rivers enter Charlotte Harbor near its northern terminus, and the Caloosahatchee River enters the harbor at its southeastern end. Considerable water is exchanged with the Gulf of Mexico through San Carlos Pass, Boca Grande Pass, and several smaller inlets. Therefore, salinity varies widely both geographically and temporally. Varying degrees of vertical stratification are seen in the estuary during the warmer months (Estevez 1998), contributing to seasonal hypoxia in the underlying water mass that may affect portions of upper Charlotte Harbor and the lower Peace River (Fraser 1997). Much of the shoreline is characterized by mangroves (principally *Rhizophora mangle* and *Avicennia germinans*), with some areas of sand beach, salt marsh (dominated by *Spartina alterniflora* and *Juncus roemerianus*), and seawalls. Substrate varies from sand to mud, with large expanses of seagrasses (*Thalassia testudinum*, *Halodule wrightii, Syringodium filiforme*, and *Ruppia maritima*) in shallow areas.

Charlotte Harbor remains one of the least altered estuaries in peninsular Florida; much of the surrounding land is protected by public ownership. However, past and present activities related to increased development in the watershed have significantly impacted the estuary (Charlotte Harbor National Estuary Program 2000). These activities include shoreline hardening, channelization, water withdrawal from tributaries and aquifers, manipulation of water-flow regimes (Caloosahatchee River), increased nutrient input, and scarring of seagrass beds by boat propellers. Development is densest near the mouths of the Caloosahatchee (cities of Cape Coral and Fort Myers) and Peace (cities of Port Charlotte and Punta Gorda) rivers.

Sample collection

Fish and certain invertebrates (crabs and shrimp of commercial importance) have been sampled in the Charlotte Harbor estuary by the FIM program since 1989; this paper includes data collected through 2007. Samples were taken seasonally (spring and fall) from 1989 to 1995 and monthly thereafter. The initial sampling area was located north of Pine Island Sound and Matlacha, including Gasparilla Sound, northern Matlacha Pass, and the tidal portions of the Peace and Myakka rivers. The sampling area was expanded in 1994 to include Pine Island Sound and in November 2003 to include southern Matlacha Pass, tidal portions of the Caloosahatchee River (upstream to Franklin Lock), and the Orange River. Until 1998, 15 fixed stations located in the upper harbor and Peace River were also sampled monthly.

Use of a range of sampling gear allowed us to sample much of the estuarine ichthyofauna. Shallow (≤1.8 m) habitats were sampled with a 21.3 m nylon bag seine (1.8 m depth, 3.2 mm mesh, 1.8 m × 1.8 m center bag). Deeper areas (>1.8 m and ≤7.6 m) were sampled with a 6.1 m otter trawl (38 mm mesh with 3.2 mm mesh liner). Gear of these types and sizes is more efficient in capturing small fishes and crustaceans (Comp and Seaman 1985) than larger, more mobile animals (Kupschus and Tremain 2001). Therefore, 183 m center—bag haul seines (3.0 m depth, 38 mm mesh), 183 m center—bag purse nets (3.3 m depth, 50 mm mesh), and 180 m gill nets (2.0 m depth, 51 to 152 mm mesh) were used periodically to sample larger fish, allowing us to sample a wide variety of sizes and types of fishes simultaneously.

A stratified-random design was used to select sampling sites. Sampling locations were chosen randomly without replacement from a universe of 0.2 × 0.2 km sites that contained suitable habitat. Samples were collected principally during the day (both day and night sampling were conducted prior to 1996) and processed in the field. All fish and selected invertebrates in each sample were identified to the lowest practical taxon and counted. A maximum of 40 randomly selected individuals of each taxon were measured to the nearest millimeter standard length (SL). Extremely large catches were subsampled with a modified Motoda box splitter after less abundant species had been removed and processed (Winner and McMichael 1997). Representative samples of most species were retained and reidentified in the laboratory for quality control; the remaining fish were returned to the water. Species that could not be identified in the field were retained and identified in the laboratory. Nomenclature follows Nelson et al. (2004).

Date, location (latitude and longitude), depth, and bottom and shoreline descriptors (e.g., substrate and vegetation type), water temperature (°C), salinity, and dissolved oxygen (mg/l) were recorded at each sampling site. The hydrologic variables were measured at the water surface and at depth intervals of 1.0 m to the bottom.

Data analysis

To examine the geographic distributions of introduced species, we plotted the locations and sizes of individual catches (fish/haul), regardless of sampling gear. We tabulated numbers of fish collected by salinity category, modified

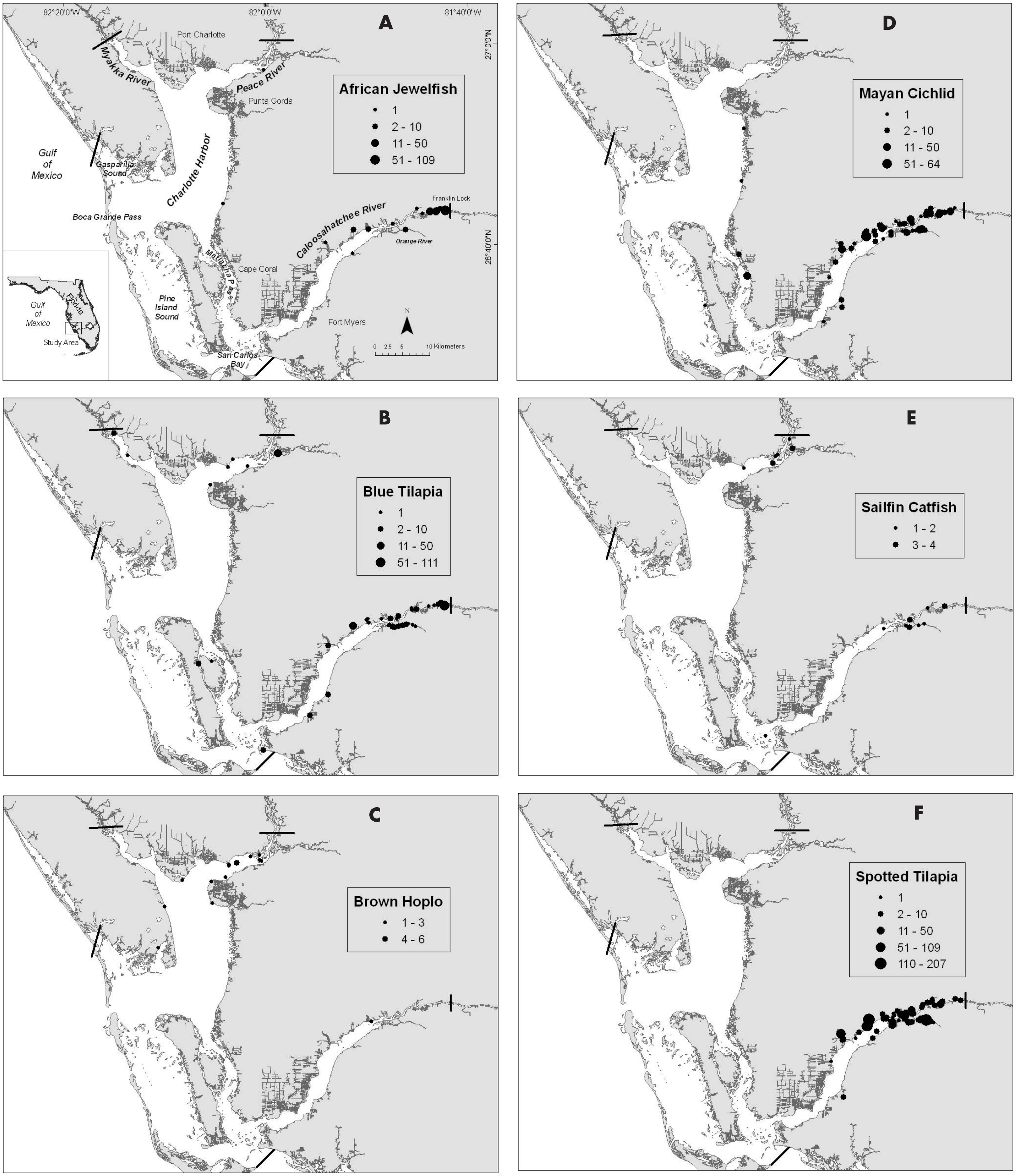

Figure 1. *Catches of introduced species made during the study period in Charlotte Harbor ("0" catches not shown). Dark bars delineate boundaries of sampling area.*

from the Venice system (Anonymous 1958): limnetic (<0.5), oligohaline (0.5—4.99), low mesohaline (5—11.99), high mesohaline (12—17.99), polyhaline (18—29.99), and euhaline (≥30). For introduced species that were collected in sufficient numbers (at least several hundred individuals), catch data from the area and sampling gear of highest abundance were analyzed as follows: catches were standardized to area sampled (fish/100 m^2), geometric mean fish density ± 95% confidence limits (Sokal and Rohlf 1981) were calculated, and these densities were plotted against month to reveal seasonal trends. Monthly lengths were overlaid on the density plots to evaluate spawning seasonality and recruitment.

Results and Discussion

We collected 21,524 samples containing 7,459,363 individuals. More than 260 taxa of fishes and commercially important crustaceans were represented, including eight species of introduced fishes. The grass carp (*Ctenopharyngodon idella*) is represented by only a single specimen, captured in the upstream portion of our sampling area in the Caloosahatchee River in June 2005. These sterile grass carp are used in Florida to help control aquatic vegetation (Shafland et al. 2008), and this fish is probably an escapee from a stocked pond or lake. The walking catfish (*Clarias batrachus*) is represented by two specimens collected in a single sample near the mouth of the Myakka River in September 1994. Although this species is established in the Peace River watershed (Fraser 2007) and is abundant in some freshwater ponds adjacent to our sampling area (pers. obs.), it has been unsuccessful in colonizing the estuarine portions of Charlotte Harbor, presumably due to poor salinity tolerance or preference for lower salinities. The six other introduced taxa collected—African jewelfish (*Hemichromis letourneuxi*), blue tilapia (*Oreochromis aureus*), brown hoplo (*Hoplosternum littorale*), Mayan cichlid (*Cichlasoma urophthalmus*), sailfin catfishes (*Pterygoplichthys* spp.), and spotted tilapia (*Tilapia mariae*)—were more abundant in the study area. Species profiles and distributional information for these fishes are given below.

African Jewelfish *(Hemichromis letourneuxi)*

The African jewelfish is a relatively small (usually <75 mm total length in Florida; Shafland 1996) cichlid native to northwest Africa, where it inhabits freshwater and brackish habitats of tidal rivers (Schofield et al. 2007). The Florida population likely was established by fish that escaped from an ornamental fish farm into Dade County waters in the early 1960s (Courtenay et al. 1974). The range of this species has expanded throughout south Florida, extending north to the Alafia River on Florida's west coast (Shafland et al. 2008).

We collected 197 African jewelfish ranging from small individuals to adults (19—53 mm SL). The first was taken in September 2003 in the Peace River. Another specimen was collected on the eastern shore of Charlotte Harbor in 2006. The rest were collected in the Caloosahatchee River and adjacent Orange River at shallow sites sampled with 21.3—m seines (Figure 1a); these collections were analyzed further. Most of the African jewelfish collected in this area were found in freshwater and oligohaline areas (Table 1). Small individuals (< 25 mm SL) were collected only in October (n = 2), November (n = 3), and December (n = 3). Although monthly trends in mean SL were not apparent, fish were most abundant in late fall and winter (Figure 2a), suggesting that spawning took place principally in fall.

TABLE 1. *Numbers of introduced species collected during 1989-2007 in Charlotte Harbor estuary by salinity category. Categories are based on the Venice System (Anonymous, 1958).*

Species	Salinity						Total
	<0.5	0.5-4.99	5-11.99	12-17.99	18-29.99	≥30.0	No.of fish
African jewelfish	160	33	1	2	1	0	197
Blue tilapia	52	200	18	10	4	0	284
Brown hoplo	16	9	3	1	0	0	29
Mayan cichlid	156	148	79	66	12	1	462
Sailfin catfish	23	5	1	0	0	0	29
Spotted tilapia	487	446	76	28	1	0	1,038

Fraser (2007) lists the African jewelfish as being established in the Peace River, based on evidence of a reproducing population in freshwater areas; however, it is not abundant (Champeau et al. 2009). This species is also present in tidal creeks on the eastern shoreline of Charlotte Harbor (A.J. Adams, unpublished data, Mote Marine Laboratory, Pineland, FL).

Blue tilapia *(Oreochromis aureus)*

The blue tilapia is native to North Africa and the Middle East and has been introduced in many parts of the world for aquaculture (Shafland and Pestrak 1982). It was released into Hillsborough County waters in the 1960s in aquatic weed control experiments. It was also promoted as a food and game species, which prompted anglers to release it in

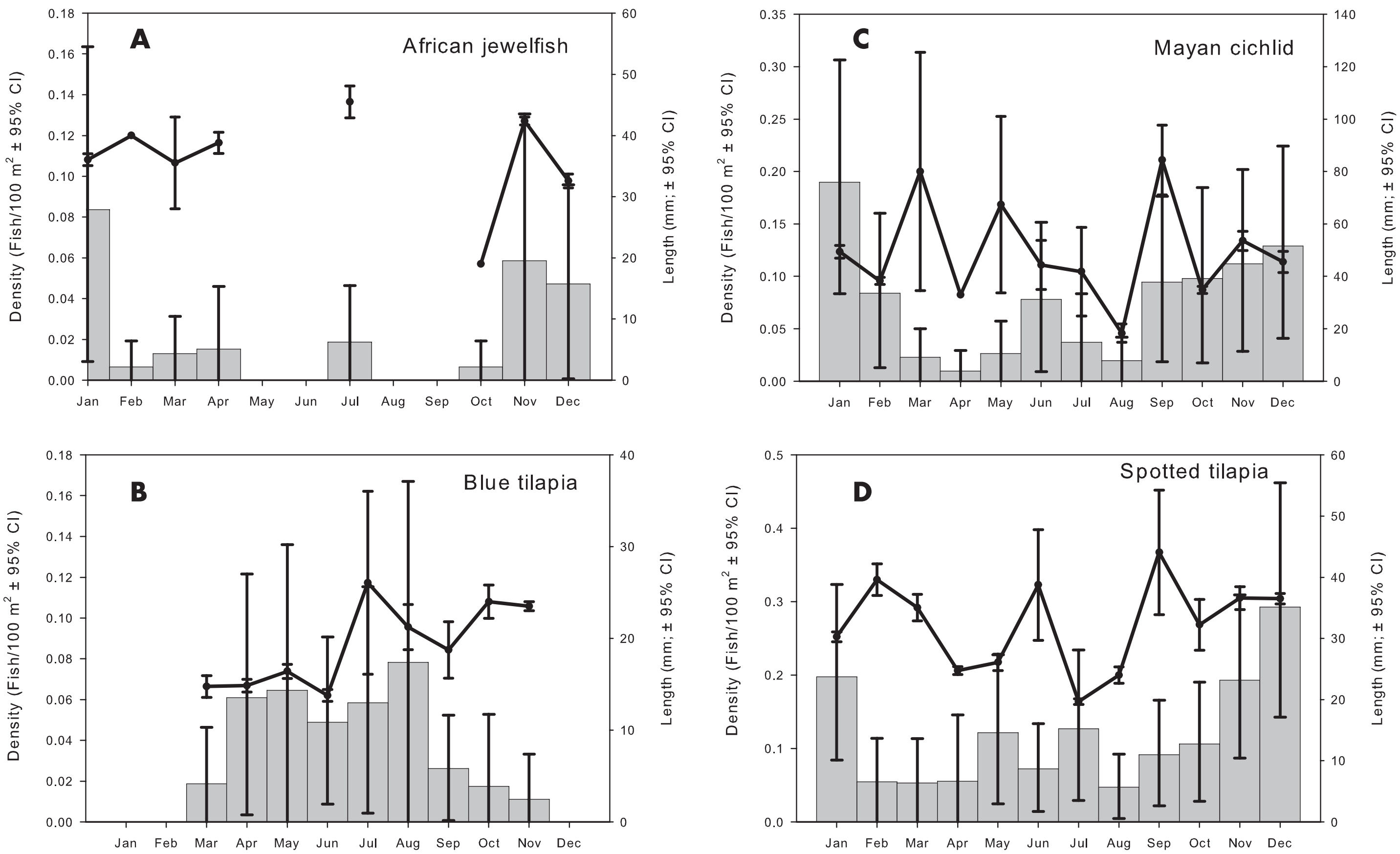

Figure 2. *Estimated densities (histogram; fish/100m²) and standard length (lines; mm; ± 95% CI) of abundant introduced species collected with 21.3—m seines during 2003—2007 in the tidal portion of the Caloosahatchee River and vicinity by month.*

other areas (Courtenay et al. 1974). It rapidly became the most widespread introduced species in Florida (Courtenay et al. 1974, Shafland et al. 2008), and in some lakes it even supports a small commercial fishery.

We collected 284 blue tilapia ranging from small individuals to large adults (9—280 mm SL). The first were collected in December 1991, when three individuals were captured on the southern shoreline of the Peace River, about 14 km above the river's mouth. The largest catch contained 111 individuals; this collection was in the upstream portion of our sampling area in the Caloosahatchee River, near Franklin Lock. Most catches were made at sites in the tidal rivers, particularly in the Caloosahatchee and Orange rivers (Figure 1b). Data collected in the Caloosahatchee area (21.3 m seine catches; n = 201) were examined in more detail. Blue tilapia in this area were almost exclusively found in low-salinity habitats (mainly < 12; Table 1). Spawning apparently takes place only during the warmer months; we collected small individuals (< 25 mm SL; n = 32) from March to October. Mean fish length was smallest from March to June, suggesting most spawning occurred during this period (Figure 2b). Few fish were collected during the rest of the year (Figure 2b). This is consistent with a reported minimum temperature of 20° for spawning (FWC 2008).

The blue tilapia has been present in the Peace River drainage since at least 1973 (Champeau 1990, Fraser 2007) and remains an established and abundant component of the ichthyofauna of the Peace River (Champeau et al. 2009) and other freshwater portions of the Charlotte Harbor watershed. Our data indicate that while individuals occasionally enter brackish areas, this species has not been successful in colonizing the Charlotte Harbor estuary.

Brown hoplo *(Hoplosternum littorale)*

The brown hoplo is native to fresh and brackish waters of northeastern South America and Panama (Nico et al. 1996). It was first reported in Florida in 1995, when 33 specimens were captured and hundreds more were observed in the Indian River Lagoon system (Nico et al. 1996). The source of this species' introduction remains unknown, although possibilities include release by hobbyists, escape from aquaculture ponds, and introduction as a food fish (Nico et al. 1996). Since this catfish was discovered, its range has expanded rapidly. It is now present throughout much of central and south Florida (Shafland et al. 2008) and has even become a major dietary item of the common snook (*Centropomus undecimalis*), an important game fish in this area (Stevens et al. 2010). The ability to breathe air by gulping has allowed it to survive in water with low levels of dissolved oxygen and has probably facilitated its spread (Nico et al. 1996).

We collected 29 brown hoplos, ranging from small individuals to adults (17—172 mm SL). The first specimen was captured in September 2001 near the mouth of the Peace River. Although in its native range this species inhabits brackish areas with salinities up to 16 (Nico et al. 1996), it appears to be confined principally to freshwater habitats in the Charlotte Harbor system, where it has become quite abundant (Fraser 2007, USGS 2008). In fact, most of our specimens were collected in or near the mouth of the Peace River (Figure 1c) shortly after the passage of Hurricane Charley (August 13, 2004), which caused massive freshwater runoff in the Peace River watershed (Stevens et al. 2006). The brown hoplo has also been documented in the Myakka and Caloosahatchee rivers (Peebles et al. 2006, USGS 2008).

Mayan cichlid *(Cichlasoma urophthalmus)*

The Mayan cichlid is native to the Atlantic slope of Central America. The origin of the Florida population is not known, although it was first reported in the Everglades in 1983 (Loftus 1987). It is well established in south Florida (Trexler et al. 2000, Matamoros et al. 2005, Shafland et al. 2008), and its range has expanded northward, with established populations to at least Melbourne and Tampa Bay on Florida's east and Gulf coasts, respectively (Paperno et al. 2008).

We first collected the Mayan cichlid in December 2003, when 11 individuals were captured in a single sample in Matlacha Pass. A few were taken on the eastern side of Charlotte Harbor near tidal creeks, and one was collected in Pine Island Sound. The largest catch, at a site on the north bank of the Caloosahatchee River about 19 km above its mouth, was 64 specimens. Most (n = 435) of the 462 specimens taken during this study were collected with 21.3 m seines in the Caloosahatchee and Orange rivers (Figure 1d), where this fish is particularly abundant in backwater areas (Stevens et al., 2010). Data from the Caloosahatchee River area were examined further. The Mayan cichlid has an affinity for brackish conditions in its native range (Martinez—Palacios et al. 1990, Chavez—Lopez et al. 2005, USGS 2008), and we also collected them at sites ranging from limnetic to high mesohaline (Table 1). The presence of both juveniles and adults (13—288 mm SL) indicates that this species is established and breeding in the Charlotte Harbor system. Most (26 of 30) small individuals (< 25 mm SL) were collected from June to December, suggesting an extended spawning season through the warmer months. Smallest mean lengths during June-August may reflect peak spawning during this period, followed by increased abundance as these young recruit to our sampling gear (Figure 2c). This contrasts with the findings of Faunce and Lorenz (2000), who noted that breeding activity of Mayan cichlids in the southeastern Everglades was limited to spring (April to June).

Adams and Wolfe (2007) also documented the presence of Mayan cichlids in tidal creeks along the eastern shoreline of Charlotte Harbor. They proposed that these tidal creeks provide connectivity between the estuarine habitats of Charlotte Harbor and altered upland habitats and concluded that populations established in upland habitats periodically (during the rainy season) invade estuarine habitats but do not appear to be established or to breed there.

Sailfin catfish (*Pterygoplichthys* spp.)

Sailfin catfish are native to South and Central America (Nico and Martin 2001). These popular aquarium fishes, known as "plecos" in the pet trade, were probably introduced into Florida by escaping or being released from ornamental fish farms or aquariums. Several species of sailfin catfishes and similar suckermouth catfishes (*Hypostomus* spp.) have been well established in south and central Florida rivers and canals since the 1980s (Shafland 1996, Hill 2002, Nico et al. 2009).

We first collected sailfin catfish in the Charlotte Harbor estuary in August 1996. We collected a total of 29 specimens, ranging from small individuals to adults (21—374 mm SL), evidence that they are established and breeding in the Charlotte Harbor system. However, they appear to be confined principally to low-salinity areas (Figure 1e), and are well-established and abundant in tributaries of Charlotte Harbor (Peebles et al. 2006, Fraser 2007, Champeau et al. 2009). Although the systematics of sailfin catfish remains unclear, at least four species, the vermiculated sailfin catfish (*Pterygoplichthys disjunctivus*), the Orinoco sailfin catfish (*P. multiradiatus*), the Amazon sailfin catfish (*P. pardalis*), and *P. parnaibae*, may occur in the estuary (R. Ruiz—Carus, pers. comm., Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL).

Spotted tilapia *(Tilapia mariae)*

The spotted tilapia is native to western Africa (Taylor et al. 1986). In Florida, it was first reported in 1974, in Dade County (FMNH 2008). It has since become abundant in canals throughout southeastern Florida (Shafland 1996), and its range has expanded north on Florida's east coast to Melbourne (Shafland et al. 2008).

We collected 1,038 spotted tilapia with 21.3 m seines from the upstream portion of our sampling area in the Caloosahatchee and Orange rivers (Figure 1f), where it was relatively abundant. Five of our catches contained more than 50 fish, and the largest catch had 207. The spotted tilapia is most numerous in backwater habitats in this area (Stevens et al., 2010). Our spotted tilapia data were examined for distributional trends. Most were collected at low-salinity (freshwater and oligohaline) sites (Table 1). Specimens ranged from small individuals to large adults (12—265 mm SL), indicating a well-established breeding population. Small individuals (< 25 mm SL) were collected in all months and were most abundant in November (n = 11) and December (n = 10), suggesting a protracted spawning period with peak reproductive activity in late fall. This spawning pattern is reflected in the absence of a clear seasonal pattern of mean fish length, and maximum fish abundance during the winter months (Figure 2d). Peak spawning of spotted tilapia is reported to take place from November to March in south Florida (FWC 2008).

Other species

Other non—native species have been reported in freshwater areas of the Charlotte Harbor watershed but were not represented in our samples. These include the Nile tilapia (*Oreochromis niloticus*), Oriental weatherfish (*Misgurnus anguillicaudatus*), and pirapitinga (*Piaractus brachypomus*) (Shafland et al. 2008, USGS 2008). Single specimens of the Guayas cichlid (*Cichlasoma festae*), Mozambique tilapia (*Oreochromis mossambicus*), and small—scaled pacu (*Piaractus mesopotamicus*) have also been reported, although these identifications are questionable (USGS 2008). Of these species, only the oriental weatherfish is thought to be established in the system (Fraser 2007, Shafland et al. 2008).

A number of introduced fishes, including the Asian swamp eel (*Monopterus albus*), blackchin tilapia (*Sarotherodon melanotheron*), and pike killifish (*Belonesox belizanus*), could eventually enter the Charlotte Harbor system. They are established in Tampa Bay and southeast Florida. The blackchin tilapia has been successful in colonizing the higher-salinity areas of Tampa Bay (Courtenay et al. 1974). Turner and Snelson (1984) found reproducing populations of the pike killifish at salinities ranging from 0 to 50 in southeast Florida, and Florida populations of the Asian swamp eel also tolerate brackish conditions (Schofield and Nico 2009).

Conclusions

Charlotte Harbor has considerably fewer introduced fish species than adjacent areas. The Tampa Bay drainage, to the north, has about twice as many introduced species, and the Dade and Broward county area of Florida, to the southeast, has about five times as many introduced species (USGS 2008). We suggest two explanations for this difference. First, these areas, although close to Charlotte Harbor, are more heavily populated and developed than Charlotte Harbor is, and the increased habitat modification associated with such urbanization is thought to facilitate the establishment of introduced species (Shafland 1996, Adams and Wolfe 2007, Leprieur et al. 2008). Second, there have been more aquaculture facilities in the Tampa Bay drainage and in southeast Florida than in the Charlotte Harbor area (UF DFAS 2008), and these facilities are thought to be the source of most fish introductions (Courtenay et al. 1974, USGS 2008).

Many of the introduced fishes reported in Florida are from tropical or subtropical areas of Africa, Asia, or South America. In Florida, particularly south Florida, these fishes have the potential to survive and become established because the climate is similar to that of their native habitat. The ranges of some of these species are thought to be restricted by limited cold tolerance (Shafland et al. 2008). For example, the distribution of the spotted tilapia, fairly abundant in our Caloosahatchee River samples but not collected farther north, may be thermally limited (lower lethal temperature = 11.2°C; Shafland and Pestrak 1982, Hill 2002, FMNH 2008). The Mayan cichlid's local range may be limited by its lower lethal temperature of 15°C (Stauffer and Boltz 1994). In contrast, the other six introduced species in the Charlotte Harbor estuary reportedly can survive temperatures of 10°C or less (Shafland and Pestrak 1982, Stauffer and Boltz 1994, Gestring et al. 2006, USGS 2008).

All the introduced fish species we collected, including those reported to inhabit brackish areas in their native ranges (African jewelfish, Mayan cichlid, and brown hoplo), appear to be restricted principally to riverine habitats in the Charlotte Harbor drainage. The reasons for their lack of success in colonizing estuarine areas are unclear. However, those with some salinity tolerance can probably use the estuary as a "saline bridge" to move between tributaries (Brown et al. 2007), particularly during periods of high precipitation and runoff.

Acknowledgements

We thank P. Stevens and the staff of the Charlotte Harbor Field Laboratory for their dedicated field assistance. This study was supported in part by the South Florida Water Management District, by funds collected from State of Florida Saltwater Fishing License sales, and by the Department of the Interior, U.S. Fish and Wildlife Service, Federal Aid for Sport Fish Restoration Grant No. F-43. We appreciate the comments of several anonymous reviewers and the editorial suggestions of J. Colvocoresses and B. Crowder.

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