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Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views

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Abstract

We summarized data from eight quantitative fish surveys conducted in southern Florida to evaluate the distribution and relative abundance of introduced fishes across a variety of habitats. These surveys encompassed marsh and canal habitats throughout most of the Everglades region, including the mangrove fringe of Florida Bay. Two studies provided systematically collected density information over a 20-year period, and documented the first local appearance of four introduced fishes based on their repeated absence in prior surveys. Those species displayed a pattern of rapid population growth followed by decline, then persistence at lower densities. Estuarine areas in the southern Everglades, characterized by natural tidal creeks surrounded by mangrove-dominated marshes, and canals held the largest introduced-fish populations. Introduced fishes were also common, at times exceeding 50% of the fish community, in solution holes that serve as dry-season refuges in short-hydroperiod rockland habitats of the eastern Everglades. Wet prairies and alligator ponds distant from canals generally held few individuals of introduced fishes. These patterns suggest that the introduced fishes in southern Florida at present may not be well-adapted to persist in freshwater marshes of the Everglades, possibly because of an interaction of periodic cold-temperature stress and hydrologic fluctuation. Our analyses indicated low densities of these fishes in central or northern Everglades wet-prairie communities, and, in the absence of experimental data, little evidence of biotic effects in this spatially extensive habitat. There is no guarantee that this condition will be maintained, especially under the cumulative effects of future invasions or environmental change.

Much has been written about the potential of introduced fishes to invade and disrupt natural aquatic communities, but recent reviews have revealed a complex reality with many invasions leading to little or no apparent effects on the native fauna (Moyle and Light 1996; Gido and Brown 1999). We examined the introduced ichthyofauna of southern Florida, USA, to evaluate the potential impact of non-indigenous fishes over a diversity of aquatic habitats, including freshwater and brackish marshes, canals, and rockland marshes. Two important contributions to the body of work on introduced fishes in southern Florida have recently been published that provide opposing perspectives on the ecological significance of the dozen or more species established there. Shafland (1996a) reported that fishes introduced into Florida have had few, if any, demonstrably negative effects on the native ichthyofauna. Further, he suggested that scientific and environmental/aesthetic views have often been confused in assessments of fish introductions (Shafland 1996b). Courtenay (1997) provided an alternative view, arguing that no effect has been documented because no quantitative data have been gathered. Both authors claimed that there were limited ecological data from southern Florida to resolve these issues. Few could disagree with Shafland that introduction of fishes is a controversial topic, where systematically gathered data and anecdotal information are freely mixed. However, Courtenay's sentiment that lack of observed damage does not equate with no damage is equally important. This discussion mirrors debates in other regions on the wisdom of authorized introductions and feasibility of management to control or extirpate introduced species (Dill and Cordone 1997).

More than 50 species of fishes have been introduced into southern Florida fresh waters during the past 40 years (Shafland 1996a; Courtenay 1997; Fuller et al. 1999). Prior to human intervention, the southern tip of Florida from Lake Okeechobee to the coastal mangrove forests was largely covered by the grassy wetlands of the Everglades. Seasonally flooded cypress forests bounded the Everglades to the west and limestone uplands to the east. By the 1960s, extensive agricultural and water-management developments had greatly diminished the area of aquatic habitats, decreased the hydroperiod of many wetlands, and added canals that provided permanent aquatic refuges unlike any native habitat (Gunderson and Loftus 1993). Introduced fishes became established in canals as early as the 1950s, when pike killifish (*Belonesox belizanus*) and oscars *(Astronotus ocellatus)* became the first introduced species recorded (Belshe 1961). Additional species were added both by accidental and intentional releases of ornamental species, as well as by intentional efforts to control aquatic weeds or to enhance sport fisheries. In 1984, the Florida Game and Fresh Water Fish Commission (GFC) introduced peacock bass (*Cichla ocellaris*), native to South America, to control other introduced species and to establish a new game fishery in canals of the southeastern urban area of the state (Shafland 1995).

The history of introduced fishes in southern Florida is marked by biologists expressing concern for native fish communities, efforts by fisheries biologists to eliminate introductions, and ultimate resignation and acceptance of their presence by fisheries managers (Courtenay and Robins 1973; Courtenay et al. 1974; Shafland and Foote 1979; Shafland 1986; Fury and Morello 1994). Though we are unaware of any additional introductions planned for southern Florida, illegal invasions continue to occur routinely (e.g., jaguar guapote *Cichlasoma managuense* (Shafland 1996b)). Presently, debate continues over the effects, or lack thereof, of introduced fishes on indigenous aquatic communities in southern Florida.

Several quantitative studies of southern Florida's freshwater and estuarine fish communities were not used either by Courtenay or Shafland in their assessments. The longest running study, begun in 1965 and continuing to present, uses pull traps to sample fishes in northern Shark River Slough in Everglades National Park (ENP; Higer and Kolipinski 1967; Kushlan 1976); four additional sampling techniques, throw traps, electrofishing, block nets, and minnow traps have been used systematically to provide quantitative data (either number of individuals m^{-2} or catch per unit effort (CPUE)) of fishes over time from fixed sampling locations. More recently, similar studies have been completed or are underway in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Water Conservation Area 1 (WCA-1) (Jordan 1996), WCAs 2A, 3A and 3B, throughout the ENP in both Taylor Slough and Shark River Slough, in the Rocky Glades area of the ENP, and from coastal habitats along northern Florida Bay (Figure 1). All of those studies sought to sample fishes

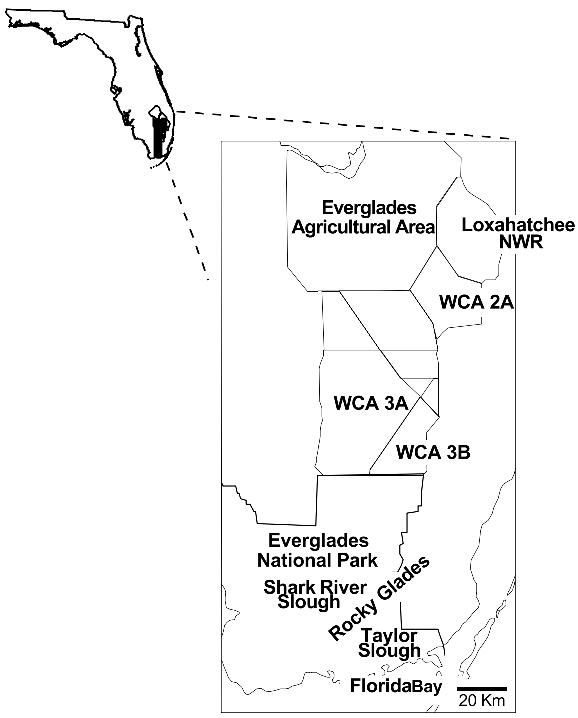

Figure 1. Map of the study area. Solid lines indicate canals.

systematically without distinction between native and introduced status, but were limited by recognized and measurable gear biases. The studies provided data on the relative abundance of introduced and native fishes over time across much of southern Florida. They documented the dynamics of invasions by four species of fishes into southern Florida, and provided insight into other species not abundant enough in the study areas to be sampled routinely. Complete analysis of native fish communities in these data is beyond the scope of a single paper. However, by drawing these quantitative data on introduced fishes in southern Florida together in one paper we hope to move forward the discourse begun by Shafland and Courtenay.

Methods

We report data from eight studies that used a variety of techniques across many of the inland aquatic habitats of southern Florida. Several studies were conducted in more than one habitat: six sampled in freshwater wet prairies, two in canals, one in alligator ponds, one in rockland solution holes, and one in mangrove-dominated estuarine marshes. Characteristics of those habitats have been described elsewhere (Odum et al. 1982; Loftus and Kushlan 1987; Loftus et al. 1992; Gunderson and Loftus 1993). We examined data collected between 1965 and 2000. Two studies are long-term monitoring efforts with periods of record exceeding two decades, long before the first nonindigenous species entered the study areas. We organized the studies by sampling techniques employed.

Throw traps. The 1-m^{-2} throw trap has been used by many biologists in southern Florida to obtain quantitative estimates of fish density and community composition in vegetated freshwater marshes. Sampling efficiency and biases of this technique have been examined in several studies (Kushlan 1981; Loftus and Eklund 1994; Chick et al. 1992; Jordan et al. 1997; Turner and Trexler 1997). Those studies concluded that the throw trap samples approximately 80% of the fishes present in an area, and is very effective in habitats with vegetative cover from 18 to 680 stems m^{-2}, the entire range examined. No other technique has fared as well in comparative studies (Kushlan 1981; Chick et al. 1992). Nevertheless, the density of large fishes (i.e., standard length (SL) $>$ 8 cm) is too low in most Everglades marshes to be estimated effectively with throw traps (Jordan et al. 1997). Thus, throw-trap data are most useful for describing small fish (i.e., SL $<$ 8 cm) density and composition. Throw traps were used to sample 1-ha grided plots, where they were thrown in randomly pre-selected locations. We examined several studies of varying duration conducted between the years 1985 and 1996. The animals trapped within were removed by a standardized protocol, generally involving bar seines and/or dip nets.

Pull Traps. Two sample sites established in Shark River Slough in 1965 have been continuously sampled to the present, usually monthly, using a rigid-frame mesh pull trap (Kushlan 1976, Figure 1). This technique, in which a net is left submerged on the marsh surface and lifted by a pulley system, has created deep-water microhabitats that attract large fishes (Loftus and Eklund 1994). In spite of this artefact, the long-term nature of the study permits comparisons of introduced species abundance over a long time scale.

Drop nets. Red mangrove trees (*Rhizophora mangle*) with complexes of exposed prop roots preclude use of throw traps in southern Florida's estuarine zone. There, permanently positioned drop nets have been employed from 1990 to 1996 (Lorenz et al. 1997). These nets are dropped to enclose 3-m $\times$ 3-m plots that are treated with rotenone to permit fish removal. Unlike throw traps, drop traps re-sample fixed locations over time.

Minnow traps. Short-hydroperiod rockland habitats bordering the Everglades are characterized by exposed limestone pitted with solution holes that serve as refuges for fishes during the dry season (Loftus et al. 1992). Today, this habitat is found in the Rocky Glades area of ENP (Craighead 1971), but is rare outside of the Park because of development. In the Rocky Glades, shallow wetlands that surround the solution holes were inundated between July and March in 1999 and 2000; the water table dropped below ground surface isolating fishes in solution holes in the intervening months. Minnow traps were the best technique to sample fishes in solution holes because of their confined space, structural complexity, and sharp edges. In 1999 and 2000, unbaited wire minnow traps with 3-mm mesh were placed in solution holes overnight. The fishes collected were fin-clipped and returned alive to the solution hole where they were captured. Nineteen solution holes were sampled weekly from January to July in 1999, and 29 holes were sampled over the same time period in 2000. Wire minnow traps are know to be relatively inefficient, often with marked interspecific variation in trap susceptibility (Pot et al. 1984; He and Lodge 1990; Jackson and Harvey 1997). In this environment, water clarity is high much of the year permitting visual surveys to accompany the minnow trap data. These surveys confirmed the general patterns of relative abundance reported here (R.M. Kobza, unpublished results).

Block nets. To sample large fishes (>8 cm SL), block nets and boat electrofishing were employed in south Florida. The block net encircled a 0.1-ha area that was treated with rotenone (Nielsen and Johnson 1983), then visited daily for two or three consecutive days to remove as many fishes as possible. Two studies using block nets have been conducted in our area. One contrasted fish communities in canals with those in nearby marshes (GFC, Fury et al. 1995). This study was conducted between 1991 and 1996 and employed a single block net to sample six canal locations and seven marsh locations from WCAs 2 and 3. Fishes in canal block nets were sampled by submerged primacord detonation. The second study was conducted in 1997 in marshes of ENP and WCA 2 and 3 (Florida International University (FIU), Chick et al. 1999). In that study, a pair of block nets were set in each of 11 different locations and dosed with rotenone (22 total). Only species exceeding 8 cm SL were enumerated to standardize data collection. The FIU and GFC marsh samples provide an interesting contrast because the FIU sites were located far from any canal, while those of GFC were located relatively near canals.

Electrofishing. Two studies have used electrofishing to sample fishes in Everglades marsh habitats. An airboat-mounted Smith-Root type VI electrofisher was used to sample alligator ponds in Shark River Slough from 1983 to 1996. The same six ponds were visited monthly (1983–1986) or semi-annually (1986–1996) during the study (Nelson and Loftus 1998). Each pond was sampled for 300 s of pedal time, and fishes were returned live to the ponds after processing. The second study used an airboat-mounted Smith-Root model GPP 9.0 electrofisher to sample large fishes in wet-prairie habitats from October 1997 to October 1999. Chick et al. (1999) described the techniques and equipment used in detail, and evaluated the effectiveness of this method. Eleven sites, corresponding to some of the throw trap sites described above, were sampled quarterly in three regions: WCA-3A, and both Shark River Slough and Taylor Slough in ENP. At each site, nine 300-s (pedal time) electrofishing transects were conducted in the vicinity of the three 1-ha grided plots. All fishes captured were allowed to recover and returned to the marsh alive.

Data presentation. We chose to forego formal statistical analyses of the data, but instead report the number of specimens of introduced species and the total number of fish examined in each survey. A strength of our study is that it draws together results of many sampling techniques to illustrate community patterns robust to gear biases and habitat differences. This is also a weakness, however, because it limits direct comparability of our data and complicates formal statistical analyses. Instead, we have chosen a narrative comparison of large-scale patterns, attempting to avoid over-interpreting our diverse data. Detailed statistical analyses of each data set will be reported elsewhere.

Results

The sampling studies we reviewed resulted in the capture of more than 150,000 fishes (Table 1). Relatively few introduced fishes were collected by throw trap in freshwater wet prairies, despite the extensive sampling efforts. Electrofishing and block nets in wet prairies revealed that introduced fishes made up from 10% to 20% of the large-fish community in both Taylor and Shark River Sloughs. Introduced fishes were also common at times in canal, estuarine, and Rocky Glades habitats. In total, three families comprised the specimens of the seven introduced species collected: Cichlidae (5 species), Clariidae (1 species), and Poeciliidae (1 species). Our data documented the population growth and decline of two species, pike killifish and black acara (*Cichlasoma bimaculatum*) at one location, and large fluctuation in abundance in a third species, the Mayan cichlid (*Cichlasoma urophthalmus*), at a different site. A fourth species, spotted tilapia (*Tilapia mariae*), invaded and increased in abundance at one site but, unlike the previous species, it has not been observed to decline. Oscars were only reported in or near canals, where they were the most commonly collected species. The remaining two species (walking catfish (*Clarias batrachus*), blue tilapia (*Oreochromis aurea*)) were infrequently collected at the sites included in this study.

Table 1. Frequency of non-indigenous fishes, relative to the total number of fishes collected reported by study.

Location and method	*N*	Study period	Total fishes	WC	PK	MC	BA	BT	ST	O	Non-native (%)
Throw traps in wet prairies											
WCA-1	1296	1990–1992	33,601	2	0	0	21	0	0	0	0.1
WCA3A	1485	1995–1996	19,664	1	0	0	7	0	0	0	0.0
SRS-N	3035	1985–1995	26,558	0	12	74	0	0	1	0	0.3
SRS-S	1029	1993–1996	18,728	0	17	85	0	1	11	0	0.6
TS	67	1996	4281	0	1	6	0	0	0	0	0.2
Rocky Glades	188	1998–2000	738	0	2	9	4	0	0	0	2.0
Pull traps in wet prairies											
ENP	371	1965–1996	49,384	0	251	17	9	0	23	0	0.6[a]
Block nets in canals[b]											
L67-A	3	1992, 1996	2655	0	0	16	0	0	47	202	10.0
L35-B	3	1993, 1996	3246	1	0	0	0	1	30	2	1.0
WCA3A	6	1994–1995	2084	0	0	14	5	0	40	67	6.0
Block nets in wet prairies[b]											
WCA2 (GFC)	2	1992	221	0	0	0	0	0	21	0	9.5
WCA3A (GFC)	19	1992–1996	3881	0	0	3	37	0	106	5	3.9
WCA2 (FIU)	2	1997	176	0	0	0	0	0	0	0	0.0
WCA3A (FIU)	3	1997	132	0	0	0	0	0	0	0	0.0
SRS-N (FIU)	1	1997	22	0	0	1	0	0	0	0	4.5
SRS-S (FIU)	2	1997	205	0	1	35	0	5	0	0	20.0
TS (FIU)	3	1997	37	0	0	6	0	0	0	0	16.2
Minnow traps in solution holes											
Rocky Glades	1151	1999–2000	3321	13	87	67	254	0	0	0	12.7
Electrofishing in wet prairies											
WCA3A	252	1997–1999	453	1	0	2	0	0	1	0	0.9
SRS-N	69	1997–1999	117	0	0	3	0	0	1	0	3.4
SRS-S	201	1997–1999	444	5	0	28	0	14	4	0	11.5
TS	207	1997–1999	118	5	0	7	0	5	0	0	14.4
Electrofishing in ponds											
SRS	52	1983–1996	10,915	39	29	4	7	0	3	0	0.8
Drop nets in mangroves											
ENP	1149	1990–2000	54,979	4	135	7527	4	1	587	0	15.0

N – number of samples collected to yield the total number of fishes, WC – walking catfish, PK – pike killifish, MC – Mayan cichlid, BA – black acara, BT – blue tilapia, ST – spotted tilapia, O – oscar, SRS-N – northern region of Shark River Slough, SRS-S – southern region of Shark River Slough, TS – Taylor Slough.

[a]The percentage of non-native fishes is underestimated here because of the long period of sampling before invasions began (see Figure 2).

[b]These data are limited to fishes with maximum standard length >8 cm to make them comparable to canal block net and marsh electrofishing data. The source of the block net data is indicated in parentheses.

Throw traps. Few specimens of introduced fishes were collected in Everglades wet prairie habitats in the five surveys we examined (Table 1). Of the 80,000 fishes collected by throw trap, only 239 (0.3% of the total) were not native to southern Florida. During the period of record (1985–1996), the number of species of introduced fishes was the greatest in the southern Everglades (Shark River Slough), where four taxa were collected. The frequency of introduced fishes was also the greatest in southern Shark River Slough (Table 1), where most specimens were collected at one study site adjacent to a natural creek at the marsh–mangrove interface. Throw-trap samples from the short-hydroperiod marshes of the Rocky Glades yielded a greater frequency of introduced fishes than throw-trap samples in wet prairies nearby (2%, Table 1).

Pull traps. From 300 to 4500 fish were collected each year by this technique. Between 1965 and 1988, no introduced species were collected. After 1988, 10–150 specimens of introduced fishes were collected each year (Figure 2a). The first introduced species, black

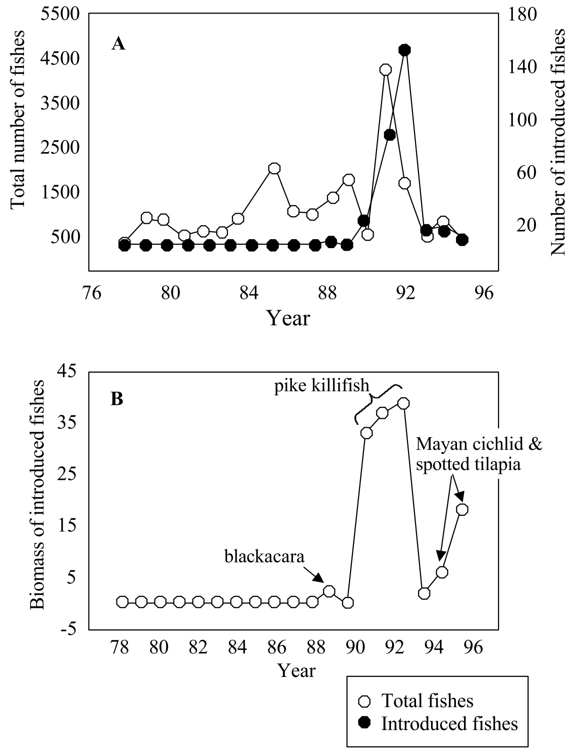

Figure 2. Freshwater pull-trap data from the ENP. A. The total number of all fishes and of introduced fishes collected per year. Samples were collected monthly and summed to yield annual totals. B. The percentage of total fish biomass that came from introduced species. Peaks in 1989, 1991–1993, and 1996 mainly resulted from the species indicated.

acara, appeared in 1989. Biomass of that species never exceeded its original level, and it has remained a minor component of the community to present (Figure 2b). In 1991, a second species, pike killifish, appeared at high frequency (35% of the biomass) and peaked at around 40% of the biomass in 1993 before returning to much lower levels (Figure 2b). Pike killifish was the most commonly collected species of introduced fish collected by this technique (Table 1). Like black acara, this species is currently a minor component of the fish community. In 1995, two additional species appeared in the pull-trap samples, Mayan cichlid and spotted tilapia. These increased in relative abundance in the final year of available data, 1996.

Drop traps. Drop-traps sampling estuarine sites along the northern border of Florida Bay yielded from 1600 to 10,000 fish per year, and captured from nearly zero to 8258 specimens of non-indigenous species (Figure 3a). The euryhaline Mayan cichlid was the

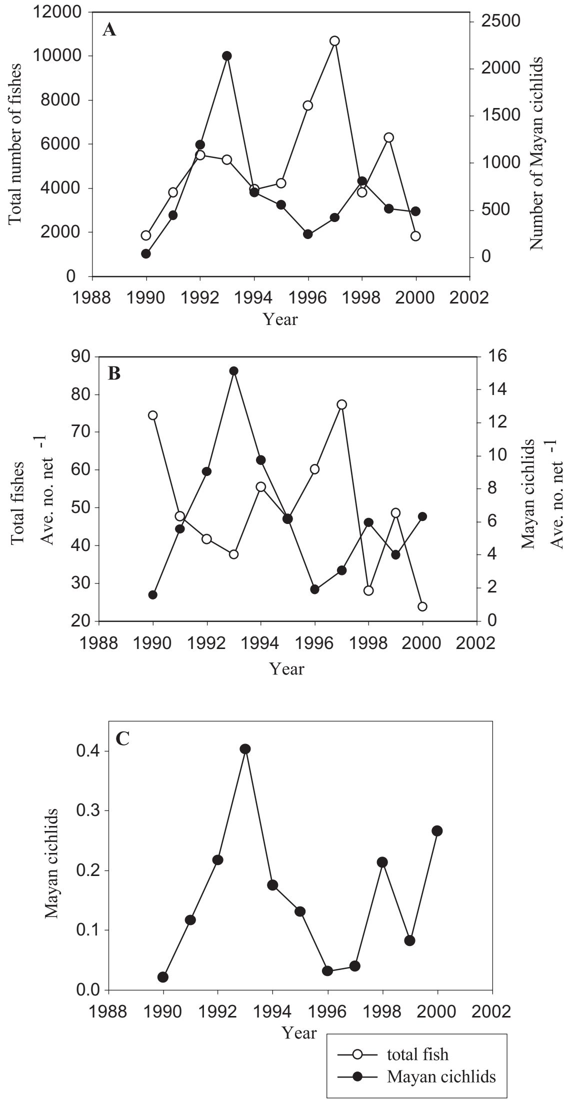

Figure 3. The temporal pattern of Mayan cichlid collections made by estuarine drop trap. A. The total number of all fishes and of Mayan cichlids collected by year. B. The average number of fishes of all species and Mayan cichlids per net sample per year. C. The proportion of all fishes that were Mayan cichlids by year.

major constituent of introduced fishes in these samples (Table 1), so we have focused on its abundance. The number of samples collected varied among years, leading us to standardize the data as the average number of fish per net-sample. The average number of all species collected per sample began very high, declined for several years before rebounding in 1996, and then fell again in 1998 (Figure 3b). The number per trap of Mayan cichlids displayed a marked ‘boom-and-bust’ pattern over the study period, in an inverse pattern to the total catch (Spearman's rank correlation, $r_s = -0.664$, $n = 11$, $P = 0.04$). Mayan cichlids increased from near zero in 1990 to approximately 44% of all fish collected in 1993, before declining to almost zero in 1996, and finally rebounding to over 20% of the catch in 1998 and the first half of 2000 (Figure 3c). Each of the declines in Mayan cichlid collection followed extreme cold events.

Minnow traps. The frequency of non-indigenous fishes collected by minnow traps in solution holes (12.7%) was high compared to contemporary collections by throw trap (2.0%) from the marsh surface nearby (Table 1). The collection of introduced fishes from solution holes varied among four study areas in the Rocky Glades and, at some sites, over the course of the dry season (Table 2). Non-indigenous fishes were never common at one of the areas (Pa-Hay-Okee), but ranged from 10% to 62% at the others (Table 2). At the Wilderness Road site, there was a marked increase in the frequency of non-indigenous fishes late in the dry season when the marsh surface was dry and fishes were restricted to solution holes. That site had the shortest hydroperiod (highest elevation) of the four studied, and the fewest fish. Black acara were very common at the Main Road and Context Road sites late in the dry season of 1999, and were the most commonly collected non-indigenous species in 2000. In general, more fishes and more non-indigenous fishes were collected in 1999 than in 2000 at these study sites, in spite of a greater sampling effort in 2000 (10 more solution holes were monitored in 2000 than in 1999). There was less rainfall and the wetlands dried more completely in 1999 than in 2000, possibly forcing fishes to spend more time in solution-hole refuges in that year.

Block nets. GFC. Over 7900 fishes were collected in block nets set in canals between 1992 and 1996. Approximately 5% of these fishes were introduced species, and the frequency ranged from 1% to 10% among study sites (Table 1). Oscars and spotted tilapia were the most commonly collected introduced species during this study. Introduced fishes comprised 4–9.5% of the fishes collected by this technique in marshes near canals. Spotted tilapia was the most common species, and oscars were rare (Table 1).

The total biomass of all fishes in block-net samples from canals averaged 579 kg/ha, while those from marshes averaged only 40.5 kg/ha (Table 3). These samples differed in the relative biomass of introduced fishes: canal samples averaged 63.5 kg/ha (12.4% of total) of introduced fishes while marsh samples averaged only 1.4 kg/ha (4.2% of total).

FIU. Paired block-net samples collected from marsh habitats in WCAs 2 and 3, and ENP indicated that introduced species were more prevalent in the southern Everglades than elsewhere (Table 1). We took no introduced fishes from the five sites in the WCAs, whereas three species were collected from Shark River and Taylor sloughs. Few fishes of any species were collected in Taylor Slough. The small number of specimens collected in Taylor Slough decreased the likelihood of detecting introduced species, although several Mayan cichlids were collected at site TS-MD, which is adjacent to a small canal.

Electrofishing. Almost 11,000 specimens were examined during the electrofishing program in northern Shark River Slough alligator ponds (Table 1). Five species of introduced fishes were collected from 1983 to 1996. Most specimens were captured between 1987 and 1996. The walking catfish was exceptional in that it was first collected in 1984, but had been recorded in the slough earlier by sampling with other techniques. Fewer than 1% of all fish collected in these alligator ponds were non-indigenous.

A total of 1132 fish were captured during the electrofishing study of wet-prairie habitats (Table 1). Four non-indigenous species were captured, comprising 6.7% of the total number of large fish captured. Of these four species, Mayan cichlid were the most frequently captured and accounted for more than 50% of all non-indigenous fish. Abundance of introduced fishes was far greater in the southern portion of the Everglades. Fewer than 1% of all large fish captured in WCA-3A were non-indigenous, whereas non-indigenous fish comprised 9.8% and 14.4% of all large fish captured in Shark River and Taylor Sloughs, respectively (Table 1). The greatest relative abundance of non-indigenous fishes in both Shark River and Taylor Sloughs occurred in the southern-most sites sampled there, within sight of the mangrove zone.

Discussion

The data we gathered indicate that introduced fishes have not flourished equally in aquatic habitats in southern Florida. We observed marked spatial variation in their prevalence across regions and habitats, which may

Table 2. Non-indigenous fishes collected by minnow traps in solution holes at four sites in the Rocky Glades, ENP, in 1999–2000.

Region	Black acara	Mayan cichlid	Walking catfish	Pike killifish	Total all species	% Non-indigenous	Black acara	Mayan cichlid	Walking catfish	Pike killifish	Total all species	% non-indigenous
	Early 1999						Late 1999					
Pa-Hay-Okee	0	0	0	0	229	0	0	14	0	14	847	3.3
Main road	6	3	4	0	29	44.8	51	4	3	12	131	53.4
Wilderness road	2	3	0	2	21	33.3	10	2	1	0	21	61.9
Context road	8	9	0	12	613	4.7	118	24	3	41	665	28.0
	Early 2000						Late 2000					
Pa-Hay-Okee	0	0	0	0	4	0	2	0	1	0	257	1.2
Main road	2	3	0	6	61	18.0	9	0	0	0	52	15.4
Wilderness road	3	1	1	0	49	10.2	22	0	0	0	35	62.9
Context road	3	2	0	0	135	3.7	18	2	0	0	172	11.6

The ‘early’ samples were collected early in the dry season when the marsh surface was still inundated (January–mid-March); the ‘late’ samples were collected after the marsh surface had dried, restricting fishes to solution holes. Table entries are the number of fishes collected and the % non-indigenous. Total all species is the total number of fishes collected during that time period.

Table 3. Biomass of fishes collected by block net by the GFC from Everglades marsh and canal habitats.

Area	Date	All fish (kg/ha)	Introduced fishes kg/ha (%)
Canals			
L67-A	5/92	1048	202.4 (19.3)
L35-B	4/93	112	13.7 (12.2)
WCA-3	5/94	167	34.2 (20.5)
WCA-3	5/94	672	63.3 (9.4)
L35-B	5/96	979	3.8 (0.4)
L67-A	5/96	501	63.9 (12.8)
Mean canal		579 ± 316	63.5 ± 57.9
Marshes			
WCA-3	10/91	41	3.1 (7.5)
WCA-2A	11/92	51	0.4 (0.7)
WCA-3A	10/92	22	1.2 (5.7)
WCA-3A	10/93	30	0.3 (5.5)
WCA-3A	11/94	53	3.0 (5.5)
WCA-3A	11/95	37	1.6 (4.4)
WCA-3A	10/96	50	0.0 (0)
Mean marsh		40.5 ± 8.7	1.36 ± 0.9

be a function of the proximity of the sampling area to the site of introduction, to preferred habitats such as canals, or regional climatic variation. For four species, we documented a pattern of early colonization and rapid population growth, followed by decline, and then persistence. The abundance of one of those species, the Mayan cichlid, appeared to fluctuate markedly, linked to annual temperature minima. These data serve as a baseline for the Everglades region, against which future changes in introduced fish abundance can be assessed. Nevertheless, descriptive sampling of this sort provides limited ability to establish causal relationships between introduced fishes and changes in the community they invade. Below, we evaluate what can be determined from these descriptive data, and briefly propose future research needed to assess effects of introduced species on community dynamics.

The use of a variety of sampling methods permits us to draw conclusions about native and introduced fish species that inhabit an extensive range of Everglades habitats. Courtenay (1997) argued that limited quantitative information on fish communities in southern Florida hindered assessment of the effects of introduced species at that time. We have demonstrated that data now exist from several habitats in southern Florida. Those data indicate that the relative abundance of introduced species is low in some habitats and regions, particularly wet prairies in the northern and central Everglades. Analysis of community composition of the native fish fauna in wet prairies across all regions also suggests no marked changes to date (Loftus 1988; Loftus and Eklund 1994; Trexler et al. 1996). Does this apparent lack of change in the native fish community in wet prairies indicate little or no effect of invaders on community regulation and dynamics? We assert that our sampling programs would have noted extinctions or dramatic ecological shifts in composition or size structure in fish communities, should any have occurred. This suggests the relative abundance of introduced species in wet prairies may not be sufficient to effect regulatory control of population size or community composition. However, examples of relatively uncommon species acting as keystone species (Ricklefs 1990) provide a caveat to this conclusion.

In contrast to wet prairies, canals offer several features that appear to favor higher population levels of introduced species. Canals provide refuge during droughts and dry seasons when marsh surfaces are exposed. Small fishes moving into canals from marshes during the dry season provide an allochthonous food source to large fishes there (Howard et al. 1995). Both native and introduced fishes inhabiting canals move into adjacent marshes in the wet season (Howard et al. 1995). Large fishes inhabiting Everglades marshes, including introduced species, may be limited by availability of deep-water refuges. The need for thermal and deep-water refuges may also explain the greater density of introduced fish in the extreme southern Everglades, where winter temperature is milder and natural tidal streams are often nearby. Because the tropically derived introduced fishes of southern Florida are susceptible to temperature stress in some winters (Loftus and Kushlan 1987), they probably find thermal refuge in deep canals. Many south Florida canals penetrate the aquifer where annual minimum temperatures are generally above 17 °C (Shafland 1989, 1995). More quantitative data on fishes in canals and adjacent marsh habitats are needed to better examine the interrelationship of these habitats. Three data sets indicated that the density of introduced species was greater in wet prairies located near habitats where they reached relatively high frequency (the mangrove zone and canals).

Although the proportion of introduced fishes is greater in Everglades regional canals than in wet prairies, they did not outnumber natives, and never exceeded 20% of the community by biomass. Both Shafland (1989) and Courtenay (1997) stated that introduced fishes dominate canals. Their assessment is probably more accurate for urban canals in southeastern

Florida (see Shafland 1999), especially those lacking connections to wetlands or extensive littoral-zones. Native fishes may be more dependent on wetlands for feeding and spawning than introduced species, and possibly are at a disadvantage in canals lacking access to wetlands. The estuarine zone of northern Florida Bay provided our only data from a natural ecosystem where introduced fishes routinely reached high densities. There, the catch of native species varied inversely with the catch of Mayan cichlids. Although this pattern does not provide proof of a cause-and-effect relationship, further research in this habitat may provide evidence of community-level effects as a result of the Mayan cichlid invasion.

Our data clearly illustrate that introduced species require time to expand across southern Florida from the point of introduction. For example, the Mayan cichlid peaked at our study site in the mangrove zone in 1993, started to become abundant at the pull-trap site in northern ENP in 1996, and were first observed in WCA-3A in 1993 (P. Shafland, personal communication) but are not yet abundant there. It seems likely that this represents a range expansion from the area of introduction to the south (Loftus 1987). Thus, assessments at any point in time during range expansion may not capture long-term effects of these dynamic new populations. Courtenay (1997) noted that rare introduced species may increase in number at a future date. The pike killifish provides a ready example: it persisted as a small population in several canals east of the Everglades for more than 20 years before expanding dramatically in the 1980s and 1990s (Courtenay 1997). A final assessment of introduced fishes in southern Florida and their effects on native aquatic communities, even if restricted to species present today, may not be written for years to come.

All fish sampling techniques have taxa and habitat biases. Drawing our data from such a diversity of sources dictates circumspection in developing general conclusions. For example, susceptibility to electrofishing varies among fish species based on their somatic characteristics (Zalewski and Cowx 1990). Cichlids are widely believed to be less susceptible to shocking than many other fishes (Chick et al. 1999). For that reason, relative-abundance estimates of non-indigenous fishes from electrofishing are likely to be conservative. There are also microhabitat and seasonal fluctuations in abundance that may yield under- or overestimates of the relative abundance of introduced fishes from sampling focused on one microhabitat. For example, we caught relatively few specimens of introduced species in the Rocky Glades during the wet season when sampling on the marsh surface in the same area where they are dominant taxa in solution holes during the dry season. We believe that black acara, pike killifish, and walking catfish seek out solution holes and are ‘over-represented’ in that local habitat, relative to their abundance in the region. However, their dominance in solution holes during the stressful dry season may have greater ecological consequences than on the marsh surface, where native fishes may be replenished by immigration from nearby wet prairies. Also, minnow traps sampling the fringes of tree islands may yield moderate frequencies of juvenile introduced species (e.g. black acara), while throw trap and block net samples in the adjacent marsh yield few, if any specimens of those taxa (Laura Brandt and the authors, personal observations). The validity and significance of such microhabitat patterns should be a topic of future research.

We found little evidence of ecological effects of introduced fishes on native freshwater fish communities in southern Florida, especially in wet prairies. While consistent with Shafland’s conclusions, this does not negate Courtenay’s (1997) observation that cryptic or delayed effects may have been overlooked. Negative results from field sampling data should not be used to infer the absence of negative biotic interactions. Experimental studies, conducted across the range of environmental conditions, are ultimately needed to delineate biotic interactions necessary to predict the impact of invading species on natives. For example, important local effects resulting from feeding or habitat disturbance may go undetected by studies conducted at an improper scale (Cowell 1984; Lodge et al. 1998). Many ecological effects that are not readily observed are possible, including a variety of interactions among introduced and native species that are negative for natives. For example, we have observed competitive interactions among substrate-spawning species (e.g., introduced blue tilapia, spotted tilapia, and Mayan cichlids interacting with native largemouth bass (*Micropterus salmoides*), warmouth (*Chaenobryttus gulosus*), and spotted sunfish (*Lepomis punctatus*) in the ENP. We have also observed nest predation by Mayan cichlids and walking catfish on native centrarchids. Although data from the Rocky Glades showed that invading species came to dominate some dry-season aquatic refuges, this outcome was not consistent across all study sites or between the two years of data gathering. Non-native species, especially the black acara, may have done better in the drier of the 2 years studied. Subtle effects on native invertebrate or aquatic plant communities are quite possible, but simply no one is looking for them.

It is likely that the balance between native and non-native species depends on local environmental conditions, and varies among years with rainfall and minimum temperature (cold winters favor natives over most species introduced at present). It is unclear how the frequency of years benign to an invading species, or the spatial ecology of beneficial habitat patches, may tip the ecological balance. Several introduced species presently in southern Florida come from habitats in Central America remarkably similar to those they now inhabit in Florida (e.g., Faunce and Lorenz 2000). The abundance of introduced fishes of Everglades wet prairies, presently all of tropical origin, may be limited by occasional droughts and cold temperatures (Shafland and Pestrak 1982) to levels too low to adversely affect native species. Indeed, the relative abundance of non-indigenous fishes in wet prairie habitats was greatest in the southern (and warmest) portion of the Everglades. Alternatively, intermittent environmental disturbances such as droughts and hurricanes, or gradual ones such as climate change, could open opportunities for invading species to overtake natives and shift the balance of community regulation (Roman et al. 1994; Moyle and Light 1996).

In some ecosystems, introduced fishes have caused catastrophic effects on communities in which they have become established. For example, introduction of fishes into North American desert streams has resulted in extinction of some native endemic species (Minckley and Deacon 1991). Why have the many introductions in southern Florida failed to produce marked effects? The reason no fish extinctions have been recorded from southern Florida introductions may ultimately lie in the composition of our native fauna. Southern Florida lacks endemic specialized species with restricted habitat requirements, the kind of species most susceptible for extinction. This community of generalists may be inherently resilient in the face of natural, and now anthropogenic, disturbances. However, this ability to cope may provide no guarantee for future persistence given the extensive cumulative alterations of the southern Florida ecosystem, including further introductions of fishes.

Complete assessments of introduced species, their costs and benefits, are not in the realm of science or the research reported here (Shafland 1996b). Instead, science provides a method of inquiry and problem solving, not a method to determine societal values of historical and anthropogenically altered fish communities. However, a systematic basis for *post facto* evaluation of ecological effects of fish introductions in southern Florida and elsewhere is needed, but has not been applied. This must include long-term quantitative sampling of communities affected and unaffected by introductions across a range of sites. Ideally, samples should be obtained before a new species expands into an area, afterward, and simultaneously in nearby areas lacking the new species (a BACI sampling design (Stewart-Oaten et al. 1986; Underwood 1994)). Sampling techniques should be sensitive and appropriate to all members of the community, but especially for small-sized and rare taxa susceptible to new predators and competitors. The importance of managing and maintaining native biodiversity must not be overlooked. Data on habitat use and feeding habits of the new species should be obtained and, ideally, experimental studies of direct and indirect effects of the new species should be carried out. The composite of monitoring studies reported here, and others underway, provide an excellent basis for assessing future introductions in southern Florida, especially if coupled with experimental analysis of community regulation.

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