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ORIGINAL PAPER

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Contrasting invasion histories and effects of three non-native fishes observed with long-term monitoring data

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Abstract Boom-bust population dynamics are long-recognized phenomena during species invasions, but few studies documented impacts of these dynamic changes. The Florida Everglades is the largest wetland in the United States, is undergoing a multi-decade hydro-restoration effort, and has been invaded by several tropical freshwater fishes. We used a 26-year dataset of small native marsh fishes and decapods to assess potential effects of African Jewelfish (*Hemichromis letourneuxi*) invasion and compared their effects to those of a more recently invading species, Asian Swamp Eels (*Monopterus albus/javanensis*), and a long-established non-native species, Mayan Cichlids (*Mayaheros urophthalmus*). Unlike boom-bust dynamics of jewelfish, swamp eel abundance increased and stabilized over the course of this study. After accounting for effects of hydrologic variation, the densities of several native species were more reduced by either jewelfish or swamp eels than by native fish predators, while effects of Mayan Cichlids were similar to those of native fish predators. Impacts of the jewelfish boom in Shark River Slough were smaller (density reductions ≤ 50%) and more temporally limited than those of swamp eels, which produced near-complete loss of four species in Taylor Slough. Following the jewelfish bust, the density of affected species approximated pre-invasion predictions based on hydrology, but their recovery is now threatened by the subsequent invasion of swamp eels in Shark River Slough. Long-term monitoring data provide opportunities to probe for population-level effects at field scales, and indicate that impacts of non-native species can be context-dependent and vary across ecosystems and temporal scales.

Keywords Boom-bust · Ecosystem resilience · Invasion time · Invasive species · Population declines · Top-down effects

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Introduction

Populations of non-native species often grow rapidly before collapsing, either in a single, solitary boom or repeated boom-bust cycles (Williamson 1996). These boom-bust population dynamics are a foundational observation in invasion biology ("outbreaks" in Elton 1958) and remain important to understanding biological invasions today (Simberloff and Gibbons 2004; Lockwood et al. 2013). While there has been debate concerning the frequency of boom-bust dynamics (Williamson 1996; Simberloff and Gibbons 2004; Strayer et al. 2017), recent work continues to document the phenomenon (Fernández 2020; Haubrock et al. 2022; Soto et al. 2023). Dramatic community responses to non-native predator species often occur when non-natives have novel traits causing native prey to become more susceptible to losses, and when factors that may limit the success of non-native species, such as higher-level predators and/or disease, are absent from an ecosystem (Ricciardi and Atkinson 2004; Callaway and Ridenour 2004; Cox and Lima 2006; Lawson and Hill 2022).

Predicting and detecting effects of non-native species can be problematic when our understanding of an invader's abundance, distribution, and function in an ecosystem is limited (Hulme et al. 2013; Ricciardi et al. 2013; Jarić et al. 2019). This may be particularly true in boom-bust invasions where invaders are common for only short time periods, giving the impression that boom-bust invasions occur in systems that naturally, without human intervention, recover from, and are resilient to, invasion. Busts in populations of non-native species are commonly attributed to pathogens and parasites, but otherwise it may be difficult to attribute the population collapse of a non-native species to any single cause (Simberloff and Gibbons 2004).

Non-native fishes began to establish in Florida during the 1950s, and established populations of novel non-native species were detected approximately every couple of years; by 2007, there were reproducing populations of at least 34 non-native species in the state (Shafland et al. 2008; Schofield and Loftus 2015). Most of southern Florida is part of the greater Everglades ecosystem, a shallow oligotrophic wetland that experiences distinct subtropical wet/dry seasonality, with crisscrossing man-made canals, that has been the focus of a multi-billion dollar restoration effort (Sklar et al. 2005). Although the exact means of introduction are not certain for all species, generally, non-native fishes have been introduced to canals and other water bodies of urban Miami as accidental or intentional releases of species kept for the aquarium industry or as food (Schofield and Loftus 2015; Nico et al. 2019). Non-native fishes arrived in Everglades National Park following dispersal through canals (Loftus 1988); by 2010 there were at least 16 species of non-native fishes in non-canal waterways of Everglades National Park (Kline et al. 2014). Water depth variation and the severity of low water levels during the dry season have direct and indirect impacts on population dynamics of fishes and macroinvertebrates (Trexler and Goss 2009; Parkos et al. 2011; Dorn and Cook 2015; Botson et al. 2016), but few studies have attempted to document the influence of non-native fishes on population dynamics of native fishes and macroinvertebrates after accounting for hydrological drivers.

More than 26 years of monitoring work indicates that most non-native fishes are encountered at low densities relative to native species in Everglades sloughs (Trexler et al. 2000; Kline et al. 2014), but three species stand out as more successful colonists of the wetlands in the two primary drainages of Everglades National Park (Shark River Slough, Taylor Slough; Fig. 1). Mayan Cichlids (*Mayaheros urophthalmus*), African Jewelfish (*Hemichromis letourneuxi*; hereafter 'jewelfish'), and Asian Swamp Eels (*Monopterus albus*/*javanensis* complex; hereafter 'swamp eels') have either reached high abundance or are/were regularly encountered in one or both sloughs (Fig. 2). Mayan Cichlids were first found in Everglades National Park in 1983 (Loftus 1987) and have been regularly encountered in both Shark River and Taylor sloughs for the past three decades except for two years following a cold spell in 2010 (Kline et al. 2014). Jewelfish have been found in Florida since the 1960s and were first found in Everglades National Park in 2000 and in Shark River and Taylor sloughs in 2002. Swamp eels were first found in two distinct populations southern Florida in 1997 and 1999 (Collins et al. 2002), and first appeared in the marsh/mangrove fringe of the southeastern Everglades in 2007 (Kline et al. 2014).

Attempts to characterize the effects of non-native fishes in the Everglades using field data on naturally occurring populations have been limited and most show modest or unquantifiable effects (Trexler et al. 2000; Kobza et al. 2004). The only exceptions so far have been swamp eels and Mayan Cichlids: swamp eels have been implicated in the near-complete loss of crayfishes (*Procambarus* spp.) and a few small fish species in Taylor Slough (Pintar et al. 2023).

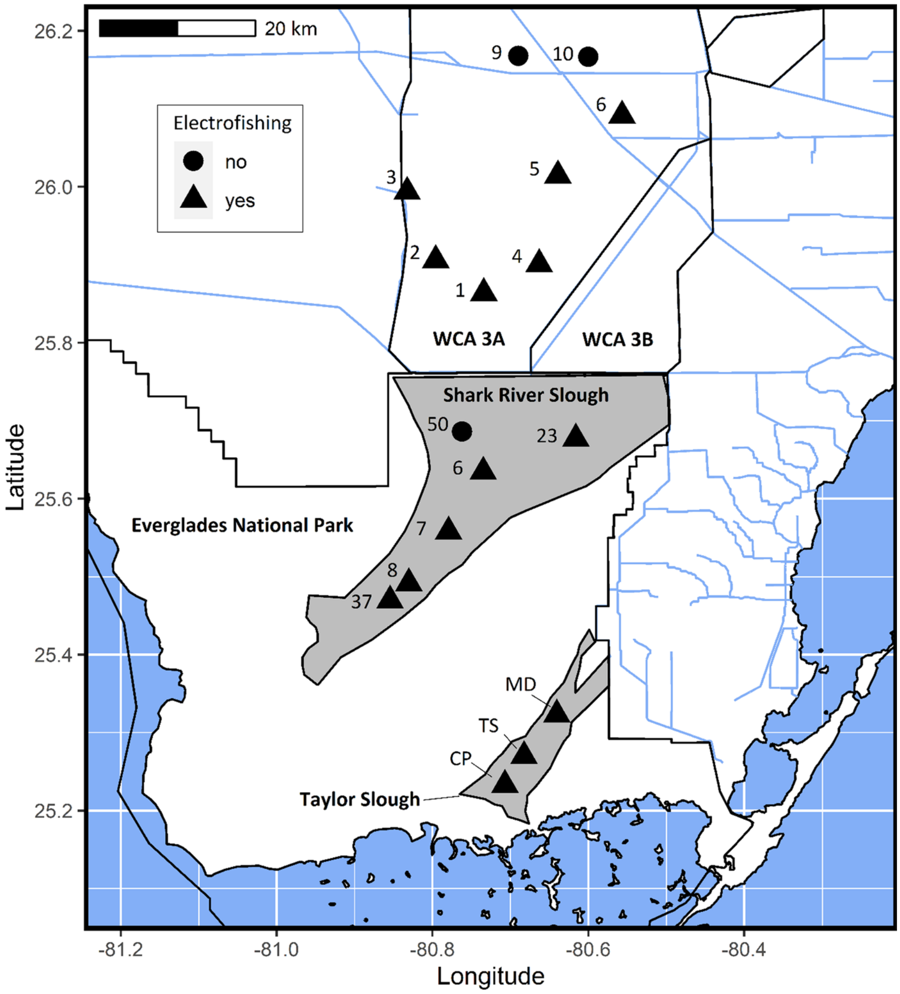
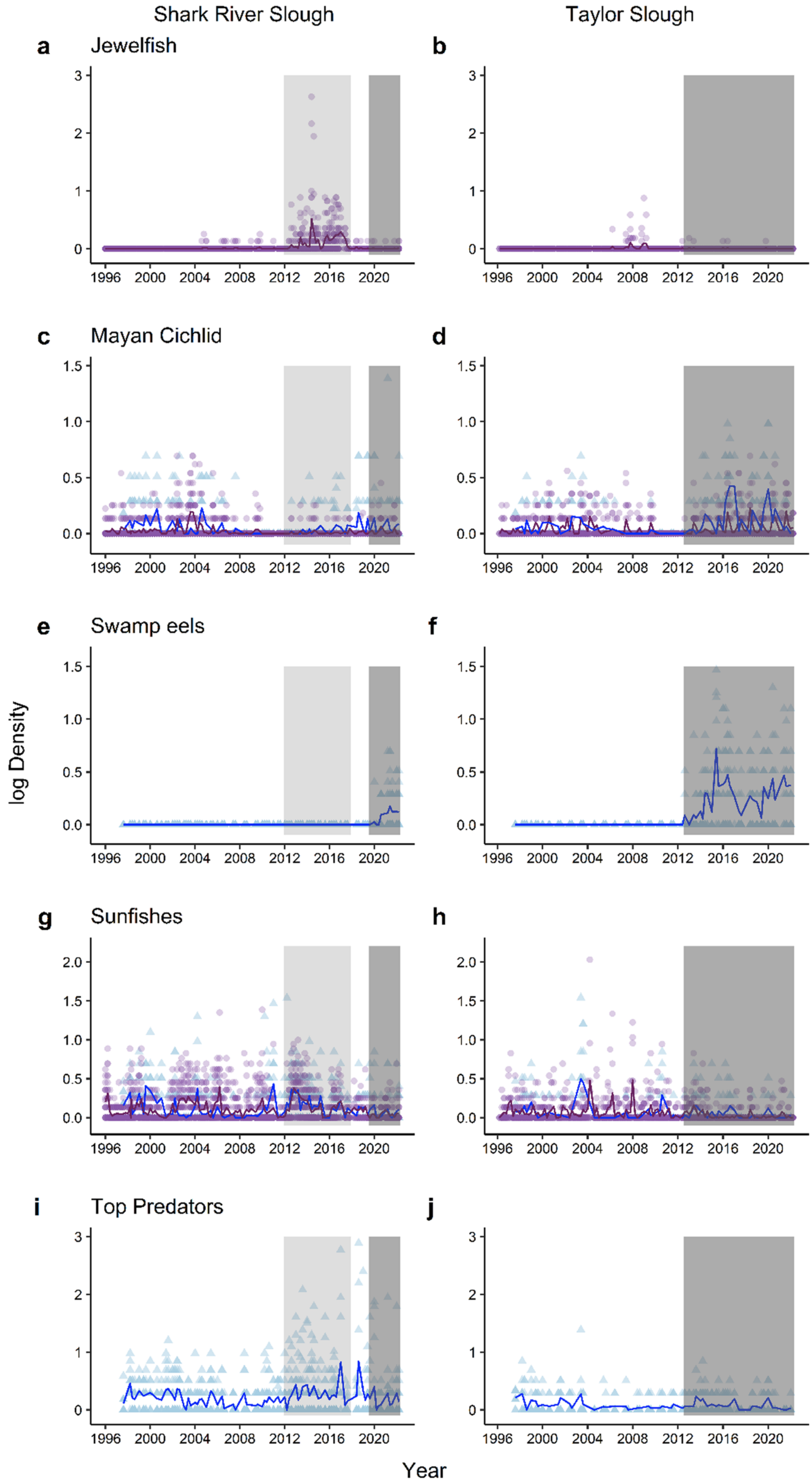


Fig. 1 Map of the study region in southern Florida. Shaded regions indicate approximate boundaries of Shark River Slough and Taylor Slough in Everglades National Park. Long-term monitoring sites used in this study are illustrated by circles (sampled by throw trapping only) and triangles (sampled by both throw trapping and electrofishing). Black lines are borders of major conservation areas (Everglades National Park, Water Conservation Areas 3A and 3B). Blue lines are major canals

Mayan Cichlids have been associated with reduced abundance of some smaller native fishes, particularly Sheepshead Minnows (*Cyprinodon variegatus*) in estuarine habitats of the southern Everglades (Harrison et al. 2013), but effects have not been detected in the freshwater marshes presumably because the species did not attain similar high abundance as observed in the mangrove/marsh and creek habitats (Trexler et al. 2000; Harrison et al. 2013). Analyses of community responses to jewelfish have been limited to experiments and the small solution-hole habitats in short-hydroperiod marshes. A field enclosure study observed that Flagfish (*Jordanella floridae*) were the only species negatively affected by jewelfish (Porter-Whitaker et al. 2012), while in a separate experiment jewelfish reduced populations of grass shrimp (*Palaemonetes* [*Palaemon*] *paludosus*), Least Killifish (*Heterandria formosa*), and two gastropods (Schofield et al. 2014). In correlational studies, the absence of many generalized, strong effects of non-native fishes on smaller natives could be due to the strong annual wet/dry cycle that regulates the population of many species (Ruetz et al. 2005; Trexler et al. 2005; Gaiser et al. 2012), cold events that disproportionately affect the mostly tropical non-native fishes (Rehage et al. 2016; Schofield and Kline 2018), or the functional similarity of non-native cichlids to native centrarchids (Montaña and Winemiller 2013). The lack of correlative evidence for effects has been misconstrued by some to indicate these species have little to no detrimental effects in the Everglades (Shafland et al. 2010). Extensive time series and comparison with non-invaded reference regions can help to uncover relationships between non-native and native

Fig. 2 Densities (natural log-transformed) of the five predatory fishes assessed in this study from 1996–2022 in Shark River Slough (left column) and Taylor Slough (right column) of Everglades National Park. Study taxa are African Jewelfish (*Hemichromis letourneuxi*; **a**, **b**), Mayan Cichlids (*Mayaheros urophthalmus*; **c**, **d**), Asian Swamp Eels (*Monopterus albus*/*javanaensis*; **e**, **f**), Sunfishes (combined *Lepomis* spp.; **g**, **h**), and combined Top Predators (Bowfin, *Amia calva*; Florida Gar, *Lepisosteus platyrhincus*; Largemouth Bass, *Micropterus salmoides*; **i**, **j**). Points are plot-level densities of throw trap (purple circles) and electrofishing catch-per-unit-effort (blue triangles) data; purple/blue lines indicate mean densities during each sampling period. Light shaded areas are the 'invasion' periods that correspond to peak jewelfish abundances in Shark River Slough; the dark shaded area is are the 'invasion' periods during which swamp eels were present in both Taylor Slough and Shark River Slough



taxa in an ecosystem (Hargrove and Pickering 1992; Simberloff and Gibbons 2004; Strayer et al. 2017; Pintar et al. 2023).

We used a 26-year dataset of aquatic animals in the Everglades to (1) Describe the invasion dynamics of three non-native fishes (jewelfish, swamp eels, Mayan Cichlids) in Everglades National Park, (2) Examine evidence for effects of these three species on small prey fishes and decapods, and (3) Compare effects of non-native fishes to those of native predators and their relation to hydrologic conditions. We focused the examination on the boom-bust dynamics exhibited by jewelfish and compared the species affected by jewelfish in Shark River Slough to those affected by the swamp eel invasion that occurred over a similar timeframe in Taylor Slough, while accounting for relationships of prey species to native predatory fishes and Mayan Cichlid variation in both regions. We hypothesized that jewelfish would have species-specific relationships with prey taxa, having inverse relationships with species such as grass shrimp, Flagfish, Eastern Mosquitofish, and Least Killifish, for which prior experimental work demonstrated negative impacts.

Methods

A summary of the methods used in this study are presented below; full methods are available in the supplements.

Study system and data collection

Sampling of fish and aquatic macroinvertebrates occurred at 24 sites throughout the Everglades from July 1996 through April 2022 (see Trexler et al. 2001). Here, we focused on sites in Shark River Slough (6 sites) and Taylor Slough (3 sites) of Everglades National Park, while those in Water Conservation Area 3A (WCA; 8 sites) served as a reference region (Fig. 1). Small fishes and macroinvertebrates were collected with 1-m^2 throw traps five time per year (Dorn et al. 2005), while large fishes (> 8 cm standard length) were sampled with an airboat-mounted electrofisher four times per year (Chick et al. 2004). Dry-season electrofishing was spatiotemporally more limited, so we created indices of annual predator abundances caught electrofishing by averaging the total number of fish caught across all electrofishing transects during both wet season sampling periods (July, October). These indices were used as predictor variables in analyses.

Densities (# individuals/m^2) of the three most common decapod species and nine most common small fishes caught in throw traps between both Shark River Slough and Taylor Slough were our response variables in analyses. For decapods, these species were grass shrimp, Everglades Crayfish (*Procambarus alleni*), and Slough Crayfish (*Procambarus fallax*). Seven fishes were common in both regions: Everglades Pygmy Sunfish (*Elassoma evergladei*), Golden Topminnows (*Fundulus chrysotus*), Marsh Killifish (*Fundulus confluentus*), Eastern Mosquitofish, Least Killifish, Flagfish, and Bluefin Killifish (*Lucania goodei*). Sheepshead Minnows were only common and analyzed in Taylor Slough, and Sailfin Mollies (*Poecilia latipinna*) were only common and analyzed in Shark River Slough, but we displayed time series data for all nine species in all regions regardless.

Baseline hydrologic analyses

We separately investigated effects of hydrologic conditions and non-native species in Shark River Slough, Taylor Slough, and WCA 3A due to each region's respective invasion history, hydrology, and other environmental characteristics. We established pre-invasion baseline periods in both Shark River and Taylor sloughs during which we modeled relationships between hydrologic conditions and seasonality and density of our response species, with the subsequent years forming an invasion period (Fig. 3). We modeled the density of each response species separately by region using hydrologic covariates measured at the plot scale (see Trexler et al. 2005; Dorn and Trexler 2007).

Response and predictor variables in predator analyses

Residuals from the models of hydrologic conditions were used as our response variables during analyses assessing effects of predators during the baseline period. Following the arrival of each non-native predator, we generated predictions of prey-species' density based on observed hydrologic conditions

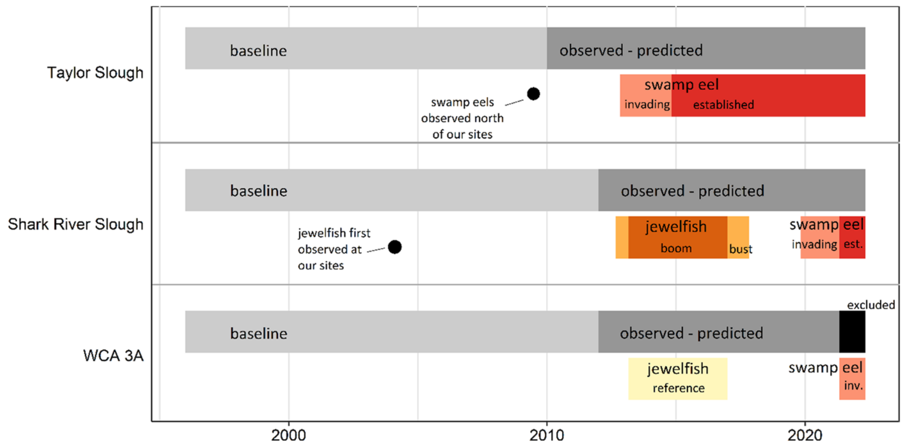


Fig. 3 Timeline of species invasions and analysis periods in the three regions of the Everglades analyzed here: Taylor Slough, Shark River Slough, and Water Conservation Area (WCA) 3A. In each region, the top illustrates the baseline period and the subsequent years for which the baseline was used to predict densities of prey species when we calculated 'residuals' of observed—predicted densities. The bottom row for Taylor Slough and Shark River Slough illustrate the timeline of the swamp eel and jewelfish invasions in those regions. The 'invading' periods are when swamp eels were detected at some but not all of our sites, while the 'established' periods are when each species was consistently detected sites across the region. In WCA 3A, the bottom row illustrates the jewelfish reference period (corresponding to the boom period in Shark River Slough when they were present at all sites) and the beginning of the swamp eel invasion in that region

and the most supported models from the baseline period. Then during the invasion period, we generated 'residuals' that were calculated as observed minus predicted densities for each prey species (Fig. 3). This approach was necessary because we were looking for evidence of the non-native species beyond the effects of hydrologic variation and because the presence of swamp eels in Taylor Slough has had dramatic effects that have eliminated the relationships between hydrologic conditions and population responses of several small animal species (Pintar et al. 2023). We assumed that our models of hydrologic conditions should continue to predict densities of prey species in the absence of the non-native predators and used them to define our expectations relative to observed densities in the absence of predator effects. Native predator effect sizes (standardized coefficients) provided a range of expected values for native predators beyond hydrology that might be expected if non-natives are similar to adding another fish of similar impacts. We looked for significantly negative standardized effects that were also larger than those of the native fishes when identifying effects of non-natives.

The three common non-native species (jewelfish, swamp eels, Mayan Cichlids) were our primary predictor variables in predator analyses, but we also assessed effects of all combined sunfish (*Lepomis* spp.; Fig. 2g, h) and the combined three largest native predatory fishes ('top predators': Bowfin, *Amia calva*; Florida Gar, *Lepisosteus platyrhincus*; and Largemouth Bass, *Micropterus salmoides*; Fig. 2i, j). Three different measures of predator abundance were used in models: annual indices of large fish catch-per-unit-effort (CPUE) from electrofishing (ef) were used for swamp eels, top predators, sunfish, and Mayan Cichlids, while densities of predators from throw-trap data from the current time period (t) and previous time period (t-1) were used for jewelfish, sunfish, and Mayan Cichlids.

Predator analyses

We used a consistent approach to analyze predator effects with separate models in Shark River Slough and Taylor Slough: one model of the baseline period (pre-invasion; Fig. 3) and two models of the full dataset: one based on abundances of jewelfish and/or swamp eels, and one based on presence/absence of those two species. Model selection was used to determine the best combination of predator species that explained changes in densities (residuals) of small fishes and decapods beyond what was already accounted for or predicted by hydrologic variables. Though some predator impacts on small fish and decapods co-vary with hydrologic variation (see Trexler et al. 2005; Dorn and Cook 2015), we limited our examination to effects distinguishable after accounting for hydrology, which would indicate effects of non-native predators that are functionally different from those of native predators.

Because of the generally small effects of jewelfish observed in Shark River Slough (see results), we then used WCA 3A to test for potential time period effects during the core of the jewelfish invasion. We used the time period during which jewelfish were considered present at all sites in Shark River Slough as a categorial variable in WCA 3A. Doing so may validate or conflict with findings of jewelfish presence/absence in Shark River Slough if concurrent changes of similar magnitude for the same species were observed in both regions. We had no way to test for jewelfish density in WCA 3A because they were effectively absent from the region during this timeframe. We did not run this same test for swamp eel presence because the presence of swamp eels in both regions overlaps during the final years of the dataset, which we otherwise excluded from WCA analyses. However, the same jewelfish reference period in WCA was used as a limited comparison for swamp eel effects in Taylor Slough because it overlaps with a large portion of the time when swamp eels were present in Taylor Slough.

Jewelfish analyses

As a final step in our assessment of the jewelfish invasion and decline in Shark River Slough, we investigated potential factors limiting jewelfish populations from when they were first detected in our dataset (2004) through the year swamp eels were first detected (2019). Residuals from the best hydrologic model for jewelfish densities were used as a response variable to assess potential effects of predators through the same predator model selection process using abundances of sunfish, top predators, and Mayan Cichlids.

Results

In the time since data on the abundances and distributions of our focal non-native species were last reported in the literature (Kline et al. 2014), the invasions of jewelfish and swamp eels in the Everglades have followed distinctively different trajectories. Jewelfish populations boomed from 2012–2017 in Shark River Slough, but declined and remained at their pre-2012, near-zero, densities from 2018–2022 (Fig. 2a), while they never established high densities in Taylor Slough and were rarely caught there (Fig. 2b). Prior to 2019, jewelfish were rarely caught in WCA 3A but since 2019 have become more common (Fig. S1a), though still at much lower densities than observed during their boom in Shark River Slough. In contrast, swamp eels established in Taylor Slough in 2014 (found at all sites) and have become more common than all other large fishes caught electrofishing combined (Fig. 2f). Swamp eels continued to spread across the Everglades, arriving in Shark River Slough in 2019 and were found at all electrofishing sites by 2021. Most recently, swamp eels spread into WCA 3B (2017) and 3A (2021) north of Everglades National Park (Figs. 1, S1c).

Models of predator impacts, excluding jewelfish and swamp eels, on small fish and decapod density indicated that predators accounted for little of the residual variation in species densities (marginal $R^2 < 0.1$) that was not already accounted for by effects of hydrologic condition and seasons. Densities of predatory fishes (Figs. 2, S1), decapods (Figs. 4, S2a–d), and small fishes (Figs. 5, 6, S2f–t) varied by year, season, and site in all three regions. Responses to hydrologic variables were species- and region-specific and confirmed the well-established importance of antecedent hydrologic conditions in regulating populations of aquatic animals in the Everglades; coefficients for hydrologic models are presented in the supplements (Tables S1–S3).

Responses to predators were species-, region-, and time-period specific (Figs. 4, 5, and 6, Tables S4–S8). Abundances of native predators (large predatory fishes, sunfishes) and Mayan Cichlids had both positive and negative associations with densities of most prey species, but their effects, as illustrated by the size of standardized coefficients in Figs. 4, 5 and 6, were smaller than those of either jewelfish or swamp eels for most species. Similar patterns of small positive

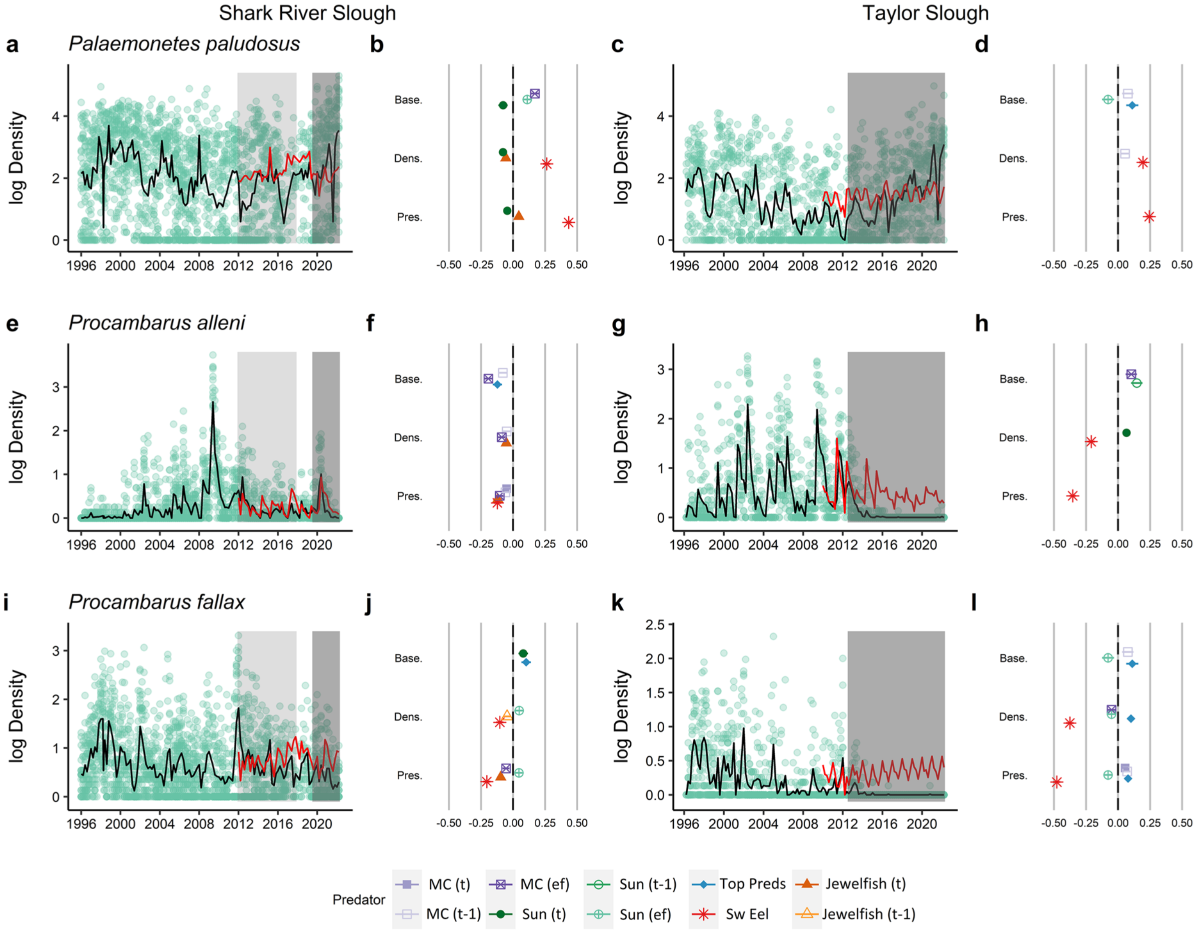


Fig. 4 Plot-level densities (natural log-transformed) over time and standardized coefficients of effects of predatory fishes on the three decapod species in Shark River Slough (left two columns) and Taylor Slough (right two columns). In density plots, the black line is the mean density of all plots during each sampling period; the red line is the mean density predicted by the parameterized hydrologic models from the baseline period (error bars are excluded for clarity). Light shaded areas are the 'invasion' periods that correspond to peak jewelfish abundances in Shark River Slough (Fig. 2a); the dark shaded area are the 'invasion' periods during which swamp eels were present in Shark River Slough (Fig. 2e) and Taylor Slough (Fig. 2f). The baseline period in each region is all years prior to the invasion period in Shark River Slough (1996–2011) and prior to detection of swamp eels upstream of our sites in Taylor Slough (1996–2009). Coefficient plots illustrate the mean standardized coefficient (±SE) for effects of predators with $P < 0.10$ included in final models (Tables S3, S5). Legend abbreviations: MC = Mayan Cichlid, Sun = Sunfish; Sw Eel = Asian Swamp Eel; t = predator densities during current sampling period; t-1 = predator densities during previous sampling period; ef = index of predator densities from electrofishing

and negative effects of predators were observed in WCA 3A in the absence of jewelfish and swamp eels (Fig. S2). Coefficients for invader presence/absence are presented in the figures illustrating species effects, but they are not directly comparable to coefficients of continuous abundance variables (densities reported in Tables S4–S8).

In Shark River Slough, we observed consistent significant ($P \leq 0.05$) negative effects of jewelfish density and presence/absence on Eastern Mosquitofish, Least Killifish, Flagfish, and Sailfin Mollies and consistent positive associations for Everglades Pygmy Sunfish. When accounting for potential (marginal, $0.05 < P < 0.10$) effects, there were also indications of negative associations for Slough Crayfish and Bluefin

Killifish. Higher lagged jewelfish density (t-1) was associated with lower density of Golden Topminnows; higher contemporary jewelfish density (t) was associated with lower density of Grass Shrimp and Bluefin Killifish, along with higher density of Golden Topminnows. Jewelfish presence during the boom period was associated with significantly lower densities of Everglades Crayfish and Slough Crayfish.

During the entire study period in Taylor Slough, consistent effects of both swamp eel densities and presence/absence were observed for all species in which there were any statistically significant results. There were significant negative associations for Everglades Crayfish, Slough Crayfish, Sheepshead Minnows, Everglades Pygmy Sunfish, Golden Topminnows, Marsh Killifish, Eastern Mosquitofish, and Flagfish. There were significant positive associations with Grass Shrimp and Least Killifish and no detected effects on Bluefin Killifish.

Swamp eels have been known to be present at our sites in Shark River Slough for the last 2.5 years of our dataset (December 2019–April 2022), and during this period we have begun to see signs of declines consistent with the most dramatic declines observed in Taylor Slough. Consistent effects of both presence/absence and swamp eel CPUE were observed for Slough Crayfish, Marsh Killifish, Flagfish, Sailfin Mollies (all negative), and Grass Shrimp (positive).

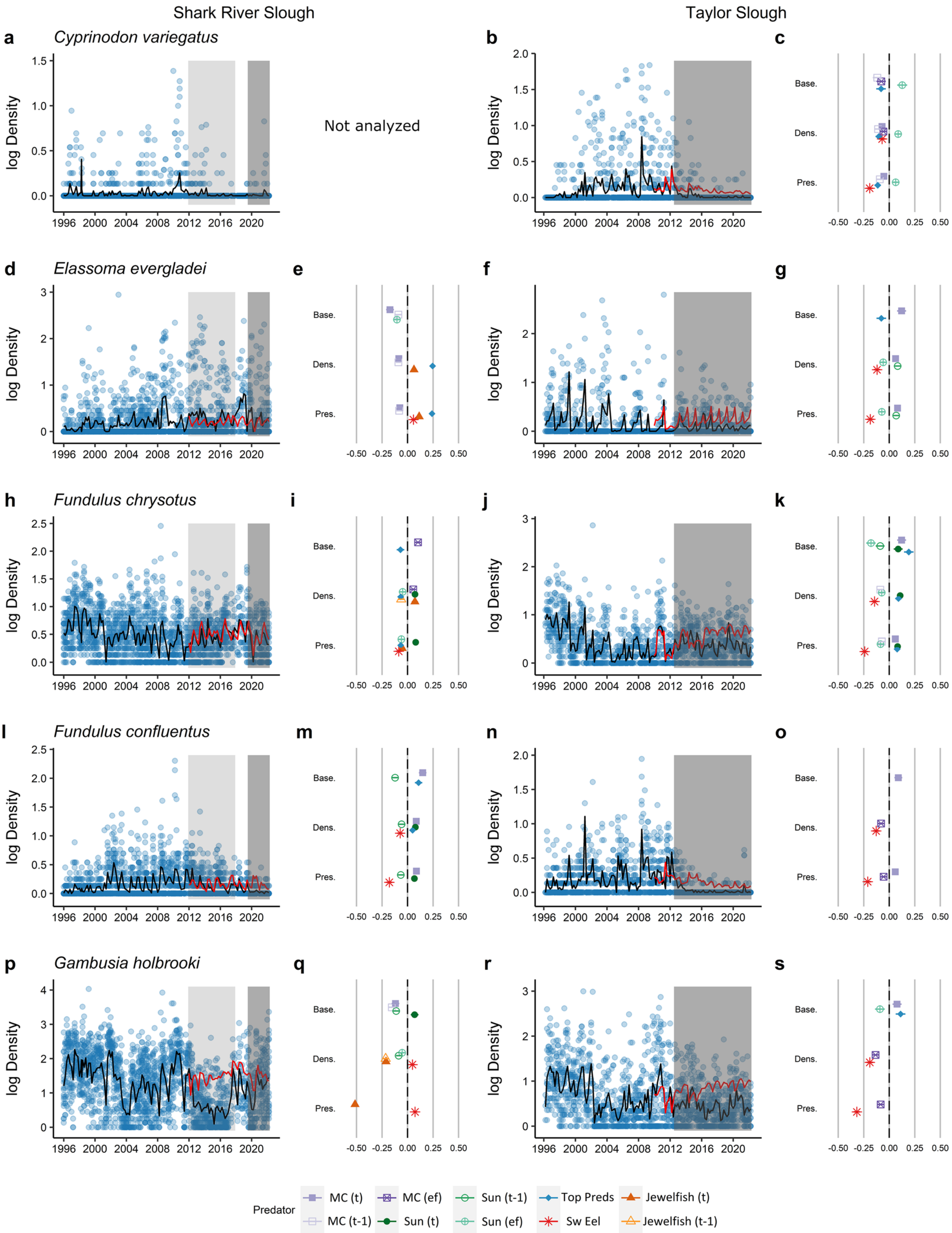
In our secondary analyses of the nine common species in WCA 3A, the jewelfish invasion period (comparison using the boom period in Shark River Slough) was not included in the final selected model for Least Killifish, had a significant positive association with densities of grass shrimp, and had significant negative associations with densities of slough crayfish, Everglades Pygmy Sunfish, Golden Topminnows, Eastern Mosquitofish, Flagfish, and Sailfin Mollies (Table S8). Everglades Crayfish, Sheepshead Minnows, and Marsh Killifish were not common enough to be analyzed in WCA 3A. For three of the four species that seemed to decline in SRS during the boom period of jewelfish, they also seemed to decline at the same time in WCA 3A. However, for all three species that were less abundant during the boom in both regions (Eastern Mosquitofish, Flagfish, Sailfin Mollies) the standardized coefficients were always larger in SRS with jewelfish present (coefficients in SRS: -0.515, -0.286, -0.368, respectively) than in the reference WCA region without jewelfish (WCA: -0.109, -0.173, -0.095, respectively).

Finally, the best fitting model of hydrologic/seasonal conditions that regulated jewelfish populations (Table S9) indicated that jewelfish densities were negatively associated with longer dry seasons and negatively associated with days since dry. The only predator groups retained in the most supported model of jewelfish densities were top predators (significant positive association) and Mayan Cichlids (t-1 throw trap densities, non-significant coefficient; Table S10).

Discussion

Despite their overall importance, boom-bust dynamics have often been neglected due to their challenging nature to study and limited availability of temporal data (Strayer et al. 2017; Haubrock et al. 2022). Less documented yet are the impacts of these dynamics on native species and persistence of the impacts following the initial explosive growth of the invading species (Soto et al. 2023). Our time series analyses in the Everglades has illustrated that some small fish species strongly negatively impacted by rapid population growth ('boom') of a non-native species can recover following declines ('bust') in abundances of the same invader. This study provides hope that the initial population-level impacts of some invasive fish may be reversible and that the fish and macroinvertebrates are somewhat resilient (Chaffin et al. 2016).

In the Everglades, jewelfish and swamp eels had contrasting invasion histories, taxon-specific impacts, and persistence and magnitude of effects. The boom-and-bust of non-native jewelfish in Shark River Slough was associated with lower densities of several small fishes during the boom phase. During the boom, densities of Eastern Mosquitofish, typically the most abundant fish in the ecosystem (Loftus and Kushlan 1987; Trexler et al. 2001), were as much as 50% lower than predicted by hydrologic drivers, while declines in other species were relatively smaller (Figs. 5 and 6). We also report a contrasting result from the persistent establishment of swamp eels in Taylor Slough associated with the recent collapse (declines of 90–100%) of both crayfish species and two small fishes. The difference in effects of these two non-native predators may result from differences


Shark River Slough
Taylor Slough
a
Cyprinodon variegatus
b
c
Not analyzed
d
Elassoma evergladei
e
f
g
h
Fundulus chrysotus
i
j
k
l
Fundulus confluentus
m
n
o
p
Gambusia holbrooki
q
r
s
log Density
Base.
Dens.
Pres.
Predator
MC (t)
MC (t-1)
MC (ef)
Sun (t)
Sun (t-1)
Sun (ef)
Top Preds
Sw Eel
Jewelfish (t)
Jewelfish (t-1)

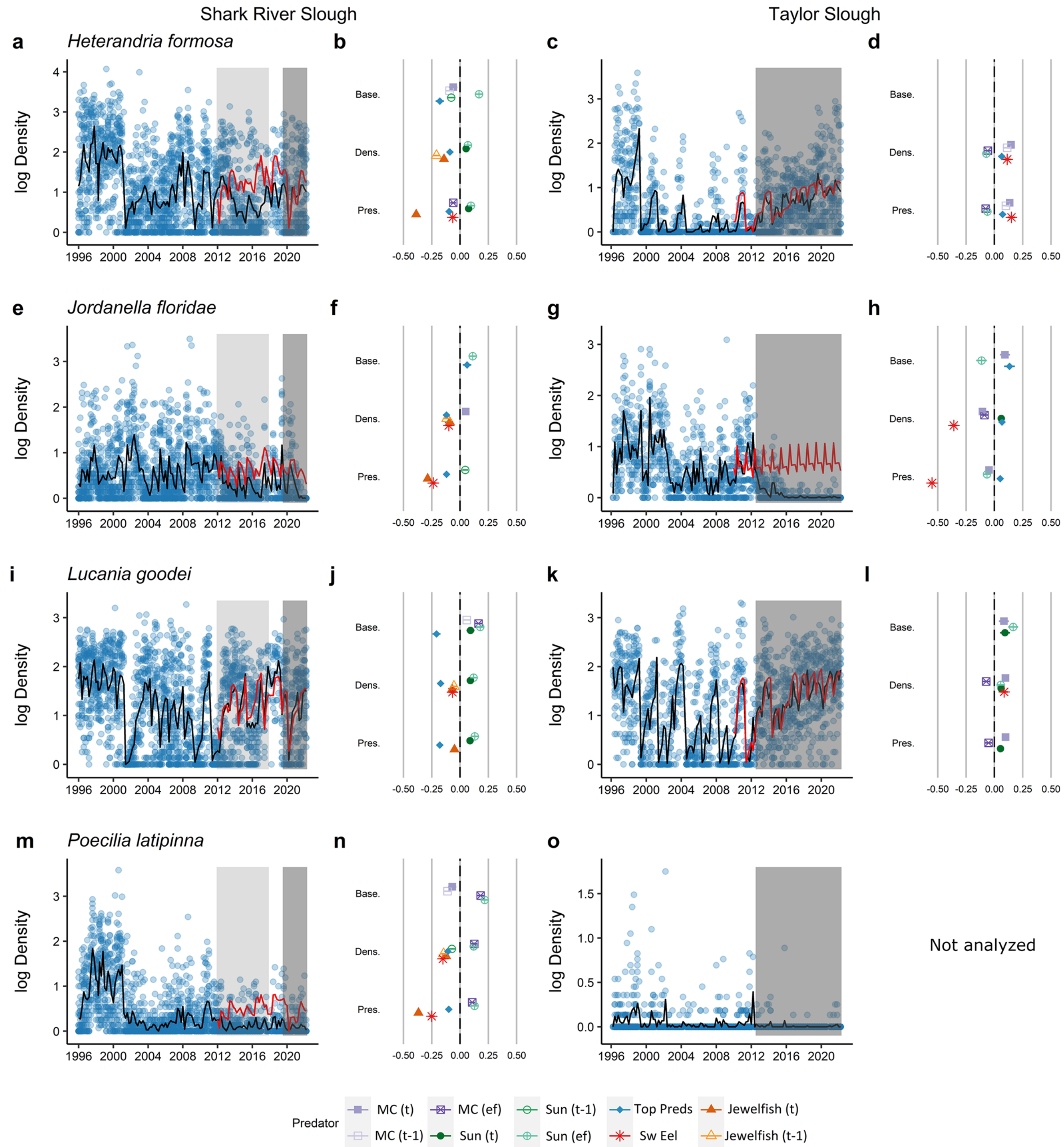
◂**Fig. 5** Plot-level densities (natural log-transformed) over time and standardized coefficients of effects of predatory fishes on the first five small fish species in Shark River Slough (left two columns) and Taylor Slough (right two columns). In density plots, the black line is the mean density of all plots during each sampling period; the red line is the mean density during/following the invasion predicted by the parameterized hydrologic models from the baseline period (error bars are excluded for clarity). Light shaded areas are the 'invasion' periods that correspond to peak jewelfish abundances in Shark River Slough (Fig. 2a); the dark shaded area is are the 'invasion' periods during which swamp eels were present in both Shark River Slough (Fig. 2e) and Taylor Slough (Fig. 2f). The baseline period in each region is all years prior to the invasion period in Shark River Slough (1996–2011) and prior to detection of swamp eels upstream of our sites in Taylor Slough (1996–2009). Coefficient plots illustrate the mean standardized coefficient (±SE) for effects of predators with $P<0.10$ included in final models (Tables S4, S6). Legend abbreviations: MC = Mayan Cichlid, Sun = Sunfish; Sw Eel = Asian Swamp Eel; t = predator densities during current sampling period; t-1 = predator densities during previous sampling period; ef = index of predator densities from electrofishing

in their life histories or body size, the timing of each invasion relative to the mediating role that hydrology plays in the Everglades, and/or the potential effects of other large predators in the system that approximate and likely covary with hydrologic effects.

We further assessed effects during the jewelfish boom period in Shark River Slough by comparing changes observed over the same time period in WCA 3A, when jewelfish were rare to absent from our sampling sites there. The standardized coefficients (effects) of this categorical presence/absence variable in WCA 3A were similar to or less than the coefficients for the densities of predators in most of these models, with effects on Flagfish and Golden Topminnows being larger than other predators. In contrast, the coefficients for categorical effects of jewelfish and swamp eels in Shark River and Taylor sloughs were often much larger than effects of other predator abundances. We suggest the significant declines reported for WCA 3A were probably attributable to residual hydrologic variation rather than being indicative of system-wide changes in populations of these species. WCA 3A has had longer hydroperiods throughout most of the monitoring period and fish densities were more difficult to statistically model using drought-based terms (Ruetz et al. 2005; Dorn and Cook 2015). The findings in WCA 3A cannot undermine the conclusions for three of the species (i.e., Eastern Mosquitofish, Least Killifish, Sailfin Molly) with consistent responses to both density and presence/absence of jewelfish in Shark River Slough. The negative association of this period on Everglades Pygmy Sunfish densities in WCA 3A contrasts with the positive associations observed for both jewelfish presence and density in Shark River Slough, while the relatively large negative effect on Flagfish in WCA 3A suggests the decline in Shark River Slough correlated with jewelfish may have confounding causes.

In spite of the overlapping impacts of jewelfish and swamp eels on the most abundant small fish and decapods in Everglades sloughs and the persistent presence of Mayan Cichlids, we did not observe a 'meltdown' (Simberloff and Holle 1999) of the native community in Shark River Slough. We observed a marked resilience of the native community to jewelfish in Shark River Slough, rebounding in the bust phase of a boom-and-bust cycle of jewelfish in the presence of a second invading species, Mayan Cichlids. The non-native impacts observed in this study suggest species-specific impacts rather than a synergistic effect of the collection of three invaders.

When our results for jewelfish impacts are combined with prior examinations of their impacts in experimental systems (Porter-Whitaker et al. 2012; Schofield et al. 2014), we observed some consistency and disagreement. The negative effects observed on Least Killifish and Flagfish were consistent with the experimental results of Schofield et al. (2014), while the strongest effects we observed were on Eastern Mosquitofish, for which they observed non-significant negative trends. Porter-Whitaker et al. (2012) found that mortality of Bluefin Killifish, Least Killifish, and grass shrimp were not higher in the presence of jewelfish than when predators were absent. Some of the strongest effects Schofield et al. (2014) observed were on grass shrimp, while Rehage et al. (2014) documented detrimental effects on Eastern Mosquitofish in solution holes. In aggregate, we observed no strong impact on grass shrimp but a consistent response by Eastern Mosquitofish. Elevated effects of predators and competitors may be expected in confined habitats (solution holes) or experimental enclosures (mesocosm studies) where inter-individual encounter rates are enhanced. The different findings emphasize the importance of long-term observational studies in field conditions for determining the population-dynamical



importance of interactions between predators and prey, and in this case, non-native predators.

In Taylor Slough, swamp eels produced dramatic declines in abundance of several formerly abundant and functionally important species. The Taylor Slough community was home to a persistent population of Mayan Cichlids from the outset of this study, with few statistically demonstrable responses of any prey to their variation in abundance. In Shark River Slough, we observed some preliminary indications that swamp eels are having effects on some of the same species most affected by the longer invasion history in Taylor Slough (Slough Crayfish, Marsh Killifish, Flagfish) and are already rivaling or exceeding those of jewelfish and native predatory species observed in models (Figs. 4–6). After the decline of

◂**Fig. 6** Plot-level densities (natural log-transformed) over time and standardized coefficients of effects of predatory fishes on the last four small fish species in Shark River Slough (left two columns) and Taylor Slough (right two columns). In density plots, the black line is the mean density of all plots during each sampling period; the red line is the mean density during/following the invasion predicted by the parameterized hydrologic models from the baseline period (error bars are excluded for clarity). Light shaded areas are the 'invasion' periods that correspond to peak jewelfish abundances in Shark River Slough (Fig. 2a); the dark shaded area are the 'invasion' periods during which swamp eels were present in both Shark River Slough (Fig. 2e) and Taylor Slough (Fig. 2f). The baseline period in each region is all years prior to the invasion period in Shark River Slough (1996–2011) and prior to detection of swamp eels upstream of our sites in Taylor Slough (1996–2009). Coefficient plots illustrate the mean standardized coefficient (±SE) for effects of predators with $P<0.10$ included in final models (Tables S4, S6). Legend abbreviations: MC = Mayan Cichlid, Sun = Sunfish; Sw Eel = Asian Swamp Eel; t = predator densities during current sampling period; t-1 = predator densities during previous sampling period; ef = index of predator densities from electrofishing

jewelfish (bust period; 2018–2019) in Shark River Slough, populations of the most-affected species appeared to have recovered (particularly Eastern Mosquitofish, Least Killifish, and, prior to 2021, Flagfish), with predicted densities more closely matching observed densities (Figs. 5 and 6). There was no evidence for a swamp eel bust and no recovery of native species in in Taylor Slough where swamp eels have persisted at abundances higher than any other large fishes (> 8 cm TL). Indeed, the dramatic effects of swamp eels in Taylor Slough and hint of effects in Shark River Slough may paint a bleak picture for the future of the Everglades small animal communities as swamp eels continue to spread.

Life history differences of jewelfish and swamp eels may explain their different dynamics and community-level impacts. Although both species are reported to consume wide ranges of small fishes and invertebrates in Florida, the measured impacts were on different species, and swamp eels grow to much larger sizes and have larger gapes whereas jewelfish can be aggressive to competitors (Hill and Watson 2007; Shafland et al. 2010; Schofield et al. 2014; Rehage et al. 2014). The dramatic predation effects of swamp eels are probably related to their ability to persist in sediment when the water above recedes from marshes during the dry season (Graham 1997; Chew et al. 2005). This makes swamp eels functionally unique additions to the Everglades that place pressure on species that rely on predator-free times immediately after re-inundation for reproduction and recruitment through juvenile stages; the drought tolerance of swamp eels provides a unique trait to these invaded communities (i.e., weapon against natives; Callaway and Ridenour 2004). Jewelfish density models suggest they were sensitive to hydrological drought like native fishes. Although limited published work suggests jewelfish may also have better ability to survive drier periods in marshes than native large fishes (Schofield et al. 2010; Rehage et al. 2014), they cannot burrow and survive drying like swamp eels. Therefore, jewelfish may not represent a sufficiently functionally distinct predator compared to the other fishes already found in the system, particularly other cichlids and centrarchids (Montaña and Winemiller 2013).

The causes of the boom-bust dynamic in the jewelfish population in Shark River Slough are unknown. This dynamic cycle coincides with years following two cold events (January and December 2010) and a subsequent drought (2011) that temporarily set back populations of all large non-native fishes (Fig. 2c,d) (see also Rehage et al. 2016). It is possible that the 2010/2011 cold and drought events provided a window for jewelfish populations to boom in Shark River Slough in the absence of larger predatory cichlids, and Mayan Cichlids in particular, sensu the enemy release hypothesis (Keane and Crawley 2002). If correct, this explanation implies Mayan Cichlids provide a degree of biotic resistance to further non-native fish invasions in the marshes of the Everglades, or at least to smaller cichlid species such as jewelfish. Other potential explanations for the jewelfish bust include disease, inbreeding, or increased avian predation (Evans and Gawlik 2020), but effects of any such limiting factors are unknown at this time.

The Everglades is an ecosystem where seasonal and hydrologic variation regulate most changes in the populations of aquatic animals (Chick et al. 2004; Ruetz et al. 2005; Dorn and Trexler 2007; Gaiser et al. 2012; Boucek and Rehage 2013). Swamp eels, at least to a certain extent, can escape this hydrologic limitation whereas jewelfish cannot. The link between hydrology (especially recent drying) and fish population dynamics means that attribution of effects of fish predators, native or non-native, can be challenging (Dorn and Cook 2015). This may explain why we observed small positive and negative coefficients (effects) of native and even non-native predators on prey densities in both regions. For instance, if dry conditions are disturbances for both predator and prey fish populations (see Trexler et al. 2005), we would expect mostly positive relationships between the two even though the predators are consuming prey. This may complicate conclusions reliant on detecting inverse correlations between taxa in order to determine detrimental impacts of a non-native species. The ability to detect residual negative covariation between prey and predator density after accounting for hydrological effects in the Everglades depends on the relative resistance and resilience of predator and prey to drying and the net effect of increased predator–prey encounter rates as water levels drop compared to simple concentration of both species; if relatively more prey migrate into a hydrological refuge than the predators are able to consume (even as predator numbers also increase), the net effect is positive on both groups and the consumptive effect is swamped. The situation for crayfish populations, which can resist direct effects of drying by burrowing, is different and has been conceptualized as an resilience-based example of the consumer-stress model – population release from fish predation after dry periods (Dorn and Cook 2015) such that predatory fish impacts and slough permanence are mostly correlated for crayfish in the pre-swamp eel Everglades. Invading species, such as swamp eels, that are able to disrupt the link between hydrology and fish/decapod population dynamics (Dorn and Trexler 2007) are those that may have the largest effects (Pintar et al. 2023).

The arrival and spread of non-native fishes in Florida and the Everglades have drawn the attention of biologists and land managers for decades (Loftus and Kushlan 1987; Kline et al. 2014). Our 26-year dataset suggests that, perhaps thanks to the natural wet/dry seasonality of the Everglades, jewelfish have had effects lasting only the few years when they were exceptionally abundant. Jewelfish provided a clear period of abundance (boom) and near absence (pre-invasion, bust) – a contrast in densities and presence/absence that may have helped elucidate potential effects. Contrary to the repeated rapid repeated variation in densities of Mayan Cichlids in some sites of the marsh/mangrove areas near Taylor Slough that was used to determine the ecological impacts observed by Harrison et al. (2013) on some small native fishes, there was not as much clear variation in densities and presence/absence for Mayan Cichlids in the large freshwater sloughs.

Perhaps the more important message of this work is that risks and effects of a non-native species continue to be difficult to predict (Jarić et al. 2019; Lawson and Hill 2021). Results from experimental or short-duration field studies can be helpful as first proxies and mechanism tests, but short-term results mostly affecting survival or recruitment variation should provide no reason to fail to monitor native communities or avoid implementing programs to limit the spread of the invader. Long-term community-level monitoring programs are critical to tracking the presence, spread, and abundance of non-native species, as well as the native taxa they may impact (Schofield and Loftus 2015). When swamp eels were restricted to, and studied predominantly in, canals, some suggested they would be innocuous invaders in Florida (Shafland et al. 2010). Yet today they represent perhaps the biggest threat to the trophic dynamics of the freshwater Everglades and the monumental efforts to restore its trophic links to wading birds (e.g., Boyle et al. 2014).

Jewelfish were at their peak ~ 50% of the fish collected at multiple long-term monitoring sites in Everglades National Park and appeared to be a major disrupter of the food-web supporting endangered wading birds and other species of concern. And then, for unknown reasons, their numbers crashed and the native fish species they impacted subsequently recovered. Identifying any such patterns and relationships among current and future non-native species is dependent on consistent long-term data and monitoring programs like the dataset analyzed here. For the Everglades and other systems undergoing restoration and management of system drivers (e.g., hydrology, fire, nutrients) long-term monitoring programs are invaluable for parsing out the simultaneous effects of non-native species, climate/rainfall variation, and water management (Trexler and Goss 2009).

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Author Contributions NJD, JLK, and JCT managed the project and data collection. MRP analyzed the data with input from NJD, JCT, and JLK. MRP led the writing of the manuscript and all authors contributed to revisions.

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Data availability Data are archived on the FIU Florida Coastal Everglades LTER website through the Environmental Data Initiative (https://doi.org/10.6073/pasta/b5038017157f91ef92ff495dde6122b0).

Declarations

Conflict of interests The authors declare no competing interests.

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