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POPULATION TRENDS AND TROPHIC ECOLOGY OF THE INVASIVE PEACOCK EEL (*MACROGNATHUS SIAMENSIS*) IN THE FLORIDA EVERGLADES

By
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Abstract

Invasive species threaten the ecological integrity of ecosystems worldwide, including the Florida Coastal Everglades. This study investigated the ecological role of the peacock eel (*Macrognathus siamensis*) within this ecosystem, emphasizing its population trends and the environmental factors that affect its population performance, and the potential for interactions with native fish assemblages and coastal food webs. I used 19 years of electrofishing data to investigate the population trends of peacock eels at the marsh-mangrove ecotone of the Shark River Estuary, Everglades National Park (Florida, USA). I found that peacock eel populations have increased since their first detection in 2002, and their populations are strongly affected by hydroclimatic regimes—with warmer water temperatures and greater marsh inundation periods explaining greater abundance. I used stable isotope analysis of carbon, nitrogen, and sulfur to provide insights into the basal resource contribution to peacock eels and to determine peacock eel niche size and overlap with native species using hypervolume analysis. With these analyses, I found that peacock eels have the potential to compete with native sunfishes (*Lepomis spp*.). The trophic niche of peacock eels, though significantly smaller in volume, overlaps 98.8% with that of native sunfishes. Competitive interactions between peacock eels and native sunfishes could disrupt the niche of sunfishes and subsequently alter marsh prey subsidies on which coastal fisheries rely. In recent years, the catch of peacock eels has outnumbered the catch of all species of native sunfish combined. Peacock eel populations are expected to increase as the climate continues to change and cold weather events that are currently limiting their population growth become less frequent.

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Introduction

List of Symbols and Acronyms:

ENP – Everglades National Park

FCE – Florida Coastal Everglades

SRS – Shark River Slough

UFWS – US Fish and Wildlife Service

$\delta^{13}C$ – Heavy-to-light isotopic ratios of carbon

$\delta^{15}N$ – Heavy-to-light ratios of nitrogen

$\delta^{34}S$ – Heavy-to-light isotopic ratios sulfur isotopes

The Florida Everglades encompasses 1.5 million acres of South Florida and consists of expansive sawgrass marshes that drain into mangrove coastlines and out to Florida Bay and the Gulf of Mexico (Junk et al. 2006; Stabenau and Pearlstine 2011). It was the first U.S. national park to be established with the primary objective to protect and preserve biological resources and is now recognized as a Natural World Heritage site and a wetland of international importance (Junk et al. 2006; Kline et al. 2014). However, the Everglades is a highly threatened system, experiencing 50% loss in wetland area due to drainage and impoundment associated with urban development, agriculture, flood protection and the extensive hydrological alterations associated with water management systems (Rudnick et al. 1999; Junk et al. 2006; Kline et al. 2014). The Everglades is also highly vulnerable to invasions of exotic species due to its close proximity to aquarium trade routes and its subtropical climate allowing tropical invaders to thrive

(Junk et al. 2006; Episcopio-Sturgeon and Pienaar 2020). The coastal and aquatic systems are particularly susceptible to widespread invasions due to the intricate canal system that enables non-native species to rapidly spread into areas that were previously inaccessible (Courtenay and Miley 1975; Loftus and Kushlan 1987; Kline et al. 2014). With continued hydrological and ecological changes, the Everglades are becoming increasingly susceptible to non-native and invasive species (Junk et al. 2006; Pintar et al. 2023).

The recent introduction of non-native peacock eels (*Macrognathus siamensis*) in the Everglades is of growing concern. The peacock eel was first collected in the canals of South Florida in 2002 and has since been deemed established in the Everglades by the US Fish and Wildlife Service (Shafland et al. 2008; USFWS 2018). The ornamental fish is highly sought after for its unique body shape, coloration, and playful behavior and was likely imported to the U.S. for the aquarium trade (Das and Kalita 2003; USFWS 2018; Sinha et al. 2020). Peacock eels are native to Southeast Asia where they inhabit freshwater rivers, canals, ponds, and inundated fields (Sultana et al. 2017). In their invaded range, they can now be found throughout Everglades National Park (ENP) within the canals, freshwater marshes, and mangrove creeks (Shafland et al. 2008; Kline et al. 2014). The spread of this species is of particular concern due to its potential to compete with native species such as sunfishes (*Lepomis spp*.) that are a critical prey source for economically important migratory fish (Boucek and Rehage 2013; Rezek et al. 2023).

The Florida Coastal Everglades (FCE) naturally undergoes seasonal variation in freshwater input and marsh inundation levels which affect habitat availability and resources available to secondary consumers (Ruetz et al. 2005; Childers 2006). These variations affect species distributions and abundances, competitive interactions, and resource availability that can impact ecosystem dynamics (Rehage and Trexler 2006; Matich et al. 2017; Rezek et al. 2023). During seasonal dry-down periods, prey species originating from the freshwater marshes pulse into the estuarine creeks seeking refuge (Boucek and Rehage 2013; Matich and Heithaus 2014; Boucek et al. 2016). These pulses are important for sport fish such as common snook (hereafter snook; *Centropomus undecimalis*) that prey on these marsh fish (Boucek and Rehage 2013; Rezek et al. 2020; Massie et al. 2022). Sunfishes (*Lepomis spp*.) account for a significant portion of seasonal prey pulses in both abundance and biomass (Boucek and Rehage 2013; Boucek et al. 2016; Rezek et al. 2023) and can provide 41% of the total biomass consumed by snook inhabiting these riverine systems (Boucek and Rehage 2013). Competitive interactions between peacock eels and native sunfish could disrupt the niche of sunfishes and subsequently alter the seasonal prey pulse composition on which these major fisheries rely.

Few studies have been done on peacock eels in the Everglades, and their primary resource use in this region is largely unknown. Close evaluation of their anatomy and morphology reveals peacock eels to be carnivorous and highly adapted predators (Das and Kalita 2003; Faridi et al. 2016). Gut content analysis of peacock eels in their native habitat found their diets to consist of similar items to that of sunfish including small fish, shrimp, insects, annelids, and other benthic invertebrates (Loftus 2000; Faridi et al. 2016; Sultana et al. 2017). The US Fish and Wildlife Service risk assessment on peacock eels in the Everglades concluded that additional information is needed to determine the impact of their introduction and establishment (USFWS 2018). Based on known diets of both, peacock eels and sunfishes likely belong to the same feeding guild and may compete for resources and occupy similar trophic niches (e.g., Rubenstein 1981; Faridi et al. 2016; Sultana et al. 2017). In ecosystems where resource availability is limited, such as freshwater portions of the Everglades, competitive interactions leading to niche contraction can have substantial effects on the role species play, and lead to increased susceptibility to environmental change in species with more specialized niches (Colles et al. 2009; Clutton-Brock and Sheldon 2010; Matich et al. 2017).

Environmental changes such as altered temperature regimes and hydrological changes can have a profound impact on aquatic ecosystems and make them more susceptible to invasion (Junk et al. 2006; Boucek and Rehage 2014; Stachowicz et al. 2023). Warming water temperatures in subtropical and temperate areas can be particularly beneficial to invasive species of tropical origin, allowing them to out-compete their native counterparts (Zerebecki and Sorte 2011; Tepolt and Somero 2014) and can magnify the impacts of predation by non-native predators on native prey species (Rahel and Olden 2008). For example, bioenergetics models indicate that consumption of native salmon by non-native piscivores in the Columbia River (North America) will increase 4-6% with 1˚C increase in annual river temperatures (Petersen and Kitchell 2001). Similarly, European freshwater invasive gammarids (*Gammarus tigrinus* and *Dikerogammarus villosus*) were shown to have increased food intake with increased water temperature suggesting predation pressure on resident prey is likely to increase with ongoing climate change (Pellan et al. 2016).

Hydrological regimes can also profoundly impact the overall productivity of an ecosystem. Rezek et al. (2023) determined that the overall biomass of the prey pulse in the FCE was best explained by marsh flooding duration during the prior wet season, indicating that overall production is mediated by the hydrological regimes experienced in the marsh habitat. These regimes are expected to change in light of future water management actions (Junk et al. 2006; Flower et al. 2017) as well as climate change and sea level rise (Stabenau and Pearlstine 2011; Catano et al. 2014; Dessu et al. 2018). Understanding the long-term population trends of peacock eels and the environmental factors influencing their populations is necessary for mitigation and management of the invasion.

It is also important to investigate the potential effects the introduction of peacock eels may have on existing food webs. Various methods can be used to assess the potential impacts of an introduction on food web dynamics such as stable isotope analysis. Carbon, nitrogen, and sulfur stable isotopes are often used to understand the effects of non-native and invasive species on food webs (Vander Zanden et al. 1999; Jackson et al. 2012; Guzzo et al. 2013). The heavy-to-light isotopic ratios of carbon (denoted as $\delta^{13}C$) undergo minimal isotopic fractionation between prey and consumer making it possible to determine sources of dietary carbon in consumer tissue (DeNirot and Epstein 1981; Peterson and Fry 1987; Layman et al. 2007). Similar to carbon, the ratio of sulfur isotopes ($\delta^{34}S$) changes relatively little with trophic transfers and can be used to identify important resource pools such as those derived from fresh and saltwater sources (Canfield 2001; McCutchan et al. 2003). Heavy-to-light ratios of nitrogen ($\delta^{15}N$) exhibit stepwise enrichment with trophic transfers and can define an organism’s trophic position within a food web (DeNirot and Epstein 1981; Fry 1988; Post 2002). Unlike other methods of assessing trophic dynamics, such as gut contents analysis, stable isotope analysis can also differentiate between food that is assimilated rather than merely ingested by providing an integrated estimate of long-term food utilization (Michener and Schell 1994; Gao et al. 2006; Xia et al. 2013; Alp and Cucherousset 2022).

Stable isotope analysis can also be used to characterize the ecological role of non-native species and their potential effects on native species (Guzzo et al. 2013). With Bayesian stable isotope mixing models, the isotopic composition of a consumer can be used to determine the proportional contribution of different dietary sources and be used as a measure of trophic niche width (Bearhop et al. 2004; Swanson et al. 2015). The trophic niche of invasive species can then be compared to that of native species to identify any overlap, such as a shared food source, and can serve as an indicator of potential competition (Vander Zanden et al. 1999; Zambrano et al. 2001; Jackson et al. 2012; Córdova-Tapia et al. 2015). A common method of characterizing niche overlap based on raw stable isotope data is the standard ellipse method. This method uses the total area of a Bayesian estimated ellipse drawn around isotope values in bi-variate space as a measure of isotopic niche space (Layman et al. 2007). Standard ellipse methods have been used to evaluate the likelihood of resource competition between native and invasive species including invasive carp (*Cyprinus carpio*), in Lake Naivasha, Kenya (Jackson et al. 2012); invasive white perch (*Morone americana*) in Lake Erie, United States (Guzzo et al. 2013); and weakfish (*Cynoscion regalis*) in the Iberian Peninsula, Europe (Cerveira et al. 2021). In addition to standard ellipses and other geometric niche areas that can be dimensionally limiting, methods of hypervolume analysis have been developed that are based on stochastic geometry to represent the desired niche in greater dimensions

(Blonder et al. 2014; Blonder 2018; Lu et al. 2021). James et al. (2020) used hypervolume analysis methods based on trophic levels and source contribution information derived from Bayesian isotope mixing models to determine how trophic niche size and overlap within fish species changes in response to the availability of food sources. Rezek et al. (2020) used similar hypervolume methods for niche differentiation among migratory predators within the Everglades.

This study aimed to evaluate the magnitude of the peacock eel invasion in the Everglades and characterize the potential threat their introduction and spread may pose towards native species and existing food webs. Using an 18-year electrofishing dataset and contemporary stable isotope-based hypervolume analysis I 1) analyzed the long-term trends in abundance of peacock eels in the mangrove creeks of the Florida Coastal Everglades; 2) assessed the relationship between variation in hydrology and temperature on peacock eel abundance; and 3) quantified the trophic niche of peacock eels in their invaded range and assessed the overlap in basal resource use between peacock eels and native sunfishes—Dollar sunfish (*Lepomis marginatus*), Bluegill (*Lepomis macrochirus*), Spotted sunfish (*Lepomis punctatus*), and Redear sunfish (*Lepomis microlophus*). These data provide a better understanding of the factors regulating peacock eel populations as well as insight into the potential effects of the invasion on ecosystem structure, function and services, and may help to inform management actions.

Methods

List of Symbols and Acronyms:

AR1 – Autoregressive order 1 term

BIC – Bayesian Information Criterion

CPUE – Catch per unit effort

FCE LTER – Florida Coastal Everglades Long Term Ecological Research

FldDays – The count of days in the preceding six months of sampling where marsh inundation exceeded 30 cm

GLMM – Generalized linear mixed model

IACUC – Institutional Animal Care and Use Committee

MdWaterDp – The median water depth on the sampling day

MinTemp – The lowest temperature documented in the preceding six months of sampling

NGS – National Geological Survey

PE – Peacock eels

$R(X_H/X_L)$ –The ratio of the heavy to light isotope of the element, X

SRS – Shark River Slough

TDF – Trophic discrimination factor of nitrogen

TP – Trophic Position

w_i – Schwarz weight of linear regression models

X – Element in question, carbon nitrogen or sulfur

Δ BIC – The difference in BIC relative to the minimum

δ – The relative difference, in parts per thousand, of the isotopic ratios of a sample and of a reference standard

$\delta^{13}C$ – Heavy-to-light isotopic ratios of carbon relative the standard PeeDee Belemnite

$\delta^{15}N$ – Heavy-to-light isotopic ratios of nitrogen relative the standard atmospheric nitrogen

$\delta^{15}N_{ind}$ – The nitrogen value of an individual consumer

$\delta^{15}N_{source}$ – The nitrogen value of each basal resource

$\delta^{34}S$ – Heavy-to-light isotopic ratios of sulfur relative the standard Canyon Diablo Troilite

$\%cont_{source}$ – The proportional contribution of each source to the consumer diet

2.1 | Study site

The focus area of this study was the interface between marsh and riverine habitats in the main stem and first-order creeks of Rookery Branch located within the Shark River Slough (SRS) of Everglades National Park. The SRS is located near the southern tip of the Florida peninsula (Figure 1a) and is the largest preserved portion of the "River of Grass" (Dessu et al. 2018). The northern portions of this subtropical wetland system are dominated by freshwater sloughs and sawgrass marshes (Sultana et al. 2017) which transition to mangrove forests towards the coast and flow into mesohaline rivers that empty into the Gulf of Mexico (Ewe et al. 2006; Saha et al. 2012; Dessu et al. 2018). This system is highly oligotrophic and phosphorus-limited (Noe et al. 2003; Gaiser et al. 2023). Nutrients are primarily brought in by tidal influence carrying marine water up from the Gulf of Mexico (Fourqurean and Zieman 1992; Chen and Twilley 1999) forming a gradient of increased productivity with greater marine influence (Childers 2006; Rezek et al. 2020).

2.2 | Data Collection and Sample Processing

I used 19 years of data (2004–2022) collected as part of the Florida Coastal Everglades Long Term Ecological Research Program (FCE LTER; Childers et al. 2019). Sampling events occurred at least once during the wet season (November-December), once in the early dry season (i.e. the transitional period between marsh inundation and drying; February-March), and once in the late dry season (April-May) each year. Additional sampling occurred near monthly during the dry season. During each sampling period, fish were collected via boat-based electrofishing (Smith-Root GPP 9.0 electro fisher, Smith-Root, Vancouver, Washington, USA) at 15 sites, six located in the main stem of Rookery Branch and nine in first order creeks (Figure 1b), using methods approved by Florida International University's Institutional Animal Care and Use Committee (IACUC # 15-046).

Electrofishing was conducted along transects parallel to the mangrove shoreline for 300 seconds of pedal time (i.e., time electrofishing unit is running; Rehage and Loftus 2007). For each transect the shoreline was selected at random, right or left side, for approximately 100 m (mean = 91m, SD = 28). GPS was used to record the precise distance traveled during each sample. At each site, fish collected were identified to species, weighed, measured for total length and counted. The abundance of peacock eels is reported as a catch per unit effort (CPUE) standardized to catch per 100 m of shoreline. All peacock eels shocked during the sampling events, including those that were shocked and not landed, were included in the total catch estimate to allow for a more accurate abundance estimation, as recapture or misidentification is unlikely due to the unique shocking behavior of peacock eels. Water level and temperature data for the 180 days prior to each study period were obtained from the MO-215 hydrostation (United States Geological Survey [USGS] gauge 252820080505401) and the Bottle Creek hydrostation (USGS gauge 022908295), respectively (Figure 1b). For a more detailed sampling method summary see Boucek and Rehage (2013).

Sampling for stable isotope analysis was conducted in May and November of 2019. Dorsal muscle tissue samples of peacock eels and sunfishes (0.5-0.7 g) were taken using standard protocol. Primary producer basal resources including epiphytic microalgae and mangrove detritus were collected by hand. Phytoplankton stable isotope values were obtained from (Fry and Smith 2002), who derived them from the values of suspension feeders (mussels and barnacles) collected within approximately 5 km of our study area. All samples collected for stable isotope analysis were stored on ice until being transported to the lab and stored at -20°C until processing. Samples were dried at 55°C for 24 h, ground into fine powder, packed in tin capsules, and analyzed for carbon, nitrogen, and sulfur values using continuous flow isotope ratio mass spectrometry at the Washington State University Stable Isotope Core Laboratory. Carbon, nitrogen, and sulfur isotope values were calculated using the standard formula:

$$Equation\ 1: \qquad \delta X = \left(\frac{R(X_H/X_L)_{\text{sample}} - R(X_H/X_L)_{\text{standard}}}{R(X_H/X_L)_{\text{standard}}}\right)$$

where R(XH/XL) is the ratio of the heavy to light isotope of the element, X (Peterson and Fry 1987; Nelson et al. 2012). Isotope values are expressed in standard δ notation (Peterson and Fry 1987), using PeeDee Belemnite, atmospheric nitrogen, and Canyon Diablo Troilite as reference standards.

2.3 | Environmental factors related to peacock eel abundance

A generalized linear mixed model (GLMM) with a negative binomial distribution was used to investigate the environmental factors that may impact the abundance of invasive peacock eels in the Everglades. This model was selected due to the over dispersed count data associated with this study. The model was constructed in R (v 4.2, Development Core Team, 2020), using the 'glmmTMB' package (Brooks et al. 2017). In the model, the dependent variable was the count of peacock eels in each site sampled. The independent variables included the year of sampling, a polynomial function of the sampling month (capturing potential seasonal effects), the count of days in the preceding six months where marsh inundation exceeded 30 cm, the median water depth on the sampling day, and the lowest temperature documented in the preceding six months. The 30 cm threshold represents the lower 15% of wet season daily water depth values measured throughout the study period. Water levels greater than 30 cm at the marsh platform indicate a state of flooding (Rezek et al. 2023). The temperature at which loss of equilibrium occurs in peacock eels is 12.8 ± 1.5°C and the lower lethal temperature of peacock eels, the point at which direct mortality occurs, is 9.1°C (± 1.0°C; Schofield and Kline 2018).

To accommodate temporal autocorrelation among sites, the model includes year sampled as an AR1 (autoregressive order 1) term. An offset term was incorporated to account for sampling effort and variations in sampling distances, which was expressed as the log-transformed distance of the electrofishing transects. The model was fitted to a dataset of 1,311 observations that spanned across 15 unique sampling sites. I used the Bayesian Information Criterion (BIC) to select the most likely model from a set of candidate models. The candidate models increased in complexity with each additional model beginning with a null model and then incorporating additional independent variables including sampling year and month, temperature, and hydrology (Table 4). BIC is calculated based on model likelihood and penalizes complex models, therefore, I chose the model with the lowest BIC value as the best fit for the data. Sensitivity analysis was conducted to assess the robustness of this selection (Schwarz 1978). The DHARMa package in R was used to evaluate the goodness of fit of the model by generating scaled residuals for the model through simulation (DHARMa v0.4.6; Hartig and Lohse 2022). The model was tested for zero-inflation and overdispersion – two common issues in count data models – using tests implemented in the DHARMa package, and a Kolmogorov-Smirnov test was conducted to verify goodness-of-fit. Predictor multi-collinearity was assessed using variance inflation factors, calculated with the performance package in R (Lüdecke et al. 2021).

2.4 | Trophic Niche of Peacock Eels

To characterize the trophic niche of peacock eels and native sunfishes, the relative contribution of each distinct resource base to individuals was derived through concentration-dependent Bayesian mixing models (Wilson et al. 2010; Parnell et al. 2010). All stable isotope data were analyzed in R using the package MixSIAR (v3.1.7; Stock et al. 2018).To allow for adequate model convergence, models were run in three chains with 1,000,000 iterations, a burn-in of 500,000 and a thin of 500. Trophic fractionation factors used for each element were as follows: C = 1.3 (±0.3), N = 3.3 (±0.26), and S = 0.5 (±0.54) (McCutchan et al. 2003; Wilson et al. 2010; Rezek et al. 2020). The results of the mixing models were used to estimate the mean contribution of each basal resource to each consumer sampled during the study. Estimates are represented as a posterior distribution, which denotes the consumer's diet as a series of numerically calculated vectors and incorporates error present from isotopic measurement or ecological variability (Newsome et al. 2012). The source contributions determined by the mixing model were used to calculate the relative trophic position of each individual consumer compared to base endmembers in the mixing model. Trophic position separates consumers in resource use space by the number of trophic steps between prey sources and consumers (Levine 1980). TP was determined using the following equation:

$$\mathit{Equation}\ 2. \qquad \mathrm{TP} = \frac{\delta^{15}\mathrm{N}_{\mathrm{ind}} - \sum(\delta^{15}\mathrm{N}_{\mathrm{source}} \times \mathrm{mean\%cont}_{\mathrm{source}})}{\mathrm{TDF}} + 1$$

where $\delta^{15}N_{ind}$ is the nitrogen value of an individual consumer, $\delta^{15}N_{source}$ is the nitrogen value of each basal resource, and mean $\%cont_{source}$ is the mean proportional contribution of each source to the consumer diet (Post 2002; Wilson et al. 2010; Nelson et al. 2015), and TDF is the trophic discrimination factor of nitrogen, 3.3‰ (McCutchan et al. 2003). This calculation accounts for the fractionations that occur during trophic transfer from source to consumer in order to directly determine the relative trophic position of the consumer. Trophic niche space can then be represented as a function of the peacock eel's dietary contributions and trophic level.

To allow for standardized, comparable axes in n-dimensional space the means of the posterior distributions from each prey base to each peacock eel and their calculated trophic position were scaled (z-transformed) before hypervolume analysis (Blonder et al. 2014). The z-scored percent contribution of each basal resource and the peacock eel's trophic position were used to seed a Gaussian kernel density estimation with the Hypervolume R package (v 2.0.12, Blonder et al. 2018). The hypervolume algorithm overlays kernels around each z-scored observation in multi-dimensional space and defines the multidimensional trophic niche of the peacock eels. A quantile threshold of 0.05 was used so that each hypervolume included 95% of the total probability density. The resulting hypervolumes of peacock eels and sunfishes (individually and combined) were evaluated to determine total trophic niche volume (Blonder et al. 2014, 2018; Blonder 2018). Metrics of trophic niche overlap, including the proportion of overlap among group hypervolumes (Sørenson overlap index, Sørenson 1948) and the fraction of unique hypervolume space for each pairwise comparison are reported, and were statistically evaluated via a bootstrapping (50 resamples) protocol (Newsome et al. 2012; Blonder et al. 2014). Hypervolumes were not calculated for spotted sunfish due to low sample size (n = 2).

Results

List of Symbols and Acronyms:

CPUE – Catch per unit effort

$\delta^{13}C$ – Heavy-to-light isotopic ratios of carbon

$\delta^{15}N$ – Heavy-to-light ratios of nitrogen

$\delta^{34}S$ – Heavy-to-light isotopic ratios sulfur isotopes

3.1 | Peacock eel Population Trends

A total of 2,386 peacock eels were sampled during the study period (2004–2022, n = 95 days, n = 1311 sampling events). No peacock eels were recorded during 2004–2006 sampling events. The first peacock eels recorded in this data set were collected in March 2007 (Figure 2). Following the initial capture, no peacock eels were sampled until December 2008. The CPUE remained below 1 individual per 100 m of mangrove shoreline until February 2009 (3.41) and peaked at 23.28 in November of the same year. This peak was followed by a sharp decline and subsequent low capture rate (CPUE ≤ 1 eels/100 m) until February 2013 (2.08). CPUE remained below 2 until January 2018 (8.56). The mean capture rate fluctuated during 2018–2022 with the largest increase from May 2020 (0.31) to May 2021 (40.76). Since June 2021, the mean CPUE of peacock eels has remained below 2.6 (Figure 2).

3.2 | Environmental Factors Related to Peacock Eel Abundance

Over the study period, the annual minimums of mean daily water temperature averaged 14.5°C (SD = 1.89) with the lowest daily average recorded in the wet season of

2010 (8.30°C). Annual maximum daily mean water temperature averaged 31.9°C (SD = 0.93) with the highest recorded during the dry season of 2005 (33.5°C). The mean daily water temperature exceeded the point at which loss of equilibrium occurs in peacock eels during the dry seasons of 2008–2012, 2015, 2018, 2020, and 2022 (Figure 3a). The lower lethal temperature of peacock eels was reached during the dry season of 2010. Over the study period, the minimum daily mean water level averaged -0.1 cm (SD = 13.4) with the lowest daily average recorded during the dry season of 2011 at (-14.0 cm). The maximum daily mean water level averaged 64.1 cm (SD = 13.4 cm) and the highest was recorded during the wet season of 2017 at (94.5 cm). The greatest number of days that the marshes were in a state of flooding occurred in 2016 and totaled 366 days and the lowest occurred in 2015 (107 days; Figure 3b). Model results suggest minimum daily water temperature and the mean daily water level over the 180 days prior to sampling were the most related to peacock eel abundance (Figure 4b,4d). Flooding duration over the previous 180 days and the month sampled were also found to be related to peacock eel abundance (Figure 4c, 4e). Peacock eel CPUE was shown to increase by 25% annually for every 1°C increase in minimum water temperature and by 4% for each additional day of marsh flooding (Table 1). The best fit model included the minimum daily water temperature, mean daily water level over the 180 days prior to sampling, flooding duration over the previous 180 days, and the year and month sampled (Figure 4a, Table 4).

3.3 | Stable Isotope Analysis and Mixing Models

Mean δ^{34}S values of native sunfishes ranged from 23.8 in spotted sunfish to 16.5 in dollar sunfish. Mean δ^{13}C values ranged from -31.5 in bluegill to -27.8 in dollar sunfish.

Mean $\delta^{15}N$ values ranged from 11.0 in bluegill to 9.1 in dollar sunfish. The average $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ values of peacock eels were 21.2, -28.8, and 9.4 respectively (Table 2). Of the basal resources, phytoplankton had the greatest mean δ34S value (24.5) and epiphytic microalgae was the lowest (13.5). Epiphytic microalgae had the highest mean $\delta^{13}C$ (-29.0) and $\delta^{15}N$ (7.0) values and phytoplankton had the lowest ($\delta^{13}C$ -35.5, $\delta^{15}N$ 5.8; Table 2).

Dollar sunfish had the highest mean basal resource contribution of epiphytic microalgae (47.6%) and spotted sunfish had the lowest (19.7%). Redear sunfish had the highest contribution of detritus (27.9%) and bluegill had the lowest (15.9%). Phytoplankton was most used by spotted sunfish (60.1%) and least used by dollar sunfish (26.3%). The mean resource contributions for peacock eels were 32.6% for epiphytic microalgae, 29.7% for detritus, and 37.7% for phytoplankton (Figure 5b). The average relative trophic position (z-score) of the native sunfishes were 0.788 for bluegill, 0.514 for spotted sunfish, -0.132 for redear sunfish, and -0.623 for dollar sunfish. The average relative trophic position of peacock eels was -0.296 (Figure 5a).

3.4 | Trophic Niche and Hypervolume Analysis

Peacock eels had the smallest trophic niche volume of the species assessed in this study (35.3). Dollar sunfish had the largest trophic niche volume at 295.1, followed by redear sunfish (271.1) and bluegill (247.7). Spotted sunfish were not used for individual species niche metrics due to insufficient sample size but were included in combined sunfish values. The combined trophic niche space of all sunfishes was 402.8 (Table 3). The Sørenson overlap index value for peacock eels and bluegill was the highest of the species assessed at 0.231 ($P < 0.001$). The overlap between peacock eels and dollar sunfish had the lowest Sørenson overlap index value of 0.194 ($P < 0.05$). The Sørenson overlap for peacock eels and the combined sunfish hypervolume was 0.162 ($P < 0.001$). Peacock eels did not have a significant amount of unique hypervolume space compared to any of the sunfish species assessed. Peacock eels had the highest fraction of unique hypervolume space when compared to redear sunfish with peacock eels having 10% ($P < 0.01$) unique space and had the lowest fraction of unique hypervolume space when compared with Bluegill (7% unique space, $P < 0.001$). Compared to the combined value of the sunfishes, peacock eels had 1.2% unique space and sunfishes had 91.1% unique space ($P < 0.001$; Table 3, Figure 6).

Discussion

List of Symbols and Acronyms:

CPUE – Catch per unit effort

FCE – Florida Coastal Everglades

4.1 |Peacock Eel Population Trends

The effects of the introduction and spread of the invasive peacock eel in the Florida Coastal Everglades are largely unknown. This study provides insights into the growing issue and how their populations may impact native fish assemblages and food webs. Assessment of 19 years of electrofishing data found that peacock eel abundance within the marsh and mangrove ecotone of the FCE has increased by 13.79% on average each year since their introduction. Within 3 years of detection, CPUE for the peacock eel population increased dramatically in this region (from 0.11 to 23.28 individuals/100m). Similar population spikes in invasive species in the Everglades include the notorious Burmese python (*Python bivittatus*), the African jewelfish (*Hemichromis bimaculatus*), and the Asian swamp eel (*Monopterus albus*; Lopez et al. 2012; Pintar et al. 2023).

The initial spike in the peacock eel population was followed by a sharp decline and a subsequent 8-year period (2010-2018) when population numbers remained low. This drastic population decline directly followed the historic 2010 cold snap, the most severe cold weather event documented in this region in 100 years, during which water temperatures fell to 6.2°C and air temperatures remained below -3.3°C for 12 days (Boucek and Rehage 2014; Stevens et al. 2016). The lower lethal limit for peacock eels is 9.1 (± 1.0°C), therefore this cold weather event likely caused direct mortality (Schofield and Kline 2018). However, under more favorable temperature conditions peacock eel populations spiked exemplifying their ability to thrive in this ecotone. Peacock eel populations can double in as little as 1.4 years (Forese et al. 2017), though they do not become sexually mature until three years of age (Shina et al, 2023). In 2018, peacock eel populations began to increase, and increased by 927.8% over the next 3 years.

In the Everglades, hydrology is a primary driver of wildlife population dynamics and many species are tightly tied to the hydrologic cycle making them vulnerable to changes in climate and water management decisions that affect the availability of freshwater habitats. In this study, it was found that when water levels in the marsh were low, peacock eel populations in the mangrove creeks were at their highest. This trend also occurs with the seasonal freshwater prey pulse, suggesting that peacock eels are also seeking refuge in the mangrove creeks during seasonal dry down periods. Peacock eel abundance was also associated with longer periods of marsh inundation. The positive effect of increased flooding duration on peacock eels is consistent with data on native species in the system, indicating that increased duration of marsh habitat availability may increase production of peacock eels as well. Rezek et al. 2023 suggests this may be because of the increased access to floodplain-associated resources and habitat when water levels remain above a certain threshold for longer periods of time. However, the extent and timing of the subsequent dry down period will mediate the biomass and composition of the pulse of freshwater fishes to the mangrove creeks (Rezke et al., 2023). Similar to the FCE, pulsing hydrology is a major factor affecting fish communities in the river-floodplain ecosystems of South East Asia where peacock eels are native (Chea et al. 2020). Little is known about the biology of peacock eels, but the movement of peacock eels in the FCE likely mimics their behavior in their native range as peacock eels are known to inhabit inundated fields during the monsoon season (Sultana et al. 2017) and would likely seek refuge in the rivers during seasonal dry downs.

Both hydrological and temperature regimes are expected to change in light of climate change. Increasing temperatures could increase the time between cold weather events that currently limit expansion and abundance of peacock eels as well as other subtropical and tropical non-native species (Catano et al. 2014). Modeled climate change scenarios for the Greater Everglades Ecosystem predict temperature to increase by 1.5 °C, sea level to increase by 1.5 feet (46 cm), and +/-10% change in precipitation by 2060 (Obeysekera et al. 2014; Koch et al. 2014). Catano et al. (2014) predicted these conditions will have severe negative effects on native species and increase the risk for further invasion and establishment by non-native species. As temperatures continue to increase and the frequency of cold weather events decreases, it is likely peacock eel populations will expand.

4.2 |Stable Isotope and Hypervolume Analysis

Stable isotope analysis provided novel insights into the trophic ecology of peacock eels in the Florida Coastal Everglades including the species' relative trophic level, trophic niche size, and trophic niche overlap with native species. Based on diets from their native range, peacock eels have the potential to compete for resources and occupy similar trophic niches as ecologically important native species in the Everglades

(Rubenstein 1981; Faridi et al. 2016). Competitive interactions between peacock eels and native sunfishes could disrupt the niche of sunfish and subsequently alter the seasonal prey pulse composition on which major fisheries rely. Peacock eels feed at a similar trophic level as redear and dollar sunfish, suggesting that they are likely to compete for prey items. However, peacock eels have a significantly smaller trophic niche volume than that of the native sunfishes, indicating that they use a smaller variety of resources. This was an unexpected result as successful invaders often are generalist species and utilize a wide variety of resources (Brandner et al. 2013; Dehnhard et al. 2020). This finding may prove beneficial for native sunfishes, as direct competition may not be occurring. However, with increasing peacock eel populations and their non-generalist or specialized feeding characteristics, some prey species populations may be significantly affected as seen with the swamp eel invasion and could lead to trophic niche shifts in sunfishes (Kelly and Jellyman 2007; Ke et al. 2008).

In the Florida Costal Everglades, the basal resources primarily utilized by peacock eels were found to be phytoplankton and epiphytic microalgae. Epiphytic microalgae are one of the main basal resources used by aquatic animals in freshwater ecosystems and are likely incorporated in the peacock eel's diet through consumption of macroinvertebrates, snails, and small fish that consume the epiphytes growing on aquatic plants (Lv et al. 2022). Peacock eels, however, have no apparent structural adaptations for filtering phytoplankton and large quantities of fresh phytoplankton in their stomachs has not been documented. Similar unexpected results were found when determining the dietary sources of carbon in characiforms in the Amazon. Forsberg et al. (1993) concluded that for Amazonian characiforms to derive the majority of their carbon from phytoplankton they must be selectively consuming or assimilating detritus from this source. In the Everglades, detritus was not found to be a major trophic pathway for peacock eels so this may be attributed to the consumption of benthic invertebrates that consume phytoplankton or bio-flocculants.

Stable isotope analysis reflects the primary trophic channels being utilized by species and can determine which sources are being assimilated rather than merely ingested; however, gut content studies on peacock eels would be helpful for understanding specific dietary contributions in their invaded range. Such studies have been done for peacock eels in the FCE but were inconclusive due to the heavily digested state of the gut content (J.R. Blanchard, unpublished data). The trophic niche of peacock eels was not significantly different from any of the sunfishes in question and when compared to sunfishes as a whole, there were almost no unique differences in trophic niche space and was almost entirely nested within the trophic niche space of the combined sunfish value (98.8%) indicating that the trophic channels peacock eels are relying on are also being used by native sunfish. This is consistent with data on the known diets of both (Rubenstein 1981; Faridi et al. 2016; Sultana et al. 2017) and suggests competition is possible.

4.3 | Peacock eel potential impact

Competition imbalances favoring invasive species can not only displace natives but can also disrupt the stability of an ecosystem and have cascading effects on existing food webs (McKinney and Lockwood 1999; Guzzo et al. 2013; Jackson et al. 2016). Sunfishes account for a significant portion of seasonal prey pulses and can provide 41% of the total biomass consumed by common snook (*Centropomus undecimalis*) inhabiting riverine systems (Boucek and Rehage 2013; Rezek et al. 2020). Rezek et al. (2023) evaluated the abundance of sunfish from 2004–2020 in this system, finding an average annual peak abundance of 11.2 (± 2.5) n/100 m of mangrove shoreline in comparison to 2.5 (± 1) n/100 m for peacock eels in this study. Alarmingly, peacock eel abundance was greater than that of all sunfishes combined during their initial peak in 2009 and again in 2020 (Rezek et al. 2023), with the highest abundance of peacock eels in the dataset occurring in 2021.

The significant trophic niche overlap between peacock eels and the native sunfishes found in this study suggests that there is potential for resource competition (Vander Zanden et al. 1999; Kelly and Jellyman 2007; Córdova-Tapia et al. 2015). The overlap found in this study, however, does not necessarily mean direct competition is occurring. The shared resources being used may not be limiting or the species may have different behavioral adaptations to avoid competition such as habitat utilization or nocturnality. This may be the case as peacock eels are known to be nocturnal hunters (Das and Kalita 2003), where many sunfishes tend to be diurnal (Reynolds and Casterlin 1976). Peacock eels may directly impact native sunfishes if food becomes limiting and if they are unable to readjust their diet and habitat use to avoid competition (Cerveira et al. 2021); however, because sunfishes have a significantly larger trophic niche volume, they are using a larger number of trophic channels and may be able to adjust their diet more easily with changes in prey abundance (Sharma and Borgstrøm 2008; Ke et al. 2008; Córdova-Tapia et al. 2015). In some cases, invasive species may become an important prey resource to native predators and can have a positive effect on their abundance (Maerz et al. 2005; Dijkstra et al. 2013; Pintor and Byers 2015). In the Great Lakes, the invasive Round goby (*Neogobius melanostomus*) has been linked to improved body condition and growth in some native species (Crane et al. 2015; Crane and Einhouse 2016); however, it has significantly re-engineered local food webs (Campbell et al. 2009; Rush et al. 2012; Crane et al. 2015) and has resulted in a decreased abundance of native benthic prey fishes (Janssen and Jude 2001; Lauer et al. 2004). These results are similar to the swamp eel invasion that is credited for the collapse of four different populations of native benthic prey species within the Everglades. The implications of the loss of these species may include a re-organization of the local food web and food-production system which supports apex predators including wading birds and alligators (Pintar et al. 2023). The potential for peacock eels to serve as an alternative prey source for migratory predators that rely on the seasonal prey pulse remains unknown.

5 | Conclusions

This study provides an ecological dataset about peacock eel populations and trophic ecology in their non-native range within the Florida Coastal Everglades. Peacock eel populations are increasing and are expected to continue to increase under favorable temperature and hydrological regimes. Temperature and hydrological regimes in the FCE are expected to change in light of climate change which may further favor peacock eel population growth. Based on hypervolume analysis, peacock eels have the potential to compete with ecologically important native sunfishes and in recent years the catch of peacock eels has outnumbered the catch of native sunfish species. Further research should be done to determine if there is a correlation between peacock eel abundance and sunfish abundance as well as how temperature trends influence competition and community dynamics. Additional studies should also be done to assess the impacts of the peacock eel introduction on native prey species, other impacts on native fish assemblages, as well as their potential to become prey for larger predator fisheries species. It is imperative that peacock eel populations continue to be monitored and that further studies be conducted to determine additional impacts of their introduction to predict and mitigate the effects on local food webs and native species.

Figures

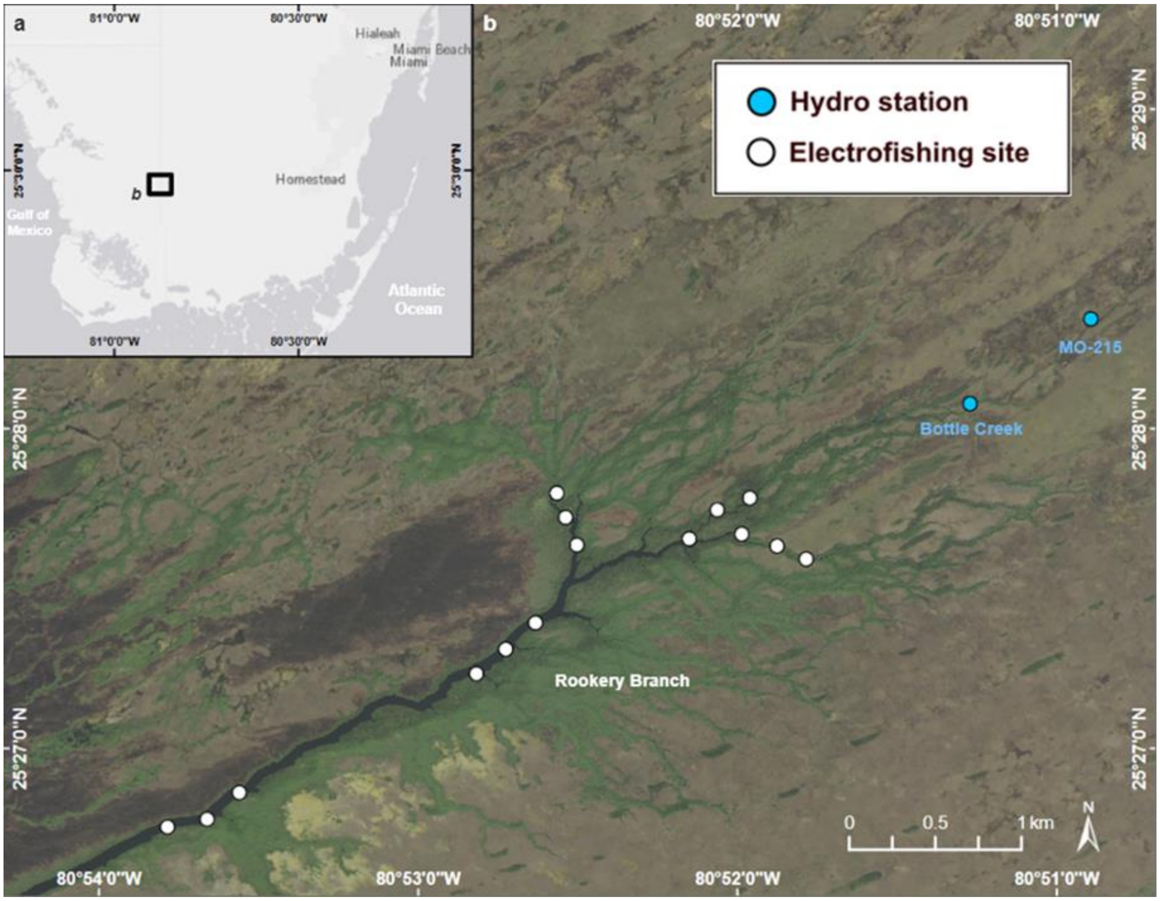

Figure 1. Map of the study region in Everglades National Park (a) map of the electrofishing sites represented by white dots and the USGS Bottle Creek and MO-215 hydro stations (b).

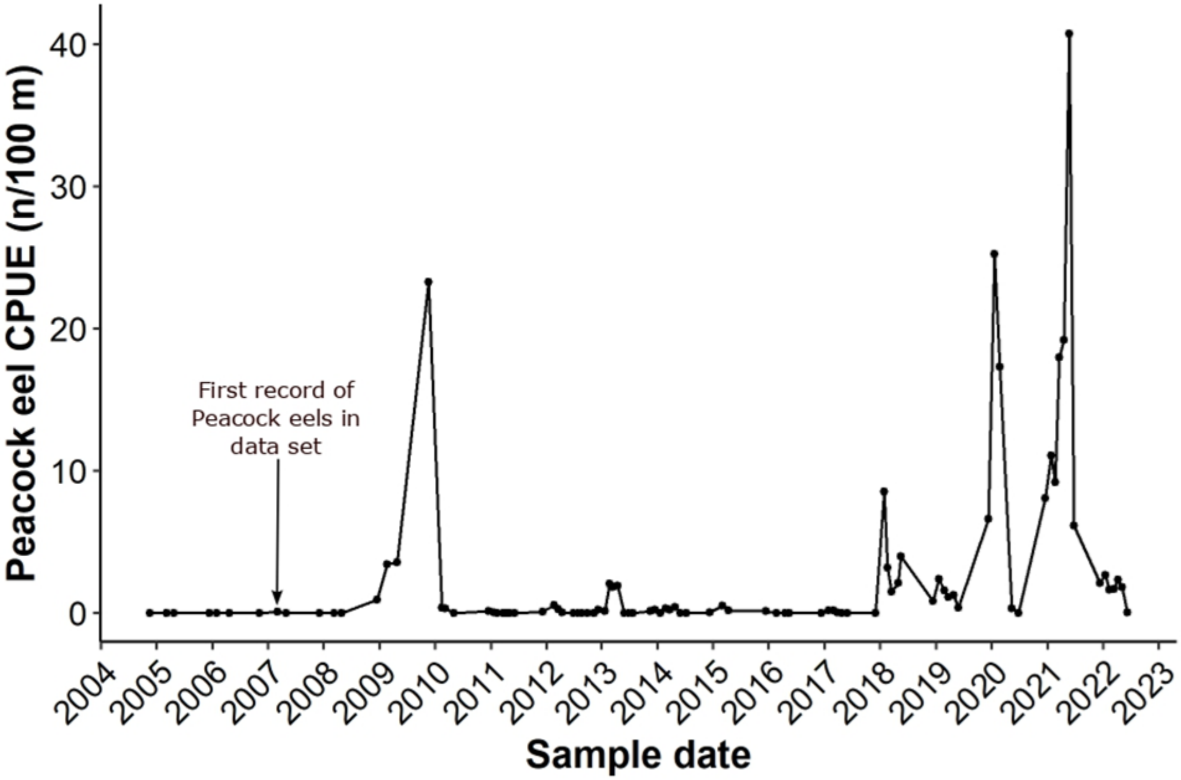

Figure 2. Mean peacock eel abundance per 100 m of river shoreline from all sampling events (*n*= 95) over the 19-year time series (2004-2022). The dashed arrow indicates the date of the first peacock eel sampled in the study area.

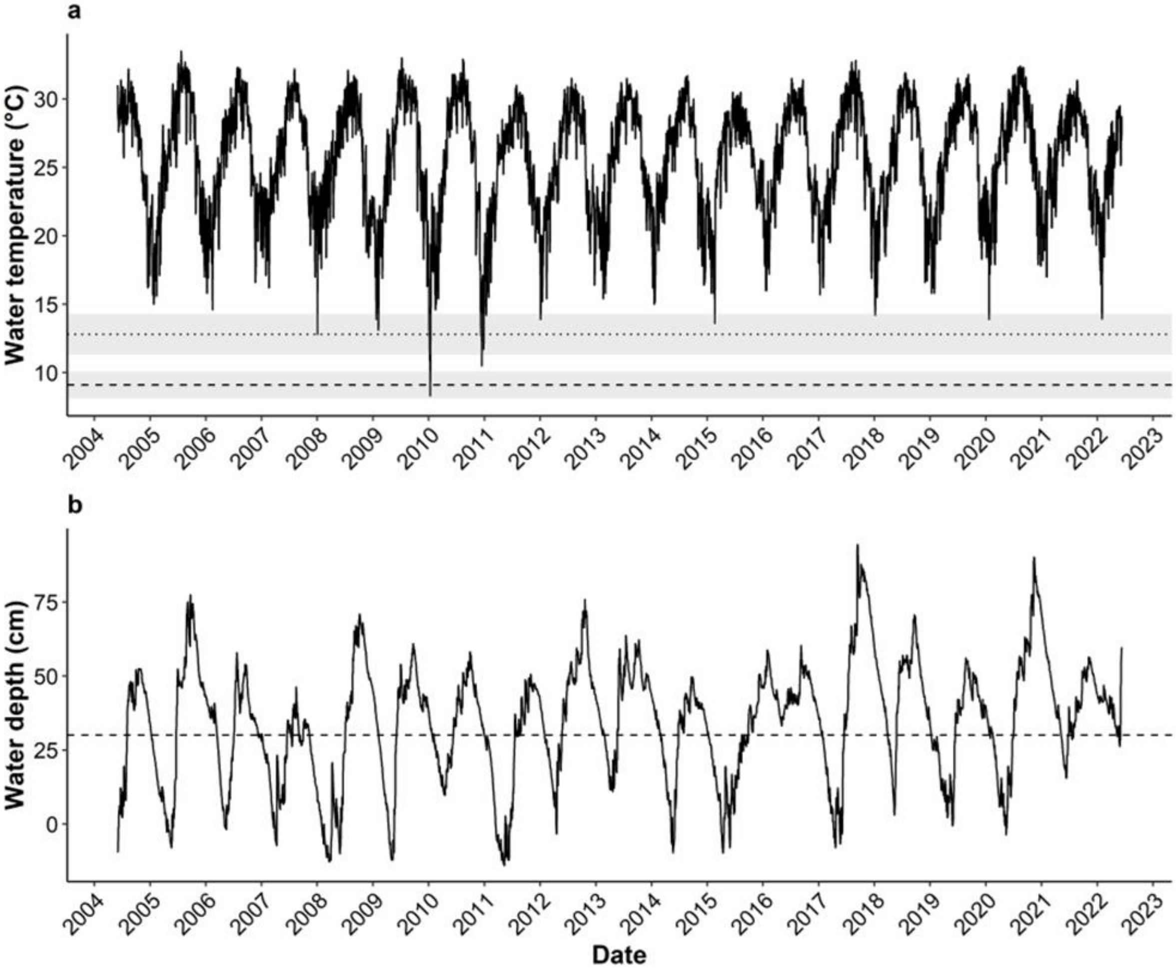

Figure 3. Hydrological data of the study area over the time series. (a) The mean daily water temperature recorded from the Bottle Creek hydro station over the study period. The dotted line represents the temperature at which loss of equilibrium occurs in peacock eels (12.8 ± 1.5°C), the dashed line represents the lower lethal temperature at which direct mortality occurs (9.1°C; Schofield and Kline 2018) and the gray areas represent the SD; (b) The mean daily water depth recorded from MO-215 hydro station over the study period. The dashed line indicates the 30 cm water depth when the marsh is considered fully inundated. The average marsh ground elevation at MO-215 is -9.8 cm relative to NAVD88.

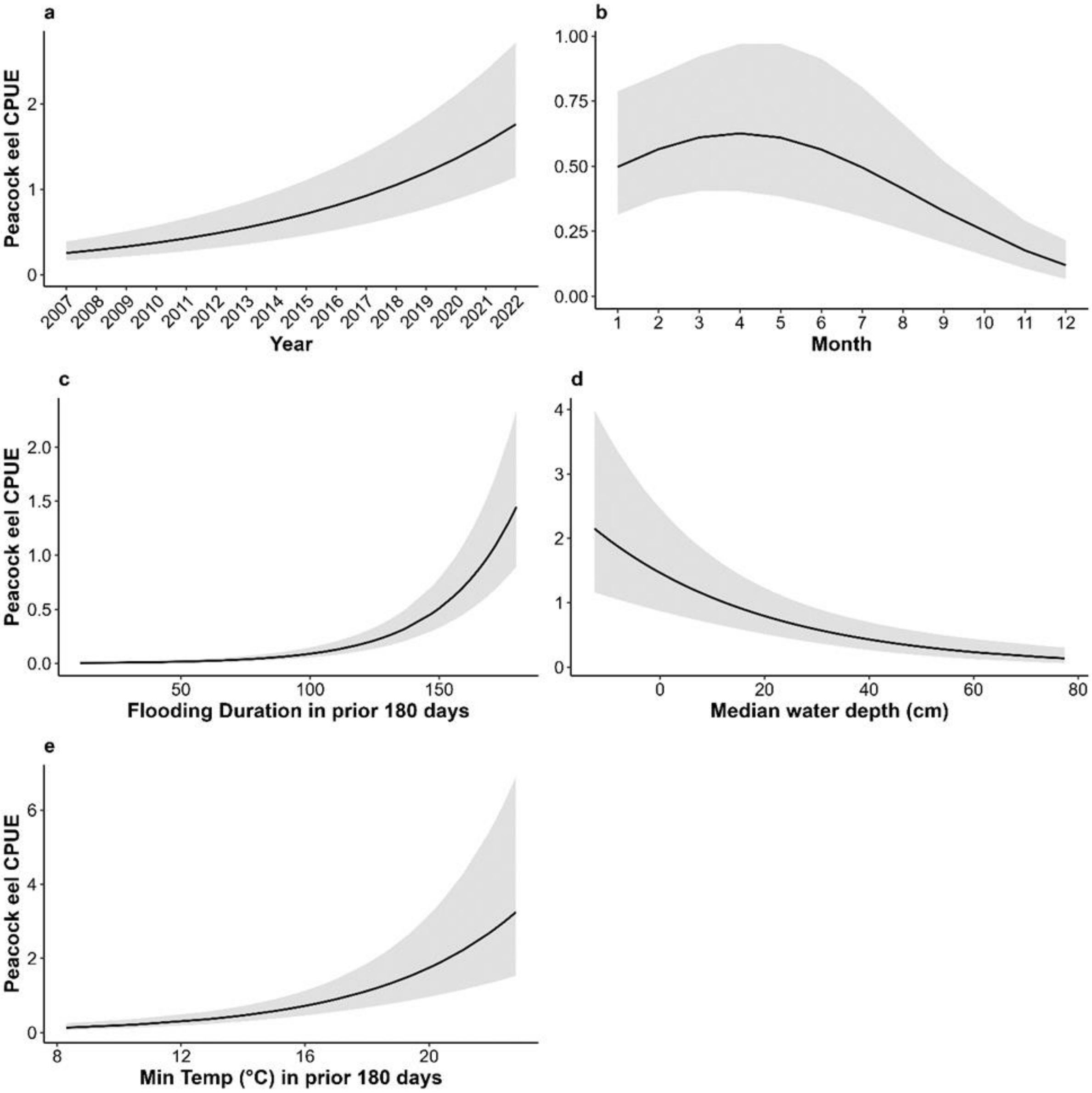

Figure 4. Marginal effects of parameters assessed with GLMM on peacock eel CPUE (catch per electrofishing bout) representing (a) sampling year, (b) the month when sampling occurred, (c) the number of days the median daily water level at the marsh platform was above 30 cm (fully inundated), (d) median daily water depth on the sampling date, (e) minimum daily mean water temperature recorded within the 180 days prior to sampling date.

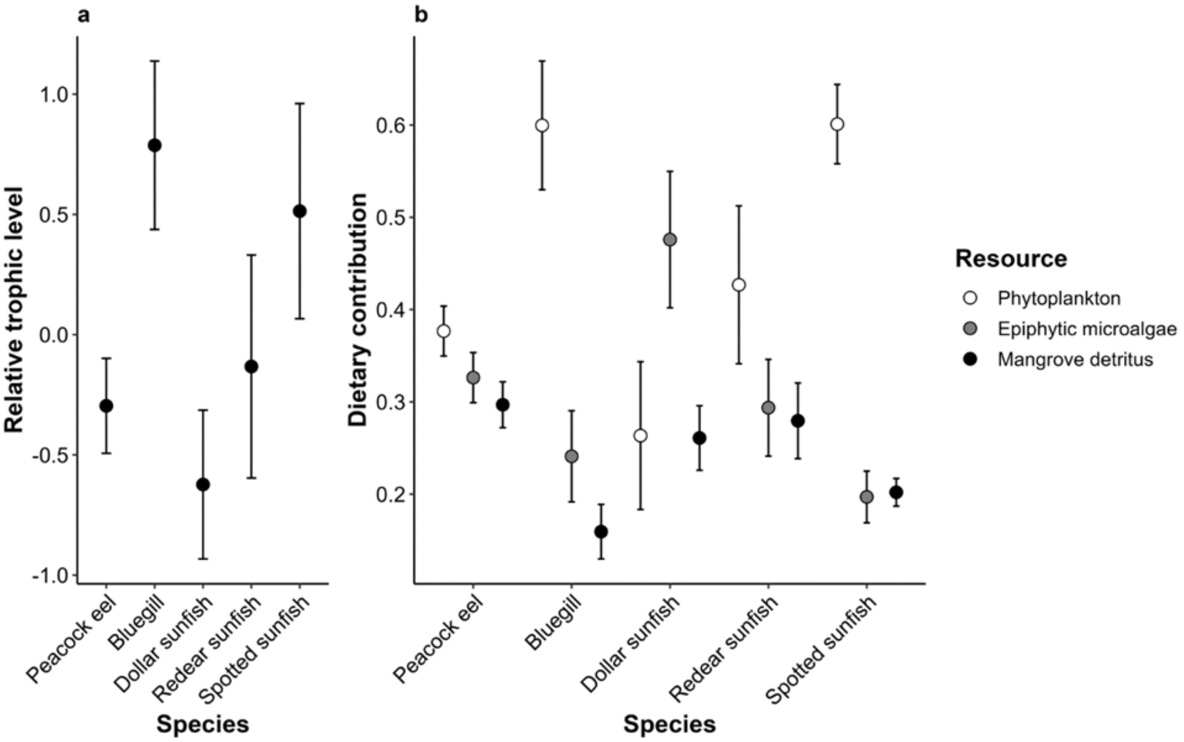

Figure 5. Mixing model outputs (a) the relative trophic position (z-score) of the invasive peacock eel (*Macrognathus siamensis*) and native dollar sunfish (*Lepomis marginatus*), bluegill (*Lepomis macrochirus*), redear sunfish (*Lepomis microlophus*), and spotted sunfish (*Lepomis punctatus*) in Rookery Branch; (b) source contributions of each basal resource to each species in question. Open points represent individual values and solid points represent mean and standard error.

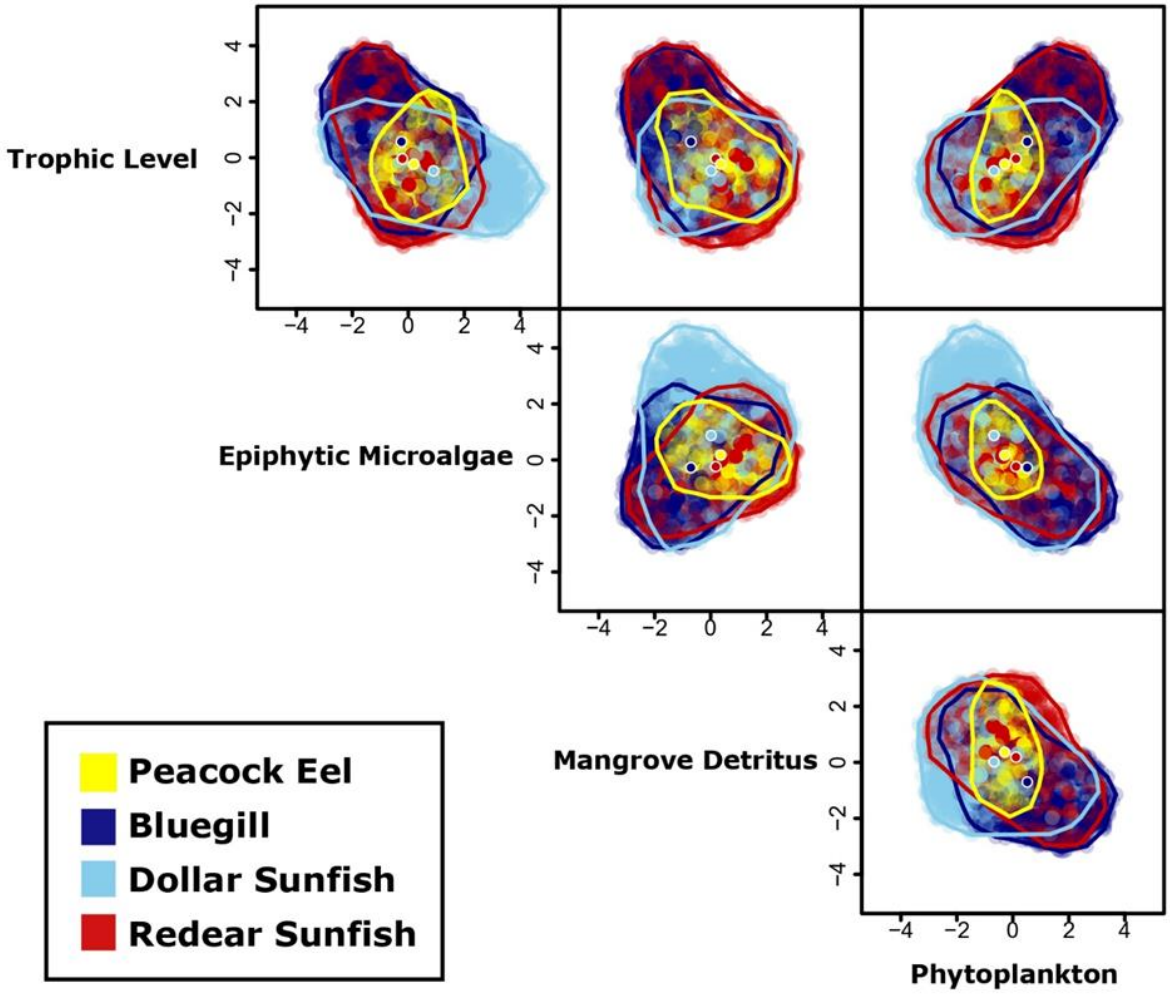

Figure 6. Trophic niche hypervolumes of the invasive Peacock eel (*Macrognathus siamensis*) vs. native Dollar sunfish (*Lepomis marginatus*), Bluegill (*Lepomis macrochirus*), and Redear sunfish (*Lepomis microlophus*) in Rookery Branch. Axes represent z-scores of estimated dietary contributions (mixing model posterior means) or trophic positions.

Tables

Table 1. Mixed effects negative binomial regression model results. Variables include the year sampling occurred, the month sampling occurred, the number of days the marsh was flooded within the 180 days prior to sampling, the median daily water depth, and the minimum water temperature over the 180 days prior to sampling.

	Coefficient	**SE**	**z-value**	***P-value***
(Intercept)	-273.6	85.88	-3.186	< 0.001
Year	0.129	0.043	3.027	0.002
poly(Month|1)	-18.58	3.092	-6.008	< 0.001
poly(Month|2)	-10.26	3.459	-2.966	0.003
Flooding duration 180 days	0.0349	0.003	11.89	< 0.001
Median water depth	-0.0306	0.006	-4.868	< 0.001
Minimum water temp 180 days	0.2214	0.038	5.808	< 0.001

Table 2. Stable isotope data for each consumer species and basal resource.

Species	**$\delta^{13}C$**	**SD**	**$\delta^{15}N$**	**SD**	**$\delta^{34}S$**	**SD**	***n***
Peacock eel	-28.8	1.4	9.4	1.0	21.2	1.5	10
Bluegill	-31.5	1.4	11.0	1.5	22.2	4.0	9
Dollar sunfish	-27.8	1.9	9.1	1.1	16.5	4.7	7
Redear sunfish	-29.3	1.3	9.6	1.6	20.9	4.0	6
Spotted sunfish	-30.0	0.8	10.5	1.0	23.8	1.5	2
Basal Resources							
Phytoplankton[a]	-35.5	3.0	5.8	1.3	24.5	2.1	2
Epiphytic Microalgae	-29.0	1.7	7.0	1.5	13.5	5.3	4
Mangrove Detritus	-29.2	0.3	5.9	0.8	18.5	4.0	6

[a] Values from Fry et al. (2002), see methods for details.

Table 3. Hypervolume metrics for the Peacock eel (*Macrognathus siamensis*), Dollar sunfish (*Lepomis marginatus*), Bluegill (*Lepomis macrochirus*), and Redear sunfish (*Lepomis microlophus*). Metrics include the total volume of each species' hypervolume representative of their trophic niche, the Sørenson overlap value between peacock eels (PE) and each sunfish species (SF), and the fraction of unique hypervolume space for each species compared. (P < 0.05 = *, < 0.01 = **, < 0.001 = ***)

Species	**Trophic Niche Volume**	**Sørenson overlap with PE**	**Fraction Unique PE**	**Fraction Unique SF**
Peacock eel	35.3	-	-	-
Bluegill	247.7	**0.231*** **	0.071	**0.868*** **
Dollar sunfish	295.1	**0.194***	0.093	**0.892** **
Redear sunfish	271.1	0.207	0.100	**0.883** **
Sunfish (combined)	390.3	**0.162*** **	0.012	**0.911*** **

Table 4. Model selection table for dependent variable (DV) catch per unit effort of peacock eels (CPUE, *n* 100 m^{-1}), based on 18-year electrofishing dataset from 15 sites in the mangrove-lined creeks of Rookery Branch, Florida Coastal Everglades, USA. Independent variables included the year of sampling (Yr), a polynomial function of the sampling month (Mo), the count of days in the preceding six months where marsh inundation exceeded 30 cm (FldDays), the median water depth on the sampling day (MdWaterDp), and the lowest temperature documented in the preceding six months (MinTemp). The table includes the number of model parameters (K), the small sample size corrected Bayesian Information Criterion (BIC), the difference in BIC relative to the minimum (Δ BIC), and the Schwarz weight (w_i) of linear regression models.

	K	**BIC**	**Δ BIC**	w_i
DV: n 100 m^{-1}				
AR1+Yr+ MinTemp+FldDays+ Mo +MdWaterDp	10	3120.89	0.00	1
AR1+Yr+MinTemp+FldDays+Mo	9	3139.82	18.93	0
AR1+Yr+MinTemp+FldDays	8	3141.06	20.17	0
AR1+Yr	5	3298.39	177.49	0
AR1+Yr+MinTemp	6	3299.26	178.36	0
AR1 only	4	3328.08	207.19	0

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