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ORIGINAL PAPER

Trophic niche of a nonnative invader and environmental drivers of its increasing populations in the coastal Everglades

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Abstract The Florida Everglades is a critically important, but highly threatened ecosystem that is becoming increasingly susceptible to the invasion of non-native species. This study investigated the ecological role of the invasive peacock eel (*Macrognathus siamensis*) within this ecosystem using 15 years of electrofishing data and stable isotope analysis. We investigated the population trends of peacock eels at the marsh-mangrove ecotone of the Shark River Estuary, the environmental factors contributing to their abundance, and the potential interactions they may have with native fish assemblages and coastal food webs. We used stable isotope analysis to provide insights into the basal resource contribution to peacock eels and hypervolume analysis to determine peacock eel trophic niche size and overlap with native species. Results of this study found that peacock eel abundance has rapidly increased, and their populations are strongly related to hydroclimatic regimes. Peacock eel abundance was positively associated with warmer water temperatures and greater marsh inundation periods. The trophic niche of peacock eels was significantly smaller in volume than that of native sunfishes (*Lepomis* spp.) indicating lower intraspecific resource use variability and suggesting a limited potential for inter-specific competition with these taxa. However, in recent years, the catch of peacock eels has outnumbered the catch of all native sunfishes combined. The feeding habits and pervasiveness of

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peacock eels in the coastal Everglades could lead to a decrease in abundance of benthic prey items targeted by peacock eels and alter food web dynamics in the system. Based on these data, peacock eel populations are predicted to continue to increase, highlighting the importance of continued monitoring of their potential impact on native fish assemblages and food webs.

Keywords Invasive species · Food web ecology · Stable isotope ecology · Peacock eel · Spotfin spiny eel · Everglades

Introduction

The Florida Everglades is a critically important ecosystem that 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). The Everglades is recognized as a Natural World Heritage site and a wetland of international importance for its role in carbon sequestration (Jerath et al. 2016) and was the first U.S. national park to be established with the primary objective to protect and preserve biological resources (Junk et al. 2006; Kline et al. 2014). The Everglades is home to 68 federally listed threatened or endangered species and serves as an important breeding ground for migratory birds as well as spawning ground for ecologically and economically important fishes (Brown et al. 2006; Trexler and Goss 2009; Howell et al. 2023). However, the Everglades is a highly threatened system and has experienced a 50% loss in wetland area due to urban development, agriculture, flood protection, and extensive drainage and impoundment (Rudnick et al. 1999; Junk et al. 2006; Kline et al. 2014). With continued hydrological and ecological changes, the Everglades are also becoming increasingly susceptible to non-native and invasive species that threaten the biodiversity and resilience of the ecosystem (Junk et al. 2006; Pintar et al. 2023).

The Everglades is 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 of the Everglades 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). Nonindigenous and invasive species can impact native species directly through predation, parasitism, niche displacement, and competition (Mooney and Cleland 2001; Córdova-Tapia et al. 2015). Competitive interactions favoring invasive species can not only displace natives but can have cascading effects on existing food webs and disrupt the stability of an ecosystem (McKinney and Lockwood 1999; Guzzo et al. 2013; Jackson et al. 2016).

Various approaches can be used to assess the potential impacts of an introduction on food web dynamics and native species (David et. al 2017). Stable isotope analysis can differentiate between basal resources that are assimilated by consumers providing an integrated estimate of long-term resource use (Michener and Schell 1994; Gao et al. 2006; Xia et al. 2013; Alp and Cucherousset 2022). 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 overlap, such as shared food sources, serving as an indicator of potential competition (Vander Zanden et al. 1999; Zambrano et al. 2001; Jackson et al. 2012; Córdova-Tapia et al. 2015). Previous work has used stable isotope analysis to evaluate the niche overlap and the likelihood of resource competition between native and invasive species including invasive common 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), using Bayesian ellipse methods based on raw isotope data. Recent studies have incorporated hypervolume analysis, a method based on stochastic geometry to evaluate niches in high dimensional space (Blonder et al. 2014; Blonder 2018; Swanson et. al 2015; Lu et al. 2021), using trophic levels and stable isotope mixing model-based dietary contribution estimates as the dimensions to characterize the trophic niche of consumers. James et al. (2020) used stable isotope mixing model-based hypervolume analysis methods to determine how trophic niche size and overlap among fishes change in response to the availability of food sources, Rezek et al. (2020) used similar hypervolume methods for niche differentiation among migratory predators in the coastal Everglades, and Livernois et al. (2024) used these methods to investigate the trophic dynamics of co-occurring estuarine fish in the Northern Gulf of Mexico. In invasion ecology, hypervolume analysis may be a useful tool in assisting species risk assessments and help determine their potential impacts on native species.

The peacock eel, also known as the Spotfin Spiny Eel (*Macrognathus siamensis*), was first introduced to South Florida in 2002, but little is known about their population dynamics or trophic ecology in its invasive range. Peacock eels are native to Southeast Asia where they inhabit freshwater rivers, canals, ponds, and inundated fields (Sultana et al. 2017). This ornamental fish is highly sought after for its unique behavior and appearance and was likely imported to the U.S. for the aquarium trade (Das and Kalita 2003; USFWS 2018; Sinha et al. 2020). Since spreading into the Everglades, they can now be found throughout Everglades National Park (ENP) in canals, freshwater marshes, and mangrove creeks (Shafland et al. 2008; Kline et al. 2014) and have been deemed an established invasive species by the US Fish and Wildlife Service (Shafland et al. 2008; USFWS 2018). The US Fish and Wildlife Service conducted a risk assessment, but it was inconclusive due to insufficient data (USFWS 2018). 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) and gut content analysis from their native range found their diets to consist of small fish, shrimp, insects, annelids, and other benthic invertebrates (Faridi et al. 2016; Sultana et al. 2017). Few studies have been done on peacock eels in the Everglades, and their primary resource use in this region is unknown.

The spread of peacock eels in the coastal Everglades is of particular concern due to its potential to compete with ecologically important native species such as sunfishes (*Lepomis* spp.) that likely belong to the same feeding guild as peacock eels based on known diets of both (e.g., Rubenstein 1981; Faridi et al. 2016; Sultana et al. 2017; Flood et al. 2023). During seasonal drying in the coastal Everglades, sunfishes 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 dry-season pulses of sunfishes are important for recreational fishes such as common snook (*Centropomus undecimalis*) that prey on these marsh fish (Boucek and Rehage 2013; Rezek et al. 2020; Massie et al. 2022). One study found that sunfishes can provide 41% of the total biomass consumed by common snook inhabiting these coastal riverine systems during dry downs (Boucek and Rehage 2013). Competitive interactions between invasive peacock eels and native sunfishes could disrupt the niche of these sunfishes and subsequently disrupt the energy flow from sunfishes to these higher trophic level fisheries species.

This study aimed to evaluate the magnitude of the peacock eel invasion in the Florida Coastal Everglades, evaluate the hydroclimatic variables that mediate their abundance patterns, and characterize the potential threat their introduction and spread may pose to native sunfishes and existing food webs using stable isotope-based hypervolume analysis. Using a 15-year electrofishing dataset we: 1) analyzed the long-term trends in abundance of peacock eels in the mangrove creeks of the coastal Everglades; 2) assessed the relationship between variation in hydrology and temperature and peacock eel abundance; and 3) quantified the trophic niche of peacock eels in their invaded range within the coastal Everglades 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*).

Methods

Study site

The focal area of this study was the interface between marsh and riverine habitats in the main stem and first-order creeks of the upper Shark River within the Shark River Estuary of Everglades National Park (Fig. 1a). The Shark River Slough is the main drainage of the southern Everglades and is 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

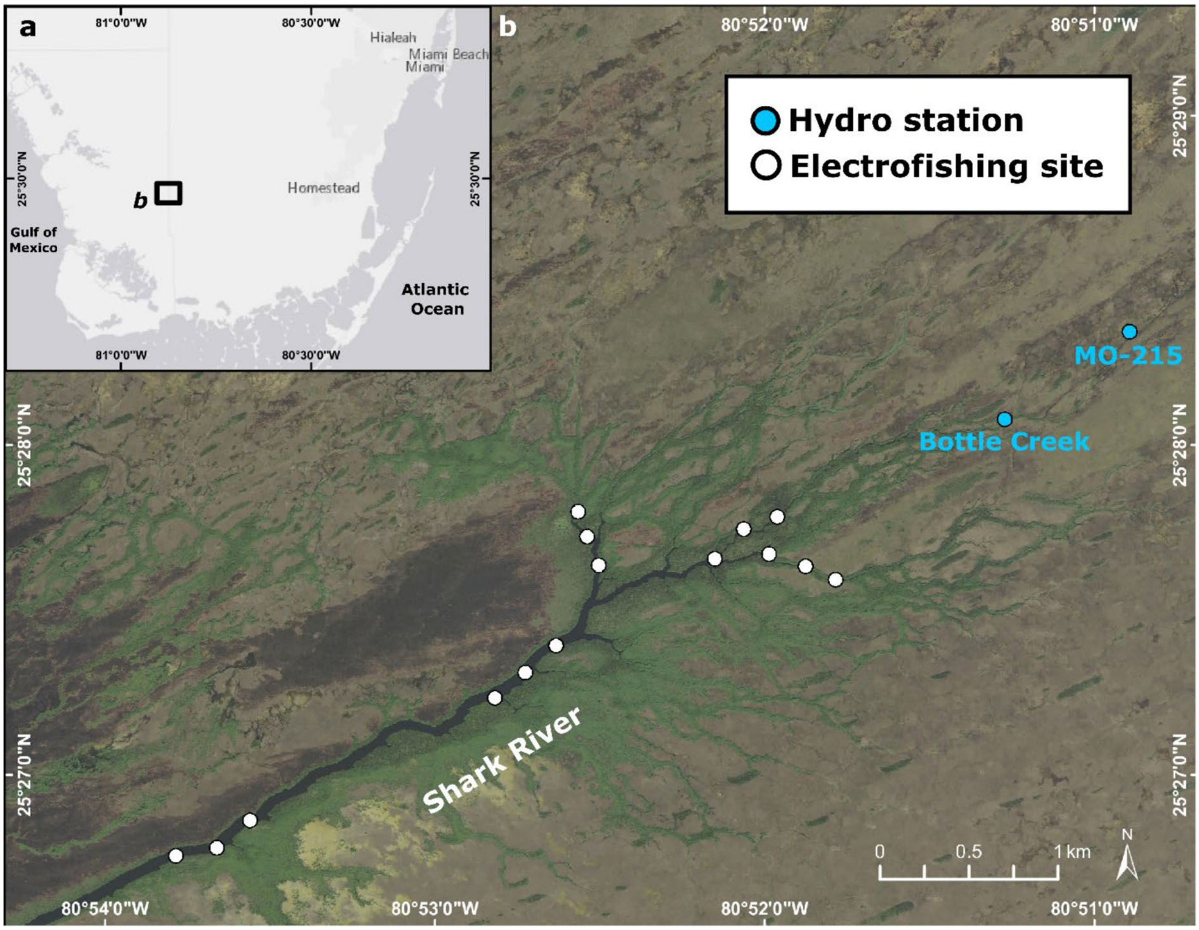


Fig. 1 Map of the study region. **a** The location of the study site within Everglades National Park; **b** Map of the upper Shark River including the fifteen electrofishing sites (white symbols) and USGS Bottle Creek and MO-215 hydro stations (blue symbols)

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 increasing productivity with greater marine influence (Childers 2006; Rezek et al. 2020).

Data collection and sample processing

We assessed 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; Rehage 2023). Sampling events were conducted at least once during the wet season in November or December. During the dry season (defined as January to May in this study), sampling happened at least twice annually: once during the transition from marsh inundation to drying (typically between February and March) and once in the late dry season (April to May). Additional monthly sampling events were conducted in most years (up to 9 per year), totaling 89 trips between March 2007, when peacock eels were first collected, and June 2022, averaging 5.5 trips per year over this 15-year timeframe. During each sampling period, fishes were collected via boat electrofishing (Smith-Root GPP 9.0 electro fisher, Smith-Root, Vancouver, Washington, USA) at 15 sites, six located in the main stem of the Shark River and nine in first order creeks (Fig. 1), using methods approved by Florida International University's Institutional Animal Care and Use Committee (IACUC # 15–046).

Electrofishing was conducted parallel to the mangrove shoreline for 300 s of pedal time at each site (i.e., time electrofishing unit is running; Rehage and Loftus 2007). The side of the shoreline that was shocked was selected at random, right or left side, for approximately 100 m (mean = 91 m, SD = 28 m). GPS was used to record the length of shoreline sampled. At each site, fish collected were identified to species, counted, weighed, and measured. The abundance of peacock eels is reported as a catch per unit effort (CPUE) standardized to catch per 100 m of shoreline (additional details described in Boucek and Rehage 2013). All peacock eels shocked during the sampling events, including those that were shocked and not landed, were included in the CPUE estimate to allow for a more accurate abundance estimation, as recapture or misidentification is unlikely due to the unique body shape and shocking behavior of peacock eels. Water level relative to marsh mean marsh elevation (− 9.7 cm NAVD88) 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 (Fig. 1).

Samples used for stable isotope analysis were collected during sampling trips in May and November of 2019. Dorsal muscle tissue samples of peacock eels and sunfishes (0.5–0.7 g) were taken post collection and analyzed individually. Primary producer basal resources including epiphytic microalgae and mangrove detritus were collected by hand at each site. 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:

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

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

Environmental factors affecting peacock eel abundance

A generalized linear mixed model (GLMM) with a negative binomial distribution was used to investigate the environmental factors related to peacock eel CPUE. 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 peacock eel CPUE at each site sampled. The independent variables included the year of sampling, a second-degree polynomial function of 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 median daily water depth values relative to the marsh platform elevation throughout the study period. Rezek et al (2023) suggests this threshold represents inundation of most, if not all, of the marsh habitat surrounding the mangrove creeks due to elevation differences between prairie slough and higher elevation sawgrass-dominated ridges and identified this threshold to be the most important predictor of the biomass of subsequent spatial prey subsidies. The temperature at which loss of equilibrium occurs in peacock eels is 12.8 °C ± 1.5 °C (mean ± SD) 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).

The model included random intercept term for site to accommodate repeated measurements, and an offset was based on the log-transformed distance of each electrofishing bout was included to account for variation in sampling effort. The model was fitted to a dataset of 1,308 electrofishing bouts across 89 sampling trips between 2007 (first Peacock eel collection) and 2022. Bayesian Information Criterion (BIC) was used to select the most parsimonious model from a set of candidate models. Forward model selection was used to identify the most likely model, where candidate models increased in complexity with each additional model beginning with a null model and then incorporating the independent variables (sampling year and month, temperature, and the two hydrology terms). BIC is calculated based on model likelihood and penalizes complex models; therefore, the model with the lowest BIC (greatest Schwarz weight) was selected as the most likely model of the models examined. Sensitivity analysis was conducted to assess the robustness of this selection (Schwarz 1978). The final model was evaluated for goodness of fit through a series of tests using the DHARMa package, which is specifically designed for assessing model diagnostics (DHARMa v0.4.6; Hartig and Lohse 2022). A test for uniformity of residuals was conducted using the testUniformity() function, which applies the Asymptotic One-Sample Kolmogorov–Smirnov Test. This non-parametric test determines if the residuals from the fitted model conform to a uniform distribution, comparing the variance of these residuals against those generated under the model's assumptions. Dispersion in the model was evaluated through the testDispersion() function, which conducts a non-parametric test on the variance of the residuals, comparing the standard deviation of the residuals from the fitted model to that of residuals from simulated data. Zero inflation was assessed using the testZeroInflation() function, which tests whether the number of zeros in the model's residuals exceeds what would be expected based on the model's assumptions. The testOutliers() function was used to detect extreme values that could disproportionately influence the model estimates. Finally, the evaluation of quantile adherence was performed using the testQuantiles() function, which fits quantile regressions to the residuals of the model and tests that the model's predictions align across the entire range of the response variables. Predictor multi-collinearity was assessed using variance inflation factors calculated with the performance package (Lüdecke et al. 2021). This package was also used to calculate the final models R2 value to estimate explanatory power of the model. The GLMM R2 was calculated using methods outlined in Nakagawa et al. (2017) which reflects both the marginal R2, which quantifies the variance explained solely by the fixed effects, and the conditional R2, which represents the variance explained by the entire model including both fixed and random effects. Marginal effects plots for the final model were generated using the ggeffects R package and represent the predicted values for each independent variable while holding other independent variables at their mean value (Lüdecke 2018).

Trophic niche space and overlap

To characterize the trophic niche of peacock eels and native sunfishes, the relative contribution of each basal resource (mangrove detritus, epiphytic microalgae, and phytoplankton) to individuals was derived through Bayesian stable isotope mixing models (Wilson et al. 2010; Parnell et al. 2010). Model estimates represent the contribution of the basal resources through consumer intermediaries or directly. No significant differences in peacock eel isotope values were found between seasons (Mann–Whitney U test $P > 0.05$, for C, N, and S), and individuals were pooled between seasons. 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: $C = 1.3 \pm 0.3$, $N = 3.3 \pm 0.26$, and $S = 0.5 \pm 0.54$ (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 individual sampled during the study. Estimates are represented as the mean of posterior distributions, which reflect 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). Mixing model estimates were evaluated for convergence using Gelman-Rubin diagnostics, with values greater than 1.05 considered indicative of poor convergence and problems with parameterization (Gelman and Rubin 1992). The source contributions determined by the mixing model were used to calculate the relative trophic position of each individual consumer compared to the 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:

$$\mathrm{TP} = \frac{\delta^{15}\mathrm{N}_{\mathrm{ind}} - \sum\left(\delta^{15}\mathrm{N}_{\mathrm{source}} \times \mathrm{mean\%cont}_{\mathrm{source}}\right)}{\mathrm{TDF}} + 1$$

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 (Post 2002). Trophic niche space can then be represented as a function of a species dietary contributions and trophic level (Bearhop et al. 2004).

To allow for standardized, comparable axes in n-dimensional space the means of the posterior distributions from each source to each consumer 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 consumer'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 multidimensional space and defines the multidimensional trophic niche of the consumers. 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 each sunfish species as well as a combined value for all sunfishes 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 hypervolumes (Sørenson overlap index, Sørenson 1948) and the fraction of unique hypervolume space for pairwise comparisons are reported, and were statistically evaluated via bootstrapping (50 resamples) (Newsome et al. 2012; Blonder et al. 2014). Hypervolumes were not calculated for spotted sunfish due to low sample size.

Results

Peacock eel population trends

A total of 2,386 peacock eels were sampled during the study period (2007–2022, n = 1,308 sampling bouts). No peacock eels were recorded during 2004–2006 sampling events. The first peacock eels were collected in March 2007 (Fig. 2) and within 3 years of detection the population of peacock eels in this region increased from 0.11 to 23.28 CPUE (n/100 m). This initial spike in peacock eel abundance was followed by a sharp decline and a subsequent 8-year period (2010–2018) when population numbers remained low (CPUE ≤ 2 n/100 m). During 2018–2022 the mean CPUE increased, with the largest increase occurring from May 2020 (0.31 n/100 m) to May 2021 (40.76 n/100 m). Since June 2021, the mean CPUE of peacock eels has remained below 2.6 n/100 m (Fig. 2).

Environmental factors related to peacock eel abundance

Over the study period, the annual average minimum daily water temperatures were 14.5 °C ± 1.89 (Mean ± SD, 2 SD = 3.78), with the lowest daily

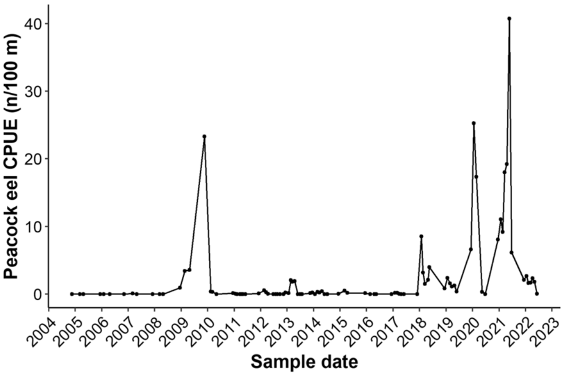


Fig. 2 Mean peacock eel CPUE (number per 100 m of river shoreline) from all electrofishing sampling events (*n* = 95) over the 19-year time series (2004–2022). The first peacock eels were collected in this system in 2007

average recorded in the wet season of 2010 (8.30 °C). Annual maximum daily water temperature averaged 31.9 °C ± 0.93 (2 SD = 1.82), with the highest recorded during the dry season of 2005 (33.5 °C). The mean daily water temperature dropped below the point at which loss of equilibrium occurs in peacock eels (12.8 ± 1.5 °C) during the dry seasons of 2008–2012, 2015, 2018, 2020, and 2022 (9 of the 15 years in the time series, Fig. 3a). The lower lethal temperature of peacock eels (9.1 ± 1.0 °C) was reached during the dry season of 2010. Over the study period, the annual minimum daily mean water level averaged − 0.1 cm ± 13.4 (2 SD = 26.8) 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 ± 13.4 (2 SD = 26.8), and the highest was recorded during the wet season of 2017 at 94.5 cm. The greatest number of days that the marshes were above 30 cm occurred in 2016 and totaled 366 days, while the lowest occurred in 2015 (107 days; Fig. 3b).

The most likely model included the year, month, flooding duration over the previous 180 days, mean daily water level at on the sampling date, and the

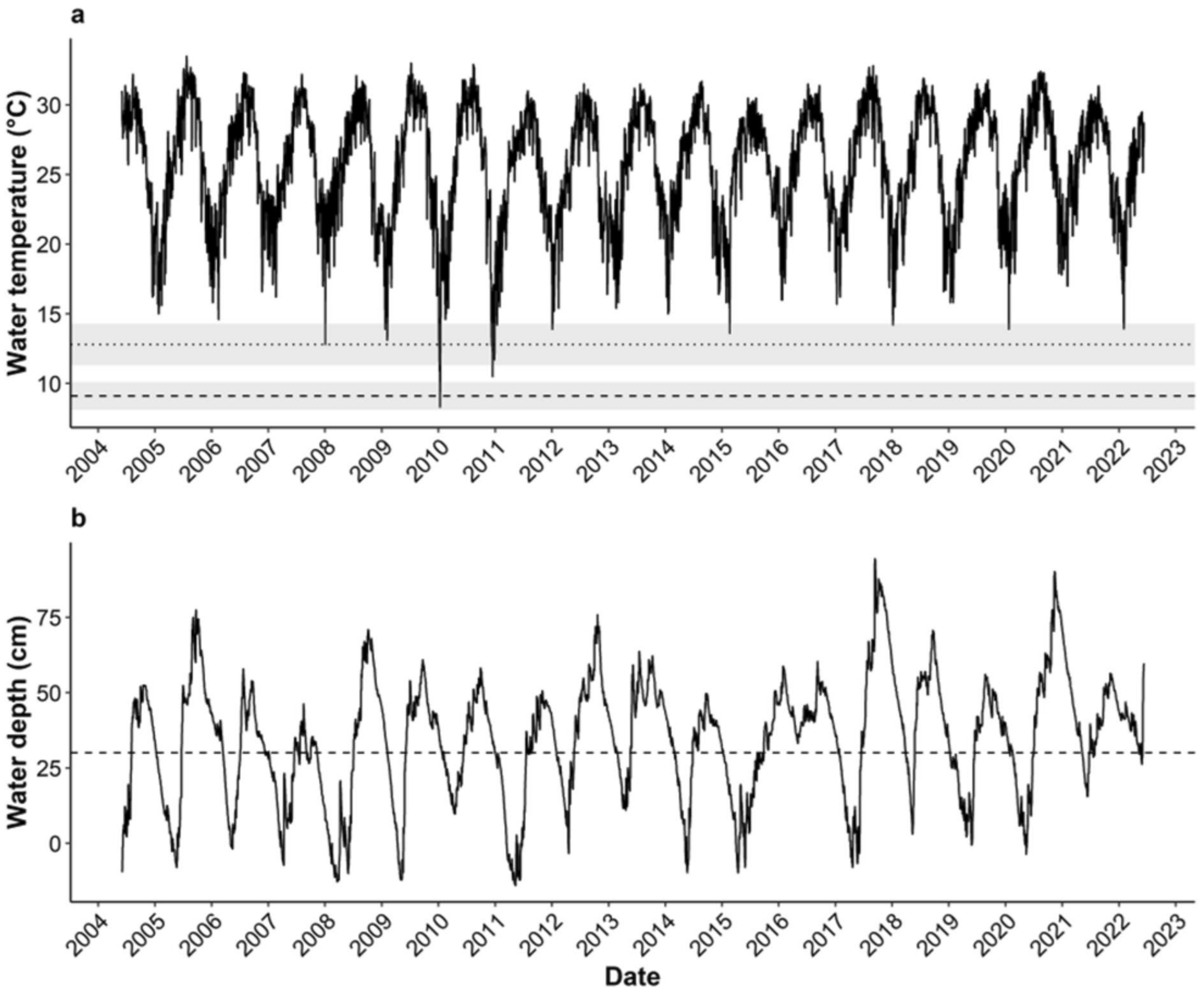


Fig. 3 Hydrological data of the study area over the time series. **a** The mean daily water temperature recorded from the Bottle Creek hydro station over the study period. The dotted line represents the temperature at which loss of equilibrium occurs in peacock eels (12.8 ± 1.5 °C), the dashed line represents the lower lethal temperature at which direct mortality occurs (9.1 °C ± 1.0; Schofield and Kline 2018) and the gray areas represent the reported SD. **b** The mean daily water depth relative to average marsh elevation recorded from the MO-215 hydro station over the study period. The dashed line indicates the 30 cm water depth threshold at which the marsh is considered fully inundated

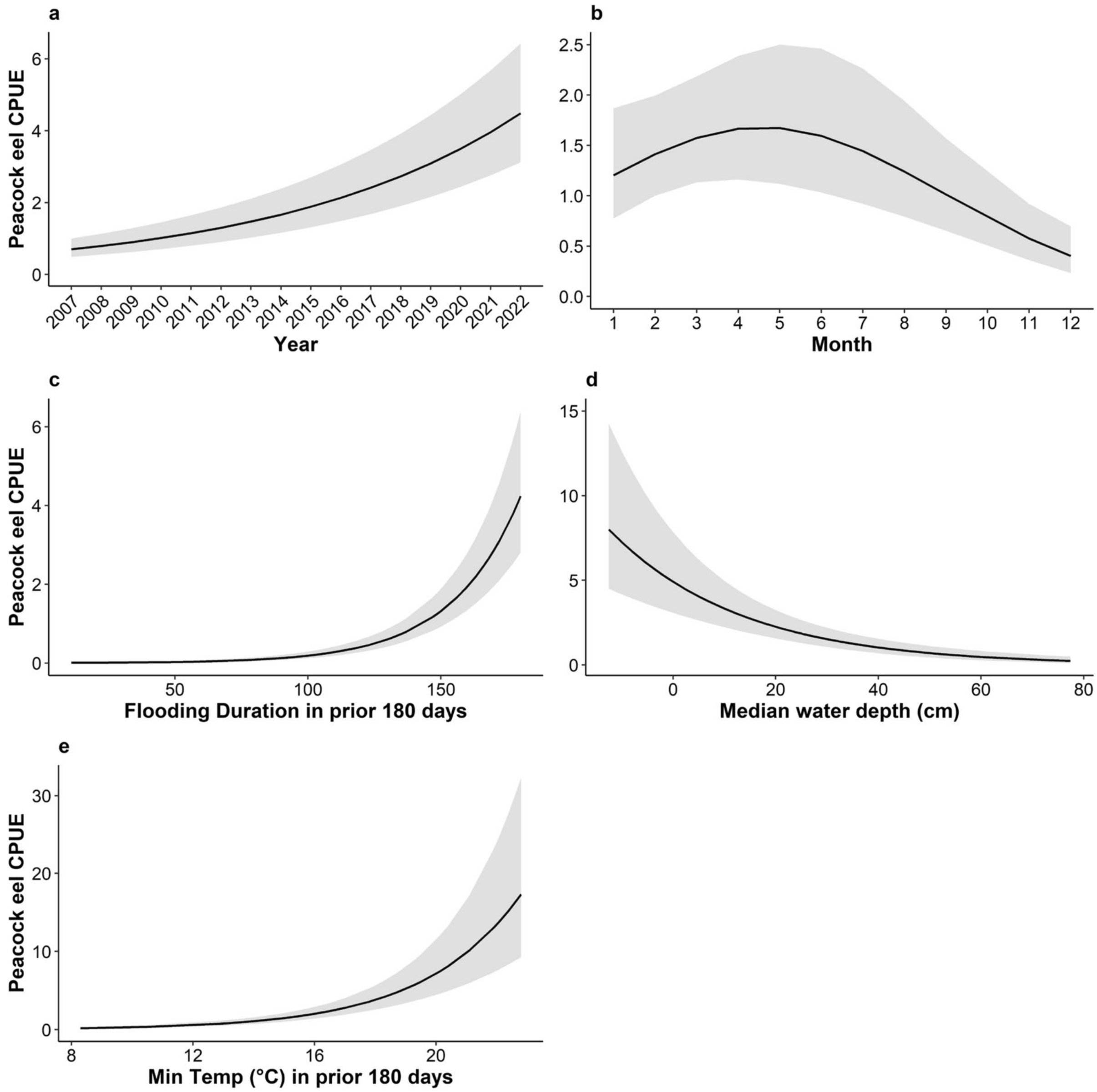


Fig. 4 Marginal effects plots for the generalized linear mixed model (GLMM) assessing each predictor of catch per unit effort (CPUE; peacock eels per 100 m of shoreline) based on electrofishing at trips conducted between 2007 and 2022 (n = 88) at 15 sites. Plots represent estimates for each predictor with other all other model predictors held at their mean values. Each subplot represents the predicted CPUE values based on the effects of: **a** sampling year, **b** sampling month, **c** number of days the marsh median daily water levels were above 30 cm, **d** median daily water depth on the sampling date, **e** minimum daily mean water temperature recorded within the 180 days prior to sampling. Gray area represents 95% confidence intervals of the estimates

minimum mean daily water temperature in the 180 days prior to sampling (Fig. 4a, Table S1 in Online Resource 1). This model passed all goodness of fit tests outlined in the methods ($p > 0.05$). The model fixed effects alone explained for a substantial portion of the variance in peacock eel CPUE, with a marginal R2 of 0.475. The conditional R2, considering both fixed effects and the random effect of site,

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)	− 262.5	36.14	− 7.264	< 0.001
Year	0.123	0.018	6.855	< 0.001
poly(Month|1)	− 14.704	3.610	− 4.075	< 0.001
poly(Month|2)	− 10.270	3.832	− 2.680	0.007
Flooding duration 180 days	0.0389	0.003	12.893	< 0.001
Median water depth	− 0.0390	0.007	− 5.833	< 0.001
Minimum water temp 180 days	0.313	0.037	8.477	< 0.001

was 0.514. The model indicated increasing peacock eel CPUE over years and that peak abundance of peacock eels in the mangrove creeks occurs between the months March–May (Fig. 4a, b). Peacock eel CPUE was positively related to minimum water temperature and with the duration of marsh flooding (Fig. 4c, Table 1). Higher mean daily water depths were shown to be related to lower peacock eel CPUE accounting for a 3.8% decrease for every 1 cm increase in median water depth (Fig. 4d). Higher minimum daily water temperatures were associated with an increase in peacock eel CPUE with an increase of 36.7% annually for every 1 °C increase in minimum water temperature (Fig. 4e, Table 1).

Stable isotope analysis and mixing models

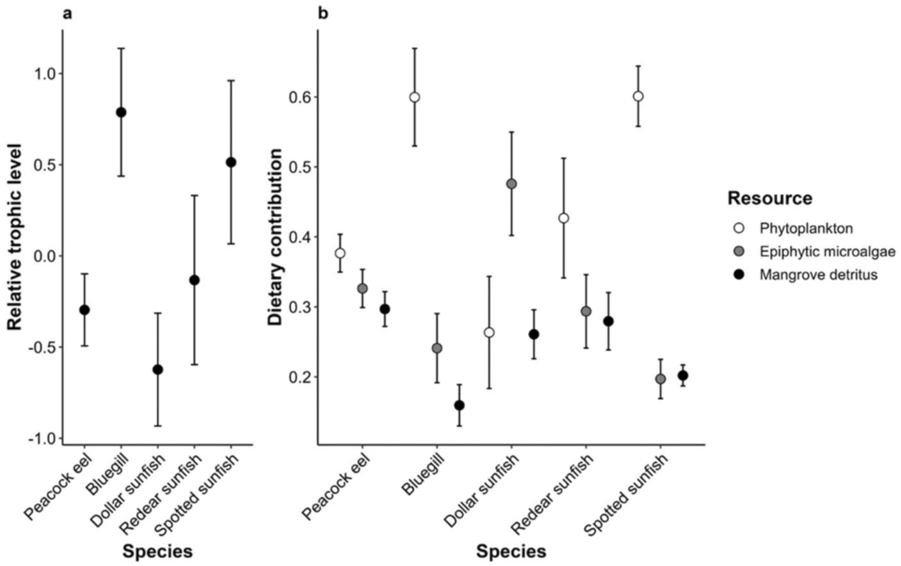
The average δ^{34}S, δ^{13}C, and δ^{15}N values of peacock eels were 21.2‰, − 28.8‰, and 9.4‰ respectively (Table 2). Mean δ^{34}S values of native sunfishes ranged from 23.8‰ in spotted sunfish to 16.5‰ in dollar sunfish. Mean δ^{13}C values ranged from − 31.5‰ in bluegill to − 27.8‰ in dollar sunfish. Mean δ^{15}N values ranged from 11.0‰ in bluegill to 9.1‰ in dollar sunfish. Of the basal resources, phytoplankton had the greatest mean δ^{34}S value (24.5‰) and epiphytic microalgae was the lowest (13.5‰). Epiphytic microalgae had the highest mean δ^{13}C (− 29.0‰) and δ^{15}N (7.0‰) values, whereas phytoplankton had the lowest (δ^{13}C − 35.5‰, δ^{15}N 5.8‰; Table 2). The average relative trophic position (z-score) of the native sunfishes were 0.79 for bluegill ($n = 9$), 0.51 for spotted sunfish ($n = 2$), 0.13 for redear sunfish ($n = 6$), and − 0.62 for dollar sunfish ($n = 7$). The average relative trophic position of peacock eels was − 0.30 ($n = 10$; Fig. 5a). Gelman-Ruban diagnostics were below 1.01 for all Bayesian stable isotope mixing model estimates, indicating good model convergence and appropriate parameterization (Philips et al. 2014). Mean basal resource contribution of epiphytic microalgae was greatest for dollar sunfish (47.6%) and lowest for spotted sunfish (19.7%). Mean basal resource contribution of detritus was highest in redear sunfish (27.9%), and the lowest

Table 2 Stable isotope data for consumer species and basal resources, with consumer total lengths (TL) and sample size (n) in May (My) and November (No) sampling periods of 2019

Species	δ^{13}C	SD	δ^{15}N	SD	δ^{34}S	SD	TL (cm)	SD	n (My/No)
Peacock eel	− 28.8	1.4	9.4	1.0	21.2	1.5	23.8	3.3	10 (5/5)
Bluegill	− 31.5	1.4	11.0	1.5	22.2	4.0	11.8	5.6	9 (6/3)
Dollar sunfish	− 27.8	1.9	9.1	1.1	16.5	4.7	4.3	0.7	7 (1/6)
Redear sunfish	− 29.3	1.3	9.6	1.6	20.9	4.0	15.0	2.8	6 (1/5)
Spotted sunfish	− 30.0	0.8	10.5	1.0	23.8	1.5	11.3	1.9	2 (0/2)
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

Fig. 5 Mixing model output showing: **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*), and **b** the source contributions of each of the three basal resources to each consumer species



for bluegill (15.9%). Phytoplankton was used most by spotted sunfish (60.1%) and least used by dollar sunfish (26.3%). Mean resource contributions for peacock eels were 32.6% for epiphytic microalgae, 29.7% for detritus, and 37.7% for phytoplankton (Fig. 5b).

Trophic niche and hypervolume analysis

Peacock eels had the smallest trophic niche volume of the four 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; Table 3, Fig. 6). The Sørenson overlap index was greatest between peacock eels and bluegills 0.231 ($P < 0.001$), and lowest for peacock eels and dollar sunfish 0.194 ($P < 0.05$). Peacock eels did not have a significant amount of unique hypervolume space compared to any of the sunfish species assessed. In contrast, all sunfish species had significantly unique hypervolume space relative to Peacock eels, ranging from 86 to 89% (Table 3, Fig. 6).

Discussion

Peacock eel population trends & relation to environmental conditions

This study provides a better understanding of the factors associated with peacock eel relative abundance in the coastal Everglades as well as insight into the potential effects of this invasion on ecosystem structure, function, and services, with implications for invasive species management. Although peacock eel abundance within the marsh-mangrove ecotone of the

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**

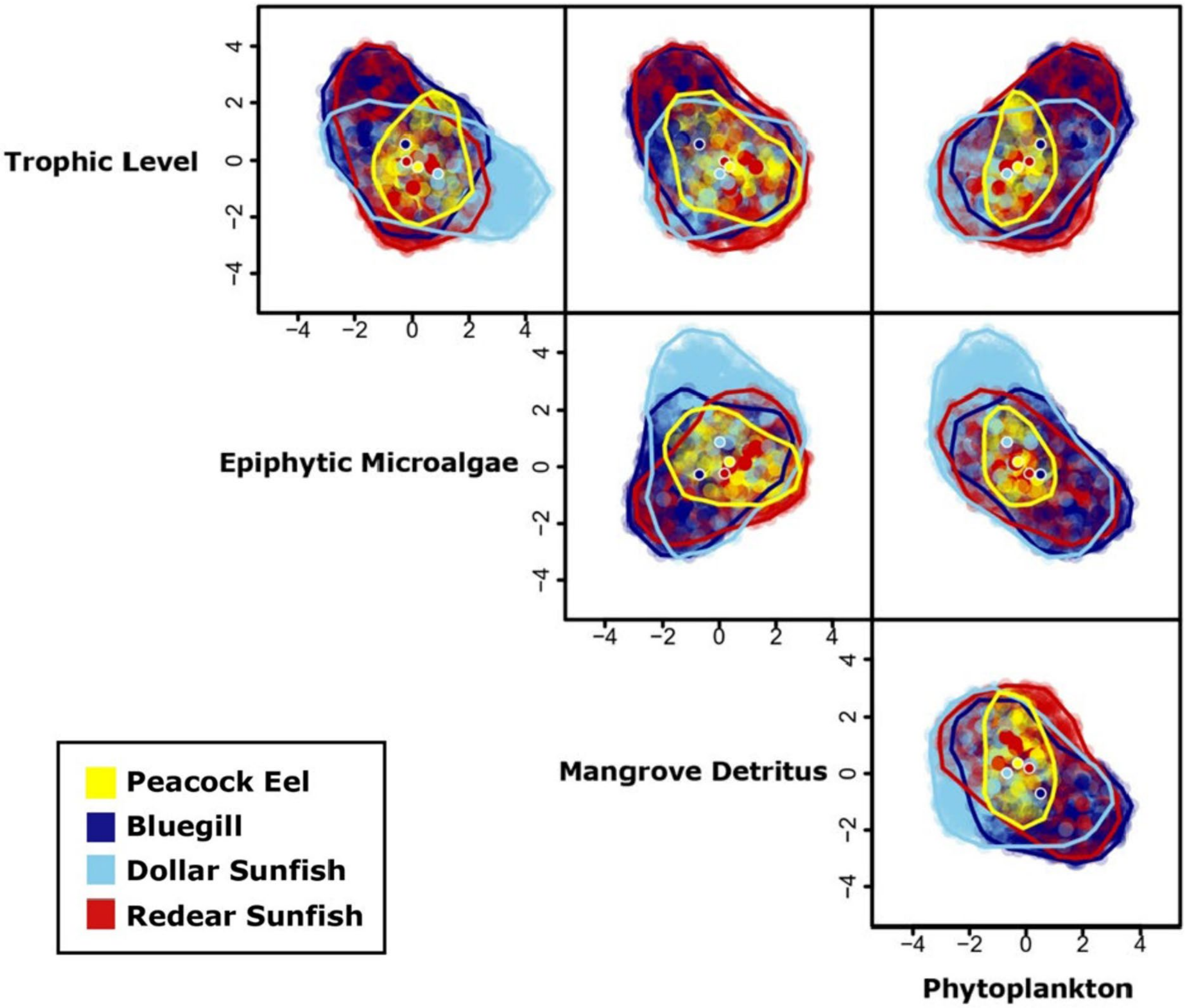


Fig. 6 Trophic niche hypervolumes of the invasive Peacock eel (*Macrognathus siamensis*) vs. native dollar sunfish (*Lepomis marginatus*), Bluegill (*Lepomis macrochirus*), and Redear Sunfish (*Lepomis microlophus*) in Rookery Branch. Axes are the z-scores of estimated dietary contributions of the three producers (mixing model posterior means) and of trophic position

Florida coastal Everglades exhibited high variability over the study period, the model identified an increasing trend in abundance and suggests their populations will continue to grow. Within the time series, peacock eel populations underwent periods of rapid increase that were followed by sharp declines and years of low abundance in between. This trend is commonly seen in invasives species populations and referred to as “boom and bust” cycles, where periods of rapid population growth are followed by declines due to a limiting resource (Elton 1958; Williamson 1996; Strayer et al. 2017). However, our model suggests these patterns are related primarily to variations in hydroclimatic characteristics of the system, which explained more than half of the variation observed in peacock eel CPUE over the time-series.

Low water levels in the marsh during seasonal drying periods were associated with high peacock eel abundances in the mangrove creeks. This trend also occurs with the native sunfish species that migrate to deeper riverine refuge during drying periods and form an ecologically important prey pulse (Boucek and Rehage 2013; Massie et al. 2022; Rezek et al. 2023). This finding suggests that peacock eels also seek refuge in the mangrove creeks during seasonal dry down periods, with a substantial portion of the population likely returning to the marsh when water levels increase during the onset of the wet season. The lack of a substantial dry-down in 2022 could explain the low abundances of peacock eels in the mangrove creeks despite otherwise favorable conditions and high abundances in the preceding years.

Peacock eel abundance was also positively associated with longer periods of marsh inundation. The positive relationship between abundance and increased flooding duration on peacock eels is also consistent with data on native species in the system, indicating that increased duration of marsh habitat availability may increase production of peacock eels. Rezek et al. (2023) hypothesized 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. Similar to the coastal Everglades, hydrology is a major factor affecting fish communities in the river-floodplain ecosystems of Southeast Asia where peacock eels are native (Chea et al. 2020). The movement of peacock eels in the coastal Everglades may mimic their behavior in their native range, as peacock eels are known to inhabit inundated fields during the monsoon season (Sultana et al. 2017) and likely seek refuge in rivers during seasonal dry downs.

Water temperature was a particularly important predictor of peacock eel abundance, which was exemplified by the drastic decrease in peacock eels directly following the historic 2010 cold weather event. This extreme weather event was later described as the most severe cold weather event documented in this region in 100 years (Boucek and Rehage 2014). During this time, water temperatures fell to 6.2 °C and air temperatures remained below −3.3 °C for 12 days (Boucek and Rehage 2014; Rehage and Blanchard 2016; Stevens et al. 2016). The lower lethal limit for peacock eels is 9.1 (± 1.0 °C); therefore, any peacock eels exposed to such temperatures for an extended period of time would have experienced direct mortality (Schofield and Kline 2018). In contrast, when temperatures did not exceed peacock eel's lower lethal limit or loss of equilibrium threshold (12.8 ± 1.5 °C) abundance increased substantially, demonstrating their ability to thrive in this region under ideal conditions. Peacock eel populations can double in as little as 1.4 years (Froese et al. 2017), though they do not become sexually mature until 3 years of age (Sinha et al. 2023), possibly explaining a lagged effect of cold temperatures on peacock eel abundance.

Both hydrological and temperature regimes are expected to change in light of climate change and may support the growth of peacock eel populations in the future. 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). 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 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 gammarid amphipods (*Gammarus tigrinus* and *Dikerogammarus villosus*) were shown to have increased food intake with increased water temperature suggesting predation pressure on native prey species is likely to increase with ongoing climate change (Pellan et al. 2016). Increasing temperatures could also increase the time between cold events that currently limit expansion and abundance of peacock eels (Catano et al. 2014; Rehage and Blanchard 2016). Based on the results of this study, as annual average water temperatures continue to increase, it is likely peacock eel populations will continue to expand. In addition to the shifts in regional average conditions, global climate change forecasts predict increases in the frequency and intensity of extreme weather events (Easterling et al., 2000; Karl et al., 2008; Boucek and Rehage 2014). Increased frequency of extreme weather events such as cold snaps may help to regulate peacock eel populations.

High abundance of peacock eels may impact populations of native species in this system. Sunfishes were evaluated as the primary component of the seasonal prey subsidy in the coastal Everglades due to their high abundance in mangrove creeks during dry down periods (Rehage and Loftus 2007; Boucek and Rehage 2014), their dominance in the gut contents of migratory predators (Boucek and Rehage 2013; Boucek et al. 2016), and their high relative abundance in the electrofishing dataset used for this study—representing over 90% of the native small-bodied freshwater fish landings (Rezek et al. 2023). Rezek et al. (2023) evaluated the abundance of sunfishes in this system during 2004–2020 finding an average annual peak abundance of 11.2 ± 2.5 (n/100 m) in comparison to only 2.5 ± 1 (n/100 m) for peacock eels in this study. However, 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). When peacock eel populations were at their highest (40 ± 17 n/100 m), sunfish abundance peaked at 3.5 ± 1.4 (n/100 m).

Stable isotope and hypervolume analysis

Stable isotope analysis provided novel insights into the trophic ecology of peacock eels in the coastal Everglades including the species' relative trophic level, trophic niche size, and trophic niche overlap with native species. Despite being found to have similar basal resource contributions to redear sunfish and feeding at a similar trophic level as both redear and dollar sunfish, peacock eels were found to have a significantly smaller trophic niche volume than that of the native sunfishes. This indicates relatively little intraspecific variation within the diets of individual peacock eels compared to that of native sunfishes. This was an unexpected result as successful invaders often are generalist species and use a wide variety of resources (Brandner et al. 2013; Dehnhard et al. 2020). Though significantly smaller in volume, assessment of overlap showed that the trophic niche of peacock eels was almost entirely nested within that of each of the sunfish species assessed in the study with little unique niche space suggesting that some of resources peacock eels are heavily relying on may also be used by native sunfishes. This is consistent with data on the known diets of both (Rubenstein 1981; Faridi et al. 2016; Sultana et al. 2017).

Although peacock eels trophic niche overlaps with that of sunfishes, this does not necessarily imply direct competition (Vander Zanden et al. 1999; Kelly and Jellyman 2007; Córdova-Tapia et al. 2015). The significantly larger trophic niche volume of sunfishes suggests a limited potential for competition, as they are able to incorporate a wider variety of resources into their diet which could allow them to adapt to changes in prey abundance and to avoid competition (Sharma and Borgstrøm 2008; Ke et al. 2008; Córdova-Tapia et al. 2015). Additionally, these species may be consuming prey from different functional groups, shared resources being used may not be limiting populations, 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 (Roberts 1986; Das and Kalita 2003), where many sunfishes tend to be diurnal (Reynolds and Casterlin 1976). Stable isotope analysis reflects the primary trophic channels being utilized by species and can determine which sources are being assimilated; however, it cannot necessarily distinguish specific dietary contributions from various prey taxa as with gut content analysis studies. Such studies have been done for peacock eels within their invaded range of the Florida coastal Everglades but were inconclusive (J.R. Blanchard, unpublished data).

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). A similar decrease in abundance of benthic prey species has been documented in the Everglades since the introduction of swamp eels and researchers now credit the invasion for the collapse of four different populations of native prey species (Pintar et al. 2023). Pintar et al. (2023) suggests 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. The results of our study found peacock eels to be relative specialists and feed on a smaller variety of prey items. Because of this, there could be a decrease in abundance of benthic prey items that are targeted by peacock eels as seen with the swamp eel invasion. Other potential impacts of increased peacock eel populations, such as the potential for peacock eels to serve as an alternative prey source for mobile predators remain unknown. With increasing peacock eel populations and their relative specialist feeding characteristics, populations of some benthic prey species targeted by peacock eels may be significantly affected and could lead to bottom-up trophic cascades (Kelly and Jellyman 2007; Ke et al. 2008; Wahl et al. 2011).

Conclusions

This study provides novel insights into peacock eel populations and their trophic ecology within the Florida Coastal Everglades. Peacock eel populations are increasing and are expected to continue to increase under favorable temperature and hydrological regimes. Further research to determine if there is a correlation between peacock eel and sunfish abundance as well as how temperature trends influence competition and community dynamics is warranted (Petersen and Kitchell 2001; Pellan et al. 2016). Additional studies should also be done to assess the impacts of the peacock eel introduction on native benthic prey species, other impacts on native fish assemblages, their potential to become prey for larger predator fisheries species, as well as other potential effects on food web dynamics. Given the ability of this species to rapidly increase in population under ideal conditions, peacock eel populations should continue to be monitored and further studies should be conducted to determine additional impacts of their introduction to predict and mitigate their potential effects on ecosystem structure, function, and services.

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Author contributions All authors contributed to the study conception and design. Material preparation and data collection were performed by Jennifer S. Rehage, Jordan A. Massie, James A. Nelson, Rolando O. Santos, Natasha M. Viadero, W. Ryan James, Ross E. Boucek, Grace Kahmann, and Ryan Rezek. Analysis was performed by Grace Kahmann and Ryan Rezek. The first draft of the manuscript was written by Grace Kahmann and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Datasets generated and analyzed during the current study are available through the Florida Coastal Everglades Long Term Ecological Research Program under the Environmental Data Initiative at https://doi.org/https://doi.org/10.6073/pasta/373d8f95186f2bf17939b5dd09cd8f7c. Hydrostation data used in this study are available from https://waterdata.usgs.gov.

Declarations

Conflict of interest The authors have no conflict of interest to declare.

Ethics approval The care of animal subjects was in accordance with institutional guidelines (IACUC-18-002-CR01).

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