

Trophic niche overlap & increasing populations of a nonnative invader 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 (*Macrogathus siamensis*) within this ecosystem using 19 years of electrofishing data. We investigated the population trends of peacock eels at the marsh-mangrove ecotone of the Shark River Estuary, emphasizing 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 methods to determine peacock eel niche size and overlap with native species. Results of this study found that peacock eel abundance has rapidly increased, and their populations are strongly affected by hydroclimatic regimes—with warmer water temperatures and greater marsh inundation periods explaining greater abundance. We found that the trophic niche of peacock eels, though significantly smaller in volume, overlaps 98.8% with native sunfishes (*Lepomis* spp.) suggesting a potential for inter-specific competition. In recent years, the catch of peacock eels has outnumbered the catch of all native sunfishes combined. Peacock eel populations are predicted to continue to increase, highlighting the importance of continued monitoring of their impact on native fish assemblages and food webs.

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 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 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; Episcopo-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 & 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 (Vander Zanden et al. 1999; Jackson et al. 2012; Guzzo et al. 2013). Unlike other methods of assessing trophic dynamics, such as gut contents analysis, stable isotope analysis can differentiate between food that is assimilated rather than merely ingested by providing an integrated estimate of long-term resource utilization (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 likelihood of resource competition between native and invasive species including for: 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). However, these studies used standard ellipse methods, which can be dimensionally limiting and may not accurately represent the desired niche. To address this shortcoming, hypervolume analysis, based on stochastic geometry, has been developed to represent a consumer's trophic niche in greater dimensions (Blonder et al. 2014; Blonder 2018; Lu et al. 2021). James et al. (2020) used hypervolume analysis methods to determine how trophic niche size and overlap among fishes changes in response to the availability of food sources, and Rezek et al. (2020) used similar hypervolume methods for niche differentiation among migratory predators in the coastal Everglades. Yet, hypervolume analysis methods have yet to be used in invasion ecology.

The peacock eel (*Macrogathus siamensis*), named for its unique markings (ocelli) that resemble a peacock's plumage is a recent introduction to the Everglades. Peacock eels are native to Southeast Asia where they inhabit freshwater rivers, canals, ponds, and inundated fields (Sultana et al. 2017). The 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). The peacock eel was first collected in the canals of South Florida in 2002 and quickly spread into the Everglades where 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). They have since been deemed an established invasive species by the US Fish and Wildlife Service, though the risk assessment that was conducted was inconclusive (Shafland et al. 2008; USFWS 2018). Few studies have been done on peacock eels in the Everglades, and their primary resource use in this region is 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) 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).

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; Loftus 2000; Faridi et al. 2016; Sultana et al. 2017). During seasonal dry-down periods 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). Sunfishes can provide 41% of the total biomass consumed by common snook inhabiting these coastal riverine systems (Boucek and Rehage 2013). Competitive interactions between invasive peacock eels and native sunfishes could disrupt the niche of these sunfishes and subsequently alter the seasonal prey pulse composition on which major fisheries rely.

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 species and existing food webs using contemporary stable isotope-based hypervolume analysis. Using an 19-year electrofishing dataset we: 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 and 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 this invasion on ecosystem structure, function, and services, with implications for invasive species management.

Methods

2.1 | 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 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

We 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 nearly 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 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 seconds 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 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).

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 post collection. 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:

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

where $R(X_H/X_L)$ 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 Pee Dee Belemnite, atmospheric nitrogen, and Canyon Diablo Troilite as reference standards.

2.3 | Environmental factors affecting peacock eel abundance

A generalized linear mixed model (GLMM) with a negative binomial distribution was used to investigate the environmental factors affecting peacock eels 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 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 median daily water depth values measured 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 $12.8 \pm 1.5^\circ\text{C}$ and the lower lethal temperature of peacock eels, the point at which direct mortality occurs, is 9.1°C ($\pm 1.0^\circ\text{C}$; 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 bout at each site. The model was fitted to a dataset of 1,311 electrofishing bouts that spanned across 15 sampling sites and 15 years of sampling. Bayesian Information Criterion (BIC) was used to select the most likely model from a set of candidate models. Forward model selection was used to identify the best 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 value was selected 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 multicollinearity was assessed using variance inflation factors, calculated with the performance package in R (Lüdtke 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 basal resource (mangrove detritus, epiphytic microalgae, and phytoplankton) 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 individual 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 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:

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

where $\delta^{15}\text{N}_{\text{ind}}$ is the nitrogen value of an individual consumer, $\delta^{15}\text{N}_{\text{source}}$ is the nitrogen value of each basal resource, and $\text{mean \%cont}_{\text{source}}$ 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 the peacock eel's 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 multi-dimensional 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 (Sørensen overlap index, Sørensen 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.

Results

3.1 | Peacock eel Population Trends

A total of 2,386 peacock eels were sampled during the study period (2004–2022, n = 1,311 sampling bouts). No peacock eels were recorded during 2004–2006 sampling events. The first peacock eels were collected in March 2007 (Fig. 2). Following this 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 (3.41/100 m) and peaked at 23.28/100 m in November of the same year. This peak was followed by a sharp decline and subsequent low capture rate (CPUE $\leq$ 1 eels/100 m) until February 2013 (2.08/100 m). CPUE remained below 2/100 m until January 2018 (8.56/100 m). The mean capture rate increased during 2018–2022, with the largest increase from May 2020 (0.31/100 m) to May 2021 (40.76/100 m). Since June 2021, the mean CPUE of peacock eels has remained below 2.6/100 m (Fig. 2).

3.2 | Environmental Factors Related to Peacock Eel Abundance

Over the study period, the annual average minimum daily water temperatures were 14.5°C (SD = 1.89), with the lowest daily average recorded in the wet season of 2010 (8.30°C). Annual maximum daily 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 dropped below the point at which loss of equilibrium occurs in peacock eels (12.8°C) during the dry seasons of 2008–2012, 2015, 2018, 2020, and 2022 (9 of the 19 years in the time series, Fig. 3a). The lower lethal temperature of peacock eels (9.1°C) was reached during the dry season of 2010. Over the study period, the annual 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 above 30 cm occurred in 2016 and totaled 366 days, while the lowest occurred in 2015 (107 days; Fig. 3b).

Model selection indicated the best fit model included the year, month, flooding duration over the previous 180 days, mean daily water level over the 180 days prior to sampling, and the minimum daily water temperature (Fig. 4a, Table S1 in Online Resource 1). Model results suggest that peacock eel CPUE will increase over time and that peak abundance occurs between months 3–5 (Fig. 4a, b). Peacock eel CPUE was shown to increase with increasing minimum water temperature with an increase of 4% for each additional day of marsh flooding (Fig. 4c, Table 1). Higher median water depths were shown to be related to lower peacock eel CPUE (Fig. 4d). Higher minimum daily water temperatures were associated with an increase in peacock eel CPUE with an increase of 25% annually for every 1°C increase in minimum water temperature (Fig. 4e, Table 1).

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

3.3 | Stable Isotope Analysis and Mixing Models

Mean $\delta^{34}\text{S}$ values of native sunfishes ranged from 23.8‰ in spotted sunfish to 16.5‰ in dollar sunfish. Mean $\delta^{13}\text{C}$ values ranged from - 31.5‰ in bluegill to -27.8‰ in dollar sunfish. Mean $\delta^{15}\text{N}$ values ranged from 11.0‰ in bluegill to 9.1‰ in dollar sunfish. The average $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values of peacock eels were 21.2‰, -28.8‰, and 9.4‰ respectively (Table 2). Of the basal resources, phytoplankton had the greatest mean $\delta^{34}\text{S}$ value (24.5‰) and epiphytic microalgae was the lowest (13.5‰). Epiphytic microalgae had the highest mean $\delta^{13}\text{C}$ (-29.0‰) and $\delta^{15}\text{N}$ (7.0‰) values, whereas phytoplankton had the lowest ($\delta^{13}\text{C}$ -35.5‰, $\delta^{15}\text{N}$ 5.8‰; Table 2). 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‰ (Fig. 5a). Dollar sunfish had the highest mean basal resource contribution of epiphytic microalgae (47.6%), while 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 used most 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 (Fig. 5b).

Species	$\delta^{13}\text{C}$	SD	$\delta^{15}\text{N}$	SD	$\delta^{34}\text{S}$	SD	<i>n</i>
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.							

3.4 | 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). 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 Sørensen 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 Sørensen overlap index value of 0.194 ($P < 0.05$). The Sørensen 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 due to the larger volume ($P < 0.001$; Table 3, Fig. 6).

Table 3
Hypervolume metrics for the Peacock eel (*Macrogathus 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 Sørensen 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	Sørensen 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***

Discussion

4.1 | Peacock Eel Population Trends

Although Peacock eel abundance at the mangrove ecotone of the FCE exhibited high variability over the study period, the model identified a 13.8% mean annual increase since their first detection. Notably, there are 2 periods of rapid population increase in the time series with years of low abundance in between. First, within 3 years of detection, the population of peacock eels in this region increased dramatically (from 0.11 to 23.28 individuals/100m). Peacock eel populations can double in as little as 1.4 years (Froese et al. 2017), though they do not become sexually mature until three years of age (Sinha et al. 2023). The initial spike in peacock eel abundance, however, was followed by a sharp decline and a subsequent 8-year period (2010–2018) when population numbers remained low. The drastic population decline directly followed the historic 2010 cold snap, which was later described as the most severe cold weather event documented in this region in 100 years. 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 ($\pm 1.0^\circ\text{C}$); 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, under more favorable temperature conditions peacock eel populations spiked exemplifying their ability to thrive in this ecotonal habitat under ideal conditions. In 2018, peacock eel populations began to increase again, and increased by 928% over the next 3 years. 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 of mangrove shoreline in comparison to only 2.5 (± 1) n/100 m for peacock eels in this study. 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 May 2021 (40 ± 17 n/100

m). Sunfish abundance peaked at $3.5 (\pm 1.4)$ n/100 m the same year; however, the highest recorded CPUE for sunfish during this data set occurred in March 2014 with $90 (\pm 24)$ n/100 m.

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 gammarid amphipods (*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). 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 (Ruetz et al. 2005; Catano et al. 2014).

In this study, it was found that when water levels in the marsh were low in association with seasonal drying periods, 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 also seek refuge in the mangrove creeks during seasonal dry down periods. Peacock eel abundance was also associated with longer periods of prior marsh inundation. The positive effect of 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 as well. 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. However, the extent and timing of the subsequent dry down period also mediates the biomass and composition of the pulse of freshwater fishes to the mangrove creeks (Rezek et al. 2023). Similar to the FCE, pulsing 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). 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 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 extreme cold events that currently limit expansion and abundance of peacock eels as well as other subtropical and tropical non-native species (Catano et al. 2014; Rehage and Blanchard 2016). 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 $\pm 10\%$ 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. 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.

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. Our results revealed that peacock eels have similar basal resource contributions to redear sunfish and feed at a similar trophic level as both redear and dollar sunfish suggesting there is potential for competition. 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). Though significantly smaller in volume, assessment of overlap showed that the trophic niche of peacock eels was almost entirely nested within that of the combined sunfish value (98.8%) indicating that the trophic channels peacock eels are relying on are also being used by native sunfishes. This is consistent with data on the known diets of both and suggests competition is possible (Rubenstein 1981; Faridi et al. 2016; Sultana et al. 2017). Despite the utilization of similar dietary resources, other aspects of peacock eel resource use within the Everglades need to be investigated in the future to better understand any inter-specific interactions that may be occurring to facilitate coexistence.

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, likely because peacock eels are nocturnal feeders and collection occurred during the day (J.R. Blanchard, unpublished data). The significant trophic niche overlap between peacock eels and the native sunfishes found in this study suggests that there is potential for resource competition; however, it does not definitively indicate direct competition is occurring (Vander Zanden et al. 1999; Kelly and Jellyman 2007; Córdova-Tapia et al. 2015). 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 resources become limiting or if the shared food resources are the most energetically important and they are unable to readjust diet, behavior, or 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 Borgström 2008; Ke et al. 2008; Córdova-Tapia et al. 2015). However, with increasing peacock eel populations and their non-generalist or specialized feeding characteristics, some prey species populations may be significantly affected and could lead to trophic niche shifts in sunfishes or bottom-up trophic cascades (Kelly and Jellyman 2007; Ke et al. 2008; Wahl et al. 2011).

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 of the Everglades, which is credited 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 potential for peacock eels to serve as an alternative prey source for highly mobile predators that rely on the seasonal prey pulse (e.g., Boucek and Rehage 2013, Massie et al. in review) as well as the effects that they may have on benthic prey species remains unknown.

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. 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 (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. It is of importance that peacock eel populations continue to be monitored and that further studies be conducted to determine additional impacts of their introduction in order to predict and mitigate the effects on ecosystem structure, function, and services.

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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References

1. Alp M, Cucherousset J (2022) Food webs speak of human impact: Using stable isotope-based tools to measure ecological consequences of environmental change. *Food Webs* 30:1–11. <https://doi.org/10.1016/j.fooweb.2021.e00218>
2. Bearhop S, Adams CE, Waldron S, et al (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73:1007–1012. <https://doi.org/10.1111/j.0021-8790.2004.00861.x>
3. Blonder B (2018) Hypervolume concepts in niche- and trait-based ecology. *Ecography* 41:1441–1455. <https://doi.org/10.1111/ecog.03187>
4. Blonder B, Lamanna C, Violle C, Enquist BJ (2014) The n-dimensional hypervolume. *Global Ecology and Biogeography* 23:595–609. <https://doi.org/10.1111/geb.12146>
5. Blonder B, Morrow CB, Maitner B, et al (2018) New approaches for delineating n-dimensional hypervolumes. *Methods Ecol Evol* 9:305–319. <https://doi.org/10.1111/2041-210X.12865>
6. Boucek RE, Rehage JS (2013) No free lunch: Displaced marsh consumers regulate a prey subsidy to an estuarine consumer. *Oikos* 122:1453–1464. <https://doi.org/10.1111/j.1600-0706.2013.20994.x>
7. Boucek RE, Rehage JS (2014) Climate extremes drive changes in functional community structure. *Glob Chang Biol* 20:1821–1831. <https://doi.org/10.1111/gcb.12574>

8. Boucek RE, Soula M, Tamayo F, Rehage JS (2016) A once in ten-year drought alters the magnitude and quality of a floodplain prey subsidy to coastal river fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1672–1678. <https://doi.org/10.1139/cjfas-2015-0507>
9. Brandner J, Pander J, Mueller M, et al (2013) Effects of sampling techniques on population assessment of invasive round goby *Neogobius melanostomus*. *J Fish Biol* 82:2063–2079. <https://doi.org/10.1111/jfb.12137>
10. Brooks ME, Kristensen K, Van Benthem KJ, et al (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J* 9/2:378–400
11. Brown MT, Cohen MJ, Bardi E, Ingwersen WW (2006) Species diversity in the Florida Everglades, USA: A systems approach to calculating biodiversity. *Aquat Sci* 68:254–277. <https://doi.org/10.1007/s00027-006-0854-1>
12. Campbell LM, Thacker R, Barton D, et al (2009) Re-engineering the eastern Lake Erie littoral food web: The trophic function of non-indigenous Ponto-Caspian species. *J Great Lakes Res* 35:224–231. <https://doi.org/10.1016/j.jglr.2009.02.002>
13. Catano CP, Romañach SS, Beerens JM, et al (2014) Using Scenario Planning to Evaluate the Impacts of Climate Change on Wildlife Populations and Communities in the Florida Everglades. *Environ Manage* 55:807–823. <https://doi.org/10.1007/s00267-014-0397-5>
14. Cerveira I, Dias E, Baptista V, et al (2021) Invasive fish keeps native feeding strategy despite high niche overlap with a congener species. *Reg Stud Mar Sci* 47:1–8. <https://doi.org/10.1016/j.rsma.2021.101969>
15. Chea R, Pool TK, Chevalier M, et al (2020) Impact of seasonal hydrological variation on tropical fish assemblages: abrupt shift following an extreme flood event. *Ecosphere* 11:1–15. <https://doi.org/10.1002/ecs2.3303>
16. Chen R, Twilley RR (1999) Patterns of Mangrove Forest Structure and Soil Nutrient Dynamics Along the Shark River Estuary, Florida. *Estuaries* 22:955–970. <https://doi.org/10.2307/1353075>
17. Childers DL (2006) A synthesis of long-term research by the Florida Coastal Everglades LTER Program. *Hydrobiologia* 569:531–544. <https://doi.org/10.1007/s10750-006-0154-8>
18. Childers, D. L., Gaiser, E., & Ogden, L. A. (Eds.). (2019). *The Coastal Everglades: the dynamics of social-ecological transformation in the south Florida landscape*. Oxford University Press, USA.
19. Córdova-Tapia F, Contreras M, Zambrano L (2015) Trophic niche overlap between native and non-native fishes. *Hydrobiologia* 746:291–301. <https://doi.org/10.1007/s10750-014-1944-z>
20. Courtenay WR, Miley WWI (1975) Range Expansion and Environmental Impress of the Introduced Walking Catfish in the United States. *Environ Conserv* 2:145–148
21. Crane DP, Einhouse DW (2016) Changes in growth and diet of smallmouth bass following invasion of Lake Erie by the round goby. *J Great Lakes Res* 42:405–412. <https://doi.org/10.1016/j.jglr.2015.12.005>
22. Crane DP, Farrell JM, Einhouse DW, et al (2015) Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. *Freshw Biol* 60:111–124. <https://doi.org/10.1111/fwb.12473>
23. Das SK, Kalita N (2003) Captive Breeding of Peacock Eel, *Macrognathus aculeatus*. *Aquaculture* VIII:17–18. <https://library.enaca.org/AquacultureAsia/Articles/July-Sept-2003/6peacockeels-sept03.pdf>
24. Dehnhard N, Achurch H, Clarke J, et al (2020) High inter- and intraspecific niche overlap among three sympatrically breeding, closely related seabird species: Generalist foraging as an adaptation to a highly variable environment? *Journal of Animal Ecology* 89:104–119. <https://doi.org/10.1111/1365-2656.13078>
25. Dessu SB, Price RM, Troxler TG, Kominoski JS (2018) Effects of sea-level rise and freshwater management on long-term water levels and water quality in the Florida Coastal Everglades. *J Environ Manage* 211:164–176. <https://doi.org/10.1016/j.jenvman.2018.01.025>
26. Dijkstra JA, Lambert WJ, Harris LG (2013) Introduced species provide a novel temporal resource that facilitates native predator population growth. *Biol Invasions* 15:911–919. <https://doi.org/10.1007/s10530-012-0339-1>
27. Episcopio-Sturgeon DJ, Pienaar EF (2020) Investigating Support for Management of the Pet Trade Invasion Risk. *Journal of Wildlife Management* 84:1196–1209. <https://doi.org/10.1002/jwmg.21867>
28. Ewe SML, Gaiser EE, Childers DL, et al (2006) Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia* 569:459–474. <https://doi.org/10.1007/s10750-006-0149-5>
29. Faridi AA, Rizvi MM, Serajuddin M (2016) Food and feeding habits of peacock eel, *Macrognathus aculeatus* (Bloch, 1786) from Eastern Uttar Pradesh, India. *Int J Fish Aquat Stud* 4:130–134
30. Fourqurean JW, Zieman JC (1992) Phosphorus limitation of primary production in Florida Bay: Evidence from C : N : P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology Oceanography* 37:162–172. <https://doi.org/10.4319/lo.1992.37.1.0162>
31. Froese R, Demirel N, Coro G, et al (2017) Estimating fisheries reference points from catch and resilience. *Fish and Fisheries* 18:506–526. <https://doi.org/10.1111/faf.12190>
32. Fry B, Smith TJ (2002) Stable isotope studies of red mangroves and filter feeders from the shark river estuary, Florida. *Bull Mar Sci* 70:871–890. https://www.researchgate.net/profile/Thomas-J-Smith-lil/publication/230955281_Stable_isotope_studies_of_Red_Mangroves_and_filter_feeders_from_the_Shark_River_estuary_Florida/links/09e415060a351disotope-studies-of-Red-Mangroves-and-filter-feeders-from-the-Shark-River-estuary-Florida.pdf
33. Gaiser, E., D. Childers, R. Travieso. 2023. Sawgrass Above and Below Ground Total Phosphorus from the Shark River Slough, Everglades National Park (FCE LTER), Florida, USA, September 2002 - ongoing. Environmental Data Initiative. <https://doi.org/10.6073/pasta/8bcc9c9a041dfa943f16db2d77648301>. Dataset accessed 2023-12-02.

34. Gao Q-F, Shin PKS, Lin G-H, et al (2006) Stable isotope and fatty acid evidence for uptake of organic waste by green-lipped mussels *Perna viridis* in a polyculture fish farm system. *Marine ecology progress* 317:273–283. <https://doi.org/10.3354/meps317273>
35. Guzzo MM, Haffner GD, Legler ND, et al (2013) Fifty years later: Trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. *Biol Invasions* 15:1695–1711. <https://doi.org/10.1007/s10530-012-0401-z>
36. Hartig F, Lohse L (2022) Package “DHARMA” Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models
37. Howell H, Searcy C, Howell HJ, Searcy CA (2023) The Role of Invasive Species and Charismatic Megafauna in Everglades Herpetofaunal Research. *Herpetol Conserv Biol* 18:128–139. https://www.herpconbio.org/Volume_18/Issue_1/Howell_Searcy_2023.pdf
38. Jackson MC, Donohue I, Jackson AL, et al (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. *PLoS One* 7:1–12. <https://doi.org/10.1371/journal.pone.0031757>
39. Jackson MC, Grey J, Miller K, et al (2016) Dietary niche constriction when invaders meet natives: evidence from freshwater decapods. *Journal of Animal Ecology* 85:1098–1107. <https://doi.org/10.1111/1365-2656.12533>
40. James WR, Lesser JS, Litvin SY, Nelson JA (2020) Assessment of food web recovery following restoration using resource niche metrics. *Science of the Total Environment* 711. <https://doi.org/10.1016/j.scitotenv.2019.134801>
41. Janssen J, Jude DJ (2001) Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *J Great Lakes Res* 27:319–328. [https://doi.org/10.1016/S0380-1330\(01\)70647-8](https://doi.org/10.1016/S0380-1330(01)70647-8)
42. Jerath M, Bhat M, Rivera-Monroy VH, et al (2016) The role of economic, policy, and ecological factors in estimating the value of carbon stocks in Everglades mangrove forests, South Florida, USA. *Environ Sci Policy* 66:160–169. <https://doi.org/10.1016/j.envsci.2016.09.005>
43. Junk WJ, Brown M, Campbell IC, et al (2006) The comparative biodiversity of seven globally important wetlands: A synthesis. *Aquat Sci* 68:400–414. <https://doi.org/10.1007/s00027-006-0856-z>
44. Ke Z, Xie P, Guo L (2008) In situ study on effect of food competition on diet shifts and growth of silver and bighead carps in large biomanipulation fish pens in Meiliang Bay, Lake Taihu. *Journal of Applied Ichthyology* 24:263–268. <https://doi.org/10.1111/j.1439-0426.2008.01060.x>
45. Kelly DJ, Jellyman DJ (2007) Changes in trophic linkages to shortfin eels (*Anguilla australis*) since the collapse of submerged macrophytes in Lake Ellesmere, New Zealand. *Hydrobiologia* 579:161–173. <https://doi.org/10.1007/s10750-006-0400-0>
46. Kline JL, Loftus WF, Kotun K, et al (2014) Recent fish introductions into Everglades National Park: An unforeseen consequence of water management? *Wetlands* 34. <https://doi.org/10.1007/s13157-012-0362-0>
47. Koch MS, Coronado C, Miller MW, et al (2014) Climate Change Projected Effects on Coastal Foundation Communities of the Greater Everglades Using a 2060 Scenario: Need for a New Management Paradigm. *Environ Manage* 55:857–875. <https://doi.org/10.1007/s00267-014-0375-y>
48. Lauer TE, Allen PJ, McComish TS (2004) Changes in Mottled Sculpin and Johnny Darter Trawl Catches after the Appearance of round Gobies in the Indiana Waters of Lake Michigan. *Trans Am Fish Soc* 133:185–189. <https://doi.org/10.1577/t02-123>
49. Levine S (1980) Several Measures of Trophic Structure Applicable to Complex Food Webs. *J Theor Biol* 83:195–207. [https://doi.org/10.1016/0022-5193\(80\)90288-X](https://doi.org/10.1016/0022-5193(80)90288-X)
50. Loftus WF (2000) Accumulation and fate of mercury in an Everglades Food Web. Dissertation, Florida International University
51. Loftus WF, Kushlan JA (1987) Freshwater fishes of Southern Florida. *Prog Nucl Energy* 6 Biol Sci 31:147–344
52. Lu M, Winner K, Jetz W (2021) A unifying framework for quantifying and comparing n-dimensional hypervolumes. *Methods Ecol Evol* 12:1953–1968. <https://doi.org/10.1111/2041-210X.13665>
53. Lüdtke D, Ben-Shachar M, Patil I, et al (2021) Performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *J Open Source Softw* 6:3139. <https://doi.org/10.21105/joss.03139>
54. Maerz JC, Karuzas JM, Madison DM, Blossey B (2005) Introduced invertebrates are important prey for a generalist predator. *Divers Distrib* 11:83–90. <https://doi.org/10.1111/j.1366-9516.2005.00125.x>
55. Massie JA, Santos RO, Rezek RJ, et al (2022) Primed and cued: long-term acoustic telemetry links interannual and seasonal variations in freshwater flows to the spawning migrations of Common Snook in the Florida Everglades. *Mov Ecol* 10. <https://doi.org/10.1186/s40462-022-00350-5>
56. Matich P, Heithaus MR (2014) Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. *Journal of Animal Ecology* 83:199–213. <https://doi.org/10.1111/1365-2656.12106>
57. McCutchan JHJ, Lewis WMJ, Kendall C, McGrath CC (2003) Variation In Trophic Shift for Stable Isotope Ratios of Carbon, Nitrogen, and Sulfur. *Okios* 102:378–390
58. McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Tree* 14:450–453
59. Michener RH, Schell D (1994) *Stable Isotopes in Ecology and Environmental Science*, Second Edition. Blackwell Publishing, Boston
60. Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. *PNAS* 98:5446–5451 <https://doi.org/10.1073/pnas.09109339>
61. Nelson J, Wilson R, Coleman F, et al (2012) Flux by fin: Fish-mediated carbon and nutrient flux in the northeastern Gulf of Mexico. *Mar Biol* 159:365–372. <https://doi.org/10.1007/s00227-011-1814-4>
62. Nelson JA, Deegan L, Garritt R (2015) Drivers of spatial and temporal variability in estuarine food webs. *Mar Ecol Prog Ser* 533:67–77. <https://doi.org/10.3354/meps11389>
63. Newsome SD, Yeakel JD, Wheatley P V., Tinker MT (2012) Tools for quantifying isotopic niche space and dietary variation at the individual and population level. *J Mammal* 93:329–341. <https://doi.org/10.1644/11-MAMM-S-187.1>

64. Noe GB, Scinto LJ, Taylor J, et al (2003) Phosphorus cycling and partitioning in an oligotrophic Everglades wetland ecosystem: A radioisotope tracing study. *Freshw Biol* 48:1993–2008. <https://doi.org/10.1046/j.1365-2427.2003.01143.x>
65. Obeysekera J, Barnes J, Nungesser M (2014) Climate Sensitivity Runs and Regional Hydrologic Modeling for Predicting the Response of the Greater Florida Everglades Ecosystem to Climate Change. *Environ Manage* 55:749–762. <https://doi.org/10.1007/s00267-014-0315-x>
66. Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: Coping with too much variation. *PLoS One* 5:. <https://doi.org/10.1371/journal.pone.0009672>
67. Pellan L, Médoc V, Renault D, et al (2016) Feeding choice and predation pressure of two invasive gammarids, *Gammarus tigrinus* and *Dikerogammarus villosus*, under increasing temperature. *Hydrobiologia* 781:43–54. <https://doi.org/10.1007/s10750-015-2312-3>
68. Petersen JH, Kitchell JF (2001) Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. *The Canadian Journal of Fisheries and Aquatic Sciences* 58:1831–1841. <https://doi.org/10.1139/cjfas-58-8-1831>
69. Peterson BJ, Fry B (1987) Stable Isotopes in Ecosystem Studies. *Annu Rev Ecol Syst* 18:293–320 <https://doi.org/10.1146/annurev.es.18.110187.001453>
70. Pintar MR, Dorn NJ, Kline JL, Trexler JC (2023) Hydrology-mediated ecological function of a large wetland threatened by an invasive predator. *Science of the Total Environment* 857:. <https://doi.org/10.1016/j.scitotenv.2022.159245>
71. Pintor LM, Byers JE (2015) Do native predators benefit from non-native prey? *Ecol Lett* 18:1174–1180. <https://doi.org/10.1111/ele.12496>
72. Post DM (2002) Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology* 83:703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
73. Rahel FJ, Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22:521–533. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
74. Rehage, J. (2023) Seasonal Electrofishing Data from Rookery Branch and Tarpon Bay, Everglades National Park (FCE LTER), Florida, USA, November 2004 - ongoing. Environmental Data Initiative. <https://doi.org/10.6073/pasta/373d8f95186f2bf17939b5dd09cd8f7c>. Dataset accessed 2024-01-16.
75. Rehage JS, Blanchard JR (2016) What Can We Expect from Climate Change for Species Invasions? *Fisheries (Bethesda)* 41:405–407. <https://doi.org/10.1080/03632415.2016.1180287>
76. Rehage JS, Loftus WF (2007) Seasonal fish community variation in headwater mangrove creeks in the southwestern everglades: an examination of their role as dry-down refuges. *Bull Mar Sci* 80:625–645. https://digitalcommons.fiu.edu/cgi/viewcontent.cgi?article=1084&context=fce_lter_journal_articles
77. Reynolds WW, Casterlin ME (1976) Locomotor Activity Rhythms in the Bluegill Sunfish, *Lepomis macrochirus*. *Am Midl Nat* 96:221–225. <https://doi.org/10.2307/2424581>
78. Rezek RJ, Massie JA, Nelson JA, et al (2023) The effects of temperature and flooding duration on the structure and magnitude of a floodplain prey subsidy. *Freshw Biol*. <https://doi.org/10.1111/fwb.14145>
79. Rezek RJ, Massie JA, Nelson JA, et al (2020) Individual consumer movement mediates food web coupling across a coastal ecosystem. *Ecosphere* 11:1–11. <https://doi.org/10.1002/ecs2.3305>
80. Rubenstein DI (1981) Population density, resource patterning, and territoriality in the everglades pygmy sunfish. *Animal Behavior* 29:155–172. [https://doi.org/10.1016/S0003-3472\(81\)80162-5](https://doi.org/10.1016/S0003-3472(81)80162-5)
81. Rudnick DT, Chen Z, Childers DL, et al (1999) Phosphorus and Nitrogen Inputs the Everglades Watershed to Florida Bay: The Importance of. *Estuaries* 22:398–416
82. Ruetz CR, Trexler JC, Jordan F, et al (2005) Population dynamics of wetland fishes: Spatio-temporal patterns synchronized by hydrological disturbance? *Journal of Animal Ecology* 74:322–332. <https://doi.org/10.1111/j.1365-2656.2005.00926.x>
83. Rush SA, Paterson G, Johnson TB, et al (2012) Long-term impacts of invasive species on a native top predator in a large lake system. *Freshw Biol* 57:2342–2355. <https://doi.org/10.1111/fwb.12014>
84. Saha AK, Moses CS, Price RM, et al (2012) A Hydrological Budget (2002–2008) for a Large Subtropical Wetland Ecosystem Indicates Marine Groundwater Discharge Accompanies Diminished Freshwater Flow. *Estuaries and Coasts* 35:459–474. <https://doi.org/10.1007/s12237-011-9454-y>
85. Schofield PJ, Kline JL (2018) Lower Lethal Temperatures for Nonnative Freshwater Fishes in Everglades National Park, Florida. *N Am J Fish Manag* 38:706–717. <https://doi.org/10.1002/nafm.10068>
86. Schwarz G (1978) Estimating the dimension of a Model. *The Annals of Statistics* 6:461–464. <https://doi.org/10.1214/aos/1176344136>. <http://www.jstor.org/stable/2958889>
87. Shafland PL, Gestring KB, Stanford MS (2008) Florida's exotic freshwater fishes-2007. *Florida Scientist* 71:220–245. https://www.jstor.org/stable/24321403?casa_token=ROGZBKofPDAAAAAA%3A0zkVJ4148OW50bEneSuYIQn4QeEROLFQAJU8td3tp692dEvVoO62GBuHR0xLYw-NYq3v04DASel-kx2wyB90-ix64rxQTy2yDhjhm80RJ_h6E8tyg
88. Sharma CM, Borgström R (2008) Shift in density, habitat use, and diet of perch and roach: An effect of changed predation pressure after manipulation of pike. *Fish Res* 91:98–106. <https://doi.org/10.1016/j.fishres.2007.11.011>
89. Sinha A, Swain HS, Bhattacharya S (2020) Freshwater eels: a candidate indigenous ornamental fish species of India. *Aquaculture Spectrum* 3:27–31. <http://krishi.icar.gov.in/jspui/handle/123456789/59039>
90. Sinha A, Swain HS, Das BK (2023) First report on successful captive breeding of peacock eel, *Macrogynathus aral*. *Aquaculture* 27:30–33. <https://enaca.org/?id=1278>
91. Stabenau E, Pearlstine LG (2011) Sea-level rise: Observations, impacts, and proactive measures in Everglades National Park. *Park Sci* 28:26–30. https://www.researchgate.net/profile/Leonard-Pearlstine/publication/286374988_Sea-

level_rise_Observations_impacts_and_proactive_measures_in_Everglades_National_park/links/577c0e2008ae355e74f16a08/Sea-level-rise-Observations-impacts-and-proactive-measures-in-Everglades-National-park.pdf

92. Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW (2023) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *PNAS* 99:15497–1550. <https://doi.org/10.1073/pnas.242437499>
93. Stevens PW, Blewett DA, Boucek RE, et al (2016) Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in Southern Florida. *Ecosphere* 7:. <https://doi.org/10.1002/ecs2.1400>
94. Stock B, Semmens B, Ward E, et al (2018) Package “MixSIAR” Title Bayesian Mixing Models in R
95. Sultana S, Nahar K, Bir J, et al (2017) A Quick View on Biology of Near Threatened Peacock Eel (*Macrogynathus aculeatus*) in Khulna Region of Bangladesh. *American Journal of Zoological Research* 5:38–46. <https://doi.org/10.12691/ajzr-5-2-4>
96. Swanson HK, Lysy M, Power M, et al (2015) A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* 96:318–324. <https://doi.org/10.1890/14-0235.1>
97. Tepolt CK, Somero GN (2014) Master of all trades: Thermal acclimation and adaptation of cardiac function in a broadly distributed marine invasive species, the European green crab, *Carcinus maenas*. *Journal of Experimental Biology* 217:1129–1138. <https://doi.org/10.1242/jeb.093849>
98. Trexler JC, Goss CW (2009) Aquatic fauna as indicators for Everglades restoration: Applying dynamic targets in assessments. *Ecol Indic* 9:. <https://doi.org/10.1016/j.ecolind.2008.11.001>
99. USFWS (2018) Peacock Eel (*Macrogynathus siamensis*) Ecological Risk Screening Summary
100. Vander Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464–466. <https://doi.org/10.1038/46762>
101. Wahl DH, Wolfe MD, Santucci VJ, Freedman JA (2011) Invasive carp and prey community composition disrupt trophic cascades in eutrophic ponds. *Hydrobiologia* 678:49–63. <https://doi.org/10.1007/s10750-011-0820-3>
102. Wilson RM, Chanton J, Lewis FG, Nowacek D (2010) Concentration-dependent Stable Isotope Analysis of Consumers in the Upper Reaches of a Freshwater-dominated Estuary: Apalachicola Bay, FL, USA. *Estuaries and Coasts* 33:1406–1419. <https://doi.org/10.1007/s>
103. Xia B, Gao Q, Li H, et al (2013) Turnover and fractionation of nitrogen stable isotope in tissues of grass carp *Ctenopharyngodon idellus*. *Aquac Environ Interact* 3:177–186. <https://doi.org/10.3354/aei00061>
104. Zambrano L, Scheffer M, Martínez-Ramos M (2001) Catastrophic response of lakes to benthivorous fish introduction. *Oikos* 94:344–350. <https://doi.org/10.1034/j.1600-0706.2001.940215.x>
105. Zerebecki RA, Sorte CJB (2011) Temperature tolerance and stress proteins as mechanisms of invasive species success. *PLoS One* 6:. <https://doi.org/10.1371/journal.pone.0014806>

Figures

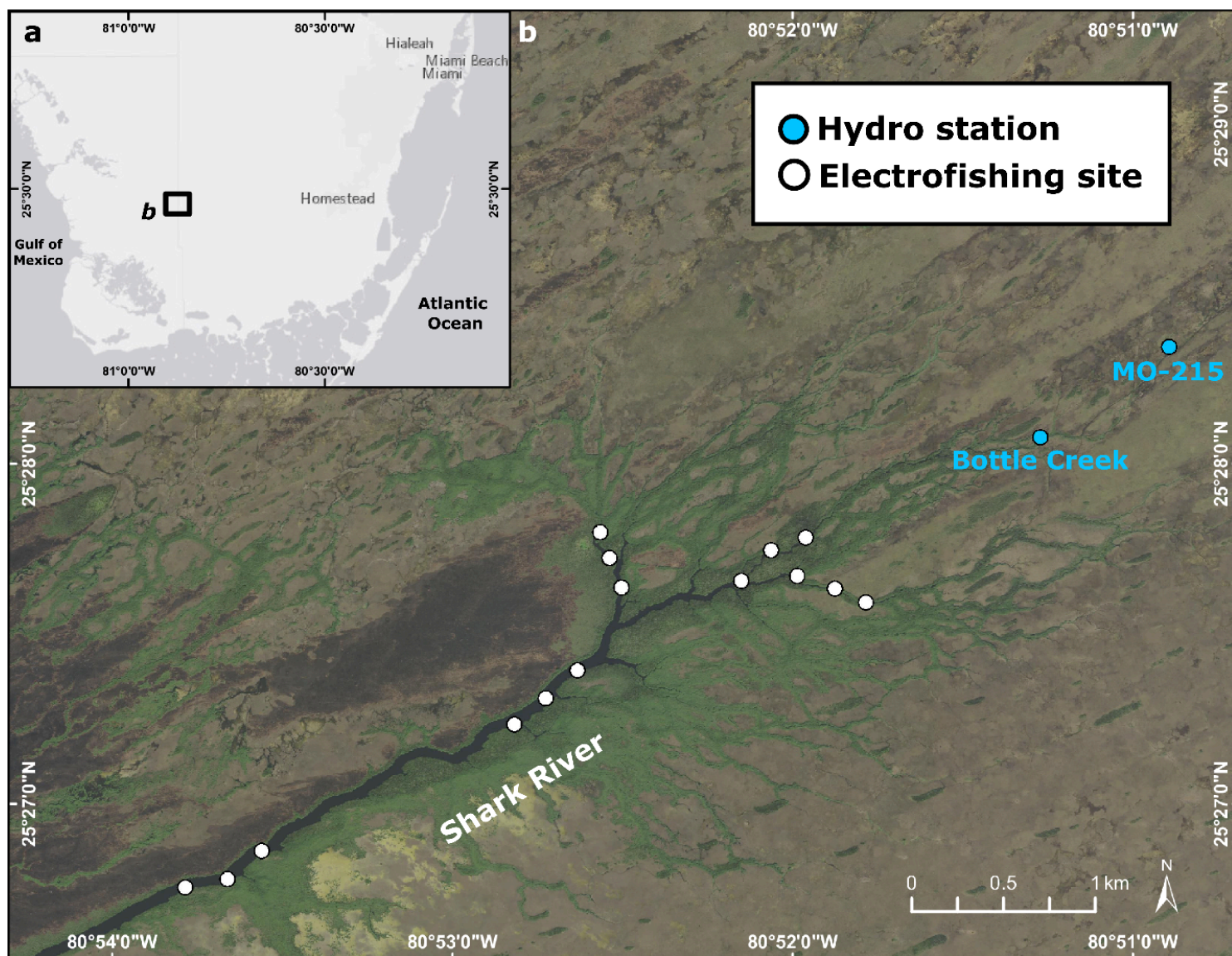


Figure 1

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)

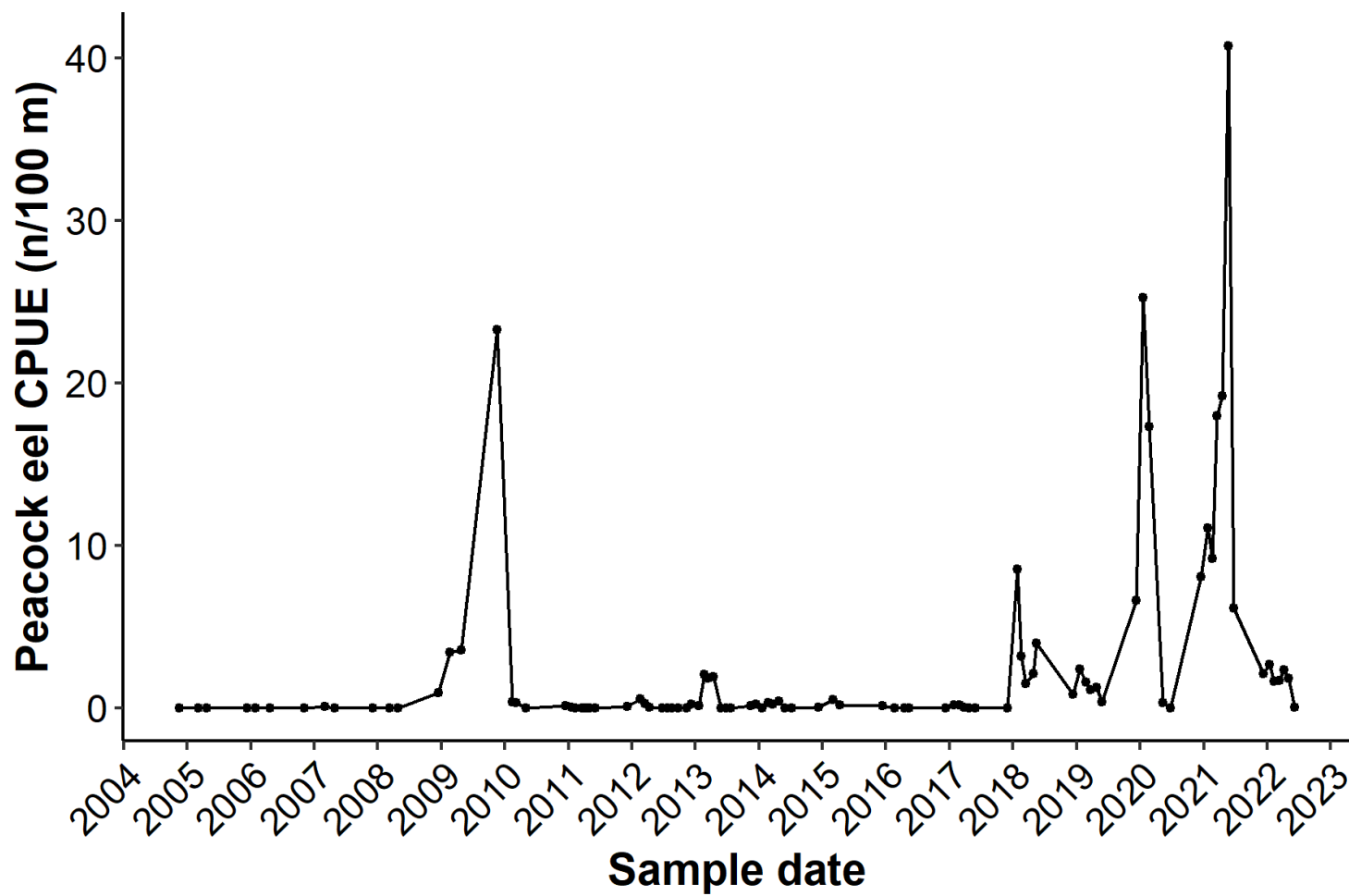


Figure 2

Mean peacock eel CPUE (number per 100 m of river shoreline) from all sampling events ($n= 95$) over the 19-year time series (2004-2022)

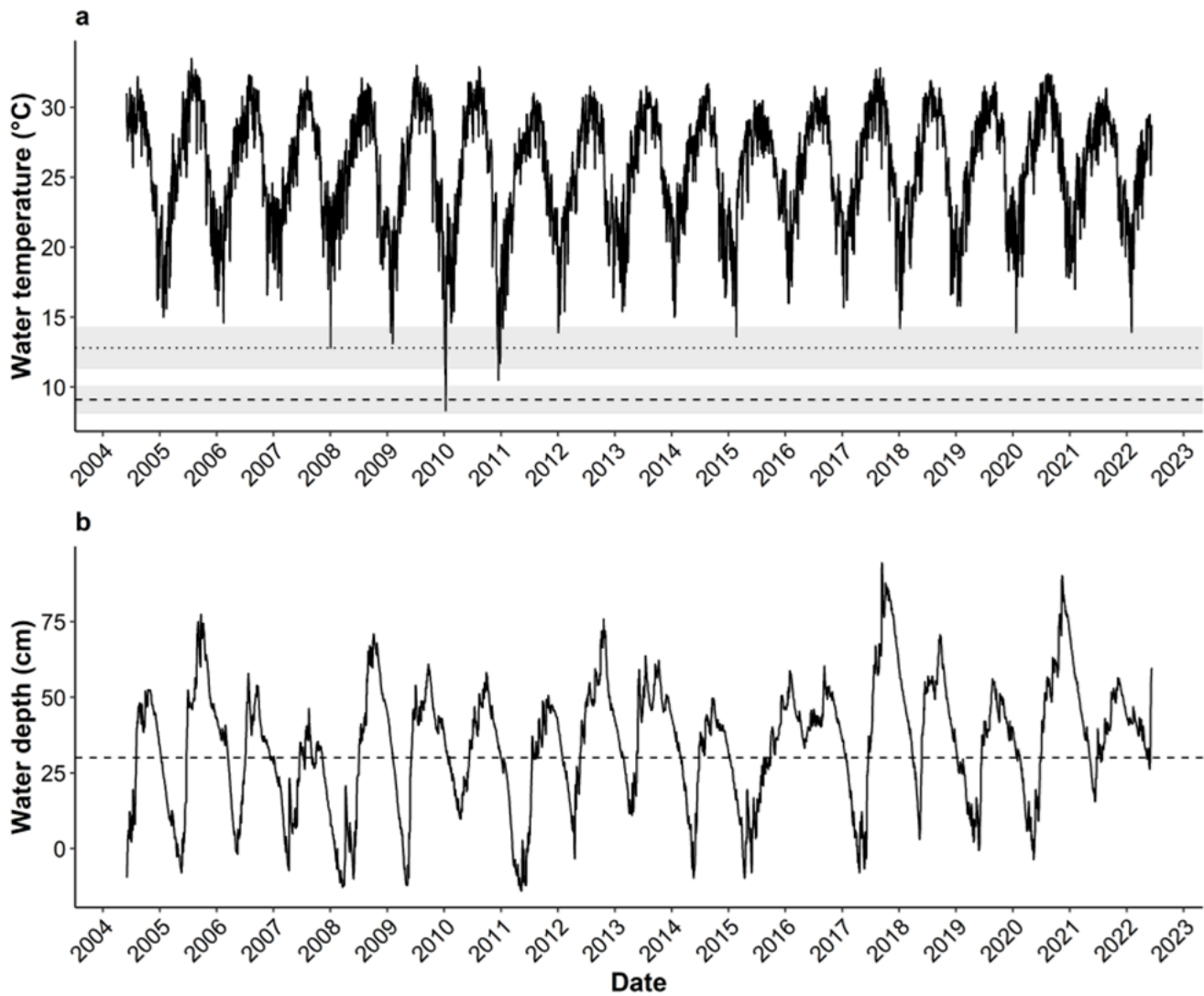


Figure 3

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 ($12.8 \pm 1.5^{\circ}\text{C}$), the dashed line represents the lower lethal temperature at which direct mortality occurs ($9.1^{\circ}\text{C} \pm 1.0$; Schofield and Kline 2018) and the gray areas represent the reported 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 threshold

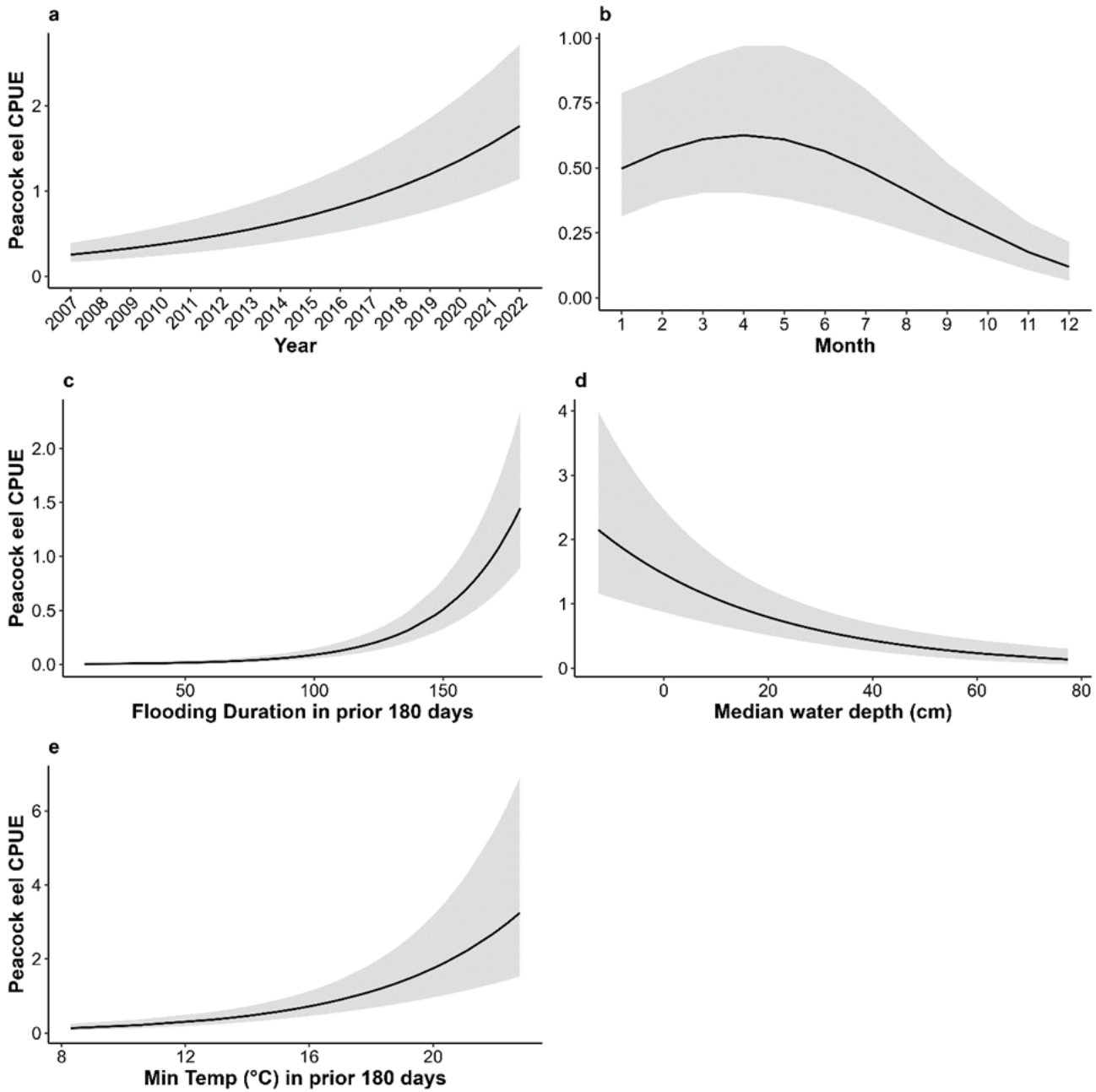


Figure 4

Marginal effects of parameters assessed with the GLMM on peacock eel CPUE (catch per 100 m of shoreline) (a) sampling year, (b) sampling month, (c) the 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 date

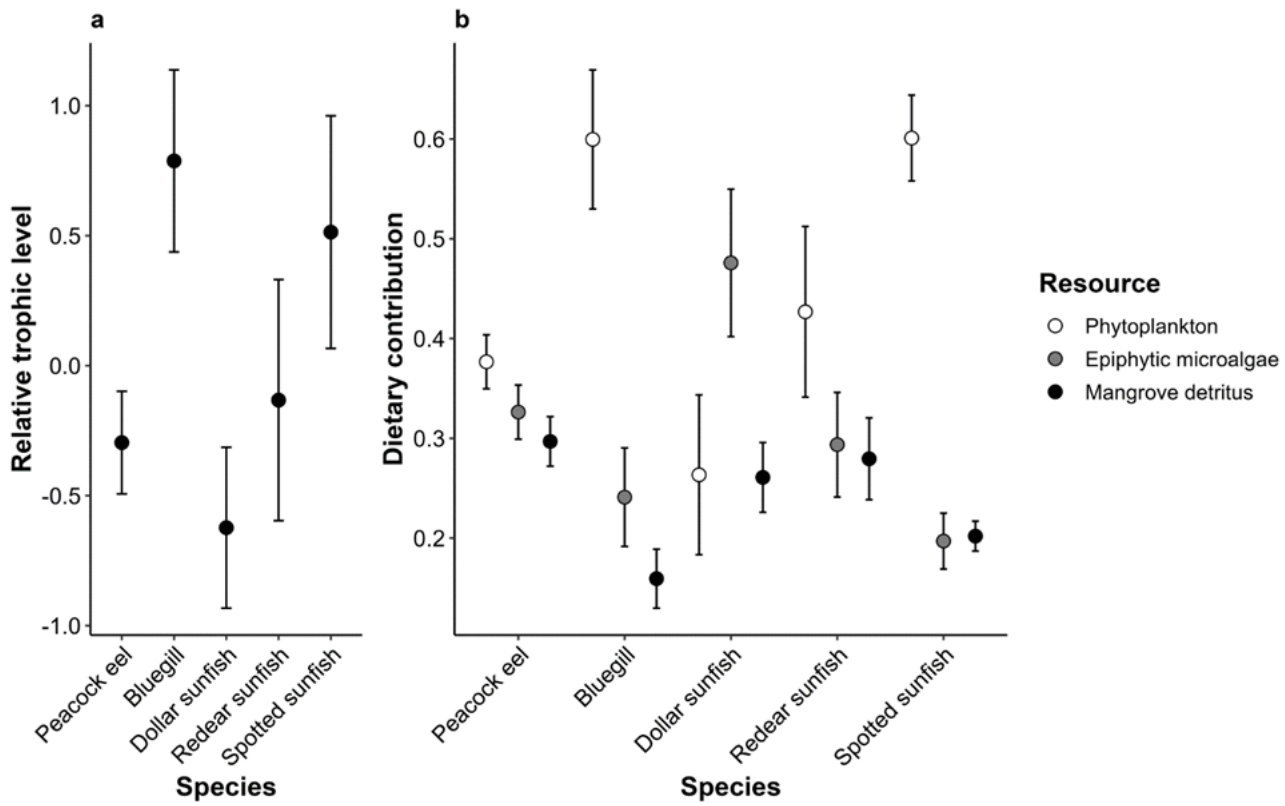


Figure 5
Mixing model output showing: (a) the relative trophic position (z-score) of the invasive peacock eel (*Macrogathus siamensis*) and native dollar sunfish (*Lepomis marginatus*), bluegill (*Lepomis macrochirus*), redeer sunfish (*Lepomis microlophus*), and spotted sunfish (*Lepomis punctatus*), and (b) the source contributions of each of the three basal resources to each consumer species

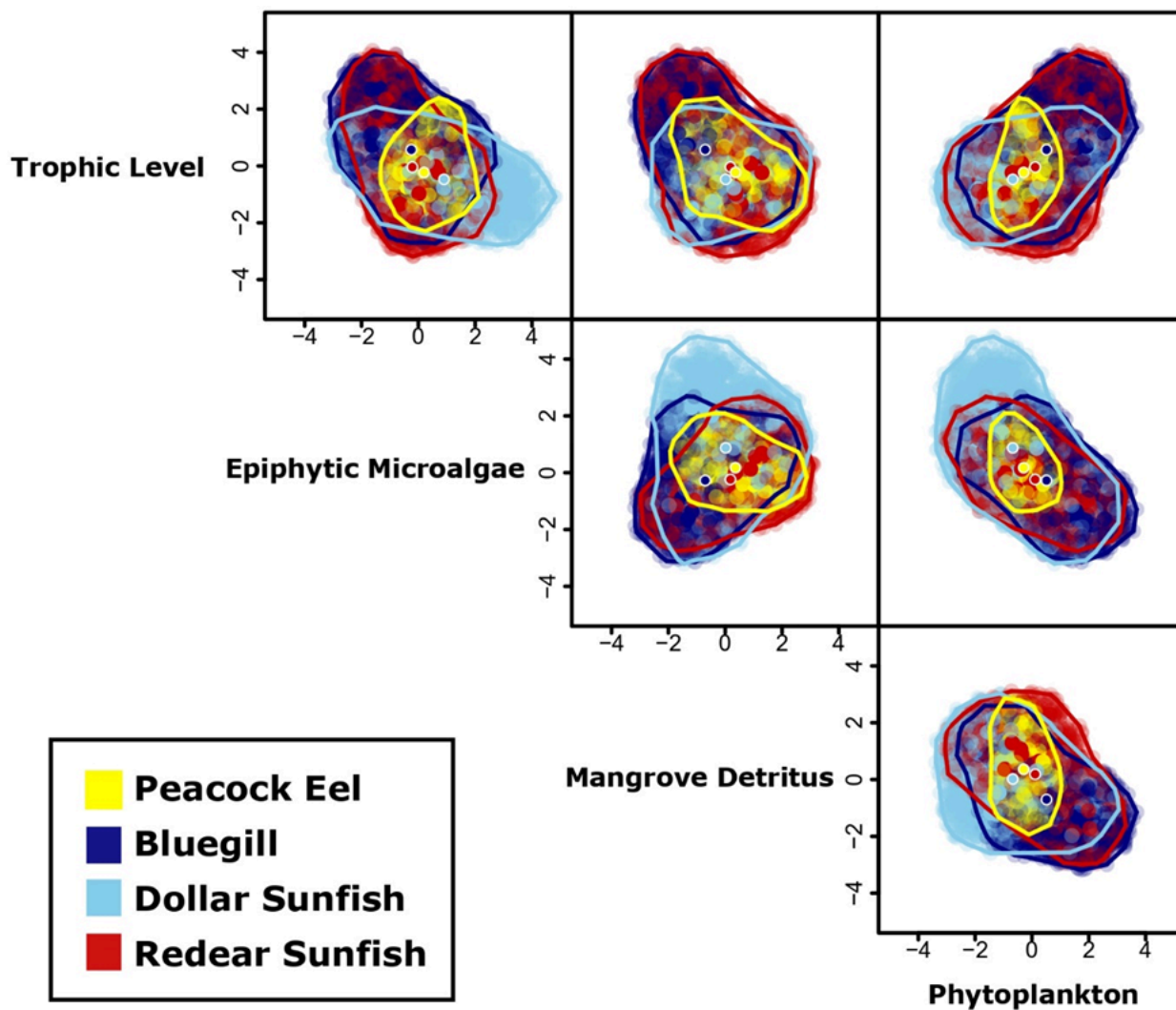


Figure 6

Trophic niche hypervolumes of the invasive Peacock eel (*Macrogathus 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

Supplementary Files

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