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The effects of temperature and flooding duration on the structure and magnitude of a floodplain prey subsidy

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Abstract

1. Riverine floodplains serve as an important link between terrestrial and aquatic systems, as the rising and falling of water drive spatial food web subsidies that are critical to the functioning and stability of ecosystems. As these systems are increasingly impacted by hydrological alterations and climate change, it is important to understand how floodplain spatial food web subsidies may respond to changing environmental conditions.
2. Here, we examine the interannual variation in the structure of a sunfish (*Lepomis* spp.) prey subsidy from freshwater marshes into the mangrove-lined creeks of Rookery Branch in the Florida Coastal Everglades that occurs during seasonal dry downs. We evaluate how the structure of this subsidy relates to prior temperature and hydrological regimes based on a 16-year electrofishing dataset. We also characterise the intra-annual relationship between marsh water depths and sunfish migration patterns that underlie this subsidy.
3. We found that interannual variation in the abundance and diversity of the sunfish prey subsidy was best explained by the minimum water temperature occurring within 90 days prior to peak abundance sampling periods, with lower minimum water temperatures associated with higher sunfish abundance and diversity. In contrast, interannual variations in the biomass of the sunfish prey subsidy were positively related to marsh flooding duration over 30 cm depth during the prior wet season. Intra-annual models estimated peak sunfish abundance and biomass values in riverine habitats to occur during the transition between wet and dry periods when marsh depths are between 10 and 15 cm.
4. Multivariate analysis of community abundance and biomass composition revealed that minimum water temperatures played an important role in structuring the prey subsidy, while the effect of flooding duration was weak. These results provide important insight into how floodplain prey subsidies may be altered under future climate and hydrological regimes and inform ecosystem-based water management decisions.

KEYWORDS
Everglades, floodplain, *Lepomis*, marsh, spatial subsidy, sunfish

1 | INTRODUCTION

Riverine floodplains are among the most diverse and productive habitats on Earth, and their role as a link between terrestrial and aquatic systems underlies a variety of important ecosystem functions and services (Dudgeon, 2010; Poff, 2018; Tockner & Stanford, 2002). Floodplains are highly dynamic systems that are in a continual state of expansion or contraction based on seasonal inundation patterns, with the timing, duration, and extent of flood pulses as principal drivers of productivity and transport of terrestrial resources to adjacent aquatic habitats (Junk et al., 1989; Poff et al., 1997; Tockner et al., 2000). Water inundation serves to mobilise nutrients, increase primary production, and increase secondary production by providing aquatic organisms access to these resources (Poff et al., 1997; Tockner et al., 2000). The exchange of organic matter and organisms between floodplains and rivers drives spatial food web subsidies and can have a strong regulatory effect on the productivity and trophodynamics of the recipient habitat, particularly in oligotrophic riverine systems (Polis et al., 1997).

The seasonal flooding of lowlands adjacent to rivers provides many species with temporary access to highly productive habitats that serve as important feeding grounds, nursery habitats, and refuges from predation (Poff et al., 1997). As waters recede, the movement of aquatic animals from previously inundated floodplains to deeper riverine refuges drives a spatial prey subsidy that couples terrestrial and aquatic food webs (Agostinho & Zalewski, 1995; Farly et al., 2021; Górski et al., 2011; Jardine et al., 2012; Lindholm et al., 2007; Rehage & Loftus, 2007). These prey subsidies are vital for supporting riverine predator populations, redistributing nutrients across landscapes, and stabilising food webs (Polis et al., 1997; Rooney et al., 2006, 2008). As the hydrological patterns that maintain the ecological functioning of riverine floodplains are increasingly altered by freshwater diversion, landscape alteration, and climate change, understanding how flooding dynamics and other physical drivers influence spatial food web subsidies is important for making evidence-based management and restoration decisions (Bayley, 1995; Dudgeon, 2010; Poff & Zimmerman, 2010; Tockner & Stanford, 2002).

The Shark River Slough (SRS) of the Florida Coastal Everglades (FCE), U.S.A., is an extensive oligotrophic riverine floodplain system, where freshwater marshes are inundated during wet seasons and drain into red mangrove-lined creeks and rivers during the dry season (Saha et al., 2011). Lower trophic level consumers feed primarily on periphyton and detritus in freshwater marshes during periods of inundation (Belicka et al., 2012), while seasonal dry downs concentrate and transfer this productivity into riparian habitats as consumers retreat into deeper riverine refuges (Rehage & Loftus, 2007). The movement of prey across habitat boundaries provides a spatial food web subsidy that supports economically and ecologically important migratory predators such as common snook (*Centropomus undecimalis*), tarpon (*Megalops atlanticus*), and juvenile bull sharks (*Carcharhinus leucas*) (Boucek et al., 2016; Boucek & Rehage, 2013; Griffin et al., 2018; Matich et al., 2017; Matich & Heithaus, 2014).

Sunfish (*Lepomis* spp.) are an important component of this spatial prey subsidy and are among the most abundant small-bodied freshwater species landed from minnow traps and electrofishing sampling in mangrove creeks at the freshwater marsh boundary in this region (Rehage & Loftus, 2007). Sunfish abundance in mangrove creeks exhibits punctuated peaks as marsh water levels recede during the transition from wet to dry seasons, or *dry-down* periods, characteristic of the seasonal migration patterns of many marsh fish to deeper water refuges as marshes dry down (Boucek et al., 2016; Rehage & Loftus, 2007; Rehage & Trexler, 2006; Trexler et al., 2005). This sunfish pulse represents a particularly important spatial prey subsidy to migratory euryhaline predators, accounting for 80% of prey biomass in common snook gut contents in mangrove creek habitats of Rookery Branch during dry-down periods (Boucek & Rehage, 2013). The importance of this prey subsidy is further illustrated by a reduction in the proportion of full stomachs observed in common snook from 83% to 43% along with an associated decrease in body condition index after dry-down periods when sunfish abundance in riverine habitats declines (Boucek & Rehage, 2013). This subsidy in turn supports a trophic relay as predators redistribute these nutrients throughout the estuary and into the Gulf of Mexico through migration (Rehage et al., 2022; Rezek et al., 2020).

Temperature and hydrological regimes are important regulators of biotic communities (Tockner et al., 2000), and can mediate spatial food web subsidies in riverine floodplain systems (Farly et al., 2021; Górski et al., 2011; Jardine et al., 2012; Schramm & Eggleton, 2006). For instance, in the Shark River Estuary, a prolonged drought in 2011 reduced the abundance of sunfish that take refuge in mangrove creeks and diminished the magnitude and quality of the floodplain prey subsidy to riverine predators, while a severe cold front in 2010 was associated with an increase in abundance of some sunfish species (Boucek et al., 2016; Boucek & Rehage, 2014). The FCE is currently the subject of the largest hydrological restoration in the U.S.A. through the Comprehensive Everglades Restoration Program (CERP), which is focused on increasing freshwater deliveries to the system, restoring natural flow regimes, and responding to the threats of sea level rise (Childers, 2006; National Academies of Sciences Engineering and Medicine, 2021; Zhao et al., 2020). However, increasing temperatures associated with climate change are likely to substantially reduce marsh inundation periods (Nungesser et al., 2015; Obeysekera et al., 2014). As the system is subject to changing hydrodynamics and altered temperature regimes, it is important to work towards a predictive understanding of how these factors will impact the floodplain prey subsidies that link and support the functioning of food webs across the system.

The objective of this study was to evaluate the influence of interannual variation in flooding dynamics and temperature regimes occurring prior to seasonal dry downs on the structure of the sunfish floodplain prey pulse. To accomplish this, we analyse sunfish catch information from a 16-year electrofishing dataset from the mangrove riverine habitats adjacent to the freshwater marshes of the upper Shark River Estuary (SRE). We specifically ask how variations in the duration and magnitude of marsh inundation and low-temperature events influence the abundance, biomass, diversity, and composition of the dry season prey subsidy to better understand how shifts in environmental conditions may impact the trophodynamics of the system in the future. In addition, we evaluate the intra-annual relationships between marsh water depths and sunfish abundance/biomass values to characterise the effect of seasonal variations in water level on the migration patterns of sunfish into deeper water refuges.

2 | METHODS

2.1 | Study site

The SRS is the primary drainage within the Everglades National Park. It is a 1,700-km^2 low-lying slowly flowing subtropical wetland system characterised by expansive freshwater marshes consisting of a mixture of wet prairie sloughs dominated by spike rush (*Eleocharis cellulosa*) and higher elevation ridges dominated by sawgrass (*Cladium jamaicense*) (Busch et al., 1998; Trexler et al., 2005). These marshes empty into the red mangrove (*Rhizophora mangle*)-lined creeks that flow into the brackish downstream rivers of the SRE and ultimately the Gulf of Mexico (Saha et al., 2012) (Figure 1). The SRS, along with the smaller Taylor Slough to the east, are the subject of the FCE Long Term Ecological Research programme (fcelter.fiu.edu; Childers et al., 2019). The SRS and the fresh headwater creeks of the SRE are oligotrophic and phosphorus limited (Childers, 2006). The study took place in the oligohaline creeks and main stem of the Rookery Branch, a network of channels 2–50 m in width and 1–3 m in depth that lies at the interface between the marsh and riverine habitats (Boucek & Rehage, 2013).

2.2 | Sampling procedures

Electrofishing sampling trips took place over 16 years (2004–2020) and were conducted at least three times per year, once in the early dry season (February–March), once in the late dry season (April–May), and once in the wet season (November–December), with the exception of 2004, which was sampled once in the wet season. Supplemental sampling trips took place during most years, at approximately monthly intervals in the dry season, for a total of 80 sampling trips evaluated over the 16-year study. In each sampling period, electrofishing was conducted at 15 sites, six of which were located in the main stem of the Rookery Branch, and nine of which

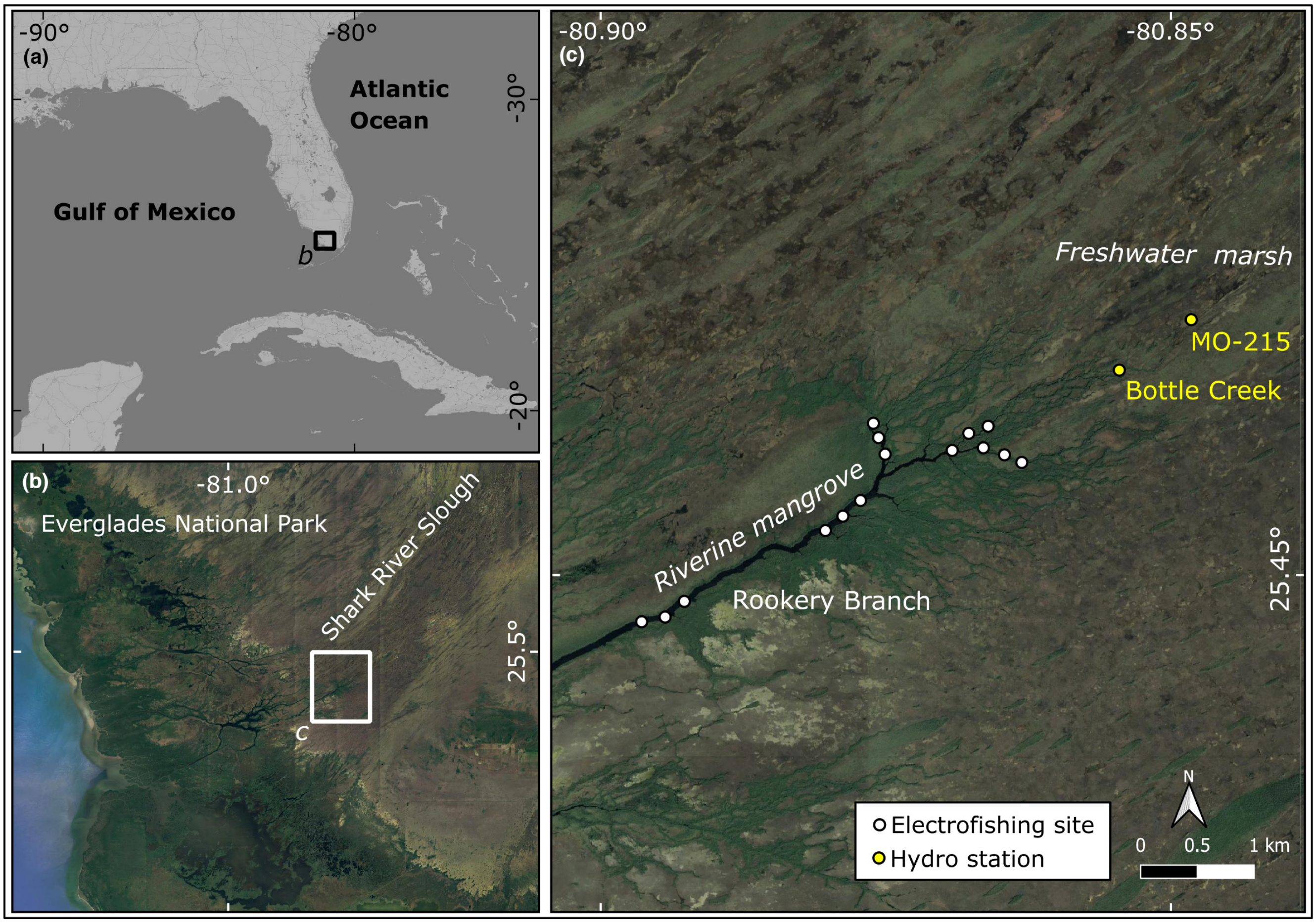

FIGURE 1 Map of the study region (a), the Shark River Slough in the Everglades National Park (b), and the study site in Rookery Branch at the interface between freshwater marsh and riverine mangrove habitats (c).

were located in first order-creeks (Figure 1c). Sunfish were evaluated as the primary component of this prey subsidy due to their high abundance in mangrove creeks during dry-down periods (Boucek & Rehage, 2014; Rehage & Loftus, 2007), their dominance in the gut contents of migratory predators (Boucek et al., 2016; Boucek & Rehage, 2013), and their high relative abundance in the electrofishing dataset used for this study—representing over 90% of the native small-bodied freshwater fish landings.

Sampling was conducted with a boat-mounted, generator-powered electrofisher (two-anode, one-cathode Smith-Root 9.0 unit, Smith-Root, Vancouver, Washington, U.S.A.). At each transect, the vessel was run at idle speed at a randomly selected shoreline and 5 min of pedal time was applied (Rehage & Loftus, 2007). Power output was standardised to 1500 W, based on the temperature and conductivity measured at the start of each transect (Burkhardt & Gutreuter, 1995). Transect distance was targeted to be approximately 100 m, and the precise distance travelled during each sample was recorded using a GPS. Electrofishing catch per unit effort was standardised to a 100-m distance and is reported as the catch or biomass per 100 m of shoreline. Sunfish were shocked, landed, enumerated, and measured for standard length, and a subset was weighed for wet-weight biomass and released at the site of collection. Sunfish that were shocked but missed (i.e., not landed) were included in the calculations of catch per 100 m of shoreline. The electrofishing sampling protocol was approved by Florida International University's Institutional Animal Care and Use Committee (IACUC # 15-046).

Median daily water level data over the study period was obtained from the MO-215 hydrostation (USGS 252820080505401; Figure 1c) and the average ground elevation of the marsh platform at the station (−9.8 cm NAVD88) was used to calculate marsh water depth. Mean daily water temperature values were obtained from the Bottle Creek hydrostation (USGS 022908295; Figure 1c).

2.3 | Data analysis

For sunfish that were measured for standard length but not weighed in the field (58%), wet biomass was estimated using species-specific length–weight relationships ($W=aL^b$) based on study data, with the exception of bluespotted sunfish (*Enneacanthus gloriosus*) and dollar sunfish (*Lepomis marginatus*), whose length–weight relationships were taken from literature based in the Everglades region (Table S1). Length–weight relationships were calculated based on methods outlined in (Klassen et al., 2014), using wet weight biomass (g) and standard length (cm) values, and regression outliers were removed on standardised residuals with values greater than 2 or less than −2. Biomass values for individuals that were shocked within the sampling area but not landed (16%), and thus could not be weighed or measured, were imputed with mean individual biomass values of the species (if identified), or the mean of all sunfish (if unidentified) caught within the same sampling period.

Peak sunfish abundance and biomass sampling periods occurring in the dry season (considered 1 January to 31 May for this study) of each year were used to analyse the effects of prior environmental conditions on the prey pulse community at an interannual scale. Annual peak abundance and biomass periods were used to best characterise the magnitude of the prey pulse and were identified as the sampling periods with the greatest mean of site values for sunfish n/100 m and g/100 m, respectively. The effects of prior water temperature and flooding characteristics on dependent variables of peak sunfish abundance, biomass, and Shannon Diversity Index (from peak abundance sampling periods) were evaluated in terms of both their magnitude and duration with multiple linear regression. For hydrological variables, maximum water level; the greatest median daily water depth measured on the marsh platform surface, and flooding duration; the number of days with median marsh water depth values greater than 30 cm, during the prior year's wet season (1 June to 31 December) were included in models to evaluate the effect of marsh flooding dynamics. To account for potential sources of variation in sunfish metrics associated with hydrological conditions at the time of measurement, the variable of median marsh water depth on the peak sunfish metric sampling dates was also included in all models. The minimum mean daily water temperature value and the number of days where mean daily water temperature remained below 18°C during the 90 days prior to the peak biomass/abundance sampling period were included in models to evaluate the potential effect of thermal stress. The 18°C temperature threshold represents the lower 5% of daily temperature values and the 30-cm water level threshold represents the lower 15% of wet season median daily water depth values throughout the study period. The 5 independent variables (three hydrological and two temperature variables) were included in multiple linear regression models for each dependent variable.

To characterise the intra-annual relationship between marsh depths and sunfish migration patterns into the Rookery Branch, polynomial regression was used to relate mean sunfish abundance (n/100 m) and biomass (g/100 m) to daily median marsh water level values measured on each electrofishing sampling date. Sunfish abundance and biomass were $\log_{10}(y+1)$ transformed to meet assumptions of residual normality for this analysis. A single outlier in marsh water level measured during a sampling period on 12/01/2017 that was associated with Hurricane Irma (September 2017) was removed from this analysis ($n=79$). For all regression models, Backward model selection was conducted using small sample size adjusted Akaike information criterion values, with best-fitting models identified as those with the lowest value (Hurvich & Tsai, 1989). Parametric model assumptions of residual normality were verified with Breusch-Pagan tests (Breusch & Pagan, 1979) and by examining residual versus fitted value plots.

To evaluate the influence of environmental variation on community composition, significant predictors of annual peak sunfish abundance, biomass, and diversity from regression models were evaluated using distance-based redundancy analysis (dbRDA). This method tests the significance of individual terms in linear regression models with multivariate response variables and allows for non-Euclidian dissimilarity indices (Legendre & Anderson, 1999).

The dbRDA analysis was performed on a Bray–Curtis dissimilarity matrix of square root transformed multivariate abundance and biomass data from the peak dry season abundance/biomass sampling period in each year, and the significance of the environmental variables was tested through permutation (n=9,999). An ordination plot is presented to visualise the dbRDA results. All multivariate analyses were conducted with the vegan R package (Oksanen et al., 2016). All statistical analysis was conducted using R v4.0 (R Development Core Team, 2020).

3 | RESULTS

3.1 | Environmental parameters and sunfish metrics

Over the course of the 16-year study period, daily median marsh water depth ranged from −14.0 to 94.4 cm, with a dry season mean of 15.1 cm and a wet season mean of 42.1 (Figure 2a). Wet season flooding duration (days over 30 cm marsh depth) ranged from 98 to 214 days (mean = 182 days), and peak daily median marsh depths over the wet season ranged from 46.5 to 94.4 cm (mean = 62.2 cm). Mean daily water temperature ranged from 8.3 and 33.5°C and averaged 25.6°C across all years, and annual minimum daily water temperatures ranged from 8.3 to 16.2°C (mean = 14.2°C; Figure 2b). In total, 6935 sunfish were sampled from 80 sampling periods over the 16-year study period, with 54 occurring in the dry season and 26 in the wet. Mean abundance in dry season sampling periods ranged from 0.3 to 90.0 n 100/m, with an interannual mean of 11.2 ± 2.5 n/100 m, and wet season abundance ranged from 0 to 4.7 n/100 m with an interannual mean of 1.0 ± 0.2 n/100 m (Figure 3a). Mean biomass in dry season sampling periods ranged from 15.5 to 985.1 g/100 m, with an interannual mean of 317.0 ± 35.4 g/100 m, and wet season biomass ranged from 0 to 193.6 g/100 m with an interannual mean of 57.1 ± 10.0 g/100 m (Figure 3b, Table S2). Mean Shannon diversity in dry season sampling periods ranged from 0.00 to 0.99, with an interannual mean of 0.48 ± 0.03; wet season values ranged from 0 to 0.87 with an interannual mean of 0.22 ± 0.4.

3.2 | Univariate analysis

Model selection based on multiple linear regressions indicated the best models for predicting peak dry season sunfish abundance and Shannon diversity included the single independent variable of minimum water temperature within 90 days prior to sampling, while the best model for peak dry season sunfish biomass included only prior wet season flooding duration (days over 30-cm marsh depth; Table S3). Minimum water temperature was negatively related to peak sunfish abundance ($F_{1,14}=7.85$, $R^2=0.314$, $p=0.014$; Figure 4a) and Shannon diversity ($F_{1,14}=6.11$, $R^2=0.254$, $p=0.027$; Figure 4b), indicating that increasing minimum temperatures (i.e., warmer conditions) were associated with lower values. Peak sunfish biomass was positively related to prior wet season flooding durations ($F_{1,14}=7.63$, $R^2=0.306$, $p=0.015$; Figure 4c), indicating that increased flooding durations were associated with higher peak biomass values.

Model selection indicated that quadratic polynomial regression models best explained the intra-annual relationships between both

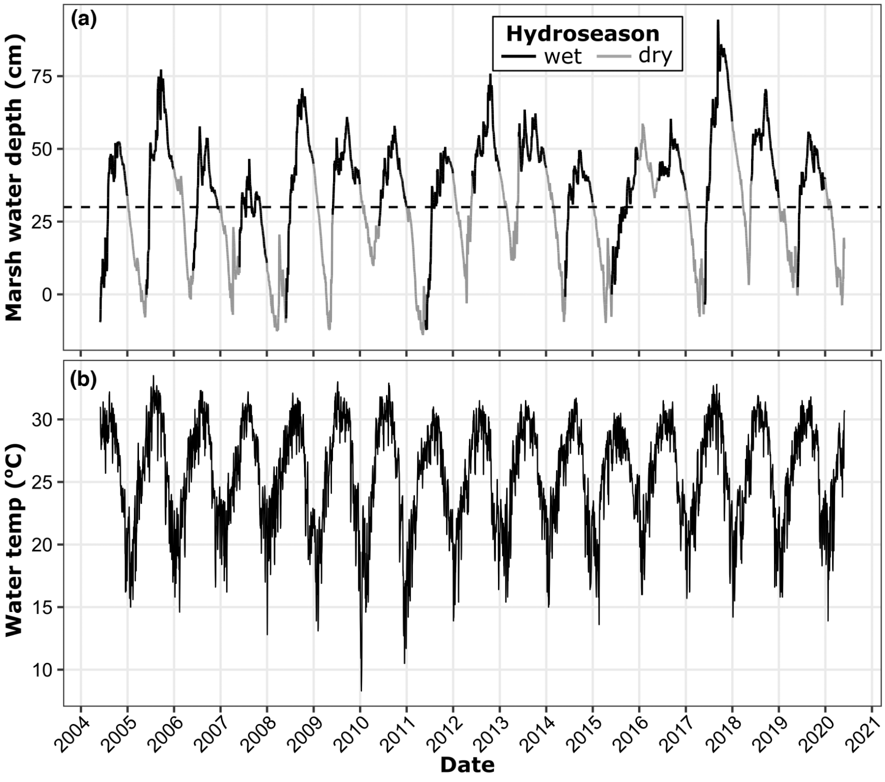

FIGURE 2 Mean daily marsh water depth from MO-215 hydro station (a) and water temperature from Bottle Creek hydro station (b) during the study period. The dry season indicated is from 1 January to 31 May, the dashed line indicates the 30 cm water depth when the marsh is considered flooded, and the average marsh ground elevation at MO-215 is −9.8 cm relative to NAVD88.

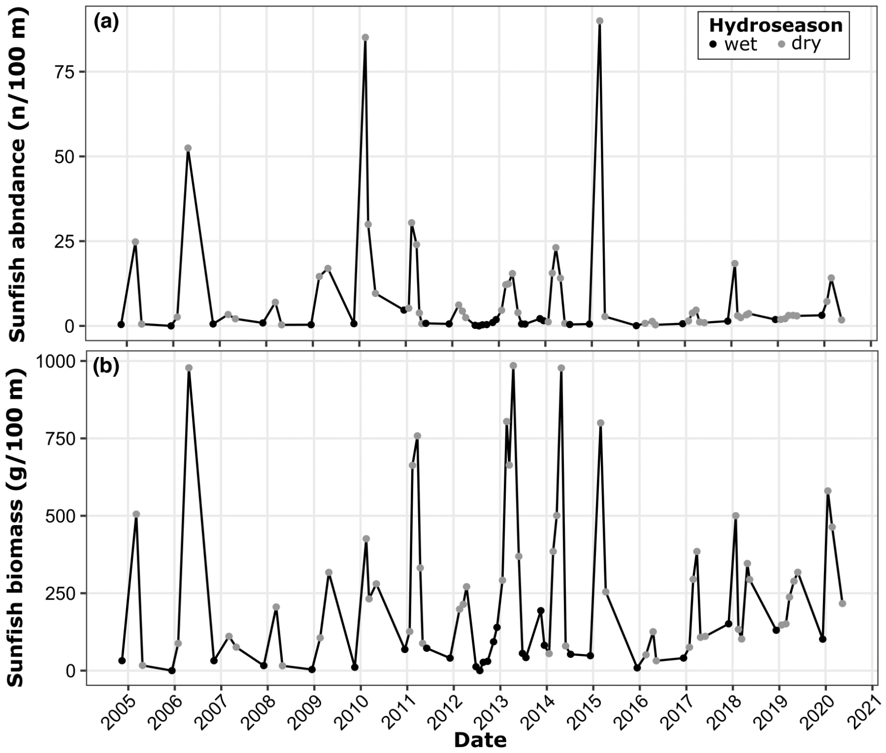

FIGURE 3 Mean sunfish abundance (a) and biomass (b) per 100 m of river shoreline in the Rookery Branch from all electrofishing sampling periods ($n = 80$) over the 16-year time series. The dry season indicated is from 1 January to 31 May.

sunfish abundance and biomass to the daily median marsh water level on each sampling date. The sunfish abundance model estimated greatest values occur when the daily median marsh water depth was 15.1 cm, with decreasing abundance values predicted as water levels increased or decreased from this value ($F_{2,76} = 13.34$, $R^2 = 0.240$, $p < 0.001$; Figure 5a). The sunfish biomass model exhibited a similar relationship, with peak values estimated to occur at marsh water depths of 10.0 cm ($F_{2,76} = 9.23$, $R^2 = 0.289$, $p < 0.001$; Figure 5b).

3.3 | Multivariate analysis

The sunfish community during peak dry season abundance was composed primarily of dollar sunfish (*Lepomis marginatus*; mean = 10.9 *n*/100 m), followed by spotted sunfish (*Lepomis punctatus*; mean = 7.3 *n*/100 m), redear sunfish (*Lepomis microlophus*; mean = 1.9 *n*/100 m), bluegill (*Lepomis macrochirus*; mean = 0.9 *n*/100 m), warmouth (*Lepomis gulosus*; mean = 0.4 *n*/100 m), and bluespotted sunfish (*Enneacanthus gloriosus*; mean = 0.1 *n*/100 m; Figure 6a, Table S4). The biomass composition of the sunfish community during peak dry season sampling events was composed primarily of redear sunfish (mean = 205.6 g/100 m), followed by bluegill (mean = 114.8 g/100 m), spotted sunfish (mean = 81.0 g/100 m), dollar sunfish (mean = 23.0 g/100 m), warmouth (mean = 19.5 g/100 m), and bluespotted sunfish (mean = 0.4 g/100 m; Figure 6b, Table S5). The mean (±*SE*) standard length of sunfish species, from largest to smallest, were 13.1 ± 0.1 cm for redear sunfish, 12.1 ± 0.2 cm for bluegill, 8.6 ± 0.4 cm for warmouth, 5.7 ± 0.1 cm for spotted sunfish, 3.9 ± 0.1 cm for dollar sunfish, and 3.6 ± 0.1 cm for bluespotted sunfish.

The dbRDA results indicated that minimum water temperature during the prior 90 days was a significant predictor of multivariate community abundance composition ($F_{1,13} = 4.81$, $R^2 = 0.218$, $p = 0.012$), and flooding duration during the prior wet season was a weak predictor of community composition ($F_{1,13} = 2.67$, $R^2 = 0.068$, $p = 0.071$; Figure 7a). Similarly, the minimum water temperature was a significant predictor of multivariate community biomass composition ($F_{1,13} = 3.38$, $R^2 = 0.129$, $p = 0.019$), and flooding duration was a weak predictor of biomass composition ($F_{1,13} = 2.34$, $R^2 = 0.062$, $p = 0.079$; Figure 7b). Species scores indicated that bluegill and redear sunfish abundance and biomass and were associated with higher minimum water temperatures (i.e., warmer conditions) and that dollar and spotted sunfish abundance was associated with lower minimum water temperatures (Figure 7).

4 | DISCUSSION

4.1 | Influence of hydrological regimes

The relationship between hydrodynamics and the functioning riverine floodplain ecosystems are well established and maintaining natural inundation regimes has long been considered critical to maintaining ecosystem integrity and services (Junk et al., 1989; Poff et al., 1997; Richter et al., 1997; Tockner et al., 2000). Aspects of flooding dynamics that exert an important influence on secondary production supported by floodplain habitats and subsequent transport to riverine habitats include the duration of flooding, the magnitude of flooding, and the extent and timing of drying phases (Boucek & Rehage, 2015; Farly et al., 2021; Gutreuter et al., 1999; Lindholm

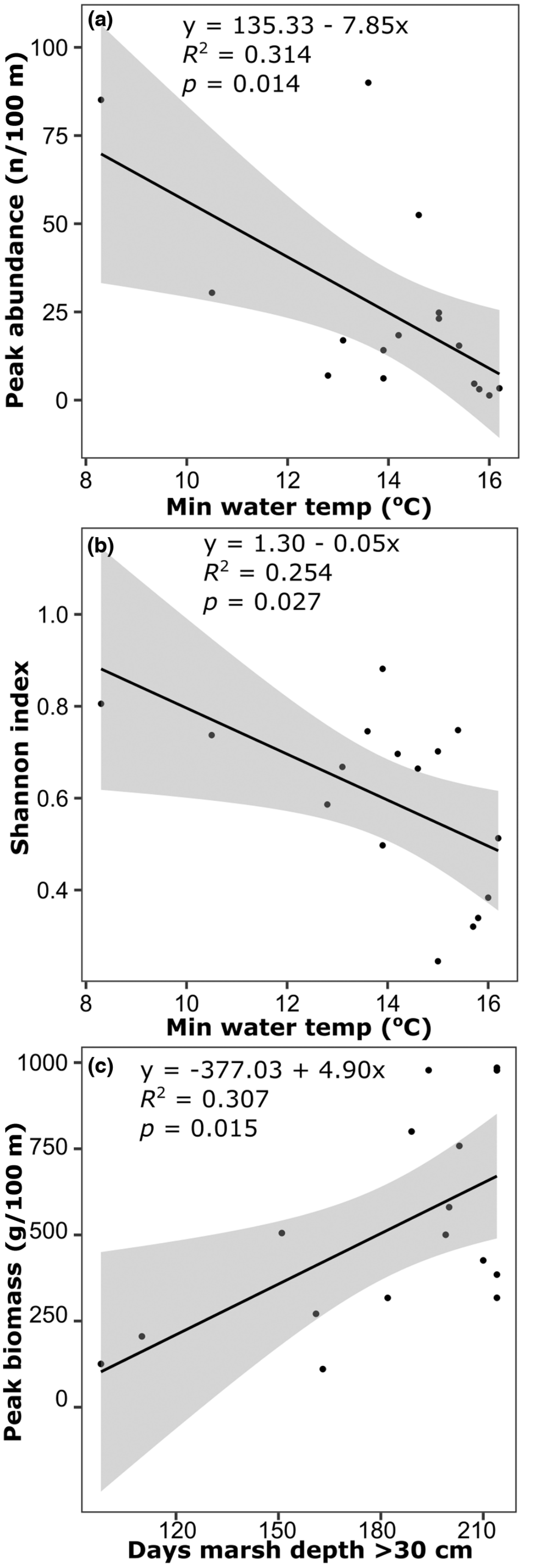

FIGURE 4 Regression results relating peak dry season sunfish abundance per 100 m of river shoreline (a) and Shannon diversity index at peak abundance (b) in each year to the minimum water temperature within the prior 90 days and relating peak dry season sunfish biomass per 100 m of river shoreline (c) to flooding duration (number of days median marsh depth was greater than 30 cm) during the prior year's wet season (1 June to 31 December).

et al., 2007; Palmer et al., 1997; Rehage & Loftus, 2007). Flooding duration above a certain threshold controls the time consumers have access to floodplain-associated resources, the magnitude of flooding is closely related to the areal extent of accessible habitat, and the extent and timing of drying phases can mediate the transport of floodplain resources across habitat boundaries.

Previous research has emphasised the importance of flooding magnitude/areal extent (Lindholm et al., 2007) or the interaction between flooding magnitude and duration (Farly et al., 2021; Gutreuter et al., 1999; Schramm & Eggleton, 2006) as primary regulators of cross-boundary subsidies. Our analysis identified wet season flooding duration over a 30-cm threshold as the most important predictor of the biomass of subsequent spatial prey subsidies, with flooding magnitude (i.e., maximum water level) failing to explain variations in abundance, diversity, or biomass. Flooding duration over this threshold may be a better predictor of spatial prey subsidies than flooding magnitude in this system due to the low relief topography of SRS marsh habitats. The elevation difference between the wet prairie slough and the higher elevation sawgrass-dominated ridges is generally 10–25 cm (Trexler et al., 2005), thus, the 30-cm flooding threshold used in this study is expected to represent inundation of most, if not all, of the marsh habitat surrounding the mangrove creeks. Therefore, particularly high-water elevations observed in this study (e.g., >60 cm) would not be expected to substantially increase the areal extent of accessible habitat to sunfish in the vicinity of the study site. Similarly, Boucek and Rehage (2015) found the abundance of riverine predators that consume marsh prey subsidies was positively related to wet season flooding duration, but not magnitude, in this system.

The results of our analysis of sunfish abundance and biomass as it relates to intra-annual patterns in marsh water depths demonstrates the role that seasonal dry downs play in driving marsh consumers into deeper riverine refuge habitats comport with findings from research across the Everglades (Boucek et al., 2016; Boucek & Rehage, 2013; Rehage & Loftus, 2007; Rehage & Trexler, 2006). The observed patterns of peak biomass and abundance of sunfish in riverine habitats occurring at marsh water depths between 10 and 15 cm are not unexpected, as other studies indicate that freshwater fish migrate to refuge habitats well before marshes completely dry (Rehage & Loftus, 2007; Rehage & Trexler, 2006). As water levels continue to fall below the mean elevation of the marsh platform, the biomass and abundance of sunfish begin to decrease. This pattern could be explained by a reduction in sunfish population due to predation by riverine consumers such as Common Snook and Largemouth Bass as they spend increasing amounts of time exposed in deep water habitats (Boucek & Rehage, 2013; Rehage & Loftus, 2007). Another factor that could contribute to this pattern is exposure to high salinities associated with very low riverine discharge events; however, salinity levels that would be lethal to sunfish in the upper reaches of Rookery Branch have only been observed in one dry season in this system over the course of the study (Boucek et al., 2016).

As water levels increase during the onset of the wet season and marshes become inundated, sunfish populations in the riverine

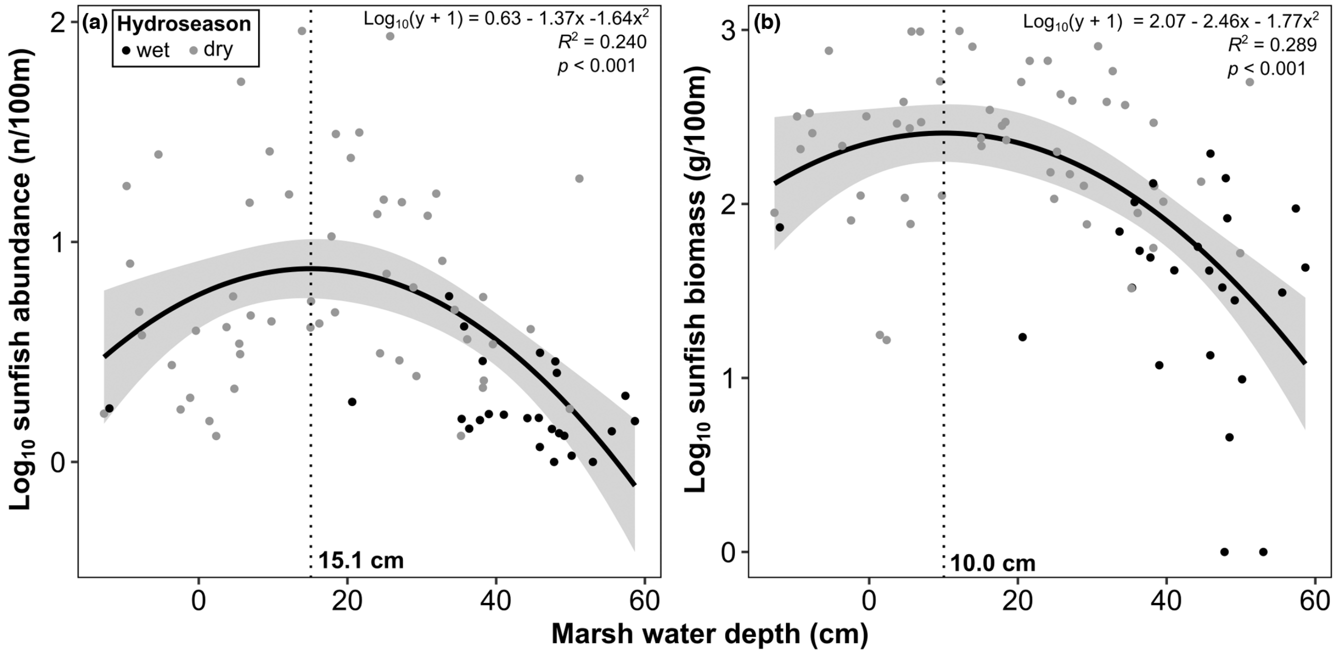

FIGURE 5 Results of polynomial regression relating $\log_{10}(y+1)$ transformed mean sunfish abundance (a) and biomass (b) per 100 m of river shoreline to median daily marsh water level measured on each electrofishing sampling date. The dotted vertical lines indicate the marsh water depths at which models predict peak sunfish abundance/biomass to occur in riverine habitats. The dry season indicated is from 1 January to 31 May.

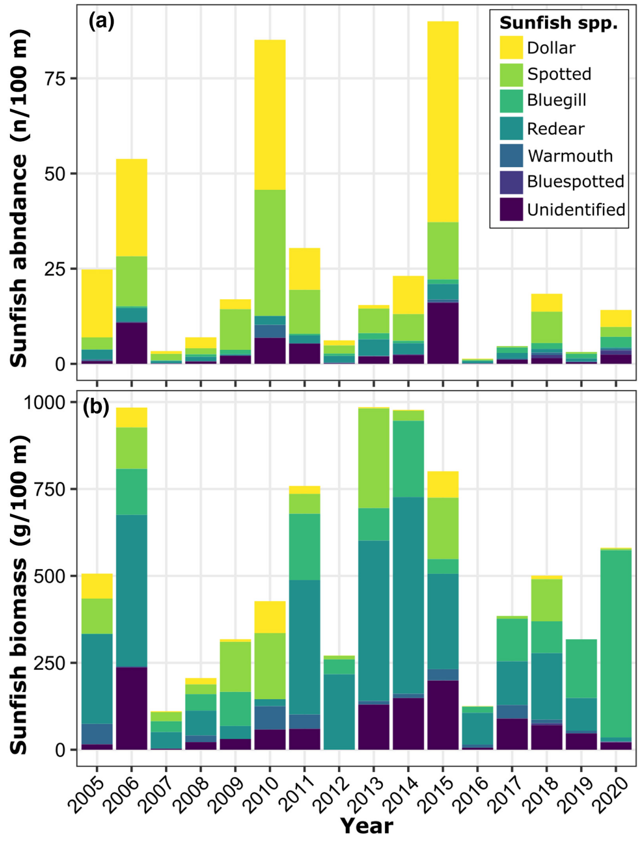

FIGURE 6 Stacked bar chart indicating the contribution of each sunfish species to total dry season annual peak abundance (a) and biomass (b) per 100 m of river shoreline.

habitats further decline, presumably influenced by the migration of the remaining sunfish back into the marsh. While marsh depths measured during peak sunfish sampling events did not explain inter-annual variations in magnitude or structure of this subsidy, results clearly demonstrate the importance of seasonal dry-down periods in mediating the migratory patterns that underlie this spatial prey subsidy. These results, in combination with the relationship identified between wet season inundation patterns and the magnitude of the sunfish prey pulse, highlight the importance of both long periods of marsh inundation during the wet season along with a period of low marsh water levels during the dry season in maintaining this spatial prey subsidy.

The SRS and the greater FCE are predicted to undergo substantial shifts in hydrology and temperature regimes in the coming decades due to climate change. Regional climate models project a 1–1.5°C increase in temperatures by 2060 in the FCE (Obeysekera et al., 2014). The most likely scenario resulting from a 1.5°C increase in temperatures is predicted to shorten inundation periods by 5%–45% and reduce median water depths by 5–114 cm due to increased evapotranspiration and decreased rainfall across the Everglades, with a reduction in median water depths of 18–24 cm in the vicinity of the study site (Nungesser et al., 2015). Based on the results of this study, the predicted shift in hydrologic conditions could drastically impact spatial prey subsidies that maintain critical ecological functions and services. Alterations in spatial prey subsidies could rewire food webs as spatial patterns of energy and nutrient flux are diminished or decoupled and the movement/feeding behaviours of mobile predators change in response, altering trophic structures,

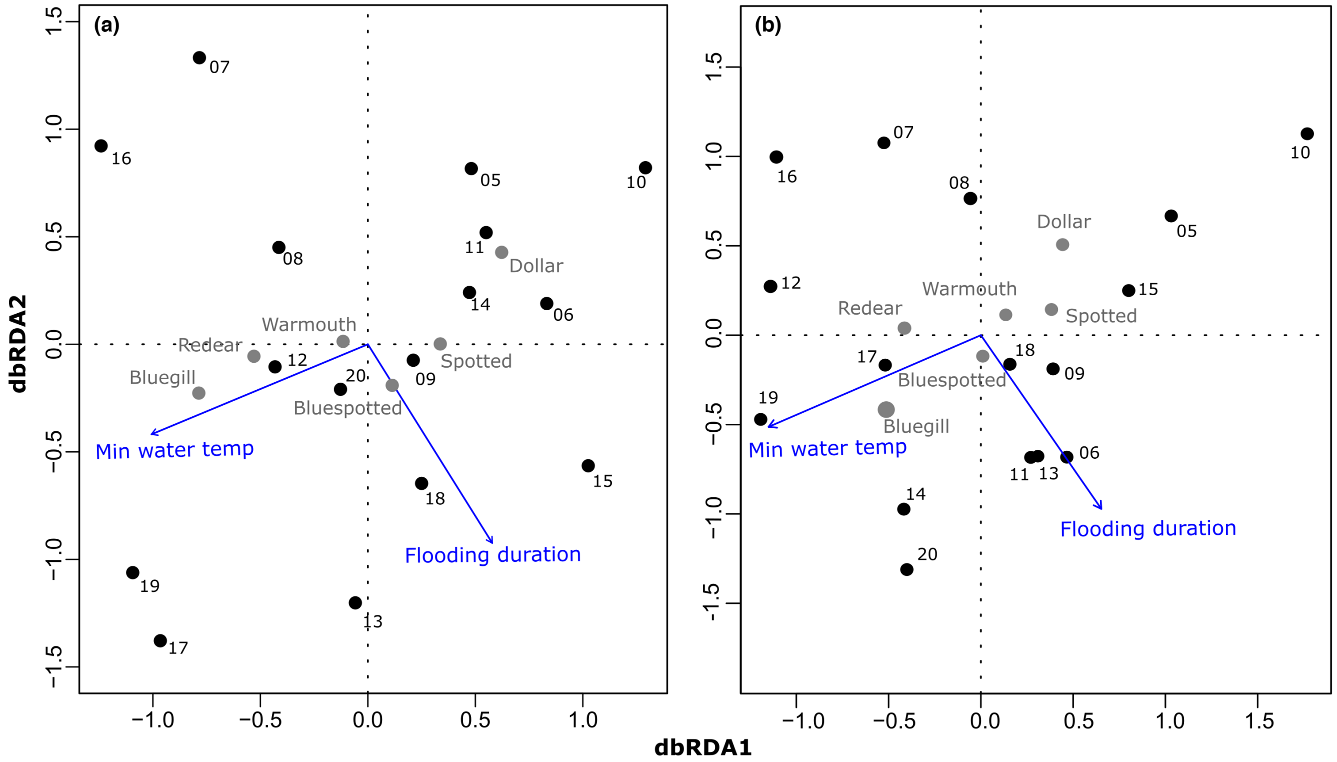

FIGURE 7 Distance-based redundancy analysis (dbRDA) ordination plot of multivariate peak dry season sunfish abundance (a) and biomass (b) data in each year of the study. Sampling years are represented by black points (20--), sunfish species scores are indicated with grey points, and environmental variable vectors of minimum temperature (within the prior 90 days) and flooding duration (days marsh water depth was greater than 30 cm in the prior wet season) represented as arrows. The minimum temperature was a significant predictor of community abundance and biomass composition ($p < 0.05$) while flooding duration had a weak effect ($0.1 > p > 0.05$) on multivariate abundance and biomass.

destabilising ecosystems, and diminishing biodiversity (Bartley et al., 2019). The results of this study emphasise the importance of maintaining appropriate inundation patterns for sustaining the ecological integrity of the SRS, which should be a principal management goal of the hydrological restoration proceeding under the CERP.

4.2 | Influence of temperature

The relationship between low prior minimum water temperatures and high abundances of dollar and spotted sunfish corresponds with previous findings of a 490% and 420% increase in abundance, respectively, following a severe cold snap in 2010 (Boucek & Rehage, 2014). This relationship could be explained by weakening predation pressure on these species while in the marsh by predators such as largemouth bass (*Micropterus salmoides*) due to metabolic and behavioural responses to low temperatures (Boucek & Rehage, 2013; Grigaltchik et al., 2012; Kishi et al., 2005). Under warmer conditions, dollar and spotted sunfish may experience higher predation mortality while in the marsh habitat due to their smaller adult size in comparison to other sunfish species such as redear or bluegill (Paller et al., 1992).

Another possible mechanism leading to this pattern could be a temperature-mediated alteration of interspecific competition (Magnuson et al., 1979; Rodtka & Volpe, 2007; Watz et al., 2019), whereby, the smaller-bodied sunfish experience lower rates of mortality associated with the intraguild competition under colder conditions. Congeners of *Lepomis* are known to compete for resources and these interactions can alter foraging behaviours, decrease growth rates, and reduce population sizes of competing species (Arendt & Wilson, 1999; Fisher Huckins et al., 2000; Werner & Hall, 1977). While temperature can have an important influence on sunfish foraging behaviour and habitat use (Wildhaber, 2001), little is known about its effect on competitive interactions among *Lepomis* spp.

A third explanation for the relationship could be that it is associated with a reduction in competitive or predatory interactions with non-native species that inhabit the marsh and mangrove creeks. Invasive species of fish, such as Mayan Cichlid (*Mayaheros urophthalmus*), African Jewelfish (*Hemichromis letourneuxi*), and Peacock eels (*Macrognathus siamensis*) are found in abundance in the marsh and mangrove creeks (Boucek & Rehage, 2014; Schofield & Loftus, 2015). These species are likely to interact with *Lepomis* spp. due to their competition for similar prey, such as gastropods, small fish, and shrimp (Dunlop-Hayden & Rehage, 2011; Harrison et al., 2013; Schofield et al., 2014). In an 8-month mesocosm experiment, Schofield et al. (2014) found that African jewelfish had a much stronger ability to reduce the biomass of several prey species in comparison to dollar sunfish. Harrison et al. (2013) found that the density of Mayan Cichlids in mangrove creeks had a negative impact on the density of several species of native small fish that are also consumed by *Lepomis* spp., although it was not found to negatively impact the density of sunfish themselves. These species, along with most other invasive species in the Everglades, are of tropical origin (Loftus, 2000), and are much more susceptible to stress and mortality associated with cold water temperatures than native species (Boucek & Rehage, 2014; Rehage et al., 2016; Schofield et al., 2010). Thus, a reduction in negative interactions with invasive species is a plausible explanation for the effects of water temperature on the composition and abundance of the sunfish prey subsidy.

Although the precise mechanisms by which temperature influences sunfish communities are uncertain, lower minimum water temperatures clearly play a significant role in maintaining biodiversity and structuring the composition of the dry season prey subsidy. While temperature variations did not influence the total export of production across habitat boundaries in terms of biomass, increasing temperatures associated with climate change may still impact the availability of resources to riverine predators through changes in prey abundance, composition, and biodiversity loss. Dollar and spotted sunfish are among the highest-quality food sources available to riverine predators in terms of energy density (Boucek et al., 2016), and a reduction in these species could decrease the foraging efficiency of riverine predators. In addition, a reduction in smaller-bodied sunfish may limit the availability of the prey subsidy to smaller predators in earlier life stages due to gape limitation (Blewett et al., 2006; Luczkovich et al., 1995). Future research addressing the impacts of temperature-mediated shifts in the composition of floodplain prey subsidies on the growth, condition, or survival of riverine predators of different size classes would shed light on their potential impacts on fisheries, biodiversity, and consumer-mediated nutrient transport.

5 | CONCLUSIONS

As floodplain systems are increasingly threatened by climate change and hydrological alterations, it is vital to understand how these factors will impact the functioning and stability of food webs and the ecosystem services they support. Based on the results of this study, increasing temperatures are predicted to affect the diversity, abundance, and composition of floodplain sunfish spatial prey subsidies in the FCE. This could potentially alter the quality and accessibility of this resource, although further research is needed to better understand the effects this might have on migratory predators. A decrease in wet season marsh inundation durations associated with climate change or water management would be predicted to reduce the transport of production in the form of sunfish biomass to riverine habitats, potentially decoupling these systems, destabilising food web interactions, and reorganising patterns of energy and nutrient transport across the system. The hydrological restoration efforts associated with the CERP and water management policies focused on providing appropriate inundation patterns will be a critical aspect of maintaining the ecological integrity of the system in the future.

AUTHOR CONTRIBUTIONS

Conceptualisation: R.R., J.N., W.J., J.R., R.S. Developing methods: R.R., R.B., J.M., N.V., R.S. Data interpretation: R.R., W.J., J.N., J.R. Data analysis, preparation of figures and tables: R.R. Conducting the research: R.R., R.B., J.R., J.M., R.S., N.V. Writing: R.R., J.R., R.S., W.J., J.N., N.V., J.M., R.B.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data used in this study is available in the supplementary materials. Hydrostation data used in this study are available from https://waterdata.usgs.gov.

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SUPPORTING INFORMATION

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