




Themed Issue on Ecology and Management of Snook *Centropomus* spp. in the Americas

Long-term patterns in the relative abundance of Common Snook as a factor of shifting environmental conditions in the Florida coastal Everglades

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ABSTRACT

Objective: Environmental variability as a factor of climate change and water management can result in fluctuations in the abundance and distribution of fish populations from year to year, with either negative or positive effects depending on behavioral and physiological requirements and the ability to adapt to changing conditions. Variability in water levels can also influence prey availability, affecting predator abundance in seasonal foraging areas. In this study, our objective was to better understand how environmental variation has affected the relative abundance of Common Snook *Centropomus undecimalis* in the freshwater/estuarine habitats of Everglades National Park.

Methods: Electrofishing data over 17 years (2004–2021) were analyzed in relation to a long-term time-series of environmental conditions, including water level, temperature, salinity, and precipitation. We used seasonal and trend decomposition via locally estimated scatterplot smoothing to isolate the effect of seasonality and identify nonlinear trends in the environmental time-series data and Common Snook abundance and Mann–Kendall trend tests to identify monotonic and directional trends over time. To identify the factors that best explain variation in Common Snook abundance, we used generalized linear models to relate relative abundance to the environmental covariates.

Results: We found significant long-term trends of increasing water level and temperature and decreasing salinity in the study area. The generalized linear models indicated that Common Snook abundance had a negative relationship with water level and a positive relationship with temperature. Common Snook abundance over the 17 years of sampling was relatively stable; however, increases/decreases in Common Snook abundance corresponded to both seasonal changes in water level and the periodic occurrence of extreme conditions (e.g., cold spells, droughts, prolonged dry-season flooding).

Conclusions: Understanding how past environmental change has affected fish populations can provide insight into how they may respond to future conditions. Our results suggest that water management decisions that maintain seasonal patterns of high/low water levels can potentially mitigate climate-driven shifts by providing conditions that promote prey production in the wet season and foraging opportunities in the dry season, increasing the relative abundance of ecologically and recreationally important species such as Common Snook.

KEYWORDS: climate change, environmental trends, estuaries, population dynamics, riverine fishes

LAY SUMMARY

Despite gradual climate-driven changes in freshwater/estuarine habitat conditions in the Everglades, the abundance of Common Snook has remained generally stable over time. However, discrete disturbances such as periodic cold spells, droughts, and flooding have resulted in a high degree of year-to-year variability.

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INTRODUCTION

In river systems, intra- and interannual variation of the flow regime are driving forces in the behavior, adaptations, and evolution of fish and other aquatic biota, influencing community interactions, physicochemical conditions, and ecosystem processes, which can affect the long-term stability of animal populations (Lytle & Poff, 2004; Palmer & Ruhi, 2019; Poff et al., 1997). Seasonal fluctuations in water level can serve as cues for movement, migration, and/or reproduction and allow access to floodplain nurseries and foraging areas that provide the resources that are required for growth, survival, and reproduction and have been linked to the productivity of fisheries (Correa & Winemiller, 2018; Gillson, 2011; Junk et al., 1989; Massie et al., 2022; Winemiller & Jepsen, 1998). In tropical coastal regions, the growth, survival, and recruitment of fishes have been linked to freshwater flows, seasonal peaks in water levels, and floodplain productivity (Jardine et al., 2015; Roberts et al., 2019; Robins et al., 2005). Furthermore, systems with alterations in flow patterns have been accompanied by declines in native species, a simplification of aquatic communities, and a loss of landscape connectivity (He et al., 2019; Ruhi et al., 2018; Ruhi et al., 2016). Collectively, water management decisions, climate change (e.g., changes in temperature, precipitation regimes), and an increase in the frequency and intensity of extreme climate events have changed the magnitude, timing, and smoothness of freshwater flows, and these changes are predicted to increase in the future (Dessu et al., 2018; Flower et al., 2017; Keellings & Hernández Ayala, 2019; Milly et al., 2008; Welcomme & Halls, 2004).

Environmental variability can result in fluctuations in the abundance and distribution of fish populations from year to year, with either negative or positive effects depending on species-specific behavioral and physiological requirements and the ability to adapt to changing conditions (Feyrer et al., 2015). Climate-driven variability in water levels can affect the recruitment and survival of riverine/estuarine fishes. For example, the abundance of early juvenile Longfin Smelt *Spirinchus thaleichthys* in the San Francisco Estuary peaks in years with high freshwater outflows, and future decreases in precipitation and outflow may have negative effects on the long-term population trajectories (Feyrer et al., 2015). Furthermore, the timing and magnitude of flow patterns can affect reproductive behavior and spawning success, with implications for reproduction and recruitment. Australian Grayling *Prototroctes maraena* have been shown to initiate spawning behavior when water levels begin to rapidly increase early in the rainy season, but spawning activity decreases under sustained high flows, suggesting that reproduction and recruitment is unlikely to occur in the absence of pulsed flow cues (Koster et al., 2018). Conversely, warming water temperatures with climate change can also result in population increases and poleward shifts in distributions for cold-limited organisms (Osland et al., 2021). Temperature-related population expansion has been documented for a number of species, including Pacific Cod *Gadus macrocephalus* in the Bering Sea (Spies et al., 2020); coral reef fishes in southeastern Australia (Booth et al., 2018); warmwater fishes in the rivers of France (Daufresne & Boet, 2007); Common Snook *Centropomus undecimalis* in the

Suwannee River, Florida (Purtlebaugh et al., 2020); and multiple temperate fish species in Tasmania (Last et al., 2011). To anticipate how fish populations may respond to future change, there is a need to understand long-term trends of the past and how populations have been affected by environmental variation and gradual climatic change over time.

The Common Snook (hereafter, “snook”) is a widely distributed tropical/subtropical fish species that is ideal for examining how environmental change in river systems affects the relative abundance of fish populations over time. Snook are euryhaline but require marine salinity for successful reproduction, and adults use coastal inlets and marine areas to spawn (Boucek, Leone, et al., 2017; Lowerre-Barbieri et al., 2014; Young et al., 2016), with juveniles moving inland to nursery habitats in tidal tributaries (creeks and rivers) and coastal wetlands (Barbour et al., 2014; Peters et al., 1998; Stevens et al., 2024; Wilson et al., 2023). Ontogenetic habitat shifts occur at 2 to 3 years of age, and larger snook recruit into the fishery as they move from backwater rearing areas into larger river channels, estuaries, and offshore reefs (Ault et al., 2021; Taylor et al., 1998; Taylor et al., 2000). Seasonal movements of adult fish between the freshwater and coastal habitats are predominantly associated with foraging and reproductive behaviors, and a contingent of the adult population occupies riverine habitats for much of the year and benefits from the seasonal increases in freshwater prey that are concentrated in the river channels during the dry season (Blewett et al., 2017; Boucek, Heithaus, et al., 2017; Boucek & Rehage, 2013; Stevens et al., 2018). Past research has illustrated how seasonal and interannual variations in environmental conditions affect both the probability and timing of freshwater-to-coast spawning migrations each year, which can influence reproduction, recruitment, and population size in subsequent years (Massie et al., 2022). Disturbances that are introduced by extreme climate events, such as tropical storms and hurricanes, can also affect the movement patterns and distribution of snook within coastal riverscapes and can have either positive or negative long-term effects on the population depending on the timing and scale of movements in relation to critical life history events and resource availability (Massie et al., 2020). Furthermore, seasonal and interannual variations in water level can dictate access to vital prey subsidies in freshwater habitats and carry implications for the health and fitness of snook (Rezek et al., 2023; Santos et al., 2025).

To better understand how environmental variation affects the relative abundance of riverine fish in freshwater/estuarine habitats, we use 17 years of electrofishing data (2004–2021) for snook in the Shark River in Everglades National Park. Our research questions were twofold: (1) What are the long-term trends in environmental conditions in freshwater/estuarine habitats of the Shark River? (2) What specific environmental conditions are most associated with snook abundance in the study area? Based on past research, we hypothesized that (1) long-term trends in environmental conditions correspond to long-term patterns of abundance for the snook population in freshwater/estuarine habitats, (2) the relative abundance of snook from year to year is a factor of annual environmental conditions (namely, water level, temperature, salinity, and precipitation), and (3) annual variation in the timing and magnitude of freshwater flows differentially affects seasonal trends in

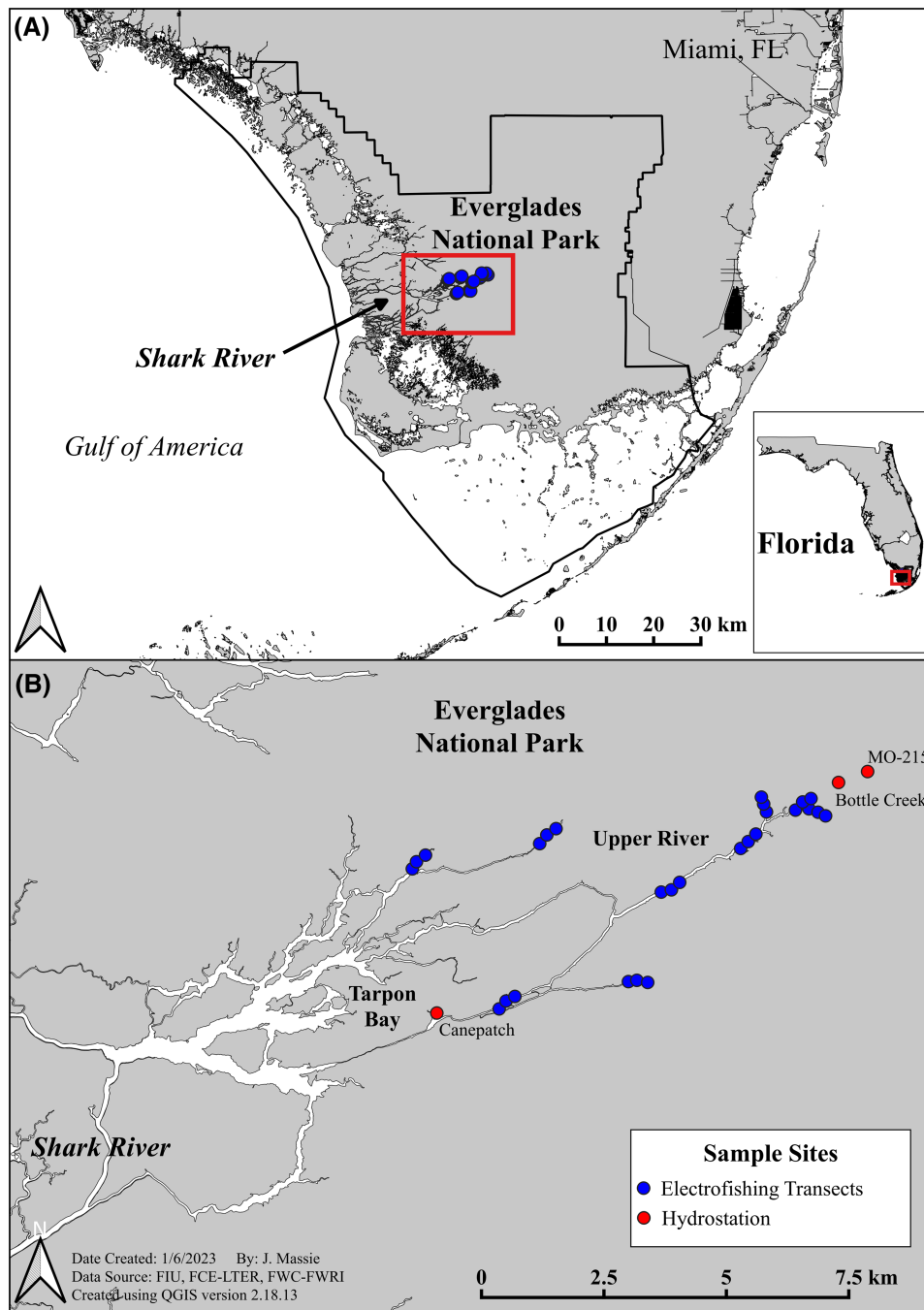


Figure 1. Map of the study area in Everglades National Park where seasonal fish community sampling was conducted between 2004 and 2021: (A) the location of the Shark River in southwest Florida and (B) the nine electrofishing sites (three transects/site) where fish were captured (27 transects total). The red circles show the location of hydrologic monitoring stations where the environmental conditions (water level, temperature, salinity, precipitation) were measured.

snook abundance in freshwater/estuarine habitats (i.e., trends in wet season abundance versus dry season abundance). To test our hypotheses, we analyzed time-series data of environmental conditions and snook abundance, isolated the effect of seasonality to identify nonlinear and directional trends in each time series, and used statistical models to relate variations in the relative abundance of snook among years/seasons to the environmental covariates.

METHODS

Study site

The Shark River is an extensive coastal river system in the southwestern region of Everglades National Park (Figure 1). The hydrologic regime is shaped by tidal cycles, the regional subtropical climate, and freshwater flows, which are driven by seasonal rainfall patterns that are influenced by atmospheric teleconnections (Abiy, Melesse, & Abtew, 2019; McIvor et al.,

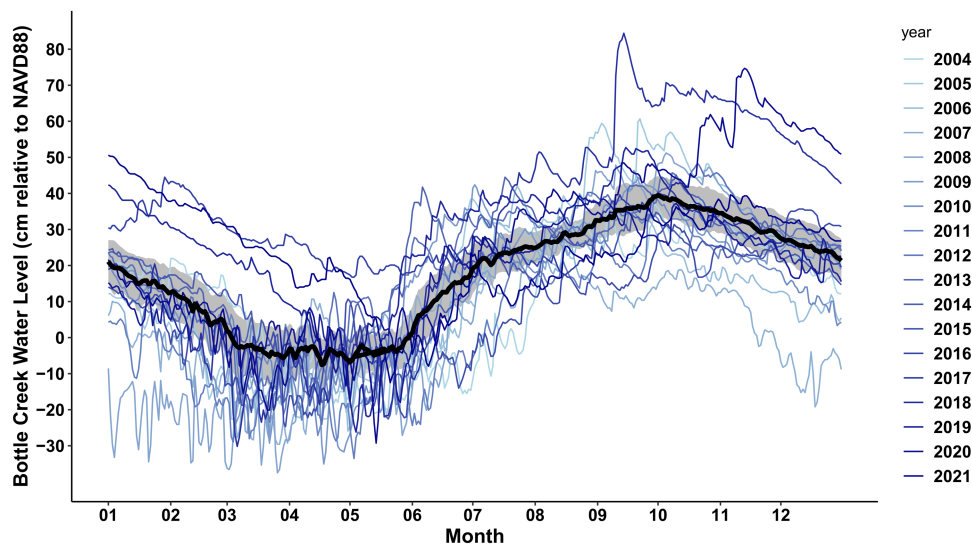


Figure 2. Hydrographs of water level in the upper Shark River at the Bottle Creek hydrostation (see [Figure 1B](#)) for each year of the study (2004–2021). Individual color-coded lines correspond to sampling year and illustrate the high degree of interannual variability in both the timing and magnitude of freshwater flows. The solid black line represents the long-term mean daily water level for the study period, with the shaded area indicating standard error in water level across the 17-year data set.

1994; Saha et al., 2012). The Shark River extends inland approximately 32 km from the coast, with a drainage area of roughly 1,700 km², and is composed of mangrove-fringed oligohaline creeks and freshwater marshes in the upper river that transition into larger mangrove forests, with progressively larger and more saline channels flowing into the Gulf of America (also known as the Gulf of Mexico; Fry & Smith, 2002; McIvor et al., 1994; Saha et al., 2012). Throughout the 20th century, drastic changes to the region's hydrology as a result of intensive water management for urban and agricultural development have reduced the volume of freshwater entering the system by roughly half (Marshall et al., 2014, 2020). However, the wet/dry seasonal pattern has been retained, with >75% of the system's rainfall occurring during the wet season in May through October (Abiy, Melesse, Abteu, & Whitman, 2019; Price et al., 2008; Saha et al., 2012).

Fish sampling

Fish sampling in the Shark River took place between November 2004 and June 2021 as part of the Florida Coastal Everglades Long Term Ecological Research Program (Childers et al., 2019; Rehage et al., 2025). Sampling occurred during three primary sampling events each year and was conducted at nine standardized electrofishing sites, with each site consisting of three replicate transects ([Figure 1B](#)). The first sampling event was conducted following the end of the wet season, when the water level was near its annual peak (one monthly sample between November and December); a second monthly event took place during the early-dry season transition of decreasing flow (between January and March); and a third monthly sampling event was in the late-dry season, when water levels neared a minimum (between April and May).

Fish were captured by boat-based electrofishing using a GPP 9.0 electrofisher (Smith Root, Vancouver, Washington, USA) following standardized methods (Boucek & Rehage, 2013; Rehage & Loftus, 2007). At each site/transect, electrofishing was performed while the boat was motored at idle speed along

a randomly selected shoreline using a pulsed 2:1 on/off power ratio for a total of 5 min of shock time to standardize sampling effort. Two netters were stationed on the bow of the boat, and once immobilized, fish were netted and immediately transferred to an onboard aerated live well. The distance sampled at each transect was recorded at the end of each transect, using GPS to calculate catch per unit effort (CPUE). Each transect sampled approximately 100 m of shoreline, but the sample distances varied based on fish catches and sampling conditions. For example, high wind speeds or the direction of tidal currents affected boat speed during sampling and increased netting time in a fixed location when large numbers of fish that were immobilized simultaneously could either increase or decrease the actual sampling distance relative to the full extent of the 100-m transect. The captured fish were measured for standard length (cm), weighed (g), and released live after being allowed to recuperate in ambient water. To compare the relative abundance of snook over time, CPUE was standardized across each sampling event, site, and transect and calculated as the number of individuals captured per 100 m of shoreline (total # snook captured in a transect / total distance sampled in meters × 100). The mean CPUE for each of the three seasonal sampling events (wet, early-dry, late-dry seasons) was then calculated to estimate overall seasonal/annual abundance and related to the environmental variables using statistical models.

Between 2004 and 2021, 51 seasonal sampling events were performed at nine sites corresponding to wet, early-dry, and late-dry season conditions (see online [Supplementary Material, Table S1](#)). Across the 51 samples and nine sites (three transects/site), 1,286 estimates for snook abundance (CPUE) were calculated and used in the analysis. For each sampling event, the specific sampling timing was based on the annual hydrologic conditions ([Figure 2](#)), and thus, the sampling dates varied across the study. In total, 1,420 individual snook were captured, ranging in size from 5.0 to 77.5 cm standard length (mean 39.5 cm ± 11.3 SD).

Environmental data

Time-series data for the environmental conditions in the Shark River (water level, water temperature, salinity, precipitation) were obtained for the entire common period where data were available for all the variables (October 2003–February 2023). Daily water level (cm relative to NAVD 88) and precipitation (cm) were queried from the Everglades Depth Estimation Network (<https://sofia.usgs.gov/eden/>) for two monitoring stations (Figure 1B), one located in a narrow creek just upstream of our upper-river sample sites (Bottle Creek) and another in the freshwater marsh just upstream from our sample sites (MO215). Additionally, time-series data for daily water temperature (°C) for Bottle Creek (Station 022908295) and salinity (psu) measurements for Bottle Creek and Canepatch (Station ENPCN) were obtained from the U.S. Geological Survey via the South Florida Water Management District's environmental database (<https://www.sfwmd.gov/science-data/dbhydro>). The time-series data contained entries where daily observations were not recorded for water level (182 of 7,006 observations, 2.5% of data), water temperature (157 of 7,006 observations, 2.2% of data), and salinity (53 of 7,006 observations, 0.7% of data). To meet the requirements for our time-series analyses, which require complete observations, we performed seasonally decomposed missing value imputation using the `na_seadec()` function from the `imputeTS` package in R statistical software (see online [Supplementary Material, Figures S1, S2, and S3; Moritz & Bartz-Beielstein, 2017; R Core Team, 2022](#)). This method isolates the seasonal component from time-series data, imputes missing values into the deseasonalized data, and then reintroduces the seasonal component. We then calculated mean monthly values for water level, temperature, salinity, and total monthly precipitation to match the temporal resolution of our relative abundance data for snook (monthly CPUE) and for use in the time-series trend analyses and statistical models. Monthly climate indices were obtained from the National Oceanic and Atmospheric Administration, with data for the El Niño–Southern Oscillation (ENSO) index queried from the National Centers for Environmental Information (<https://www.ncei.noaa.gov/access/monitoring/enso/soi>) and data for the Atlantic Multidecadal Oscillation (AMO) index from the Physical Sciences Laboratory's Climate Timeseries (<https://psl.noaa.gov/data/timeseries/AMO/>).

Modeling long-term trends

To identify the presence of either nonlinear or monotonic trends over time, we followed a three-step analytical process for both trends in environmental conditions (water level, water temperature, salinity, precipitation) and snook abundance (CPUE) using R statistical software (R Core Team, 2022). First, we used seasonal and trend decomposition via locally estimated scatterplot smoothing (STL) to isolate the effect of seasonality and determine whether nonlinear long-term trends were present in the data (Cleveland et al., 1990; Hartmann et al., 2018). This is an efficient and robust nonparametric technique that uses generalized additive modeling to identify nonlinear trends in time-series data that can be missed by other trend detection methods and has been used widely in ecological and environmental studies (Danandeh Mehr et al., 2021; He et al., 2022; Qian et al., 2000; Rojo et al., 2017). To test whether the STL models were able to

extract the seasonal and trend components from the time-series data, we examined the residuals (remainder) of the time series after removing the seasonal and trend components for normality using quantile–quantile plots, with a normal distribution of the residuals indicating that seasonal decomposition was able to extract a real trend and the residuals consisted of unquantified error in the time-series data. Second, to examine whether monotonic and directional (increasing or decreasing) environmental trends were present in the data, we performed a Mann–Kendall trend test on both observed data (monthly values calculated from raw data) and the seasonally corrected trends using the Kendall library in R (Hipel & McLeod, 1994; McLeod, 2015). This technique has been used previously to detect trends in environmental data (Abiy, Melesse, Abtew, & Whitman, 2019; Aditya et al., 2021). For snook CPUE, multiple Mann–Kendall trend tests were performed to examine the entire data set (including observations for all seasons) and subsequently for the wet, early-dry, and late-dry seasons independently to investigate whether differing trends in relative abundance were present during each sampling season. Finally, we computed a slope for the approximate linear rate of change with a 95% confidence interval using the Sen–Theil trend line slope estimate (Sen's slope) for monotonic trends that were identified by the Mann–Kendall test using the *Trend* package in R (Pohlert, 2020).

To identify the environmental factors that contribute to variation in snook abundance over time, we used generalized linear models with a Gaussian error distribution. The response variable was the mean CPUE for snook at each monthly sampling event. We selected environmental variables that influence habitat conditions in the Shark River, which vary both seasonally and annually, as well as climatic indices to consider whether atmospheric teleconnections correlate with CPUE. For the environmental conditions, we considered mean monthly water level for both Bottle Creek (river channel) and MO215 (freshwater marsh), mean monthly water temperature at Bottle Creek, mean monthly salinity at Bottle Creek and Canepatch, and total monthly precipitation measured at the MO215 monitoring station. For the climate indices, we included AMO and ENSO due to their influence on climatic and hydrologic conditions on both long and short timescales (Abiy, Melesse, & Abtew, 2019). A variable for sampling year was also included to help explain additional model variance that was not captured by our other metrics. The modeling was performed using a four-step process where we first examined all the individual variables for collinearity. Second, if collinear variables were identified, we selected a best fitting variable using corrected Akaike information criterion (AIC_c; Akaike, 1998). Third, all the selected variables were combined into a global model. Finally, the global model was reduced using backward selection to select a best fit model with the lowest AIC_c score (Anderson, 2007; Burnham & Anderson, 2003; Johnson & Omland, 2004; Symonds & Moussalli, 2011).

RESULTS

Fish sampling and CPUE

The data for CPUE were highly variable among years and seasons (Figure S4). The largest number of captured snook at a single sampling event was 91 individuals, occurring during a late-dry

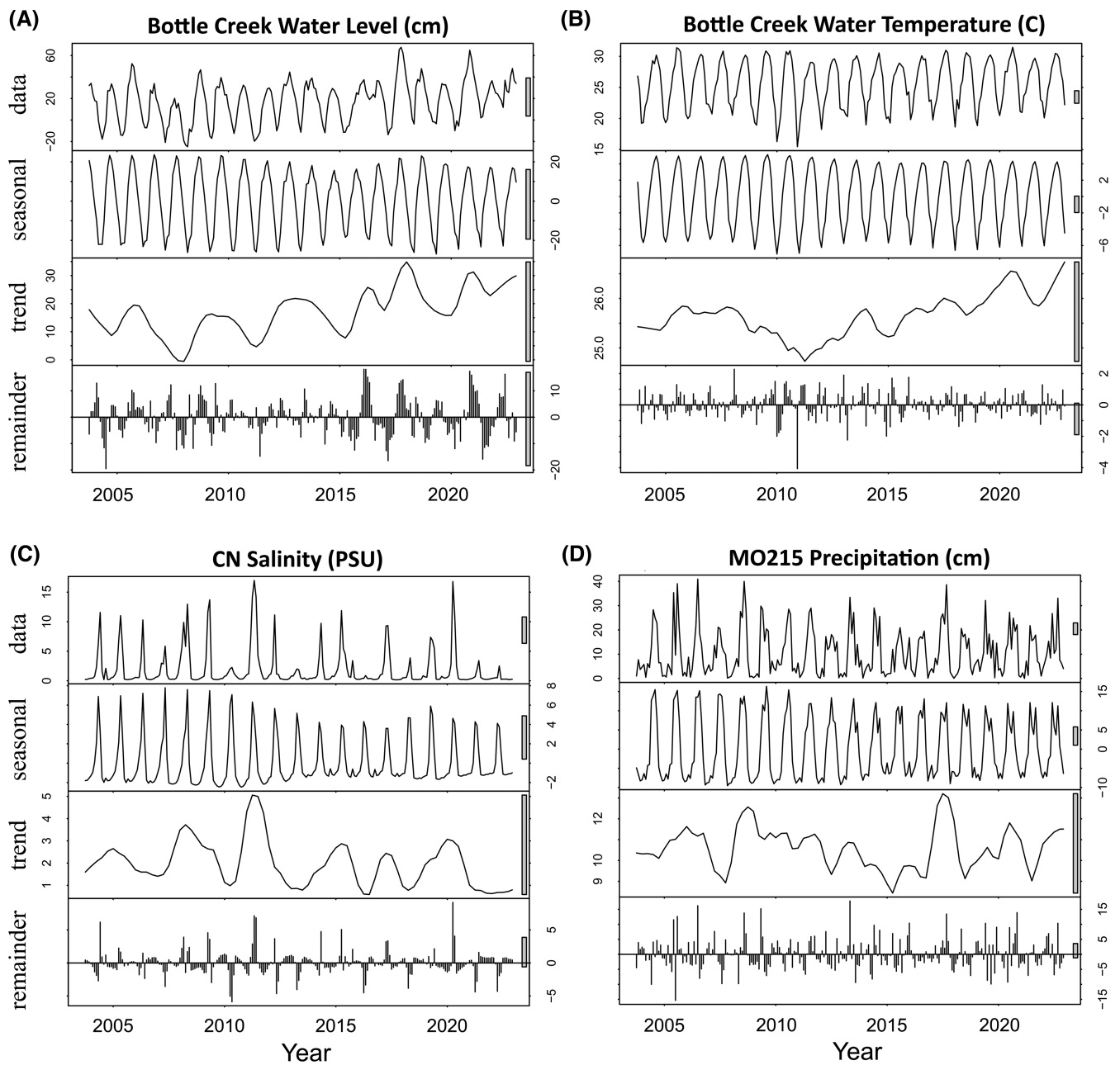


Figure 3. Results from seasonal and trend decomposition using the STL models used to identify nonlinear environmental trends over time showing measured data (data), isolated seasonal components (seasonal), nonlinear trends identified (trend), and unquantified error (remainder). Individual trends are shown for (A) water level in the upper Shark River, (B) water temperature, (C) salinity, and (D) precipitation.

season sample in April 2009, and the lowest was 0 individuals during a wet-season sample in December 2010. Mean CPUE across sites during a single sampling event ranged from 0.0 to 6.3 snook captured per 100 m of mangrove shoreline (1.3 ± 0.1 [mean \pm SE]), with catches lowest in the wet season and highest in the late-dry season. Mean CPUE ranged from 0.0 to 1.3 fish/100 m (0.5 ± 0.1) in the wet season, 0.1 to 2.6 in the early-dry season (1.0 ± 0.1), and 0.2 to 6.3 in the late-dry season (2.4 ± 0.3).

Time-series trends

We found a strong seasonal component present in the time-series data for water level, water temperature, salinity, and

precipitation (Figure 3). An evaluation of the residuals indicated that the data followed a predominantly normal distribution for water level, temperature, and precipitation to a lesser extent (precipitation quantiles deviated from normality at high values), and that STL performed well in isolating the noise and extracting the seasonal effects and trend from the data set. The remainder residuals for salinity showed large deviations from a normal distribution, indicating that the seasonally decomposed trends were less effective at extracting the nonlinear trends and seasonal components from the time-series data. Mann–Kendall trend tests indicated the presence of significant monotonic trends in the environmental data for both

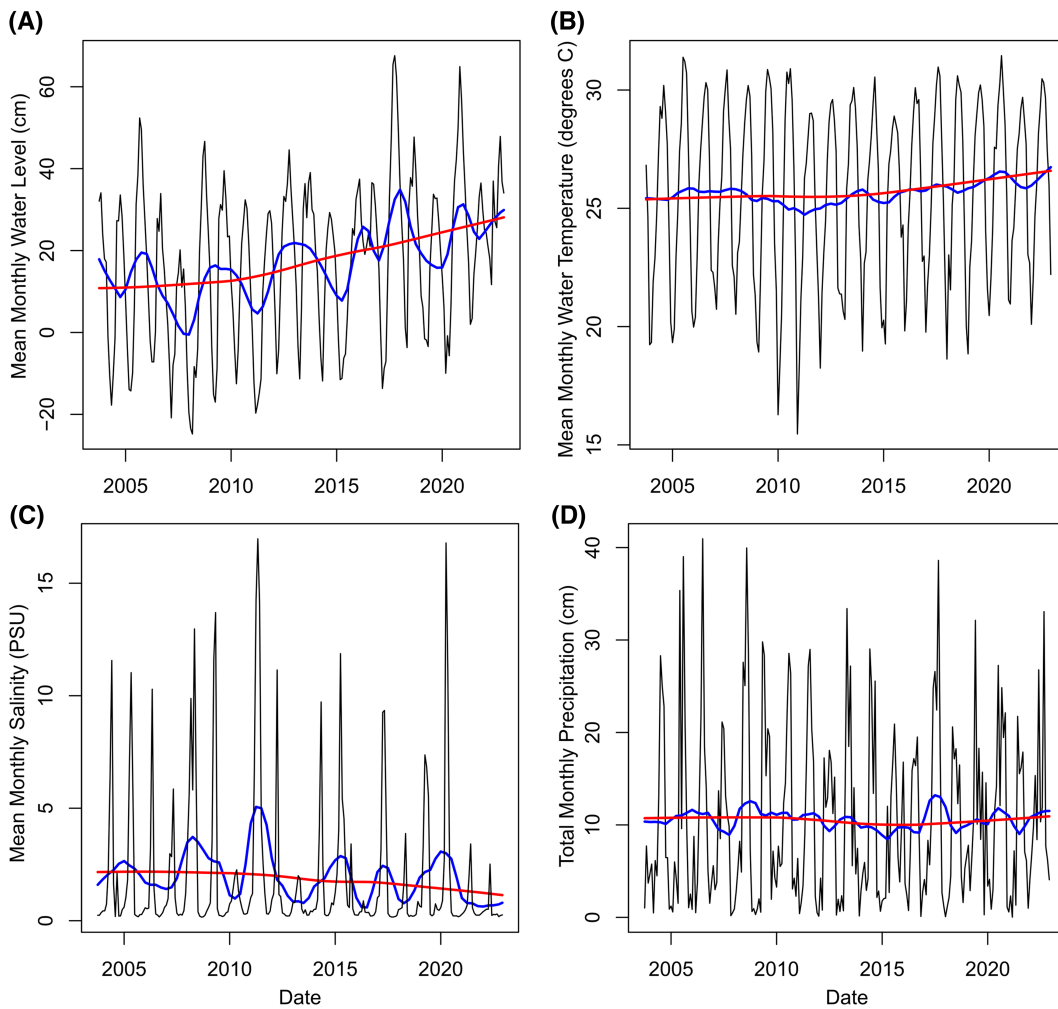


Figure 4. Environmental trends identified by Mann–Kendall trend and Sen’s slope tests for the measured environmental variables (black lines) and seasonally adjusted data (blue lines). Fitted monotonic trends (red lines) for seasonally corrected data are shown for (A) mean monthly water level, (B) mean monthly water temperature, (C) mean monthly salinity, and (D) total monthly precipitation. The monotonic trends were significant for measured water level and salinity and seasonally corrected water level, temperature, and salinity. No significant trend was found for total monthly precipitation.

Table 1. Results from the Mann–Kendall trend and Sen’s slope tests used to identify monotonic trends in the environmental data. Results are shown for both the observed (measured mean monthly water level, temperature, salinity, and total monthly precipitation) and seasonally adjusted data. Statistically significant trends are shown in bold.

Mann–Kendall trend test	Variable	Mann–Kendall trend test		Sen’s slope				
		Tau	P	Slope	Lower 95% CI	Upper 95% CI	z	P
Observed	Water level	0.184	<0.001	0.076	0.040	0.115	4.164	<0.001
Seasonally adjusted	Water level	0.280	<0.001	0.077	0.065	0.089	10.456	<0.001
Observed	Temperature	0.054	0.219	0.004	−0.003	0.012	1.230	0.219
Seasonally adjusted	Temperature	0.171	<0.001	0.004	0.003	0.004	9.158	<0.001
Observed	Salinity	−0.090	0.042	−0.001	−0.002	0.000	−2.031	0.042
Seasonally adjusted	Salinity	−0.111	0.021	−0.005	−0.006	−0.003	−5.553	<0.001
Observed	Precipitation	0.038	0.387	0.006	−0.007	0.020	0.864	0.388
Seasonally adjusted	Precipitation	0.008	0.866	−0.002	−0.004	0.000	−1.734	0.083

monthly observed (measured) data and for seasonally adjusted data (Figure 4; Table 1). Water level showed a significant positive trend over time for both the observed and seasonally adjusted data ($P < 0.001$). The trend in water temperature was

nonsignificant for the observed data ($P = 0.219$) but showed a significant positive trend for the seasonally adjusted data ($P < 0.001$). Salinity had a significant negative trend for both the observed ($P = 0.042$) and the seasonally adjusted data

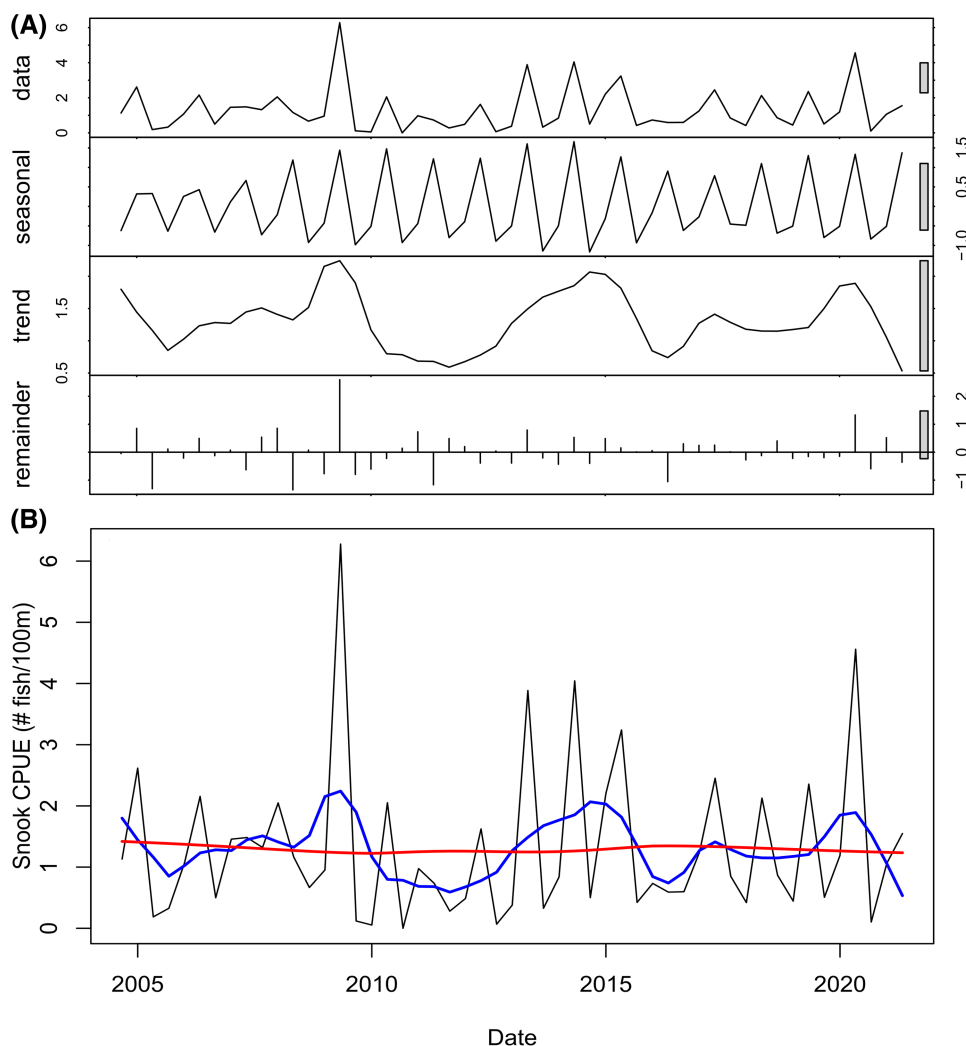


Figure 5. Trend estimates for Common Snook catch per unit effort (CPUE) data where panel A shows the results from the STL models, including raw CPUE data (data), isolated seasonal components (seasonal), the nonlinear trend identified (trend), and the noise isolated from the time-series data after the seasonal and trend components have been removed (remainder), and panel B illustrates the estimated seasonal CPUE (black line), seasonally adjusted nonlinear trend (blue line), and fitted monotonic trend line for seasonally corrected CPUE (red line). The monotonic trend from the Mann–Kendall trend test was not statistically significant.

Table 2. Results from the Mann–Kendall trend and Sen’s slope tests used to identify monotonic trends in Common Snook catch per unit effort (CPUE). The results are shown for both observed and seasonally adjusted data, and trend tests that were performed independently by season are also included.

Mann–Kendall trend test	Variable	Mann–Kendall trend test		Sen’s slope				
		Tau	P	Slope	Lower 95% CI	Upper 95% CI	z	P
Observed	Snook CPUE	0.034	0.733	0.003	−0.016	0.020	0.341	0.733
Seasonally adjusted	Snook CPUE	−0.005	0.961	0.000	−0.009	0.011	−0.049	0.961
Observed	Snook CPUE—wet	0.015	0.967	0.000	−0.047	0.048	0.041	0.967
Observed	Snook CPUE—early dry	−0.206	0.266	−0.043	−0.107	0.025	−1.112	0.266
Observed	Snook CPUE—late dry	0.191	0.303	0.085	−0.156	0.236	1.030	0.303

($P < 0.001$). No significant trend was found for either observed ($P < 0.387$) or seasonally adjusted precipitation ($P < 0.866$).

Snook CPUE also showed a strong seasonal component (Figure 5A), and the STL model performed well in isolating

the long-term trend from seasonality. However, a significant monotonic trend was not found for CPUE using the Mann–Kendall trend tests (Figure 5B; Table 2) for either the observed or seasonally adjusted data ($P = 0.733$ and 0.961 , respectively)

Table 3. Model selection results from generalized linear models examining the environmental variables affecting the relative abundance of Common Snook in the Shark River among 51 sampling events between November 2004 and 2021. The response variable for the models is the mean seasonal catch per unit effort each year (wet, early-dry, and late-dry catch per unit effort) across 17 years of electrofishing. The model shown in bold was considered the best fitting model. Abbreviations are as follows: AIC_c = Akaike information criterion; ΔAIC_c = difference in AIC_c score between each model and the lowest AIC_c model; RMSE = root mean square error; AMO = Atlantic Multidecadal Oscillation; ENSO = El Niño–Southern Oscillation.

Model variables	df	AIC_c	ΔAIC_c	R^2	RMSE
Water level + water temperature + salinity + AMO index + ENSO index + sampling year	7	150.1	4.7	0.53	0.87
Water level + water temperature + AMO index	4	145.4	0	0.49	0.90
Water level + water temperature	3	146.1	0.7	0.46	0.93
Water level	2	155.1	9.7	0.33	1.04
Water temperature	2	155.1	9.7	0.33	1.04

Table 4. Summary statistics for the top generalized linear model (see Table 3) examining the environmental variables affecting the relative abundance of Common Snook in the Shark River. The results show a significant negative relationship between catch per unit effort and water level and a positive relationship with catch per unit effort and water temperature.

Variable	Beta	SE	z	P
(Intercept)	−2.84	1.30	−2.18	0.03
Water level	−0.03	0.01	−3.46	<0.01
Water temperature	0.19	0.05	3.45	<0.01

or when the wet, early-dry, and late-dry seasons were examined independently ($P=0.967$, 0.266, and 0.303, respectively; Figure S4).

Relating environmental conditions to snook abundance

After making pairwise comparisons of each generalized linear model–variable combination, we found high collinearity between water levels at Bottle Creek and MO215 (Pearson’s correlation > 0.90), between salinity at Bottle Creek and Canepatch (Pearson’s correlation > 0.70), and between Bottle Creek temperature and precipitation (Pearson’s correlation > 0.70). We selected the data for water level and temperature from Bottle Creek for our global model to best represent the conditions that are experienced by snook in the river channels. We selected salinity data from Canepatch because it experiences more seasonal variation in salinity than Bottle Creek (Bottle Creek salinities are <1.0 psu for much of the year), allowing us to better detect salinity trends over time. After removing the collinear variables, our global model consisted of six variables (Table 3; water level, water temperature, salinity, AMO index, ENSO index, and sampling year). After model selection, the top model contained only two variables, Bottle Creek water level and water temperature (Table 4). A more complex model also containing the AMO index performed comparably. However, this more complex model was within 2 AIC_c points, and using parsimony, we chose the simpler model as our best model. This best model explained 46% of the model variance and indicated a negative relationship between snook CPUE and water level and a positive relationship with water temperature (Figure 6). An examination of univariate models for variables remaining in the best model suggested an equal contribution of water level and temperature in explaining the model variance for snook CPUE (univariate $R^2=0.33$ for both variables).

DISCUSSION

In this study, we used long-term environmental data to document trends in environmental conditions in the Shark River over time. We found an increasing trend in both water level and water temperature and a decreasing trend in salinity corresponding to higher freshwater flows. Although no clear trend was found in the snook population, the statistical models show the influence of both water level and temperature on their relative abundance. A high degree of both seasonal and interannual variation was observed for CPUE, and annual abundance oscillated over the long-term data set. Our results suggest that over long timescales, the snook population remains relatively stable but that both interannual differences in the timing/magnitude of seasonal fluctuations in water level and infrequent or pulsed environmental variation (e.g., prolonged flooding, drought, extreme cold events) can have large effects on annual relative abundance.

Our results show a negative correlation between water level and snook CPUE in the Shark River, consistent with previous findings from this and other riverine species. Water level shapes the behavior and distribution of riverine fishes, and fluctuations in water level can affect seasonal patterns in both abundance and prey availability. As water levels recede during the dry season, snook move into upper-river habitats to capitalize on freshwater prey as marshes dry and prey are concentrated in the river channels (Blewett et al., 2017; Boucek, Heithaus, et al., 2017; Boucek et al., 2016; Boucek & Rehage, 2013; Rehage et al., 2022; Rehage & Loftus, 2007). Seasonal tracking of floodplain prey has also been documented for other riverine fishes. For example, in the Cinaruco River of western Venezuela, multiple cichlid species use freshwater prey that migrate from floodplain habitats into the river channels during falling water levels (Hoeinghaus et al., 2006; Winemiller & Jepsen, 2004). Furthermore, the abundance of Barramundi *Lates calcarifer* and catfishes *Neoarius* spp. in Australia increase seasonally in freshwater habitats, corresponding to changes in water levels and access to floodplain prey resources (Crook et al., 2020; Jardine, Pettit, et al., 2012; Jardine, Pusey, et al., 2012; Roberts et al., 2019).

This study illustrates how both seasonal and interannual differences in water level affect the relative abundance of snook. Not only was CPUE lowest in the wet season across the study period, but years with exceptionally high water levels in the dry season corresponded to low abundance, which we hypothesize

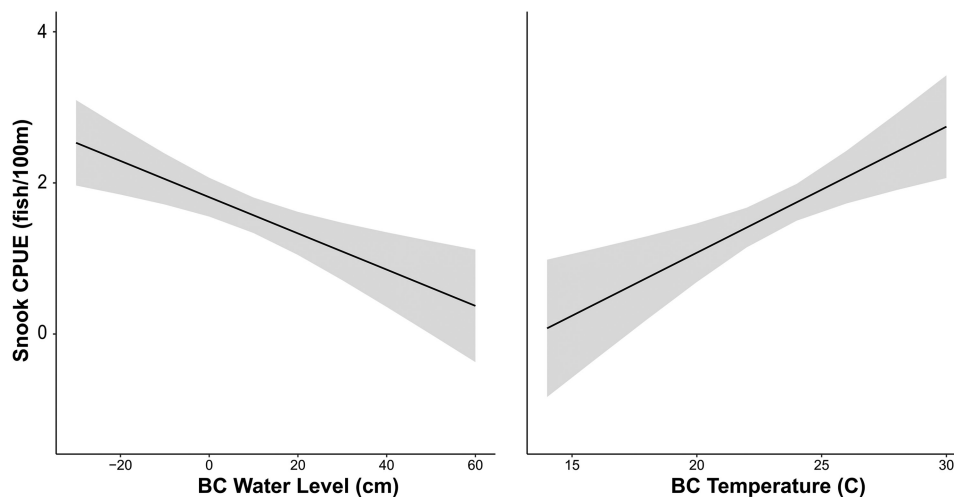


Figure 6. Bottle Creek (BC) water levels and temperature variables plotted for the best fitting generalized linear model for the relative abundance of Common Snook in the Shark River (catch per unit effort [CPUE]) bounded by a 95% CI. The individual effects of each variable that was retained in the best model were assessed by holding the other variables at a fixed mean value. Together, these variables explain 46% of the long-term variability in CPUE.

is related to decreased prey concentration. In 2016, a strong ENSO event resulted in increased dry season rainfall, prolonged high water levels, and little variation in the water level among the wet and dry seasons. This corresponded to one of the lowest late-dry season CPUE estimates for snook in our study, which was observed in May of 2016 (75% lower than the long-term seasonal mean). Furthermore, in the early-dry season of 2018, persistent high water levels that were associated with heavy rainfall during Hurricane Irma (September 2017) also corresponded to low snook CPUE in the early-dry season (60% lower than long-term seasonal mean). Conversely, the highest CPUE occurred in the late-dry season of 2009 (2.6 times greater than long-term mean), corresponding to the third-lowest water level recorded during the study period, conditions that increase the concentration of freshwater prey in the river channels. It is important to note, however, that this sampling event occurred after prolonged marsh flooding in the previous wet season, with a gradual recession of water levels throughout the spring, which corresponds to ideal conditions for both wet season freshwater prey production and enhanced foraging opportunities (Rezek et al., 2023). Also, the lowest late-dry season CPUE occurred in April 2005 (92% less than the long-term seasonal mean), where water levels were well below average in the previous wet season (34% lower than long-term mean) and began to drop rapidly beginning in early January. These findings emphasize not only the importance of seasonal drops in water level, which result in prey concentration, but also the importance of hydrologic variation that includes wet-season flooding that enhances prey production, information that could be used by water managers to maintain abundant snook populations in freshwater/estuarine habitats.

Our results demonstrate not only a positive relationship between temperature and snook abundance but also that over time temperatures have been gradually increasing in the Shark River. Snook are a tropical species, and there are populations in Florida near the northern extent of their geographic range; therefore, increasing temperatures could have a positive effect

on their abundance (Purtlebaugh et al., 2020). The upper thermal tolerance of snook has been reported at approximately 35–42°C, with thermal preferences ranging from 26°C to 29°C (Hall-Scharf et al., 2025; Paschke et al., 2018; Regil et al., 2015), well within the range of temperatures that are currently found in South Florida. However, water temperatures <10°C can be lethal for snook (Howells et al., 1990), and periodic cold events occurred within our study period. In January of 2010, a severe cold spell caused widespread mortality of snook throughout Florida (Boucek, Heithaus, et al. 2017; Boucek et al., 2023; Stevens et al., 2016), with water temperatures dropping below 10°C for a period of 3 d in the upper Shark River (January 10–12). Consequently, snook CPUE in February 2010, immediately following the cold spell, was the lowest of any early-dry sampling season in our study (90% lower than the long-term early-dry mean), and the lowest overall CPUE recorded (no snook captured) occurred in the following wet season in December 2010. Similar findings have been reported for other temperature-limited species. Booth et al. (2018) used 18 years of data for multiple coral reef fish species in southeastern Australia and found that although individuals for numerous species were observed in temperate reefs beyond their historic range corresponding to increasing water temperatures over time, many species were unable to maintain high abundance during seasonal cooling, suggesting that the establishment of a permanent population may be limited to species with higher cold tolerance (e.g., *Abudefduf* spp.). Leriorato and Nakamura (2019) also described the cold sensitivity of tropical marine fishes that had expanded into temperate waters in southwestern Japan and reported that an extreme cold event in 2018 resulted in an 80% decline in abundance. Additionally, Match et al. (2020) used long-term data to examine the abundance of Bull Sharks *Carcharhinus leucas* in Florida in relation to a 2010 extreme cold spell and found a 90% reduction in shark abundance during the cold spell. Notably, it was 5 to 7 years before CPUE returned to the levels that were observed prior to the cold spell. These results, combined with findings from the

present study, illustrate how physiological limitations that are associated with low temperatures can affect long-term population trends, suggesting that continued warming and a reduction of future extreme cold events may have positive long-term effects on thermally constrained species.

Water management, restoration efforts, and climate change are all predicted to contribute to hydrologic changes in the future (Abiy, Melesse, Abteu, & Whitman, 2019; Dessu et al., 2018, 2021; Flower et al., 2017), and shifts in habitat conditions can influence both the abundance and distribution of riverine fishes and the availability of freshwater prey resources. An analysis of long-term precipitation records suggests an overall shortening of the wet season in south Florida and that the historic bimodal rainfall patterns during the summer months may become unimodal (Abiy, Melesse, Abteu, & Whitman, 2019). Sea-level rise threatens to increase salinities in what are currently freshwater habitats, and water management practices that increase freshwater inputs from the north to keep salinity at bay could increase water depth and flooding duration in marsh habitats (Dessu et al., 2018, 2021), which could both increase the abundance freshwater prey and decrease access to this resource if dry season water levels are not low enough to result in prey concentration. Conversely, phase shifts in atmospheric teleconnections (i.e., AMO) that decrease future rainfall could result in shallower marsh depths, affecting the productivity of freshwater prey species (Abiy, Melesse, & Abteu, 2019; Boucek et al., 2016; Flower et al., 2017).

Although our findings illustrate how the periodic occurrence of extreme environmental disturbances can result in substantial fluctuations in the abundance of snook from year to year, the population is relatively stable over time and able to recover to its former population levels. However, it is apparent that maintaining the seasonal lows in the water level that concentrate prey species is an important factor in shaping abundance and distribution of fish in the freshwater/estuarine habitat of the Everglades. In a highly altered landscape where freshwater flows entering the system are carefully managed, our results emphasize how water management decisions that maintain seasonal fluctuations in water level can assist in maintaining stable and robust snook populations over time.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Marine and Coastal Fisheries* online.

DATA AVAILABILITY

The long-term fish community data sets generated and analyzed during the current study are available through the Florida Coastal Everglades Long Term Ecological Research Program under the Environmental Data Initiative (Rehage et al., 2025).

ETHICS STATEMENT

The field procedures for animal subjects were ethically reviewed and approved by Florida International University's Animal Care and Use Program under protocol numbers IACUC-20-057-CR01 and IACUC-21-003-CR01.

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CONFLICTS OF INTEREST

None declared.

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