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PATTERNS AND CUES IN THE RIVERINE MOVEMENTS OF COMMON SNOOK: INVESTIGATING THE ROLE OF ENVIRONMENTAL VARIATION AND DISTURBANCE ON MIGRATIONS AND RESOURCE USE IN THE FLORIDA EVERGLADES

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in

EARTH SYSTEMS SCIENCE

by

Jordan A. Massie

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To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Jordan A. Massie, and entitled Patterns and Cues in the Riverine Movements of Common Snook: Investigating the Role of Environmental Variation and Disturbance on Migrations and Resource Use in the Florida Everglades, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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The dissertation of Jordan A. Massie is approved.

Dean Michael R. Heithaus
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Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2023

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Massie, J.A., R.O. Santos, R.J. Rezek, W.R. James, N.M. Viadero, R.E. Boucek, D.A. Blewett, A.A. Trotter, P.W. Stevens, and J.S. Rehage. 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. Movement Ecology 10: 1-20. Permission from Springer Nature.

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DEDICATION

This dissertation is dedicated to the memory of my grandfather, Andrew Busch. It was through his patience, imparted wisdom, and respect for the natural world gained from a life spent on the water and in the woods that shaped my path in life, and ultimately my academic direction.

I also dedicate this dissertation to Joel and Janice Massie, my parents. You have been a rock throughout this long, winding, and nontraditional journey. I’ll be forever grateful for your love, support, and encouragement to become the person you always knew I could be, even when I could not see it myself.

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DECLARATION STATEMENT

I, Jordan A. Massie, declare that the dissertation entitled Patterns and Cues in the Riverine Movements of Common Snook: Investigating the Role of Environmental Variation and Disturbance on Migrations and Resource Use in the Florida Everglades is the result of my original research work, and it has been written by myself under the supervision of my advisor, Jennifer Rehage. Reference to the literature, and acknowledgement of collaborative research and discussions are made, and appropriate credit has been given within this dissertation. I confirm that this work has not been submitted for any other degree qualification.

ABSTRACT OF THE DISSERTATION

PATTERNS AND CUES IN THE RIVERINE MOVEMENTS OF COMMON SNOOK: INVESTIGATING THE ROLE OF ENVIRONMENTAL VARIATION AND DISTURBANCE ON MIGRATIONS AND RESOURCE USE IN THE FLORIDA EVERGLADES

by

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Florida International University, 2023

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Professor Jennifer Rehage, Major Professor

Understanding when, where, and why animals move is a central theme in ecology, and the timing and scale of movement can carry consequences ranging from the growth and survival of individuals to the flow of energy through ecosystems. However, gaps remain in quantitative research that links movements with environmental drivers, and that describes how key prey subsidies affect the fitness of consumers. My dissertation examined the movements of the ecologically and economically important fish species Common Snook (*Centropomus undecimalis*) in the Shark River (SR), Everglades National Park (ENP). I used eight years of acoustic telemetry data (AT) coupled with long-term community sampling data to quantify how movement patterns and foraging relate to seasonal/interannual environmental variation. First, I quantified seasonal/annual patterns in freshwater-to-coast spawning migrations using AT and related these movements to hypothesized drivers using generalized linear mixed models (GLMMs). Results showed both interannual and seasonal variation. The number of fish migrating each year was best explained by seasonal drops in water level and fish size, and the timing of migration was most correlated with water level and daily rates of change. Next, I used AT to investigate how extreme disturbance influenced movements during Hurricane Irma using generalized linear models to relate movements to hypothesized drivers representing riverine/hurricane conditions. During Hurricane Irma, 73% of tagged fish made downstream movements, and movement responses were best explained by a combination of water level and barometric pressure. I then used long-term electrofishing data to examine how the magnitude of a seasonal prey subsidy (sunfishes, *Lepomis* spp.) and seasonal/interannual environmental variation affect the body condition of Snook using GLMMs. Results showed wide year-to-year variation, with body condition increasing with higher prey biomass, lower water levels, during the wet/dry transition, and with fish size. Finally, I used time-series data of environmental conditions in the SR to examine long-term trends in environmental change and related these trends to the relative abundance of Snook over time. This research can extend beyond Snook in ENP and can help inform how other species may respond to climate change and water management in impact-prone coastal regions.

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ABBREVIATIONS AND ACRONYMS

AIC	Akaike Information Criterion
AIC_c	Akaike Information Criterion Corrected for Small Sample Size
AMO	Atlantic Multidecadal Oscillation
ANOVA	Analysis of Variance
CPUE	Catch-per-unit-effort
ENP	Everglades National Park
ENSO	El Niño Southern Oscillation
FCE LTER	Florida Coastal Everglades Long Term Ecological Research Program
GLM	Generalized Linear Models
GLMM	Generalized Linear Mixed Model
K_n	Relative Condition Factor
NAVD 88	North American Vertical Datum of 1988
OR	Odds Ratio
PSU	Practical Salinity Unit
SL	Standard Length
SPR	Spawning Potential Ratio
SR	Shark River
STL	Seasonal Trend and Decomposition using Loess
TL	Total Length
W	Weight

PREFACE

The following chapters have been published and have been formatted for those publications.

CHAPTER II

Massie, J.A., R.O. Santos, R.J. Rezek, W.R. James, N.M. Viadero, R.E. Boucek, D.A. Blewett, A.A. Trotter, P.W. Stevens, and J.S. Rehage. 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. *Movement Ecology* 10: 1-20.

CHAPTER III

Massie, J.A., B.A. Strickland, R.O. Santos, J. Hernandez, N. Viadero, R.E. Boucek, H. Willoughby, M.R. Heithaus, and J.S. Rehage. 2020. Going Downriver: Patterns and cues in hurricane-driven movements of common snook in a subtropical coastal river. *Estuaries and Coasts* 43: 1158-1173.

CHAPTER I

INTRODUCTION

Understanding animal movement is a central theme in ecology, with far-reaching implications ranging from the health and fitness of individuals to the flow of energy through food webs and ecosystems (Earl and Zollner 2017; Nathan et al. 2008; Nathan et al. 2022). A growing body of research has investigated movement in aquatic systems for a wide range of species, propelled forward by rapid advances in technology such as acoustic telemetry which have greatly facilitated animal tracking (Crossin et al. 2017; Hussey et al. 2015; Matley et al. 2021). While this has resulted in a wealth of information, there remains a need for research that provides a mechanistic understanding of the underlying drivers of movement, the extent of individual variation within animal populations, and how seasonal/interannual environmental variation affects movement, which is dependent on the availability of robust long-term datasets able to reveal these patterns (Hays et al. 2016; Nathan et al. 2008; Nathan et al. 2022; Shaw 2020).

Collectively, water management decisions, climate change, and an increase in extreme climate events (ECE) will alter environmental conditions in the future (Dessu et al. 2021; Dessu et al. 2018; Flower et al. 2017; Keellings and Hernández Ayala 2019; Welcomme and Halls 2004). Understanding how these changes affect movement, space use, and the distributional patterns of species will be critical for conservation planning and to inform management (Koster and Crook 2017; Lennox et al. 2017). Thus, the goal of my dissertation research was to draw on long-term datasets from fish communities in the Shark River (SR), Everglades National Park (ENP) to quantify fish movements, mechanistically link movement patterns to drivers, and examine the consequences of movement for foraging success and long-term population trends. More specifically, I examined how seasonal and interannual variation in environmental conditions, namely fluctuations in freshwater flow and water level, influence the movements and migrations of the popular recreational fish species Common Snook (*Centropomus undecimalis*, hereafter Snook). Further, I investigated how ECEs alter movement behaviors, and how movements into upper river foraging areas and timing/magnitude of seasonally available prey subsidies affect the body condition of Snook.

In river systems, the natural patterns of the flow regime are driving forces in the behavior, adaptations, and evolution of fish and other aquatic biota, and can influence community interactions and ecosystem processes (Lytle and Poff 2004; Palmer and Ruhi 2019; Poff et al. 1997; Poff 2018). Seasonal fluctuations in water level can serve as cues for movement, migration, and/or reproduction, allow access to floodplain nurseries and foraging areas, and have been linked to fisheries productivity (Abrahms et al. 2021; Correa and Winemiller 2018; Junk et al. 1989; Winemiller and Jepsen 1998). In tropical coastal regions, the growth, survival, and recruitment of migratory fish have been linked to high flows, seasonal peaks in water levels, and floodplain productivity (Crook et al. 2020; Jardine et al. 2015; Roberts et al. 2019). Further, systems with altered flow patterns have been accompanied by declines in native species, experienced a simplification of aquatic communities, decreased habitat connectivity, and presented barriers for migratory species (He et al. 2019; Ruhi et al. 2018; Ruhí et al. 2016). Due to the governing role of freshwater inflows in fisheries and ecological interactions, flow served as a central variable in my research for testing hypotheses investigating the drivers of Snook movements and coastal spawning migrations.

Animals frequently move in response to predictable or recurrent physiological or environmental cues (i.e., freshwater flow), including factors related to foraging, changing habitat requirements, and migration into breeding areas (Abrahms et al. 2021; Bowler and Benton 2005; Hussey et al. 2015; Secor 2015). However, animal movements can also be driven by unpredictable disturbances that cause rapid shifts in distribution and may lead to stressful conditions, a mismatch in resources, or changes in the timing of life-history events (Bailey and Secor 2016; Durant et al. 2007; Jones and Cresswell 2010; Udyawer et al. 2013). Tropical storms are examples of ECEs that have been shown to influence the movement patterns of organisms in coastal systems, resulting in redistribution and abandonment of pre-storm habitats (Bailey and Secor 2016; Heupel et al. 2003; Liu et al. 2010; Strickland et al. 2020; Udyawer et al. 2013). However, our understanding of the environmental cues eliciting movements across species, ecosystems, and ECEs remains incomplete (Bailey and Secor 2016; Hussey et al. 2015; Secor et al. 2018). To address this research gap, my dissertation examined the conditions that drove large-scale Snook movements during Hurricane Irma in September 2017.

Seasonal and interannual variation in environmental conditions driven by climate and water management can affect movement patterns, habitat use, and resource availability for both consumers and prey species (Abrahms et al. 2021; Aikens et al. 2017; Thackeray et al. 2016). Seasonally available food resources can disproportionately contribute to the growth and body condition of individuals, provide surplus energy that maximizes reproductive success, and increase the survival of offspring (Aikens et al. 2017; Merkle et al. 2016; Middleton et al. 2018; Van der Graaf et al. 2006). In riverine systems, connectivity between river channels and floodplains serves as a vector for the transport of nutrients, organic matter, and organisms that enhance productivity and can provide consumers with access to prey subsidies (Garcia et al. 2017; Hoeinghaus et al.

2006; Junk et al. 1989; Winemiller and Jepsen 1998). Understanding how variation in environmental conditions and the timing/magnitude of seasonal prey subsidies affect consumer species can provide insight into future vulnerabilities and help guide management decisions. Thus, my dissertation investigated how hydrologic variation, and the timing and magnitude of a freshwater prey subsidy concentrated into river channels as water levels recede in adjacent floodplains marshes, affects variation in Snook body condition.

Water management, restoration efforts, and climate change have all contributed to hydrologic changes in the SR and ENP over time (Abiy et al. 2019b; Dessu et al. 2021; Flower et al. 2017). Shifts in environmental cues or habitat availability can influence the movements and migrations of Snook and alter consumer-prey relationships. Long-term precipitation records suggest an overall shortening of the wet season in South Florida, and the historic bi-modal rainfall patterns during the summer months may become unimodal (Abiy et al. 2019b). 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. 2021; Dessu et al. 2018). Conversely, shifts in atmospheric teleconnections (i.e., the Atlantic Multidecadal Oscillation) that decrease future rainfall could result in shallower marsh depths, and decrease the abundance of freshwater prey (Abiy et al. 2019a; Boucek et al. 2016; Rezek et al. In Revision). To provide a better understanding of how gradual environmental change has affected animal populations over time, and gain insight into how populations may respond to future change, I used time-series data of environmental conditions (water level, temperature, salinity, precipitation) to compare long-term environmental trends to trends in the seasonal/annual relative abundance of Snook across 17 years of fish community sampling.

In each chapter of this dissertation, I investigated questions related to different aspects of how environmental variation affects the movements, migrations, and resource use of Snook, using long-term datasets and the unprecedented understanding of animal movement they provide. In Chapter II, I asked, what are the environmental drivers of reproductive migrations at both seasonal and annual scales, and does variation in river flow affect migration patterns? Chapter III asked, what was the movement response of Snook to the extreme environmental disturbance associated with Hurricane Irma, and how do the drivers of rapid behavioral changes compare to cues influencing predictable or recurrent seasonal movements? In Chapter IV, I asked, how does hydrologic variation and seasonal prey abundance affect the body condition of Snook? Finally, in Chapter V, I asked, how has gradual environmental change affected long-term trends and stability in the relative abundance of Snook over time? By quantitatively describing the environmental conditions that shape animal movement patterns, maintain access to key prey subsidies, and promote the long-term stability of coastal species, my research provides new information that can help guide conservation and management decisions that seek to maintain the stability and persistence of important fisheries for future generations.

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CHAPTER II

PRIMED AND CUED: LONG-TERM ACOUSTIC TELEMETRY LINKS INTERANNUAL AND SEASONAL VARIATIONS IN FRESHWATER FLOW TO THE SPAWNING MIGRATIONS OF COMMON SNOOK IN THE FLORIDA EVERGLADES

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ABSTRACT

Background

Spawning migrations are a widespread phenomenon among fishes, often occurring in response to environmental conditions prompting movement into reproductive habitats (migratory cues). However, for many species, individual fish may choose not to migrate, and research suggests that conditions preceding the spawning season (migratory primers) may influence this decision. Few studies have provided empirical descriptions of these prior conditions, partly due to a lack of long-term data allowing for robust multi-year comparisons. To investigate how primers and cues interact to shape the spawning migrations of coastal fishes, we use acoustic telemetry data from Common Snook (*Centropomus undecimalis*) in Everglades National Park, Florida, USA. A contingent of Snook migrate between rivers and coastal spawning sites, varying annually in both the proportion of the population that migrates and the timing of migration within the spawning season. However, the specific environmental factors that serve as migratory primers and cues remain unknown.

Methods

We used eight years of acoustic telemetry data (2012-2019) from 173 tagged Common Snook to investigate how primers and cues influence migratory patterns at different temporal scales. We hypothesize that 1) interannual differences in hydrologic conditions preceding the spawning season contribute to the number of individuals migrating each year, and 2) specific environmental cues trigger the timing of migrations during the spawning season. We used GLMMs to model both the annual and seasonal migratory response in relation to flow characteristics (water level, rate of change in water level), other hydrologic/abiotic conditions (temperature, salinity), fish size, and phenological cues independent of riverine conditions (photoperiod, lunar cycle).

Results

We found that the extent of minimum marsh water level prior to migration and fish size influence the proportion of Snook migrating each year, and that high river water level and daily rates of change serve as primary cues triggering migration timing.

Conclusions

Our findings illustrate how spawning migrations are shaped by environmental factors acting at different temporal scales and emphasize the importance of long-term movement data in understanding these patterns. Research providing mechanistic descriptions of conditions that promote migration and reproduction can help inform management decisions aimed at conserving ecologically and economically important species.

BACKGROUND

Migration is a widespread phenomenon occurring in animal populations worldwide, with examples spanning diverse habitats, in taxa ranging from terrestrial insects to marine mammals, and on scales varying from small displacements to thousands of kilometers [1-4]. Because of the diversity of organisms and contexts in which migration occurs, definitions in the literature are varied [5]. However, common themes emerge. Migration entails the collective directional movements of individuals or groups between well-defined and spatially distinct habitats, which provide favorable ecological conditions for a period of time, and frequently occurs on a cyclical or recurrent basis [4-6]. Migrations take place over a spectrum of environmental conditions and are motivated by factors related to changing resource dependencies, physiological needs, and/or seeking refuge to avoid unfavorable conditions [7-9].

Migratory patterns arise from a complex suite of genetic, physiological, behavioral, and ecological factors that are ultimately driven by the optimization of growth, survival, and reproduction [9, 10]. However, the timing and pathways of migration often occur in response to proximate *cues* related to seasonality and changes in environmental conditions [11]. Despite the increase in attention on migratory cues, research remains limited in the number/types of species investigated [9, 12]. Further, there is a need for research that addresses not only migratory cues but also how environmental conditions at broader timescales (e.g., conditions experienced in the months leading up to migration) may serve as migratory *primers*, influencing the decision to undertake reproductive migrations each year [13, 14]. Inference on migratory primers has been limited in part by a lack of long-term data that can help quantify the relative importance of environmental drivers in contributing to interannual differences in migration and associated reproduction [15-17].

Reproductive migrations commonly span environmental gradients (e.g., aquatic/terrestrial, salinity regimes), and adults move into habitats providing appropriate environmental and physiological requirements for successful breeding and development of offspring [9, 18]. For coastal fishes, seasonal fluctuations in water level dictate several key processes that may influence the spatial-temporal spawning landscape. The magnitude, duration, and abruptness of change in freshwater flows can alter productivity gradients, physicochemical environments, and tidal and current flows, all of which can influence reproductive success and recruitment [19-22]. As such, variation in freshwater flows can serve as cues for reproductive migrations.

In rivers, changes in flow have been shown to trigger spawning migrations in multiple species including Estuary Perch [*Macquaria colonorum*, 23], Australian Bass [*Macquaria novemaculeata*, 24], Australian Grayling [*Prototroctes maraena*, 15], Mary River Cod [*Maccullochella mariensis*, 25], Mulloway [*Argyrosomus japonicus*, 26], European Eel [*Anguilla anguilla*, 27], and Barramundi [*Lates calcarifer*, 28, 29]. Acoustic telemetry studies have indicated that both the probability and scale of migratory movements increase with river discharge [23, 24, 30]. Taylor et al. [26] reported that high flows drove the riverine migrations of Mulloway, potentially serving as a signal promoting the formation of spawning aggregations in the lower estuary. However, variation in migratory timing has been reported. For Australian Bass and Australian Grayling, individuals initiated migrations at different times and on distinct flow pulses during a spawning season [15, 24]. Further, the directionality and magnitude of flow may influence the strength of the migratory responses. For example, large-scale movements of neotropical prochilodontids (*Prochilodus costatus*) and large catfish (*Phractocephalus hemiliopterus*, *Pseudoplatystoma punctifer*) in Brazilian rivers were detected during the transition between dry periods and rising water levels [31, 32], and migrations of catadromous eels in New Zealand (*Anguilla* spp.) corresponded to days with increasing discharge [33].

A recurring observation in studies of spawning migrations is a high degree of interannual variability in migratory behaviors [24, 32, 34]. Relatively few studies have focused on how conditions experienced before the reproductive season (migratory primers) may influence the extent of partial migration for species that forgo spawning in a given year, often referred to as skipped spawning in fishes [9, 14, 35]. In some cases, the proportion of individuals migrating each year (hereafter referred to as intensity of the migratory response) has been linked to variability in precipitation, which could both affect the relative strength of migratory cues and result in differences in juvenile survival [32, 36]. Other studies have suggested that energetics may play an important role in the decision to migrate, with evidence for lower energy reserves increasing the prevalence of skipped spawning [13, 14]. Whether or not fish respond to environmental cues and initiate a spawning migration may be dependent on conditions experienced months earlier, with annual migration patterns reflecting the interaction between both *primers* and *cues* acting at different temporal scales. Here we propose an organizational framework that is both conceptual and analytical for addressing the primers and cues of spawning migrations (Fig. 1), and takes advantage of long-term acoustic telemetry data and the unprecedented understanding of migration patterns it provides [37].

Common Snook (*Centropomus undecimalis*, hereafter Snook) are a tropical euryhaline fish species well-suited to studies of migration. Snook are found in freshwater and marine habitats of the western Atlantic, the Caribbean, and the Gulf of Mexico, with their range extending from Brazil to Cedar Key on Florida's gulf coast and Cape Canaveral on the Atlantic coast [38-40]. The species has received considerable research attention due to their recreational and economic importance [39, 41]. While some fish reside in lower estuaries and marine waters [42, 43], a migratory portion of the population lives in riverine habitats for much of the year [34, 38, 44, 45]. Freshwater prey serve as an important seasonal resource for migrant Snook, and upriver movements into freshwater habitats correspond to drying marshes when prey are concentrated in river channels in advance of the spawning season [38, 46-49]. Snook are marine obligate spawners and require high salinity for successful reproduction [50-52]. Both estuarine and riverine contingents must move to the lower estuary and ocean inlets to spawn. In Florida, spawning occurs over a protracted period beginning in April and extending through November [43, 53-57]. Downstream migrations from freshwater habitats to coastal spawning sites have been previously documented by acoustic telemetry and indicate a high degree of variability in migratory behaviors [34, 43, 58, 59]. Not all Snook migrate each year. Studies from both the Atlantic and gulf coasts have estimated skipped spawning ranging from 24-40% [34, 58, 59]. No previous work has tied Snook migrations to specific environmental factors, and there remains a need for quantitative descriptions of the mechanisms and conditions that drive migratory behaviors to help inform fisheries management [38, 60-62].

In this study, we use eight years of acoustic telemetry data (2012-2019) to examine how environmental variability at both annual and seasonal scales influence the spawning migrations of Snook in Everglades National Park (ENP), Florida, USA. More specifically, our goal was to investigate the pre-spawning conditions that maximize the migratory responses and promote reproduction (primers) and dictate the intensity of migration, as well as the daily cues during the spawning season that act to initiate migrations as a function of hydrologic variation, and thus drive the timing of such migrations. Our research questions are twofold: Q1) how does interannual variation in hydrologic conditions influence the intensity of the migratory response each year, and do certain conditions act as primers for population-level migratory responses? (Fig. 1 – To migrate or not to migrate?), and Q2) do specific environmental cues trigger the timing of Snook migration within a given season? (Fig. 1 – When to migrate?). We hypothesized that: H1) interannual differences in hydrologic conditions preceding the spawning season, and associated variation in the timing/extent of transitions between the wet and dry season that drives access to prey pre-spawning, contribute to the intensity of the Snook migratory response, and H2) specific cues presented by changes in hydrologic conditions within the spawning season trigger the timing of Snook migrations (e.g., high flow events, temperature, salinity). To test these hypotheses and understand the intensity and timing of spawning migrations, we modeled the migratory response of Snook in relation to a suite of environmental variables. We selected explanatory variables previously reported to influence migration and reproduction in fishes [15, 16, 20, 23, 63].

METHODS

Study Area

The Shark River is an expansive, low-gradient coastal river system in the southwestern region of ENP that extends 32 km inland with a drainage area encompassing roughly 1700 km^2 (Fig. 2). The hydrologic regime is shaped by a subtropical climate and seasonal freshwater flows which are driven by tidal cycles and rainfall patterns influenced by atmospheric teleconnections on both short (El Niño/Southern Oscillation) and long (Atlantic Multidecadal Oscillation, hereafter AMO) timescales, resulting in variability in both the timing and the total amount of precipitation and annual flow characteristics [Additional File 1 Fig. S1; 64, 65, 66]. Alterations to the natural hydrology have occurred over the last century due to drainage and impoundment for urban and agricultural development that have reduced the volume of freshwater entering the system [67]. Paleo-based estimates indicate that historic flow levels were 2.1 times greater than those currently found [68, 69]. Despite these changes, the historic wet/dry seasonal pattern has been retained, and >75% of the system's rainfall occurs during the wet season in May through October, with a dry season of November to April [65, 66, 70, 71].

The headwaters of the Shark River consist of small creeks and marshes that transition into mangrove forests, with progressively larger and more saline channels approaching the coast at the Gulf of Mexico [65, 66, 72]. The system can be broadly divided into three zones with distinct habitat characteristics [46, 49, 73, 74]. The oligohaline upper river (salinity range 0-5 PSU) receives limited tidal influence and consists of shallow narrow channels bordered by a combination of mangroves and freshwater marshes [47, 75-77]. The mesohaline mid-river (salinity range 1-21 PSU) is characterized by a shallow open embayment (Tarpon Bay) with larger mangrove forests, and receives more pronounced daily tidal fluctuations relative to the upper river [47, 48]. The polyhaline lower river is the most tidally-influenced, with salinities ranging seasonally from 10-36 PSU between the wet and dry seasons [77] and contains the most productive mangrove forest of the Everglades [78].

Acoustic Telemetry

Acoustic monitoring of Snook movements in the Shark River began in January 2012 as part of the Florida Coastal Everglades Long Term Ecological Research program [67]. Fish were captured monthly via boat-based electrofishing along shoreline habitats at 15 sites in the upper Shark River and Tarpon Bay [methods detailed in 47]. Upon capture, adult Snook were placed in an aerated livewell and total length (TL, mm) and weight (whole, g) were recorded. Sex was not assigned to captured individuals. Electrofishing was primarily conducted outside of the spawning season when external indicators of sex (e.g., milt produced when pressure applied, visible oviduct opening posterior to anal slit) that are present in mature and actively spawning fish are less apparent [59, 79, 80]. Fish were then transferred to an onboard tagging station within 2-3 minutes of capture and held ventral side up in a v-shaped cradle with the head and gills submerged. Implantation of acoustic tags followed the methods of Young et al. [45, 59] which were adapted from the procedures outlined by Lowerre-Barbieri et al. [43] and have been shown to minimize stress and maximize survival for the species. Tagging consisted of a minor surgical procedure where a 30 mm incision was made in the lower abdomen and an acoustic transmitter (Vemco 69 kHz V13 or V16, Innovasea, Halifax, NS, Canada) inserted into the abdominal cavity, and the incision closed with a single Vicryl^{TM} suture. Following tagging, fish were held in water alongside the boat and allowed to regain equilibrium before release. The estimated battery life for acoustic tags was 3.7 years (1,349 days) or 6.7 years (2,435 days) for V13 and V16 tags respectively.

Between 2012 and 2019, tagged Snook were continuously monitored by an array of 37 Vemco VR2W acoustic receivers (Innovasea, Halifax, NS, Canada) placed 1-3 km apart in a gated design, allowing us to track directional movements throughout the Shark River (Fig. 2b). Each monitoring station was assigned a river distance reflecting its position relative to the coast (river km), which ranged from 0 km at the Gulf of Mexico to 32 km in the headwaters. Unique detections for individual fish were associated with a date, time, and river km within the array. Past research in the Shark River has demonstrated the efficacy of this deployment configuration for quantifying fish movement and changes in distribution over time [46, 49, 74, 81].

Identifying Migrations

To determine if and when a fish migrated, we considered acoustic detections for each individual in each spawning season they were detected. Telemetry data were screened prior to analysis and fish with less than 10 unique detections in their movement histories were excluded from analysis. This screening process allowed us to identify unreliable observations (false detections) consisting of single detections that could not be confirmed on more than one receiver, and only include fish with a sufficient record to provide inference into migratory movements [23, 59, 82]. Fish were considered migrants if they were recorded making directed downstream movements from the upper river or Tarpon Bay into the lower river towards coastal receivers during the spawning season

(Fig. 2b). If an individual moved downstream and was detected on at least one lower river receiver followed by either the end of their detection history or a time gap until subsequent re-detection in the lower river, they were presumed to have moved to coastal spawning sites. While portions of the lower river may reach salinities required for the buoyancy of fertilized eggs [>24 PSU, 43, 45], Snook spawning has been shown to take place at ocean inlets and coastal marine areas in other Florida populations [43, 45, 59], and we would expect Shark River fish to use similar marine spawning habitats. Although coastal spawning activity could not be directly confirmed, past studies have shown how movements from freshwater/estuarine to marine areas correspond to Snook spawning activity, suggesting that downstream migration during the spawning season is indicative of spawning activity [59, 79]. For our analyses, we defined the spawning season as April 1 to November 15, a window consistent with previous observations of Snook spawning activity in Florida [46, 83]. Migration timing for each individual was recorded as the year and date during the spawning season when the initiation of downstream migration occurred, which was then related to hypothesized drivers of migration using statistical models. For fish that moved persistently downstream after initiating migration, migration timing was assigned as the date that the individual entered the lower river. If an individual was detected migrating over the course of several days, migration timing was recorded as both the date of directed movement from the upper river and into Tarpon Bay, and the date of movement from Tarpon Bay into the lower river.

Environmental Data: Primers and Cues

To examine possible drivers of Snook migration, we modeled a suite of environmental covariates in relation to migratory responses from our telemetry data at both annual and seasonal scales (Fig. 1, Additional File 1 Tables S1 and S2). Environmental data consisted of flow metrics (water level, daily water level change) and key hydrologic/abiotic variables (temperature, salinity) reported to influence movement and migration in fishes [15, 20, 24, 32, 81, 84, 85]. We also included variables examining a potential phenological response (photoperiod, lunar cycle) independent of hydrologic variation. Daily time series data for mean daily water level relative to NAVD 88 were obtained from the Everglades Depth Estimation Network (EDEN, https://sofia.usgs.gov/eden/). Water level data from two different monitoring stations in the Shark River were initially considered (Fig. 2b, Bottle Creek in the upper river, Gunboat Island in the lower river) but these measurements were collinear (Pearson correlation 0.7), and exploratory models indicated better model fit using data from the upper river. Thus, the upper river monitoring station (Bottle Creek) was selected to represent water level in our final models. We also considered river discharge as a candidate flow metric, but it was highly collinear with water level (Pearson correlation 0.9). Using water level improved model performance relative to discharge, and thus water level was selected as a representative variable for flow conditions. Water level from an additional monitoring station (Fig. 2b, MO215) located in the freshwater marsh adjacent to the upper river was also included to quantify the wet/dry seasonal transition period (drydown duration), a period of prey concentration in the river channels during receding water levels [46-48]. Daily temperature and salinity data were queried from the United States Geological Survey time-series for Bottle Creek (Station 022908295) via the South Florida Water Management District’s environmental database (DBHYDRO, https://www.sfwmd.gov/science-data/dbhydro). To examine whether cumulative environmental change may better explain migratory movements relative to daily variation, we evaluated model performance of hydrologic variables (water level, water level change, temperature, salinity) for daily mean, 3-day mean, and 7-day mean data. In all cases daily mean data resulted in the best model performance. Thus, daily mean observations were selected for use in our final models.

Modeling Annual Primers: To Migrate or Not to Migrate?

To test our hypothesis that conditions prior to the spawning season act as primers influencing the intensity of the migratory response at an interannual scale, we performed logistic regression using generalized linear mixed models (GLMMs) with a binomial error distribution and unique acoustic tag numbers for each fish as a random effect. The response variable was a binary indicator for each individual and year that noted whether a fish migrated (1) or did not migrate (0) during that year. Analyses were performed in R statistical software [86] using the glmmTMB package [87].

Modeling was performed in a four-step process where we first examined all candidate variables that characterized each hypothesized driver (Fig. 1, Additional File 1 Table S1). Second, when collinearity was found among variables, Akaike's information criterion [AIC, 88] was used to select the best fitting variable. Third, the selected variables were then combined into a global model. And fourth, backward selection was performed using the step() function from the stats package in R [86] to select a final model based on the lowest AIC [89-92]. For each of our models, fit was also assessed by relative model weight and by calculating R-squared values showing the amount of model variance explained using the Performance package in R [93].

We examined a set of hypothesized drivers to explain interannual migration patterns and act as migratory primers in the months prior to migration (flow dynamics, other hydrologic/abiotic conditions), along with the role of fish size in the migratory response (Additional File 1 Table S1). Variables for migratory primers captured riverine conditions found during the preceding dry season (152-day period from November 15 in the prior year to April 1 of the current year, end of the previous spawning season to the beginning of the current spawning season). This period was selected based both on its role in the sexual maturation of Snook, and as a period shown to provide enhanced opportunities for foraging on freshwater prey as water levels drops through the dry season [38, 46, 47]. Snook are protandrous hermaphrodites, transitioning from mature males to females at sizes range from a total length (TL) of 264 to 876 mm [57, 94]. Histological analysis of female Snook indicated that the months between spawning periods correspond to the development and regeneration of oocytes, and high hepato-somatic indices suggest that sex transition and maturation is occurring outside of the spawning season [57]. Because gametogenesis and reproductive migrations are energetically costly, resource acquisition during this period can be particularly important. Results from Young et al. [57] support capital breeding to some extent for Snook, and that energy derived outside of the spawning season is used during reproduction [95]. Because the timing of peak prey concentration can vary widely from year-to-year based on the annual hydrograph (Additional File 1 Fig. S1), we included primer variables based on the full period from the end of the previous spawning season to the beginning of the current spawning season to allow for the broadest set of environmental variation. Exploratory models also included factors characterizing the annual hydrologic conditions occurring within each spawning season (April 1-Nov 15), but they showed only weak correlations and did not improve model performance. Thus, only water level and hydrologic/abiotic variables from the dry season preceding the spawning season were included in our final models.

We considered primer metrics representing the dry season maximum, minimum, and overall range of water levels, temperature, and salinity. Due to the importance of seasonal freshwater prey subsidies for Snook [38, 46, 47], we calculated a primer metric quantifying the duration of potential high-quality foraging opportunities in the upper river leading into the spawning season. This metric (drydown duration) reflected the total number of days the freshwater marshes adjacent to the river dropped below 30 cm in the dry season, a water level that has been found to correspond to increases in abundance/biomass of marsh prey seeking refuge in the creeks and channels of the upper Shark River (R. Rezek, unpublished data).

The probability of migration for Snook has been reported to increase with fish size [63, 96], and scale samples were initially collected during tagging to determine age and estimate future growth. However, laboratory analyses conducted by the Florida Fish and Wildlife Conservation Commission have shown scales to be an unreliable method for ageing Snook [94]. Scale derived estimates consistently underestimated ages determined by otolith analysis by up to three years for fish younger than 10 years old, the period during which the most rapid growth has been recorded for the species [94]. In order to provide insight on the role of size in Snook migration, we followed the methods of Young et al. [59] and estimated a total length (TL) for each fish at the beginning of each spawning season. These length-age estimates were based on von Bertalanffy growth curves derived from otolith analysis of 7,970 Snook collected as part of a fishery-independent monitoring program on Florida's gulf coast, and are reported in stock assessments for the State of Florida [39, 94]. We first calculated an estimated age for each fish based on TL at the time of tagging, then projected growth to the beginning of each spawning season in which that individual was detected. Fish age at tagging was calculated using parameters from Taylor et al. [94] and the equation:

$$t = \frac{1}{K} \ln\left(\frac{L - L_t}{L}\right) + t_0$$

Where t = age of fish when tagged, K = growth coefficient for gulf coast Snook, L = asymptotic length, L_t = length at time of capture, and t_0 = hypothetical age for a fish at length zero. A "current" age was assigned as the estimated tagging age plus the time between tagging and the beginning of a new spawning season. The above equation was then transformed and solved to determine fish size in each subsequent year of detection (new L_t) as follows:

$$L_t = -1 * (L\big(\exp\big(K(t - t_0)\big) - L\big))$$

Modeling Seasonal Cues: When to Migrate?

To identify environmental factors that influence migration timing for Snook within a spawning season, we used a second set of binomial GLMMs to test our hypothesis that specific cues, namely changes in hydrologic conditions (water level, water level change, temperature, salinity), trigger the timing of migration. Here, the response was a binary variable (1/0) for each individual and detection day indicating the timing of downstream migration during spawning season (April 1-Nov 15). A response value of 1 indicated that an individual Snook had initiated a directed downstream movement into the lower river zone from either the upper river or Tarpon Bay on that day, and a 0 value was assigned to days where no migratory movements were detected. Because the focus of these models was to identify cues prompting migratory behaviors, only fish detected making a downstream migration were included in analysis. Further, migratory status (0 or 1) was only assigned to days where fish were detected on the array in order to not draw inference where data was not available. As with our models of annual migration primers, we first assessed the best variable or variables for the hypothesized driver. Second, we removed lower fit collinear variables based on AIC. Our process consisted of an additional step compared to the annual models, and we then considered a combination of variables within each hypothesized driver (Fig. 1, flow dynamics, other hydrologic/abiotic conditions, phenology) in order to examine the relative role of that driver in predicting migration probability. We used AIC to select either the best fitting variable or combination of variables for each hypothesized driver, and then combined all best fitting variables into a global model. Last, we reduced this global model using backward selection. A final model best able to explain the timing of Snook migrations was selected based on the lowest AIC, relative model weight, and amount of variance explained.

Our models for seasonal cues consisted of variables that evaluated the relationships between migratory timing and hypothesized environmental drivers quantifying flow, other hydrologic/abiotic conditions, and phenological cues (Fig. 1, Additional File 1 Table S2). For flow, in addition to mean daily water level, we included a variable for the daily water level change to test our hypothesis that changes in flow serve as an important migratory cue [32, 33]. We considered absolute water level change in early models, but this resulted in poor model performance relative to daily water level change, which differentiates between increases and decreases in water level. Mean daily temperature and salinity were selected to represent other important hydrologic/abiotic conditions that vary throughout the spawning season and could influence migratory timing, consistent with the hypothesized drivers from our annual primer models. We also included variables examining whether migration was influenced by environmental factors independent of in-river conditions. Both photoperiod and lunar cycle were used to indicate the presence of a fixed phenological migratory response to seasonality. Further, a variable for the year was included to assess the role of interannual variability in Snook migration, capture additional variance operating at annual scale but not related to other fitted variables, and match our annual primer models.

RESULTS

Migration Patterns: Intensity of Spawning Migration

Over the course of the study, 206 individual Snook were tagged ranging in size from 416 to 1,010 mm TL (mean 690 +/- 139 mm). The number of fish tagged per year ranged from 14 to 55 (mean 26). A total of 189 individuals were subsequently detected on the array after release (92% of all tagged fish). Of these, two individuals did not meet our detection criteria to provide inference on migratory movements (minimum of 10 unique detections in movement history) and were excluded from further analysis. One of these fish had only a single detection indicating a possible false detection, and data for the second fish contained a total of nine detections, all occurring within a 24-hour period. An additional fourteen fish had no detections occurring within any of the eight focal spawning seasons (between April 1 and November 15, 2012-2019).

In total, 173 Snook were detected in at least one spawning season. Of these fish, 90 individuals (52%) were detected making downstream migrations during the spawning season, with some fish detected migrating in multiple years. Of the migrants, 78 Snook were detected migrating in only a single spawning season, 11 individuals were detected migrating in two seasons, and one fish was detected migrating in three seasons. When accounting for detections in multiple years, 297 unique fish/year combinations (migrants and non-migrants) served as the basis for our annual primer models, with 103 observed migrations included in our seasonal cues models (Additional File 1 Table S3). The proportion of fish detected migrating in a single year (number of migrants / total number of fish detected each year) ranged from a high of 53% in 2012 and 2015 to a low of 11% in 2016, with a mean annual migration rate of 35% of detected individuals between 2012 and 2019 (Fig. 3a).

Migration Patterns: Timing of Spawning Migration

Snook initiated downstream migrations in all months of the spawning season. The temporal migration patterns varied strongly from year to year, but over the course of the study more fish migrated in April, May, and June than any other month, representing > 50% of all detected migrations (Fig. 3b, Additional File 1 Table S4). The greatest number of fish were detected migrating in June (21%), and the fewest in November (7%). May and June were the only two months where migrations were observed in each of the 8 years of the study.

We found two predominant movement types in migrating Snook. Slightly less than half of the migrants (43%) moved continuously from the upper river to the coast after initiating migration and were detected on the downstream-most receivers within 48 hours of departure (examples in years 2012, 2015-2019 of Fig. 4). The other individuals made rapid and directed downstream movements from the upper river to Tarpon Bay, paused, and were then detected on receivers within the bay for between 2 days and 1 week before continuing their migration into the lower river (57% of migrants, depicted in years 2013 and 2014 in Fig. 4).

Annual Primer Models: To Migrate or Not to Migrate?

After applying our 4-step model fitting protocol, five variables were selected for our global model (Table 1). After performing backward selection, the final model consisted of only two variables, drydown duration and fish size. This best model explained a comparable amount of model variance relative to the more complex global model (R-squared 0.276 and 0.299 respectively), but with a lower AIC score. Comparisons of all models indicated a substantially higher weighting for the reduced model (AIC weight = 0.9466) relative to any univariate model or the global model. A univariate model for drydown duration explained >20% of model variance, outperforming all other variables. Both predictors from the final model indicated a significant positive relationship to annual migration probability (Table 2), with the proportion of fish migrating increasing with both drydown duration and fish size (Fig. 5).

Seasonal Cues Models: When to Migrate?

After assessing the individual and combined effects of variables for each of our hypothesized drivers affecting the timing of Snook migration, six variables were selected for the global model (Table 3). High values for collinearity (Pearson coefficient > 0.06) were not present for any variable pairings, thus variable selection for the global model was based on AIC. For flow, the best model (lowest AIC) was a combination of both water level and daily water level change. A combined model was selected for additional hydrologic/abiotic cues and included both temperature and salinity. For the variables representing a phenological response, we selected the model containing only lunar cycle. AIC was within 2 points of a combined model also including photoperiod, although photoperiod was not statistically significant ($p = 0.09$). Therefore, we chose the simpler model to combine into a global model. Additionally, a variable for the year of migration was included in the global model.

When these variables were included as covariates and reduced by backward selection, the best model included all variables except lunar cycle (Table 3). These two models were within 2 AIC points of each other indicating comparable performance; however, lunar cycle was not significant in the model ($p = 0.06$) and both models explained nearly the same amount of model variance (R-squared ~ 0.32 for both models). Thus, the simpler reduced model containing covariates for water level, daily water level change, temperature, salinity, and year was selected as our best model (Table 3). A large proportion of the model variance was explained by the variables for water level and daily water level change, which accounted for > 29% of variance. In the final model, coefficients for water level, daily water level change, and salinity showed a significant positive relationship with the probability of migration, whereas temperature showed a weak negative correlation (Table 4). These results indicate that the probability of Snook initiating downstream migrations during the spawning season increases with water level, daily water level change, and salinity, and migration probability decreases with temperature (Fig. 6).

DISCUSSION

In this study, we investigated how environmental variability at multiple temporal scales affects spawning migrations, and how annual primers which maximize migratory intensity (the proportion of the population that migrates each year) and seasonal cues that trigger migration timing interact to explain the interannual variation in the migratory response. Our results illustrate the complexity of migratory behaviors, and that decisions to migrate or not are influenced by a combination of factors that differ from those that affect when to migrate. We found correlations between Snook spawning migrations and hydrologic patterns at both interannual and seasonal scales. The proportion of Snook migrating increased in years with a longer drydown duration (specifically, the number of days with marsh water levels below 30 cm) before the spawning season, which we hypothesize is associated with enhanced feeding opportunities for floodplain prey [38, 46, 47] and results in increased energy reserves that promote migration/spawning. This suggests that water levels preceding the spawning season are an important primer for migration in the Shark River, influencing the population-level response and driving year-to-year variability in spawning, whereas water level and positive rates of change in water level (i.e., high flow events) cue the timing of migratory movements. These results add to a growing body of evidence that seasonality in the flow regime and river/floodplain dynamics are a central factor in the behavior and ecology of many coastal fishes [20-22, 97-99], yet provide an unusually detailed understanding of the dependency of spawning migrations on hydrological drivers, by pairing long-term tracking and environmental data.

While we documented a high degree of interannual and seasonal variability in the migration pattern of acoustically tagged Snook and its dependency on hydrological drivers, we recognize limits to the interpretation of our results. First, a small proportion of the population was tagged, and although samples sizes were large and adequate for multiyear analyses, they may or may not be representative of the migration patterns of the entire population. Second, because our study consisted of multiyear data and drew inference from movement patterns occurring months/years after tagging (i.e., a downriver movement to the coast constituted a spawning migration), we were not able to assess the reproductive status of tagged fish migrating each year. Moreover, we did not directly measure Snook activity along the coast where spawning aggregations may occur and were unable to confirm spawning for migrating fish. However, previous studies have shown that movements from rivers to marine areas correspond to reproductive readiness (e.g., oocyte development or postovulatory follicle sampling), suggesting that downstream migration during the spawning season can be used to indicate spawning activity [57, 79]. Further, Snook are protandrous hermaphrodites, and some skipped spawning may be related to lower energy reserves in newly transitioned females [57]. We were not able to sex tagged fish, and some individuals likely transitioned from male to female over the study period. Sex has been shown to influence spawning patterns and behaviors in Snook [59], and future work able to incorporate sex into models of migratory probability would offer valuable insight. We also acknowledge that cumulative hydrologic variation occurring at timescales longer than the daily changes included in our models could contribute to migratory timing (i.e., lagged effects). However, using daily data consistently resulted in the best model performance (lower AIC), suggesting the importance of discrete environmental cues in triggering migrations. Further, hydrological alterations affect many rivers inhabited by Snook, and these alterations may mute the environmental dependencies observed in the Shark River. Last, previous work has documented the presence of multiple contingents in Florida Snook, including riverine, coastal, and offshore marine segments of the population [42, 43], and we acknowledge that the marked dependency of spawning on freshwater flows may only apply to riverine Snook.

The presence of distinct spawning groups has been observed in other migratory fishes. Secor et al. [100] reported staggered migration timing for Striped Bass (*Morone saxatilis*) in the Hudson River, USA. Further, Koster et al. [15] found differences in migration timing for Australian Grayling. Distinct groups of tagged fish responded to separate high flow events within a single spawning season, and there was considerable variation in the proportion of Australian Grayling migrating each year (18-85% of tagged fish detected migrating annually). Differences in migration timing may be an adaptive strategy to account for environmental variation and temporal differences in spawning success, resulting in a portfolio effect that provisions for greater population stability over time [101].

Our results indicate a protracted spawning period for Snook, with migrations occurring in all months of the spawning season, consistent with patterns previously reported for the species [34, 43, 58, 59]. Yet, most of the spawning migrations were observed in earlier months (>50% migrated April-June). The decision to spawn earlier or later in the season may offer distinct advantages for Snook. Earlier spawn times may provide juveniles a longer summer growing season where growth rates have been reported to be twofold higher relative to colder winter periods [1 cm/day vs .5 cm/day, 54]. Predation risk declines with size for juvenile Snook, and increased growth may enhance overall survival for fish spawned earlier in the season [102]. However, late-season spawning provides greater access to flooded nursery habitats offering protection from predators, including adult Snook that have not yet migrated and may cannibalize juveniles [103].

Annual Primers: To Migrate or Not to Migrate?

Our results suggest a high frequency of skipped spawning in tagged Snook in the Shark River. Skipped spawning has been well documented in Florida Snook populations, although the proportion varies among systems and years [34, 57, 58]. Our annual frequencies of between 11% to 53% of Snook migrating are in line with the annual migration/skipped spawning frequencies previously reported (24-40%) but suggest a higher degree of interannual variation in the Shark River [34, 57, 58]. This may be partly explained by the longer timespan of our data which encapsulates a broader range of hydrologic variation relative to previous studies. Similar patterns of skipped spawning have also been described for Striped Bass [104], prochilodontids [32], and Australian Bass [24]. Our findings suggest that the extent of skipped spawning may be related to environmental primers in advance of the spawning season which influence migration, namely marsh drydown duration. Further, we found that fish size positively correlated with migration probability. This relationship to size has been previously reported for Snook, and for other migratory species including Barramundi in Australia and Striped Bass in Chesapeake Bay [58, 59, 100, 105]. Both drydown duration, which affects access to freshwater prey resources, and fish size can indicate available energy resources, suggesting that energy status may serves as key factor in the decision to migrate each year.

Skipped spawning, rather than an anomaly, appears to be quite common among fishes and may serve as an adaptive behavior that can help maximize lifetime reproductive potential and mitigate for environmental variability [9, 13, 106]. Models using data from a wide range of migratory taxa indicated that skipped migrations were associated with environmental stochasticity, and the increased risk of a bad year leading to lowered fecundity and poor recruitment [35]. This hypothesis may be supported by the considerable variation in hydrological conditions in the Shark River (Additional File 1 Fig. S1), including droughts (2015) and prolonged flooding (2016, 2018). A study of Arctic Haddock (*Melanogrammus aeglefinus*) proposed that skipped spawning was related to body condition, and that lower energy reserves increased the probability of skipping [14]. For Snook, access to freshwater prey originating in floodplain marshes provides an important resource in the months prior to spawning [38, 47, 48, 107]. Our models indicate that drydown duration was a key variable explaining the annual proportion of Snook migrants. In the Shark River, hydrological variation is common and results from large-scale climatic events such as flooding/droughts accompanying El Niño and AMO cycles, from tropical storm, and from freshwater management decisions [64, 70]. This variation can influence both the timing and extent of the marsh prey pulse entering the river channels. In our data, years with the highest migration had the longest marsh drydown. Years with exceptionally low migration (2016, 2018) dried only briefly prior to the spawning season, and/or showed little seasonal variation in water level. We hypothesize that this drydown duration represents access to the freshwater prey pulse established by past research [38, 46, 47]. We suspect that a gradual prolonged drydown with higher prey concentrations in the river channels directly increases Snook energy reserves, resulting in higher proportions of migrants. Conversely, in years where the marshes dry only briefly, or not at all, available energy reserves are lowered and increase the prevalence of skipped spawning. Future work aims to better link this dry season prey pulse to Snook body condition and spawning activity.

Seasonal Cues: When to Migrate?

Variation in river flow (both water level and daily water level change) was a primary cue driving the downstream migration timing of Snook. This is consistent with other studies of riverine fishes. Prochilodontids and large catfish in Brazil, long-lived eel species in New Zealand, Barramundi in Australia, and Australian Grayling undertake long-distance river migrations to spawning grounds at the onset of the rainy season, and like our findings, positive increases in water level were reported to trigger the initiation of migratory movements [15, 20, 29-33]. Harding et al. [24] also reported that high flows serve as migratory cues for Australian Bass, noting that not all fish responded to the same flow cue and multiple high flow events during the spawning season may increase the total number of individuals migrating. A migratory response to flow cues may serve as an adaptive behavior whereby elevated water levels signal the availability of high-quality juvenile rearing areas. In Australian rivers, for example, the growth rates of juvenile Barramundi increase with access to floodplain-derived resources which only become available during episodic and relatively short-duration seasonal flooding, yet account for a substantial portion (30-40%) of their diet [28, 99].

Salinity and temperature contributed to predicting the Snook migratory response in our models but explained only a small portion of model variance relative to water level and daily water level change. Temperature has been linked to the spawning activity of migratory fishes in other systems, but its relative role as a migratory cue varies. Legett et al. [16] reported that water temperature was the most consistent predictor of migratory abundance of River Herring (*Alosa* spp.) in Massachusetts. Daily increases in spring water temperature corresponded to increases in migratory activity. Conversely, Secor et al. [100] examined temperature as a driver of Striped Bass migration in the Hudson River, but concluded that while temperature did influence run timing (migration activity increased with increasing spring water temperatures), it was not tightly coupled with the migratory response and spawning was detected over a wide range of temperatures.

In Florida, Common Snook exist at the northern extent of their range and low winter water temperatures (< 10 C) can be lethal [40, 46, 108]. As a tropical species, maximum water temperature currently presents less of a threat to Florida Snook but may have some influence on reproductive timing and range expansion as waters warm under climate change. The upper thermal limits have been reported at approximately 35-42 C, with thermal preferences ranging from 26-29 C [109, 110]. Taylor et al. [56] noted that the reproductive season corresponds to periods where water temperatures are maximal, which could influence the timing of spawning for Snook. Roberts et al. [111] also suggested that an interaction between temperature and day length may play a role in stimulating gametogenesis and maturation in Snook. Conversely, Hernández-Vidal [112] did not find a strong relationship between temperature and gonadal development in

Snook. However, low temperatures indicative of non-spawning periods were associated with lower levels of sex hormones, perhaps signaling end of spawning season.

Importance to Management

Annual variation in skipped spawning frequencies resulting from differences in hydrologic conditions could affect estimates of the reproductive potential of fish populations in stock assessments. For example, the spawning potential ratio (SPR, the total number of adult fish that remain in the population after accounting for harvest) is used by fisheries managers to represent reproductive potential in a given year [113, 114]. SPR may become highly variable if a large portion of the population does not reproduce annually. Skipped spawning is not currently incorporated into Snook stock assessments in Florida [39], and an improved understanding of how temporal and spatial variations affect skipped spawning would allow SPR estimates to be calibrated based on hydrologic conditions. While our models were not assessed for predictive performance, our results illustrate a high degree of interannual variability in skipped spawning, suggesting that this variation may be appropriate to consider in future estimates of reproductive potential for Snook and other species that undertake reproductive migrations.

Findings from this study could also provide water managers information that informs controlled freshwater releases that provision for ecological function in regulated systems. For example, Koster et al. [30] showed that Australian Grayling migrate downstream during both increasing and decreasing discharge surrounding high flow events, but that fish ceased migration once water levels stabilized, indicating that short duration flow releases may not be sufficient for complete migration. Harding et al. [24] also noted a similar pattern for Australian Bass; while many fish undertook uninterrupted downstream migrations to spawning sites during increased flow, some individuals moved only part of the way downstream and required multiple high flow events to navigate barriers and reach downstream spawning grounds. Thus, increasing the number of high flow events in a single season could maximize the total number of spawning fish. We observed similar patterns in our tagged Snook, with roughly half of the migrating fish demonstrating staged migrations consisting of rapid directed movements from the upper river to Tarpon Bay, followed by a second movement event to the coast separated by days/weeks.

Quantitative descriptions of flow requirements that promote migration, reproduction, and recruitment could be used to provide conditions that enhance fisheries production. For instance, environmental flows designed to promote the migration and spawning of Australian Grayling have been informed and adapted by research revealing key flow characteristics [15]. Flow patterns initially set to trigger spawning activity were adjusted to also include cues promoting migration. In South Florida, flow patterns and water releases are highly managed for urban uses, agriculture, and flood control. Managed freshwater releases that incorporate both seasonal drawdowns maintaining access to important prey resources, coupled with pulsed increases in water level triggering migration during the spawning season, can assist in providing both the primers and cues influencing the spawning migrations of Snook.

Our study, though informative, accounts for only 27.6 % of the variance in interannual migration frequency and 31.6 % of the variance in migratory timing. However, there are areas which could help explain additional model variance. Energy status can play a key role in the decision to migrate [13, 14], and future research could expand on previous work by explicitly linking temporally variable prey landscapes and energy status to migration. Another emerging direction in studies of migration is how social cues and interactions may affect migration [115]. In many cases, migration can be a collective decision and migrating as a group can assist in navigation, conserve energy through schooling behaviors, and provide safety in numbers from predators [6, 116, 117]. For example, Furey et al. [118, 119] described how the migratory success of salmon smolts was tied to outmigration density and increased survival when high numbers increased the ability of individual fish to evade predation. Future research should focus on the role of energy status, social cues, and density dependence to provide additional insight on migratory behaviors to assist in fisheries management.

CONCLUSION

We provide evidence of how flow patterns influence migratory behavior at multiple temporal scales, serving as both environmental primers promoting the intensity of the migratory responses and seasonal cues that influence the timing of spawning migrations. Importantly, our results emphasize the critical role of long-term movement data, which can reveal patterns not apparent in shorter-duration studies and provide relevant information to natural resource managers seeking to enhance conservation efforts.

Water management, restoration efforts, and climate change are all predicted to contribute to hydrologic changes in the future [120, 121]. Shifts in environmental conditions can affect important primers and cues that influence the movements and reproductive success of migratory species [9, 100]. In Florida, analysis of long-term precipitation records suggests a shortening of the wet season, and the historic bi-modal summer rainfall patterns may become unimodal [70]. This may alter migration timing and the duration of the spawning season for species like Snook. Sea level rise threatens to increase salinities in what are currently freshwater habitats of the Everglades. Water management practices that increase freshwater inputs from the north to keep salinity at bay could increase water depth and marsh flooding duration [120]. Conversely, shifts in atmospheric teleconnections (i.e., the AMO) that decrease future rainfall could result in shallower marsh depths, and decrease the abundance of freshwater prey [64, 107, 121]. Water management can mitigate potential climate impacts, and as conditions shift under climatic change, understanding how these changes will affect animal migration and the consequences for population trends can inform conservation efforts aimed at preserving valuable fisheries. Providing natural resource managers with quantitative descriptions of both the primers and cues that influence spawning migrations can assist in maximizing reproduction and recruitment for ecologically, economically, and culturally important species, such as the Common Snook.

AVAILABILITY OF DATA AND MATERIALS

The acoustic telemetry datasets generated and analyzed during the current study are available through the Florida Coastal Everglades Long Term Ecological Research Program under the Environmental Data Initiative [122].

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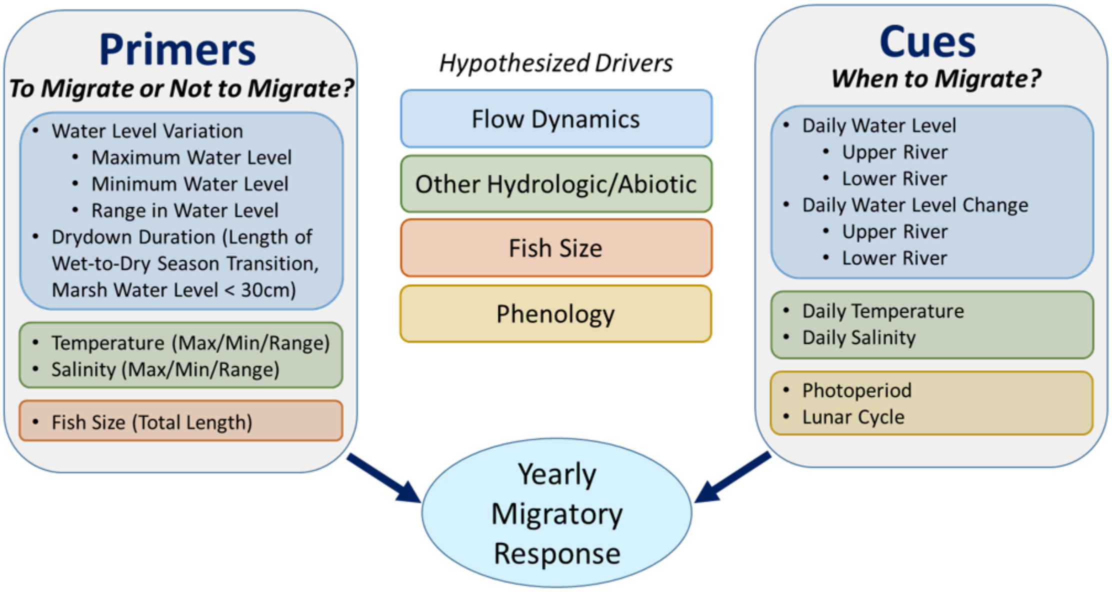

Fig. 1: Conceptual and analytical framework to investigate the environmental drivers of Common Snook migration at multiple temporal scales. We hypothesize that migration results from a combination of pre-spawning environmental conditions influencing the proportion of fish that migrate (primers), and environmental cues that determine the timing of migrations within a spawning season.

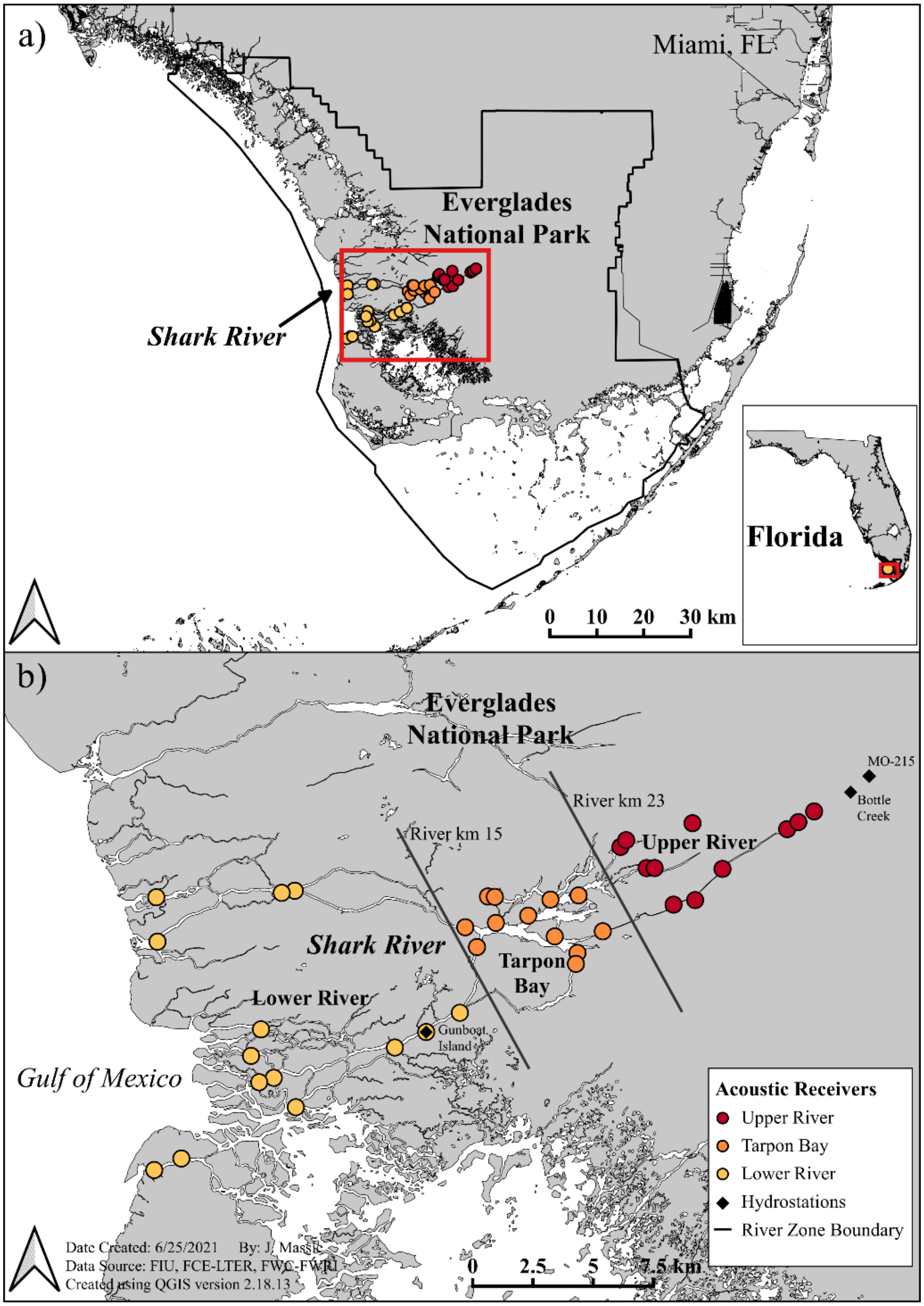

Fig. 2: Map of the study area in Everglades National Park. Panel a) shows the location of the Shark River in SW Florida, and panel b) depicts the configuration of the acoustic array used to monitor the movements of Common Snook. Black lines indicate delineation between different river zones used to identify migrations of Common Snook (upper river, Tarpon Bay, lower river), colored circles indicate the placement of acoustic receivers and river zone designation, and black diamonds show the location of hydrologic monitoring stations where environmental conditions were measured.

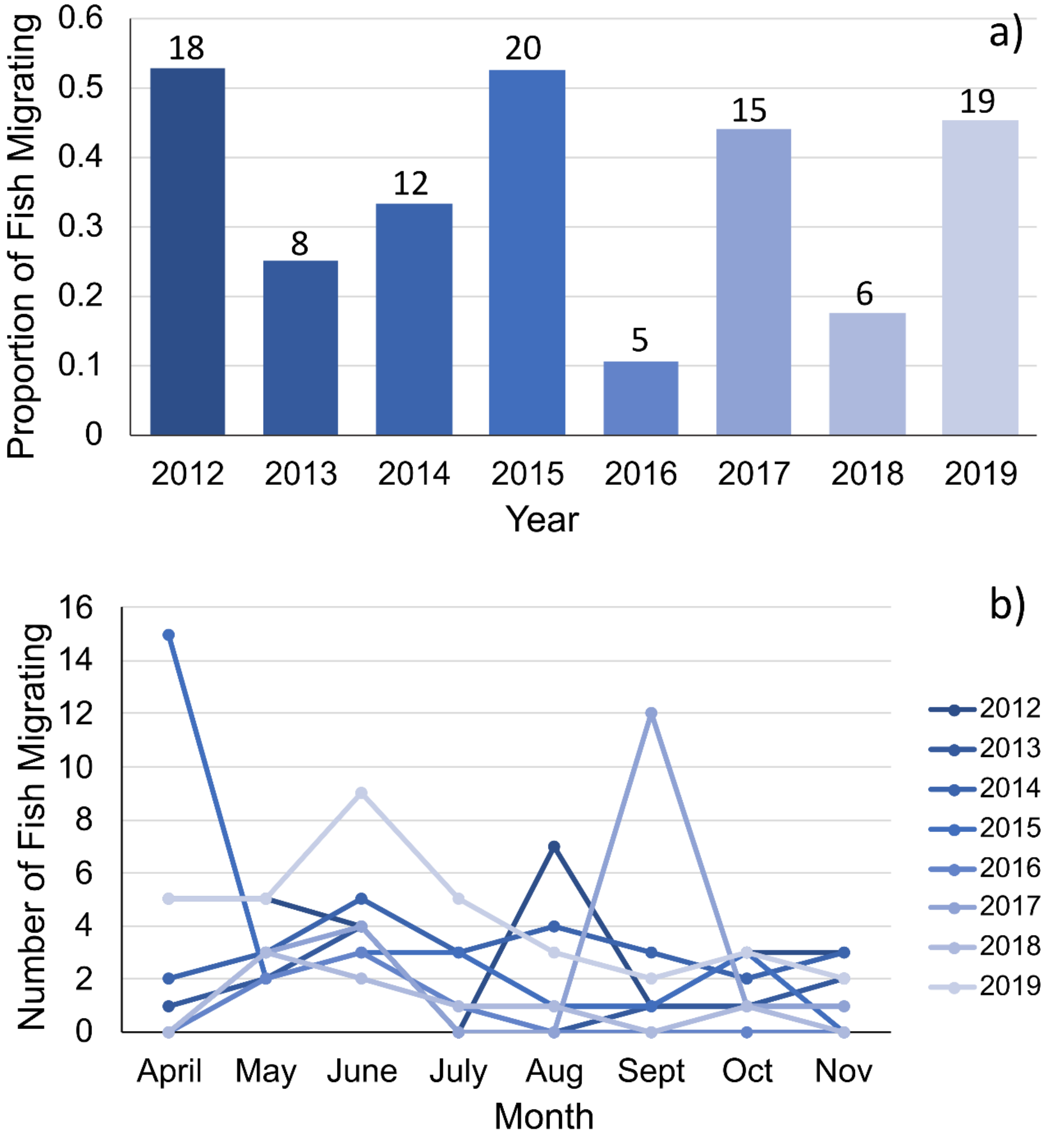

Fig. 3: Illustration of the high degree of interannual and seasonal variability in both the proportion of tagged Common Snook migrating each year, and the timing of migration within each spawning season. Panel a) depicts the proportion of fish observed migrating in each year of the study, ranging from 11% in 2016 to 53% in 2012 and 2015, with the total number of individual migrants detected each year noted above each bar. Panel b) illustrates the protracted migration period, with migrations occurring in all months of the spawning season. Each year is color coded and consistent between panels a) and b). See Additional File 1 Tables S3 and S4 for additional information.

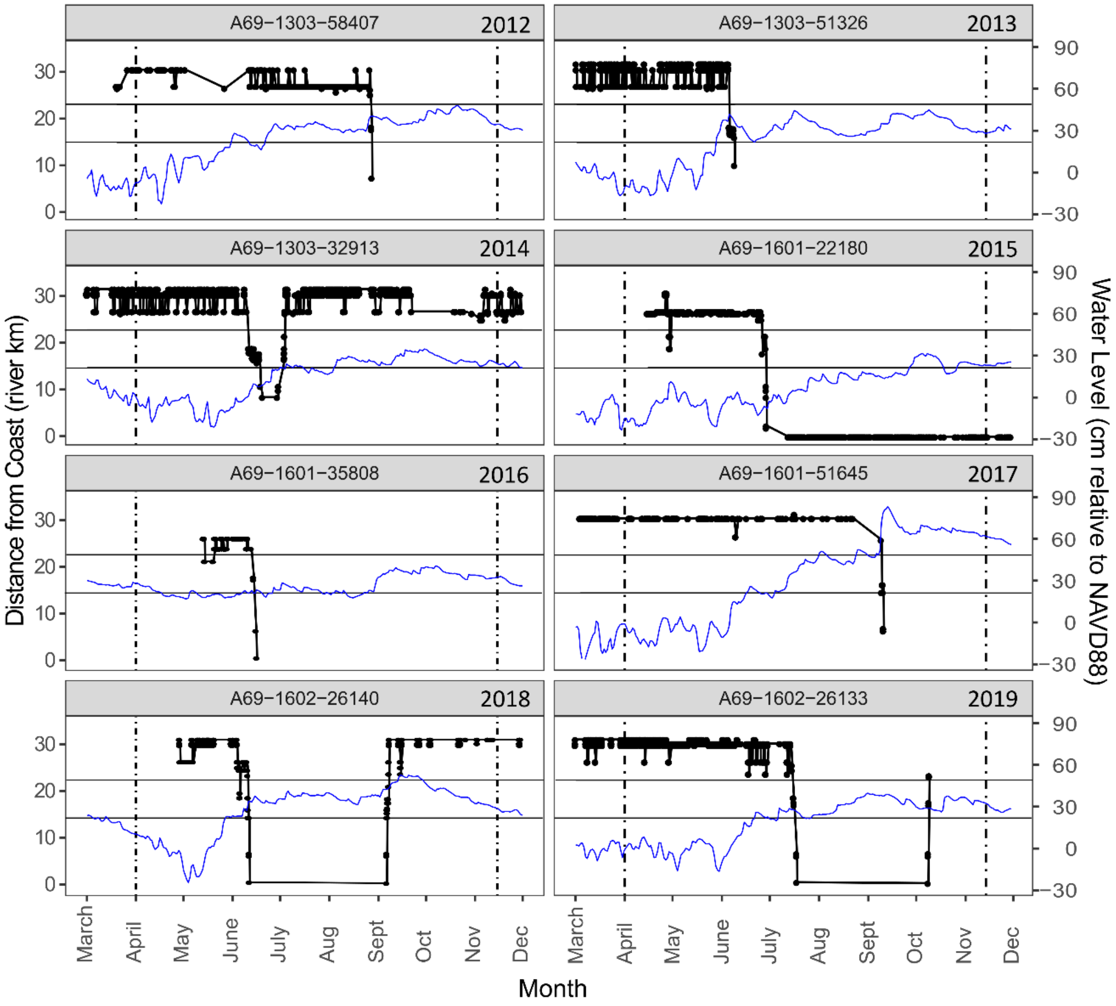

Fig. 4: Examples of individual movement tracks from acoustic detections of tagged Common Snook (fish ID number noted in each panel) showing downstream migrations during the spawning season. Solid blue lines show the measured water level at Bottle Creek in the upper river for each year. Horizontal black lines at river km 23 and 15 delineate zones boundaries between the upper river (> 23 river km), Tarpon Bay (15-23 river km), and the lower river (< 15 river km, per Figure 1), and vertical hashed lines mark the beginning and end of the spawning season (April 1-Nov 15).

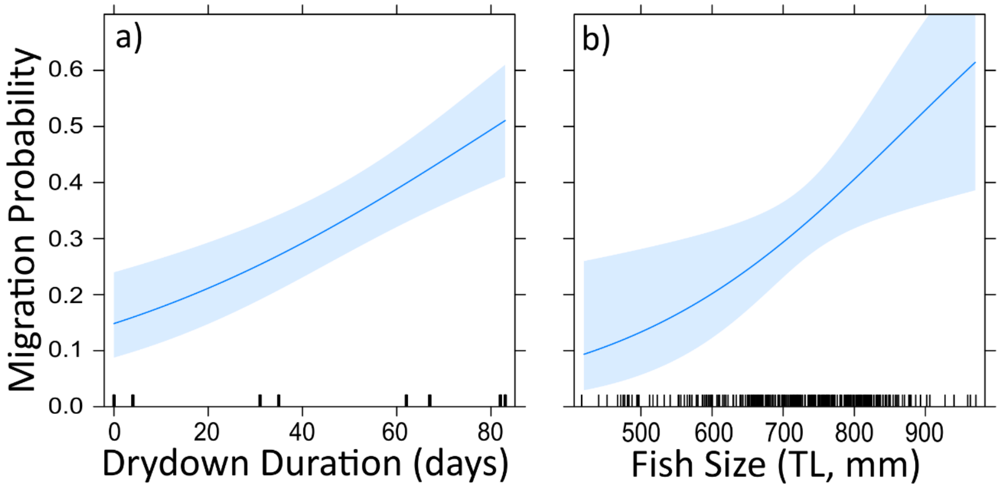

Fig. 5: Plotted variables for the best-fitting logistic regression model (Drydown Duration + Fish Size) for the annual migratory intensity of Common Snook bounded by a 95% confidence interval. Individual effects of each variable kept in the best model in Table 1 are assessed by holding the other variables at a fixed mean value. Together these variables explain 27.6% of the variability in the proportion of tagged fish migrating each year.

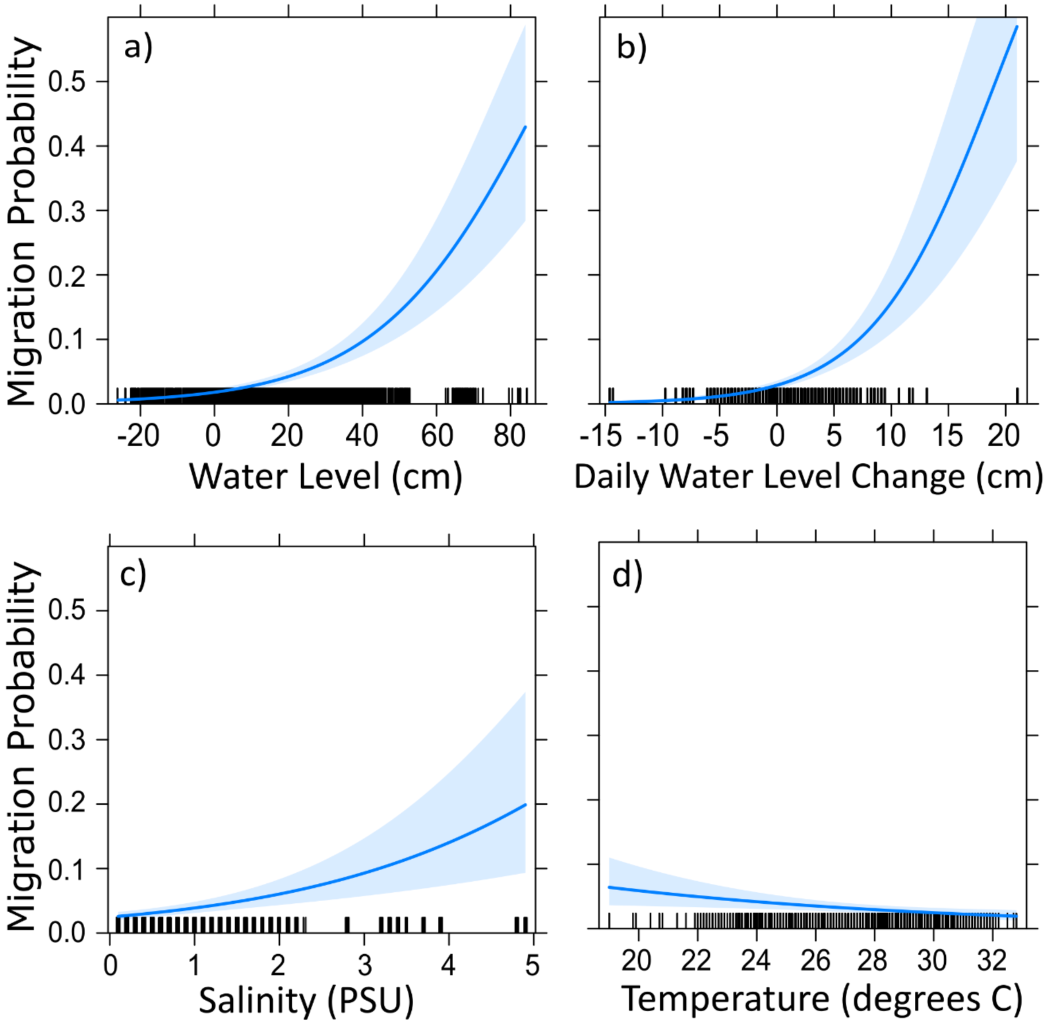

Fig. 6: Plotted variables for the best-fitting logistic regression model for the daily environmental cues predicting downstream migration timing for Common Snook during the spawning season bounded by a 95% confidence interval. Individual effects of each variable kept in the best model shown in Table 3 are assessed by holding the other variables at a fixed mean value. Together these variables explain 31.6% of the variability in the timing of migration within the spawning season. Water levels in panels a) and b) reflect gauge height relative to NAVD 88 from the Bottle Creek monitoring station.

Table 1: Model selection results based on lowest AIC value from GLMM models examining the drivers of annual migratory intensity (migratory primers) for Common Snook. The response variable for models is whether each individual fish was detected migrating or not migrating each year, across all eight years of tracking. For variable descriptions see Additional File 1 Table S1.

Hypothesized Driver	Model Variables	df †	AIC	ΔAIC ‡	AIC Weight	Conditional R^2	Marginal R^2
Flow Dynamics	Minimum Water Level	3	364.3	13.0	0.001	0.175	0.122
	Drydown Duration	3	359.4	8.1	0.017	0.204	0.135
Other Hydrologic/Abiotic Conditions	Maximum Temperature	3	379.0	27.7	< 0.001	0.079	0.048
	Salinity Range	3	369.7	18.4	< 0.001	0.147	0.083
Fish Size	Fish Size	3	372.6	21.3	< 0.001	0.151	0.085
Global Model	Minimum Water Level + Drydown Duration + Maximum Temperature + Salinity Range + Fish Size	10	357.9	6.6	0.035	0.299	0.234
Best Model	**Drydown Duration + Fish Size**	**4**	**351.3**	**0**	**0.947**	**0.276**	**0.197**

† Model degrees of freedom; ‡ Difference in AIC score between each model and lowest AIC model

Table 2: Summary statistics for the best GLMM model predicting the intensity of annual Common Snook migration (see Table 1). Results show a positive significant relationship between the proportion of fish migrating annually and the length of the transitional marsh drydown period prior to the spawning season (drydown duration) plus fish size.

Variable	Beta	SE	z-value	p-value
(Intercept)	-5.333	1.472	-3.622	< 0.01
Drydown Duration	0.022	0.005	4.371	< 0.01
Fish Size	0.005	0.002	2.593	< 0.01

Table 3: Model selection results based on lowest AIC value from GLMM models examining the environmental cues for Common Snook migration during the spawning season. The response variable is a binary indicator of whether or not each fish was detected migrating for each day detected. For variable descriptions see Additional File 1 Table S2.

Hypothesized Driver	Model Variables	df[†]	AIC	ΔAIC[‡]	AIC Weight	Conditional R^2	Marginal R^2
Flow Dynamics	Water Level	3	2082	144.2	< 0.001	0.265	0.119
	Daily Water Level Change	3	2051	112.8	< 0.001	0.119	0.086
	Water Level + Daily Water Level Change	4	1980	41.5	< 0.001	0.292	0.175
Other Hydrologic/Abiotic Conditions	Temperature	3	2174	235.3	< 0.001	0.042	0.006
	Salinity	3	2171	233.1	< 0.001	0.042	0.006
	Temperature + Salinity	4	2169	230.6	< 0.001	0.039	0.012
Phenology	Day Length	3	2176	237.6	< 0.001	0.053	0.003
	Lunar Cycle	3	2175	236.3	< 0.001	0.051	0.005
	Day Length + Lunar Cycle	4	2174	235.6	< 0.001	0.058	0.008
Interannual Variation	Year	9	2174	235.9	< 0.001	0.061	0.024
Global Model	Water Level + Daily Water Level Change + Temperature + Salinity + Lunar Cycle + Year	14	1938	0	0.680	0.319	0.247
Best Model	**Water Level + Daily Water Level Change + Temperature + Salinity + Year**	**13**	**1940**	**1.6**	**0.320**	**0.316**	**0.245**

† Model degrees of freedom; ‡ Difference in AIC score between each model and lowest AIC model

Table 4: Summary statistics for the best GLMM model (see Table 3) predicting the timing of Snook migration relative to daily environmental cues. Results show a positive significant relationship between the probability of fish initiating downstream migration and the daily water level, water level change, and salinity, and a negative relationship with temperature.

Variable	Beta	SE	z-value	p-value
(Intercept)	-1.483	0.901	-1.647	0.10
Water Level	0.044	0.005	9.338	< 0.01
Daily Water Level Change	0.184	0.021	8.568	< 0.01
Temperature	-0.090	0.033	-2.724	< 0.01
Salinity	0.466	0.102	4.571	< 0.01

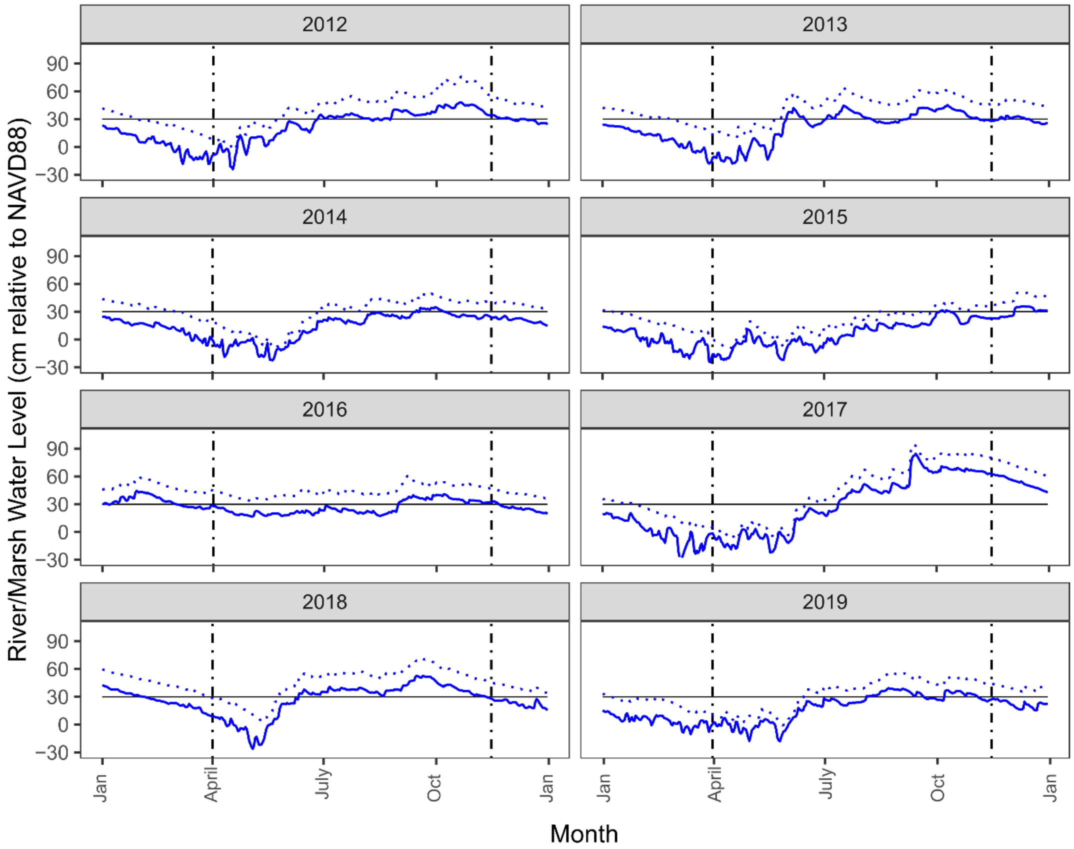

Fig. S1: Annual hydrographs for two monitoring stations in the Shark River from 2012 to 2019 illustrating the high degree of interannual variability in flow timing and magnitude. Solid blue lines show water levels at Bottle Creek in the upper river and dotted lines reflect water level in the adjacent freshwater marshes at station MO215 (see Fig. 2b for station locations). Vertical hashed lines indicate the beginning and end of the spawning season (April 1-Nov 15) used in statistical models, and the solid horizontal line shows the 30 cm water depth corresponding to the beginning of the wet/dry transitional period and marsh prey concentration in the river channels.

Table S1: Variables considered and selected for use in GLMMs for hypothesis 1, that interannual differences in hydrologic conditions preceding the spawning season (migratory primers) contribute to the intensity of the Common Snook migratory response at a broad temporal scale. Model variables are organized by hypothesized drivers, and bolded variables indicate those included in our global model, which were selected from collinear variables using lowest AIC.

Hypothesized Driver	Model Variable	Description
Flow Dynamics	Maximum Water Level	Maximum dry season water level in the upper river (cm)
	Minimum Water Level	Minimum dry season water level in the upper river (cm)
	Water Level Range	Dry season water level range in the upper river (Max - Min)
	Drydown Duration	Number of days during the spring drydown preceding spawning season where marsh water level at station MO215 was < 30 cm
Other Hydrologic/Abiotic Conditions	***Maximum Temperature***	Maximum dry season water temperature in the upper river (degrees C)
	Minimum Temperature	Minimum dry season water temperature in the upper river (degrees C)
	Temperature Range	Dry season water temperature range (Max - Min)
	Maximum Salinity	Maximum dry season salinity in the upper river (PSU)
	Minimum Salinity	Minimum dry season salinity in the upper river (PSU)
	Salinity Range	Dry season salinity range (Max - Min)
Fish Size	***Fish Size***	Total length (cm) of tagged Common Snook at the beginning of each spawning season

Table S2: Variables selected for use in GLMMs for hypothesis 2, that specific cues trigger Common Snook migration timing during the spawning season. Model variables are organized by hypothesized drivers and evaluate the relative role of flow dynamics, other hydrologic/abiotic factors, seasonality, and interannual variability in migration timing.

Hypothesized Driver	Model Variable	Description
Flow Dynamics	Water Level	Mean daily water level in cm recorded at monitoring station in the upper river at Bottle Creek
	Daily Water Level Change	Daily rate of change in water level (Current day mean - previous days mean)
Other Hydrologic/Abiotic Conditions	Temperature	Mean daily water temperature in the upper river (degrees C)
	Salinity	Mean daily salinity in the upper river (PSU)
Phenology	Photoperiod	Total hours of daylight
	Lunar Period	Numeric variable indicating the fraction of the lunar period from the full moon on that day
Interannual Variation	Year	Calendar year of spawning season

Table S3: Number of new acoustic tags deployed in the Shark River for each year of the study, the number of individual Common Snook detected during the spawning season, the number of individuals detected making a coastal migration on the acoustic array, and the annual proportion of detected fish that migrated. [†]Note: a portion of individuals were detected in multiple years, and summed annual detections include repeat observations for some fish.

Year	# New Tags Deployed	# Snook Detected	# Snook Migrating	Proportion Migrating
2012	44	34	18	0.53
2013	17	32	8	0.25
2014	20	36	12	0.33
2015	21	38	20	0.53
2016	55	47	5	0.11
2017	14	34	15	0.44
2018	21	34	6	0.18
2019	14	42	19	0.45
Total	206	297[†]	103	

Table S4: Number of Common Snook migrations detected by month and year from 2012-2019. Detections reflect individuals making directed movements from the upper river/Tarpon Bay into the lower river during the spawning season (April 1 – Nov. 15). Numbers include individuals that were detected migrating on multiple days, or those making repeat migrations within a spawning season. The proportion of total detected migrations for all years of the study are summarized by month.

Year	April	May	June	July	Aug	Sept	Oct	Nov
2012	5	5	4	0	7	1	3	3
2013	1	2	4	0	0	1	1	2
2014	2	3	5	3	4	3	2	3
2015	15	2	3	3	1	1	3	0
2016	0	2	3	1	0	0	0	0
2017	0	3	4	0	0	12	1	1
2018	0	3	2	1	1	0	1	0
2019	5	5	9	5	3	2	3	2
Proportion	0.17	0.16	0.21	0.08	0.1	0.12	0.09	0.07

CHAPTER III

GOING DOWNRIVER: PATTERNS AND CUES IN THE HURRICANE-DRIVEN MOVEMENTS OF COMMON SNOOK IN A SUBTROPICAL COASTAL RIVER

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ABSTRACT

Extreme climate events such as hurricanes can influence the movement and distribution of fish and other aquatic vertebrates. However, our understanding of the scale of movement responses and how they vary across taxa and ecosystems remains incomplete. In this study, we used acoustic telemetry data to investigate the movement patterns of common snook (*Centropomus undecimalis*) in the Florida Coastal Everglades during Hurricane Irma, which made landfall on the southwest Florida coast as a Category 3 storm on 10 September 2017 after passing in close proximity to our study site. We hypothesized that the hurricane resulted in shifts in distribution, and that these movements may have been driven by environmental cues stemming from changes in barometric pressure associated with hurricane conditions, fluctuations in water levels (stage) characterizing altered riverine conditions, or a combination of both hurricane and riverine drivers. The data revealed large-scale movements of common snook in the time period surrounding hurricane passage, with 73% of fish detected moving from the upper river into downriver habitats, and some individuals potentially exiting the river. Furthermore, regression model selection indicated that these movements were correlated to both hurricane and riverine conditions, showing increased common snook movement at higher river stage and lower barometric pressure, and stage explaining a larger proportion of model deviance. Animal movement has widespread and diverse ecological implications, and by better understanding the factors that drive movement, we may anticipate how future extreme climate events could affect fish populations in impact-prone regions.

INTRODUCTION

Understanding animal movement is a central concern in ecology. The spatiotemporal dynamics of movement influence the structure and function of populations, communities, and ecosystems, with implications ranging from the survival of individuals to the flow of energy through food webs (Nathan et al. 2008; Earl and Zollner 2017). Animals frequently move in response to predictable or recurrent physiological or environmental cues, including factors related to interspecific interactions, changing habitat requirements, or migration into breeding areas (Bowler and Benton 2005; Hussey et al. 2015; Secor 2015). However, animal movements and space use can also be driven by unpredictable disturbances or abrupt environmental changes. These rapid shifts in the distribution of animal populations may lead to stressful conditions, a mismatch in resources, or changes in the timing of life history events (Durant et al. 2007; Jones and Cresswell 2010; Hazen et al. 2013).

Tropical storms and hurricanes are examples of extreme climate events (ECE), previously shown to influence the movement patterns of organisms in marine and coastal environments (Heupel et al. 2003; Liu et al. 2010; Udyawer et al. 2013; Bailey and Secor 2016; Strickland et al. *this volume*). Advances in technology and the increased use of acoustic telemetry have propelled our ability to track animal movements; however, our understanding of the scale of movement responses across taxa, and of the environmental cues prompting these movements across events and ecosystems remains incomplete (Hussey et al. 2015; Bailey and Secor 2016; Secor et al. 2018). Models have predicted increased intensity of hurricanes with warming temperatures associated with climate change (Meehl et al. 2000; Hobday and Lough 2011; Walsh et al. 2015; Keellings and

Hernández Ayala 2019). Thus, there is a need to better understand the potential costs and benefits of ECE on animal distributions in order to inform conservation and management decisions in impact-prone coastal regions.

Previous studies have documented shifts in the movement patterns and distributions of aquatic vertebrates in response to hurricanes. Flight behaviors (i.e., rapid and directed movements) have been documented in sharks and sea snakes, with animals moving from shallow habitats in advance of approaching storms (10 to 24 hours), and into deeper offshore areas that may increase survival (Heupel et al. 2003; Liu et al. 2010; Udyawer et al. 2013; Strickland et al. *this volume*). Other studies have observed that evacuations associated with hurricanes are partial, with only a portion of the monitored individuals leaving during a hurricane, or spatially-dependent responses, with the probability of moving varying as a function of the initial location within a habitat (Bailey and Secor 2016; Secor et al. 2018; Bacheler et al. 2019). In some cases, fish movements have been significantly correlated with changing barometric pressure associated with tropical storms, with species-dependent impacts on population distribution ranging from temporary displacement to permanent movements out of previously occupied habitats (Heupel et al. 2003; Udyawer et al. 2013). In other cases, observations have indicated that fish responded to cues from increasing stream flow, and high water levels brought on by heavy rainfall during tropical storms (Bailey and Secor 2016).

In this study, we investigated the effects of Hurricane Irma on the movement of common snook (*Centropomus undecimalis*) in Everglades National Park (ENP, USA). Our research asked, (Q1) what was the movement response of common snook (hereafter snook) to hurricane conditions? and (Q2) what were the environmental cues driving these movements? To address these questions, we used acoustic telemetry data from tagged snook, and examined movements occurring before, during, and after Hurricane Irma, and the relationship of movement responses to environmental variables previously shown to correlate with hurricane-driven responses in aquatic vertebrates (Heupel et al. 2003; Liu et al. 2010; Udyawer et al. 2013; Bailey and Secor 2016). Based on these research questions, we sought to test one hypothesis regarding the snook movement response to the hurricane, and three alternative hypotheses regarding the driver or cue of the movement response: (H1) Hurricane Irma resulted in large-scale movements and redistribution of fish after the storm, deviating from expected patterns of localized foraging in the upper river, (H2) hurricane-associated snook movements were most correlated with hurricane conditions, particularly changes in barometric pressure, (H3) snook movements correspond to changes in riverine conditions, namely stage, as a result of tidal surge and rainfall during the hurricane, (H4) snook movements were best explained by a combination of both hurricane conditions and riverine conditions.

METHODS

Shark River System

We tracked the movements of acoustically-tagged adult snook in the Shark River (SR), an extensive coastal river system in the southwestern region of ENP, Florida, USA (Fig. 1). The SR is located in a subtropical climate, and is the main conduit of water through the western portion of the Everglades, with hydrology driven by rainfall and tidal cycles (McIvor et al. 1994; Saha et al. 2012). The area has been the focus of long-term ecological research, which has provided robust datasets on the hydrology and ecological characteristics of the region (Childers 2006; Danielson et al. 2017; Dessu et al. 2018).

The SR spans about 32 km with a drainage area of roughly 1,700 km^2, and is composed of graminoid marshes with oligohaline creeks in the upper reaches that transition into mangrove forests, with progressively larger and more saline channels flowing throughout the estuary and into the Gulf of Mexico (McIvor et al. 1994; Fry and Smith 2002; Saha et al. 2012). Throughout the twentieth century, drastic changes to the hydrology of the region as a function of urban and agricultural development have resulted in less than half the volume of freshwater entering the system compared to pre-drainage levels (Marshall et al. 2014). However, the characteristic wet/dry seasonal pattern has been retained, with about 80% of the system's rainfall occurring between July and November (McIvor et al. 1994; Price et al. 2008; Saha et al. 2012).

The SR can be divided into three ecologically distinct zones with varying habitat characteristics (Fig. 1b); the oligohaline upper river, the mesohaline central embayment (Tarpon Bay), and the deeper, larger, predominantly polyhaline lower river (Rosenblatt and Heithaus 2011; Boucek et al. 2017; Matich et al. 2017). The upper river (river km > 23) consists of narrow channels (2–50 m) bordered by a combination of mangrove and freshwater marshes containing a mix of sawgrass (*Cladium* sp.) and freshwater woody plant species, with depths ranging from 1–3 meters, rocky/mud bottoms, and limited tidal influence (Chen and Twilley 1999; Childers 2006; Boucek and Rehage 2013; Boucek and Rehage 2014). Tarpon Bay (river km 15–23) is marked by a transition from a predominantly freshwater fish community to one primarily consisting of estuarine species, with shallow (generally < 2 m) open (200–500 m across) habitats, and soft muddy bottoms with low submerged aquatic vegetation (Rehage and Loftus 2007; Rosenblatt and Heithaus 2011; Boucek and Rehage 2013). The lower river (river km <

15) is characterized by deeper (3–5 m) and wide riverine channels (about 100 m or greater) and is the most marine-influenced, although salinity fluctuates between the wet and dry seasons and can range from about 10–35 PSU (Childers et al. 2006). Red Mangrove (*Rhizophora mangle*) shorelines are present in all three zones; however, height and biomass increases toward the more productive, lower sections of the river (Chen and Twilley 1999; Childers 2006; Ewe et al. 2006).

Common Snook

Snook are a tropical euryhaline species found in freshwater river systems and marine habitats throughout the Caribbean, with Florida populations occurring at the northern extent of their geographic distribution (Blewett et al. 2009; Muller et al. 2015). These fish are highly targeted by anglers in the Everglades, in a largely catch-and-release fishery (> 95% of snook caught are released) that makes substantial contributions to the economy (Muller et al. 2015). About 2.5 million snook are caught in Florida each year, and the species is the fourth most targeted by anglers on the southern Atlantic coast, and third most targeted in the Gulf of Mexico (Muller et al. 2015). Reproducing adults use estuaries and marine areas to spawn, with juveniles subsequently moving upstream into nursery habitats in small creeks and freshwater marshes (Gilmore et al. 1983; Peters et al. 1998). At about two to three years old, snook enter the fishery as they leave these backwater rearing areas and move into estuaries and larger riverine channels (Taylor et al. 1998).

Adult snook use different habitats in the SR throughout the year, and seasonal movements across river zones are predominantly associated with spawning, and upper river prey availability (Boucek and Rehage 2013; Boucek et al. 2017; Stevens et al.

2018). Downstream movements are mostly attributed to reproduction, and are highest during May through August, with peak spawning activity occurring in June and July (Lowerre-Barbieri et al. 2014; Boucek et al. 2017; Matich et al. 2017; Boucek et al. 2019). Upstream movements correspond to falling water levels during the dry season (January–June), as snook move into the upper river tracking abundant prey sources that are concentrated in river channels by drying marshes (Boucek and Rehage 2013; Matich and Heithaus 2014; Blewett et al. 2017; Boucek et al. 2017; Matich et al. 2017). Not all fish make these annual migrations, and research in south Florida has indicated that > 40% of fish may express skip-spawning behavior and remain in the upper river year-round (Trotter et al. 2012; Lowerre-Barbieri et al. 2014; Young et al. 2014, Boucek et al. 2019). Past telemetry studies in the SR have indicated that snook are most frequently detected in the upper river (85% of detections, Matich et al. 2017).

Tracking Snook Movement in the Shark River

Acoustic monitoring of tagged adult snook began in 2012, with ongoing tagging efforts continuing through 2018. Fish are captured using boat-based electrofishing along shorelines in Tarpon Bay and the upper river zone (detailed in Boucek and Rehage 2013). When snook are caught, they are placed in a livewell, and transferred to an onboard tagging station within 2–3 minutes of capture. Following standardized methods (Adams et al. 2009; Trotter et al. 2012; Lowerre-Barbieri et al. 2014; Boucek et al. 2017), tagging consists of a minor surgical procedure, where a 30-mm incision is cut in the lower abdomen, and an acoustic transmitter (69kHz V13 or V16, Vemco, Halifax, NS, Canada) is implanted into the abdominal cavity. Incisions are closed with one to two sutures, and fish are held in water alongside the boat and allowed to regain full equilibrium before release. The mean interpulse delay for the transmitters is 120 seconds, resulting in a battery life of about 36 months, and previous studies have estimated that the post-release survival of snook is about 85% (Boucek et al. 2019).

Fish are tracked using passive acoustic telemetry, and are autonomously monitored by an array of VR2W receivers (Vemco, Halifax, NS, Canada). Receivers have been positioned 1–3 km apart using a gated design and are denoted by their location in the river array (river km away from the coast). This deployment arrangement allows us to track directional fish movement throughout the system. When fish swim near a receiver, their unique tag number is recorded and associated with a date, time, and detection location (hereafter river km; with values increasing from 0 at the Gulf of Mexico to 32 km at the SR headwaters). Previous studies have illustrated the efficacy of this deployment design to quantify fish movements and assess distribution over time (Rosenblatt and Heithaus 2011; Boucek et al. 2017; Matich et al. 2017). The array consists of 37 receivers (Fig. 1); however, eight receivers near the mouth of the SR and in the lower river were removed a few days prior to the storm to prevent equipment loss, and then redeployed a few weeks later (on 2 October 2017).

Hurricane Irma

Hurricane Irma developed in the eastern Atlantic about 740 km west of the Cabo Verde Islands, and reached hurricane strength on 1 September 2017. After making multiple landfalls throughout the Caribbean, Irma moved into the Florida Straits as a Category 4 storm, making landfall at about 13:00 UTC on 10 September near Cudjoe Key in the Lower Florida Keys and continuing northward, weakening to a Category 3 before making its final landfall near Marco Island, Florida at 19:30 UTC on 10

September (Cangialosi et al. 2018). Just prior to this final landfall, the hurricane reached its closest proximity to the SR (Fig. 1a), with the eye of the storm passing 60 km to the west at 15:00 UTC on 10 September 2017 (hereafter referred to as SR passage) resulting in local wind speeds approaching 38 m/s.

Snook Response to the Hurricane

In order to determine if and how snook altered their movement behaviors in response to Irma, we examined detection histories for each fish present in the acoustic array during the timing of the hurricane (hereafter hurricane window). We defined this hurricane window as the period over which we observed rapidly changing environmental conditions, namely changes in barometric pressure and altered riverine conditions (changes in flow or water level) associated with the passing of the hurricane in the vicinity of the SR. Examination of these conditions identified this hurricane window to last 67 hours, between 5:00 UTC on 9 September until 00:00 UTC on 12 September (Fig. 2). Snook were included in the analyses presented here if they had at least 10 detections in their movement histories since tagging, and at least three detections during the hurricane window. This allowed us to remove fish without a sufficient record to provide inference into movements, and also eliminate unreliable observations (false detections) consisting of single detections that could not be confirmed on more than one receiver (Clements et al. 2005; Walsh et al. 2013; Young et al. 2014). A total of 22 snook were detected at the start of the hurricane window (size range 42–70 cm standard length at time of tagging, Table 1), and all subsequent analyses focused on these fish.

We assessed movement in response to the hurricane by examining whether snook changed their location during the hurricane window. In order to distinguish between fine-scale movements within habitats and more abrupt changes in location as a result of storm conditions, we examined movements across the three major zones of the SR, following previous acoustic studies (Rosenblatt and Heithaus 2011; Boucek et al. 2017; Matich et al. 2017). The time-period of the hurricane window did not coincide with peaks in large-scale movements associated with reproduction or resource tracking (discuss in greater detail above), thus rapid and synchronous movements among river zones would be considered atypical compared to more routine within-zone movements (i.e., those related to localized foraging, as shown in Online Resource 1). To determine if snook displayed cross-zone movements, for each individual fish we first calculated an hourly mean detection distance (river km) for each hour within the hurricane window, and assigned this mean distance to a river zone. A mean distance of less than 15 km was considered the downstream zone, 15–23 km Tarpon Bay, and greater than 23 km the upstream zone (Fig. 1b). We then compared each hour's zone to the previous hour's zone during the hurricane window. If there was a change in river zone, the fish was considered to have moved in response to the hurricane. For those fish that moved, the first instance of zone change indicated the timing of initiated movement. While the majority of these mean distances were calculated from multiple detections (range of 1–33 detections/hour), in the case of a single hourly detection indicating that a zone change had occurred, we did not infer relocation if this change could not be confirmed with subsequent observations. These changes in zone were then fed into logistic regression models, where the cumulative proportion of fish that had moved over time was considered as the response variable to possible environmental cues. Last, to determine if there were persistent changes in snook distribution following the hurricane, we also compared detections during the hurricane window to those that occurred over the six months leading up to, and the six months following Hurricane Irma. This six month expanse covers any seasonality in movement that precedes or follows the hurricane in relation to foraging, mating and other drivers of movement (Boucek and Rehage 2013; Lowerre-Barbieri et al. 2014; Matich and Heithaus 2014; Blewett et al. 2017; Boucek et al. 2017; Matich et al. 2017). For each period, we calculated a mean location (river km) for the focal fish (those that were detected during the hurricane window).

Identifying Drivers of Snook Movement

To investigate the possible drivers of snook movement during Hurricane Irma, we related snook movement to a) hurricane conditions, b) riverine conditions resulting from the hurricane, and c) a combination of these cues. Modeled barometric pressure (PRESSURE, in millibars) was used for hurricane conditions based on evidence from previous studies that reported pressure as a direct or indirect (i.e., cue of other environmental conditions changing) driver of fish movements during tropical storms (Heupel et al. 2003; Udyawer et al. 2013). These studies also found correlations between movements and wind speed, but because our modeled barometric pressure estimates were calculated from wind measurements (see below), and thus highly correlated, we did not explicitly include wind as a variable in our analyses. We also considered the hourly change in barometric pressure (PRESSURE$_{\Delta}$) to examine if the magnitude of change, rather than the pressure value itself, was more aligned with the fish response. For riverine conditions, we used water level (stage), which has been described as an important driver of snook movement and habitat use in rivers (Boucek and Rehage 2013; Blewett et al. 2017; Boucek et al. 2017; Stevens et al. 2018). In order to provide a more complete picture of how the hurricane affected the entire system, stage data from two locations were included in analyses, capturing differential hurricane effects across the 32 km of the SR. Upper river stage (STAGE_U, in cm) showed increased water levels resulting from heavy rainfall, whereas lower river stage (STAGE_L, in cm) captured the storm surge (Fig. 2). Following our treatment of the PRESSURE variable, we included separate models for the hourly change in river stage in both the upper and lower river ($\text{STAGE}_{\Delta\text{U}}$ and $\text{STAGE}_{\Delta\text{L}}$).

Barometric pressure at the SR during Hurricane Irma was modeled using data obtained from the Atlantic hurricane database (HURDAT2) Best Track dataset, which records the hurricane position, minimum central pressure (millibars), maximum wind (knots), and wind radii extents (nautical miles) in six hour intervals (Landsea and Franklin 2013). Here, hourly values were estimated between these data points using linear interpolation. This modeling approach follows hurricane catastrophe models used in the insurance industry to simulate possible storm occurrences with known cyclone characteristics (Grossi and Kunreuther 2005).

In accordance with catastrophe models, Holland pressure analytical profiles can be used to produce the surface pressure (P) of a hurricane as a function of radius (r) from the storm center (spatial offset), given the radius of maximum wind (R_{max}) and the minimum central pressure (P_o, Holland 1980).

$$P(r) = P_o + (1019.0 - P_o)\exp\left\{-\left(\frac{R_{max}}{r}\right)^B\right\}$$

R_{max} was obtained from radar imagery since the radius of maximum wind has been found to be one or two nautical miles greater than the inner radius of the eye on radar (Shea and Gray 1973). The width parameter (*B*) determines the shape of the maximum wind peak, and the rate at which the wind and pressure decrease outward from the radius of maximum wind. HURDAT2 does not provide the width parameter, so subjective adjustments were made while developing the wind profile. *B* is generally around one; here it ranges from 0.8 to 1.0. Pressure was calculated for two locations in the SR, the upper and lower river, but the estimates were comparable (Fig. 2a), and only upper river pressures were included in the final analyses reported here (since all snook detected were located in the upper river at the onset of hurricane conditions).

For riverine conditions associated with the hurricane, we obtained hydrologic data from the USGS Everglades Depth Estimation Network database (https://sofia.usgs.gov/eden/). Hourly stage data were queried for two monitoring stations (Fig. 1b); STAGE_U was obtained from Bottle Creek (located in a small creek at the headwaters of the river, river km 33.5) to examine primarily upriver changes in stage driven by rainfall, and STAGE_L was obtained from Gunboat Island (about river km 10) in the lower river to track the storm surge. A preliminary analysis also examined other candidate variables representing riverine conditions (unpublished data from Gunboat Island courtesy of David Ho, University of Hawaii), but indicated either little variation over the hurricane window (water temperature, oxygen), or a high degree of correlation with stage (discharge, salinity). Furthermore, observations suggest that snook populations may not be heavily influenced by fluctuations in salinity, and can be found in waters ranging from 0 to 38 PSU (Gilmore et al. 1983; Childers 2006; Winner et al. 2010). Additionally, under non-storm conditions, SR populations are subject to daily changes in salinity due to tidal influences. Thus, stage was selected for use in the final analyses.

Relating Snook Movement to Hurricane and Riverine Conditions

We performed logistic regression using Generalized Linear Models (GLM) with a binomial error distribution and logit link function in R statistical software (R Core Team 2017) to examine if and how hurricane and riverine conditions correlated with snook movements. The response variable for these models was the cumulative proportion of fish that had moved among river zones over the course of the hurricane window (see details above). Corresponding to our hypotheses, we tested three sets of *a priori* models: 1) models assessing hurricane conditions alone, 2) those investigating riverine conditions alone, and 3) those examining combined effects. For hurricane conditions, we included one model with PRESSURE as the explanatory variable, and another with PRESSURE_{Δ}. Preliminary models examined pressure at multiple locations in the SR (Fig. 2), however, the values were very similar and did not change model outcomes. To investigate the role of riverine conditions, we considered models including only STAGE_{U} or $\text{STAGE}_{\Delta\text{U}}$ to represent the rain-driven increase in upper river water levels, models with STAGE_{L} or $\text{STAGE}_{\Delta\text{L}}$ alone to capture storm surge effects predominantly influencing the lower river, and a model including both STAGE_{U} and STAGE_{L} to consider both of these spatially discrete variables that occurred over different timeframes. For the combined stage model, we selected the best fitting variable for each river location (either measured value, or hourly change between values). Last, combined effects were assessed by evaluating two models containing both hurricane and riverine variables. One of these models combined the best fitting pressure variable (PRESSURE or PRESSURE_{Δ}) with both of the top STAGE_{U} and STAGE_{L} variables, and a second model included only the best fitting pressure and stage variables. We then used model selection to provide inference on the best explanatory mechanisms correlating with snook movements, and evaluate the relative strength of each model (Johnson and Omland 2004; Symonds and Moussalli 2011).

We conducted model selection by comparing Akaike's information criterion corrected for small sample size (AICc) for the nine logistic models of snook movement (Akaike 1998; Burnham and Anderson 2003; Anderson 2008). In addition to comparing AICc scores, we ranked models according to Akaike weights (*w*AICc), a measure of relative weight of evidence for each model as a predictor, and D^2 values (null deviance - residual deviance, analogous to R^2 in least squares models), which indicate the amount of deviance accounted for by GLMs (Guisan and Zimmermann 2000; Johnson and Omland 2004). *w*AICc and D^2 were calculated using R statistical software with the bbmle and modEvA package, respectively (Bolker and Team 2010; Barbosa et al. 2013; R Core Team 2017). The model with the lowest AICc, highest *w*AICc, and highest D^2 was considered to best explain snook movements during the hurricane.

In addition to examining relationships between environmental conditions and snook movements, we compared the mean spatial location of fish present during the hurricane window with the location of these fish in the time periods six months before and six months after the storm. To test for a significant difference in fish distribution based on these three time periods, we performed a repeated measures analysis of variance (ANOVA) using generalized least squares models (GLS) in R statistical software (R Core Team 2017), which incorporated autocorrelation and the non-independence of observations within each time period. For the six month period following the hurricane window, we also considered the individual detection records for fish that moved among river zones during the storm, in order to investigate the extent of individual variability in longer-term habitat use.

RESULTS

Hurricane and Riverine Conditions

Examination of conditions during the hurricane window showed a marked fluctuation in both barometric pressure and water levels (Fig. 2). PRESSURE was relatively stable and remained between 1017 and 1018 millibars, until a rapid decline on 9 September, marking the beginning of our hurricane window, and reached a minimum of 994 millibars in the upper river at 21:00 UTC on 10 September, six hours after the eye of the hurricane passed closest (within 60 km) to the mouth of the SR at about 15:00 UTC (Fig. 2a). After remaining near this minimum until 00:00 UTC on 11 September, barometric pressure increased as the storm moved northward and reached 1005 millibars by the end of hurricane window.

Fluctuations in river stage were spatially-dependent, and showed variable responses as a function of storm surge and rainfall. $STAGE_L$ oscillated with the tidal cycles until it began to drop from 6 cm at 20:00 UTC on 9 September to a low point of -66 cm at 8:00 UTC on 10 September, due to the anti-storm surge preceding the hurricane (Fig. 2b). As the storm surge flooded the river, $STAGE_L$ reached a maximum of 84 cm at 1:00 UTC on 11 September before beginning to recede and returning to normal tidal variation. In contrast, $STAGE_U$ did not show a signal of storm surge at the monitoring station upstream at river km 33.5, and instead remained relatively stable (between 48 and 49 cm) until 9 September, when it began to increase due to heavy rainfall, and reached 80 cm by midnight on 11 September, almost doubling pre-hurricane stage (Fig. 2c). Water levels remained high throughout September and did not begin dropping substantially until late November 2017, resulting in some of the highest prolonged stages on record for this site.

Snook Response to the Hurricane

Our acoustic data indicated that snook responded to the hurricane by making directed movements among river zones (Fig. 3). Twenty-two snook were detected at the start of the hurricane window (Table 1), with 73% (16 fish) changing zones, and all fish moving in a downstream direction. Three predominant behavioral patterns emerged: Twelve of the 22 fish (55%) moved from the upper river to Tarpon Bay (Fig. 3a), and four fish moved rapidly from the upper river to the lower river (18%) and were not re-detected further during the hurricane window (Fig. 3b). Movements for these four fish suggested a potential exit from the river to the coast. Two fish (9%) did not move, and continued to be detected on receivers in the upper river before and after the storm (Fig. 3c). Movement patterns for the four remaining fish (18%) were inconclusive, with subsequent detections occurring outside of the hurricane window, and from which we could not definitively infer movement paths during the hurricane window. All of the fish whose paths could be determined (18 fish) were initially located in the upper river zone.

Snook activity increased, and fish began moving among river zones as Irma approached the SR, with movements continuing throughout the hurricane window (Fig. 4). The majority of snook that moved did so in the hours leading up to SR passage and during peak storm conditions, with 50% of these fish changing river zones by 23:00 UTC on 10 September, eight hours after the eye of the hurricane passed the SR, and while PRESSURE remained near the minimum of 994 millibars (Fig. 4). The first fish moved downstream at 8:00 UTC on 10 September, seven hours before SR passage, and the last detected movement occurred a few days after the storm at 4:00 UTC on 13 September (61 hours later).

The results of the ANOVA analysis based on GLS models indicated that time period had a significant effect on fish location (mean river km) in the six months prior to the hurricane window, during the hurricane window, and six months following the storm ($F = 3.63$, $p = 0.027$). Before Hurricane Irma, the mean location of the detected fish was in the upper river zone at river km 27.5 ± 0.02. During the hurricane window, fish shifted position downstream and had a mean location of river km 23.1 ± 0.16, on the border between the upper river and Tarpon Bay. In the six months following the hurricane, many snook had moved back into the upper river with a mean location of river km 25.1 ± 0.02.

During the six month period following the hurricane window, detection records for the 16 snook that moved out of the upper river and among zones revealed a high degree of individual variation. Some of these fish were consistently detected within a single zone, with four returning to the upper river (25%), and one fish remaining in Tarpon Bay (6%). Three fish (19%) continued to move among zones over the next few months, making regular trips between the lower river, bay, and upper river. Additionally, three fish (19%) were detected on coastal receivers that were replaced after the storm passed, but did not move back upstream. The last five fish (31%) were detected in the days following the hurricane (between 11 September and 17 September), but were not subsequently re-detected, suggesting either mortality or undetected outmigration. In total, 11 of the 16 fish that relocated during the hurricane window were subsequently re-detected on the SR array (69%).

Relating Snook Movement to Hurricane and Riverine Conditions

Results of the regression model selection indicated that snook movements were best explained by a combination of both hurricane and riverine conditions (Table 2). A univariate model with PRESSURE_{Δ} (hourly pressure change) had a very low model weight and deviance (D^2 0.04), although the model including the PRESSURE variable (modeled value in millibars) did show a relationship with fish movement (D^2 0.43). For riverine conditions, the best fit was a combination of STAGE_{U} and STAGE_{L} (D^2 0.80), with STAGE_{U} alone providing comparable results (D^2 0.78). Both of these models outperformed those based on change in river stage between time-steps ($\text{STAGE}_{\Delta\text{L}}$ D^2 0.01, $\text{STAGE}_{\Delta\text{U}}$ D^2 0.06). The best fitting model overall was model i (Table 2), containing only PRESSURE and STAGE_{U} (D^2 0.84). Even though models h and i were within about two AICc units, indicating that both models had similar levels of support (Anderson 2008), we selected model i as the best fit model. This determination was made because model i had the highest *w*AICc (0.725), because the STAGE_{L} coefficient was not significant from 0 in model h (z value = 0.095, $p = 0.92$), and following the principal of model parsimony and selecting the simplest explanation.

In our final model, the probability of moving to a different zone increased with low barometric pressures, and higher STAGE_{U} in the upper river (Fig. 5). When plotted independently with one variable held at a fixed mean, fitted logistic curves showed that 50% of fish initiated movement among river zones with STAGE_{U} above 64.5 cm, and PRESSURE below 998 millibars (Fig. 5). Coefficient estimates from the final model indicated that for a one unit increase in STAGE_{U}, the log odds of movement among river zones during the hurricane window increases by 1.08 (SE = 0.40, $p = 0.01$). For every one unit of PRESSURE (from the minimum), the log odds of movement increases by 0.99 (SE = 0.46, $p = 0.03$). It should be noted that movements occurred both on the descending and ascending limbs of changes in barometric pressure. Seven of the 16 snook moved among river zones as PRESSURE dropped from 1008 to a minimum of 994 millibars, three while it remained near the minimum value until roughly nine hours after SR passage, and the other six continuing to initiate movement as PRESSURE returned to 1004 millibars. While the PRESSURE estimate in the final model does not show an inverse correlation (negative coefficient), results from the model isolating PRESSURE with a fixed mean STAGE_U showed a significant negative relationship (coefficient estimate = -0.32, SE = 0.06, $p < 0.001$). We calculated odds ratios (OR) for our final model and found a comparable per-unit influence between both explanatory variables (STAGE_U OR = 2.94, PRESSURE OR = 2.70), with overlapping confidence intervals (upper/lower 95% 1.60–8.20 and 1.32–8.53, respectively).

DISCUSSION

Animal movement often occurs in response to predictable or slow changing environmental cues, but movements can also be driven by unpredictable disturbances that result in rapid shifts in distribution (Bowler and Benton 2005; Durant et al. 2007; Jones and Cresswell 2010; Hazen et al. 2013). Extreme climate events such as hurricanes can influence animal movements and alter the distribution of large-bodied species such as sharks and teleosts in aquatic ecosystems. In this study, we detected 22 snook in the upper SR prior to Hurricane Irma, and the majority of fish (73%) made downstream movements among river zones during hurricane conditions. This supports our hypothesis that fish would alter their pre-storm movement behaviors. Among the tagged individuals, we found variation in the extent of movement and identified three predominant strategies; 1) movement from the upper river to Tarpon Bay (55%), 2) rapid movements from the upper river to the coast (18%), and 3) fish that were not observed to make significant movements during the hurricane (9%). Movement patterns during the hurricane could not be determined for 18% of the tagged individuals. Our logistic regression models suggest that snook movement was best explained by a combination of both high river stage (riverine conditions) and barometric pressure (hurricane conditions), with stage accounting for a higher proportion of model deviance. Further, the most relevant stage to snook movement was $STAGE_U$ (upper river), which increased with rainfall and was unaffected by storm surge.

While we observed substantial movements of tagged snook during Hurricane Irma, there are several factors that may have limited our ability to detect fish and thus our insight into the exact nature of snook movements. First, detection ranges of receivers are a general limitation of acoustic telemetry studies, particularly in large and complex systems (Rosenblatt and Heithaus 2011; Gjelland and Hedger 2013). In the SR, the detection range is about 500 m–1 km (Matich et al. 2017), exceeding channel width and allowing us to detect up or downstream movements. Array spacing (1–3 km between receivers), however, can result in fine-scale within habitat movements that may not be detected. Secondly, eight receivers at the coast and in the channels of the lower river were removed five days prior to the hurricane in order to prevent equipment loss, limiting our ability to fully track emigration from the SR or infer mortality during the hurricane window. However, these receivers were replaced several weeks later, which provided higher-resolution coverage of the lower river following the storm. It is possible that some fish may have moved downstream and continued to occupy these areas, although this increased coverage reduces the probability that they would go undetected, and fish first re-detected on coastal-most receivers in the following months provided some inference into outmigration. Thirdly, an additional caveat to acoustic telemetry is that environmental noise stemming from wind/waves/rain may interfere with acoustic receivers and reduce the ability to detect fish (Simpfendorfer et al. 2008). We acknowledge these caveats, and to provide inference into environmental cues that may drive movement we considered only fish with conclusive detection records in our regression models, and removed four fish from analysis with inconclusive movement patterns due to low detections during the hurricane window.

Movement Responses

The observed downriver movements of snook during Hurricane Irma are consistent with findings from previous studies of aquatic vertebrates during tropical storms. Heupel et al. (2003) reported that acoustically-monitored blacktip sharks (*Carcharhinus limbatus*) expressed flight behaviors and began making directed movements out of shallow estuarine habitats and into deeper coastal waters, beginning roughly six hours before landfall of a tropical storm in Terra Ceia Bay (Florida, USA). We observed a similar response in the timing of initiated movements, with the first snook moving across habitat zones seven hours before SR passage. Udyawer et al. (2013) described how three of four shark species tracked in Australia also responded to tropical storms and moved out of coastal bays within 10-24 hours of landfall. In both of these studies, all individuals showed flight responses and left the study site. While our study did not show a complete evacuation of the SR by all tagged snook, individual variability in movement responses consistent with our findings has been described in other systems. In the Hudson River (New York, USA), intrapopulation variability was described for striped bass (*Morone saxatilis*) during a series of tropical storms in 2011 (Bailey and Secor 2016). Like many of the snook we observed in the SR, striped bass located in the upper river made rapid downstream movements during the storm, but several tagged individuals remained in the river. Secor et al. (2018) also reported partial evacuations in a coastal population of black sea bass (*Centropristis striata*) during a 2016 tropical storm in the Mid-Atlantic Bight (offshore of Maryland, USA), with only half of the fish leaving the monitoring area during the storm.

Environmental Cues Driving Movement

Adult snook movements correlated with a combination of lowered barometric pressure and rainfall driven stage in the upper SR, both of which have been described as drivers of animal movement during tropical storms previously. Sea kraits (*Laticuada* spp.) were found to abandon littoral habitats at Orchid Island (Taiwan), as barometric pressure dropped (Liu et al. 2010). Both Heupel et al. (2003) and Udyawer et al. (2013) reported similar findings, with strong correlations between wind speeds, barometric pressures, and flight behaviors in coastal sharks. Because our modeled barometric pressure estimates were calculated from hurricane wind measurements, wind speed was not explicitly investigated in this study. However, it should not be ruled out as a potential movement cue. Bailey and Secor (2016) compared water levels (stage), temperature, and salinity to striped bass movement, and suggested that environmental changes stemming from high discharge rates (increased rainfall) may have driven downstream movements.

We investigated if the magnitude of hourly change in environmental conditions, rather than the stage/pressure itself, may have driven fish movement. However, our results documenting large-scale redistribution were not able to explicitly make this link. A few factors may explain the lack of model fit. First, much of the observed movement among river zones occurred in the hours leading up to and following SR passage. During this time period, barometric pressure had reached a minimum, and there was not a dramatic change between hourly estimates. Second, stage increases also began in advance of SR passage, and only three fish were detected to move among zones during the period of most rapid change (1–3 cm/hr stage increase). This does not, however, preclude the idea that rapid changes in environmental conditions may serve as movement cues. Observations of acoustically tracked bull sharks in the SR during Hurricane Irma suggested that the hourly rate of change in barometric pressure contributed to predicting evacuations from estuarine habitats (Strickland et al. *this volume*). Heupel et al. (2003) also reported that differences in the rates of pressure decline between multiple tropical storms may have helped to explain the varying strength of movement responses of blacktip sharks. Furthermore, Grammer et al. (2015) found that changes in barometric pressure corresponded to increased activity of Gulf sturgeon (*Acipenser oxyrinchus desotoi*), which made small-scale movements into estuarine staging areas preceding emigration out of rivers and into the Gulf of Mexico. Future research investigating finer-scale linkages between the initiation of behavioral responses and rates of environmental change could help provide additional insight.

Alternative Fates for Snook after Hurricane Irma

Slightly more than half (55%) of the 22 fish detected during the hurricane window remained active within the SR system, however the ten fish that were not detected immediately after may provide insight into alternative fates for snook, namely emigration or mortality. While the low density of coastal receivers during the storm limits our ability to draw definitive conclusions, we found evidence that at least some of these fish exited the SR and moved into coastal waters as a result of Irma. Four fish were last detected at receivers in the lower river and not re-detected until several months later when they were recorded on coastal receivers. These fish were among the first to move among river zones during the hurricane window, with zone changes occurring between seven hours before to six hours after SR passage. Two of these fish re-appeared on the array on 24 October and 31 October 2017, a third individual on 14 December 2017, and the fourth fish was re-detected on 11 April 2018, nearly seven months after Hurricane Irma. While these results may be suggestive and not necessarily infer movement out of the system, this last fish was recorded by an array of NOAA receivers in Faka Union Bay (Florida, USA) along the coast of the Gulf of Mexico, about 70 km north of the mouth of the SR. This provides strong evidence that fish absent from the SR array moved into coastal waters.

Another possible fate for snook is the likelihood that some degree of mortality occurred associated with disturbances introduced by the hurricane. Six of our 22 fish were never re-detected as of ten months after the hurricane. One of these fish had consistent detection records in Tarpon Bay extending back to December of 2015 and was last detected on 9 September, one day before Hurricane Irma. The other five fish were periodically detected during the hurricane window, but their final detections occurred between 11 September and 17 September, 1–6 days following peak hurricane conditions. These fish were last detected in Tarpon Bay and the lower river zones, and while undetected outmigration or fishing mortality in the following months is a possibility, mortality stemming from either the direct force of the storm or subsequent declines in habitat conditions is also a plausible explanation.

Consequences of Storm-Driven Movement

Animal movements and dispersal carry costs and involve tradeoffs in the form of energy expenditure, increased risks, availability of resources, and/or reproductive opportunities (Bonte et al. 2012). Movements driven by unpredictable disturbances such as hurricanes might lead to both positive and negative consequences if they result in alterations to normal behaviors. For snook, there are several potential costs that may arise from the rapid and atypical movements driven by hurricanes. One potential cost of the movements we observed, where snook evacuated from the upper SR to the coast, is an increased predation risk when moving into areas with higher abundances of large predators (e.g. bull sharks, *Carcharhinus leucas*, Matich and Heithaus 2015). Additionally, snook have been shown to use specific habitats throughout the year while tracking resources, and movement out of these areas could lead to both a mismatch in resources, and increased competition for food with other large bodied species like Atlantic tarpon (*Megalops atlanticus*), juvenile bull sharks, and common bottlenose dolphins (*Tursiops truncatus*) in the SR (Boucek and Rehage 2013; Matich and Heithaus 2014; Boucek et al. 2017; Matich et al. 2017). Conversely, disturbance driven movement may have resulted in some benefits to the snook population. A study of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico suggested that that large-scale movements elicited by hurricanes can result in genetic mixing between distant sub-populations of highly resident fish stocks (Patterson et al. 2001). We observed between-basin movement of at least one fish, and it is possible that major storms may contribute to genetic diversity in discrete snook populations. Another possibility is that movements resulting from the hurricane could have a benefit on snook reproduction. In December of 2017 we observed record catches of juvenile snook during electrofishing sampling (Massie and Rehage, unpublished data), and growth curve estimates suggested they were hatched shortly after the hurricane. We hypothesize that snook movements out of the SR and into coastal spawning areas may have triggered a reproductive event following Irma. This is consistent with increases in spawning activity and recruitment following hurricanes that have been previously reported for snook, Atlantic tarpon, and sand seatrout (*Cynoscion arenarius*) in Florida (Gilmore et al. 1983; Shenker et al. 2002; Locascio and Mann 2005). Additionally, the disturbance introduced by the storm may have also created new hotspots of prey productivity, and introduced additional foraging opportunities in the SR. Future work will focus on monitoring population trends in abundance and recruitment to examine the long-term effects of Hurricane Irma on snook in the Everglades.

CONCLUSION

In this study, we found that environmental conditions associated with Hurricane Irma resulted in large-scale movements of acoustically monitored snook in the Everglades. Analysis of both hurricane conditions and riverine conditions during the storm provided support for our hypothesis that a combination of these factors served as movement cues, and regression model selection indicated that high river stages and barometric pressure best described observed snook movement patterns. We found variation in the long-term response of tagged individuals, with some fish returning to habitats occupied before the hurricane, others relocating to different habitat zones, and some fish leaving the SR system. Future work should continue to examine both the immediate responses and long-term consequences of movements driven by ECE, along with variations within populations and between different aquatic species. Research investigating whether behavioral responses might be predictable based on behaviors expressed before the occurrence of ECE may be particularly insightful. With this information we may anticipate how future environmental disturbances introduced by ECE could affect movements, reproduction, and foraging of fish populations in impact-prone regions, and subsequently impact food webs and ecosystems.

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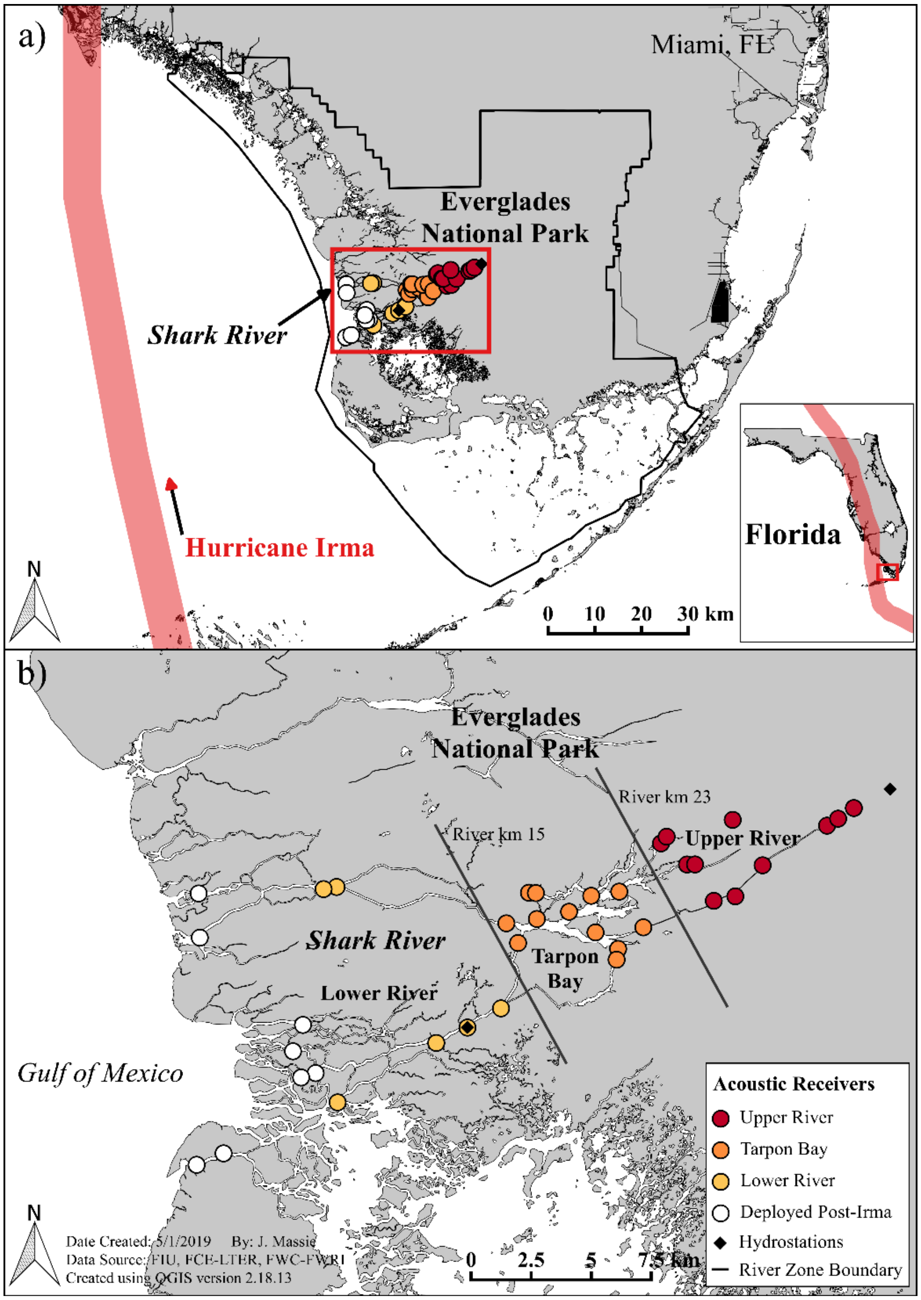


Fig. 1 Maps of the study area in Everglades National Park. a) Location of the acoustic array in the Shark River (red box) and the storm path of Hurricane Irma from south to north (indicated by red band). b) Details of acoustic receiver and hydrostation placement within the river system. Circles show receiver locations and indicate the river zones for the 37 receivers used to characterize common snook movements (upper river, Tarpon Bay, and lower river). Receivers that were not present during the hurricane window, but were replaced on 2 October 2017, are denoted by white circles (deployed post-Irma). Black diamonds mark the locations of the two hydrostations used to obtain water levels (stage) in the upper river and lower river. The upper river hydrostation is shown at the top right of the map, in a small creek just upriver of the acoustic array extent, and the lower river station shares a location with one of the acoustic receivers.

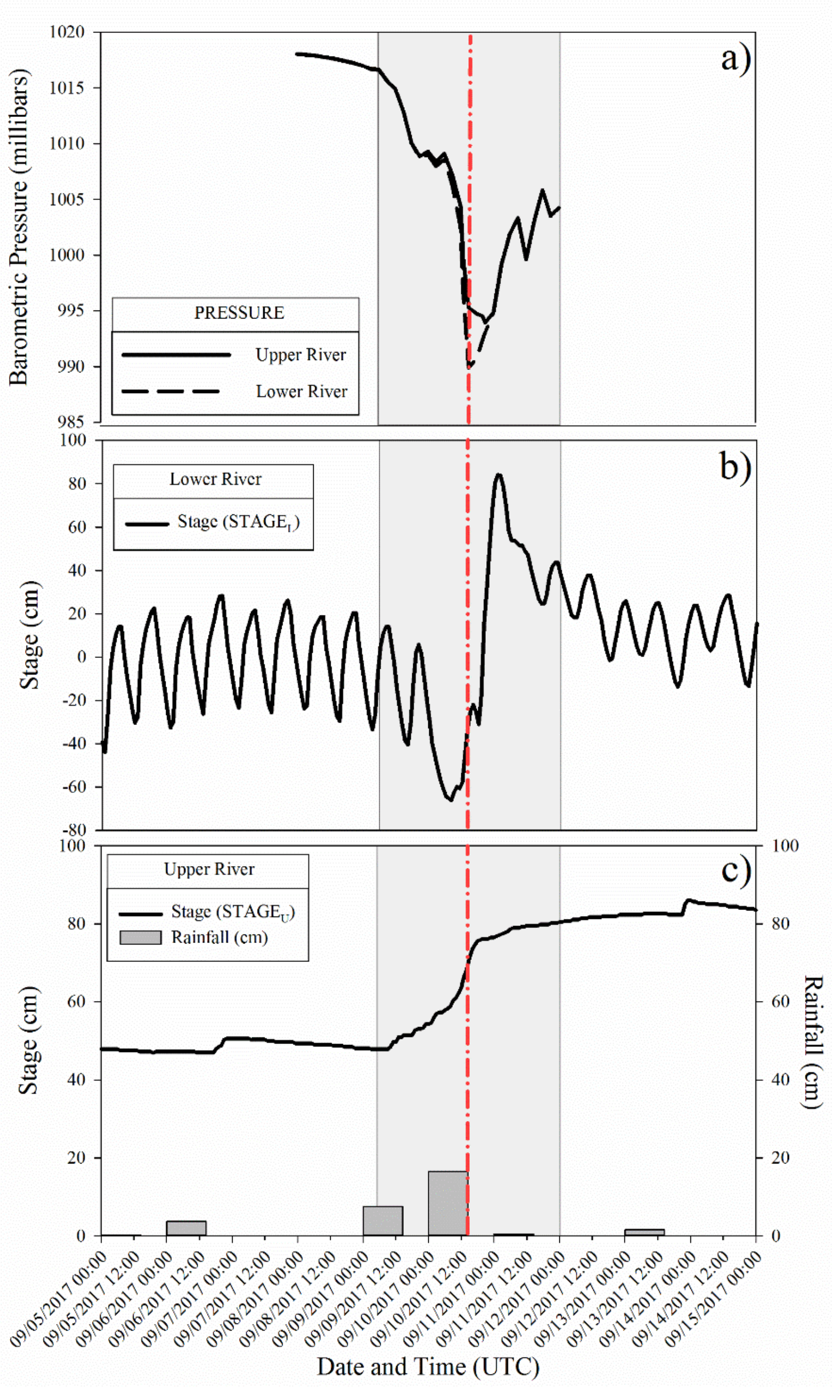


Fig. 2 Environmental conditions in the Shark River for the 10 days surrounding the passage of Hurricane Irma (15:00 UTC on 10 September 2017, red dotted line). Shading in all three panels shows the 67-hr hurricane window denoted by changes in hurricane (barometric pressure) and riverine conditions (stage). a) Modeled barometric pressures for the upper and lower river showing a rapid decline with the approaching storm. b) River stage in the lower river illustrating the drop in water level (anti-surge), and spike with storm surge. c) Stage in the upper river increasing with heavy rainfall.

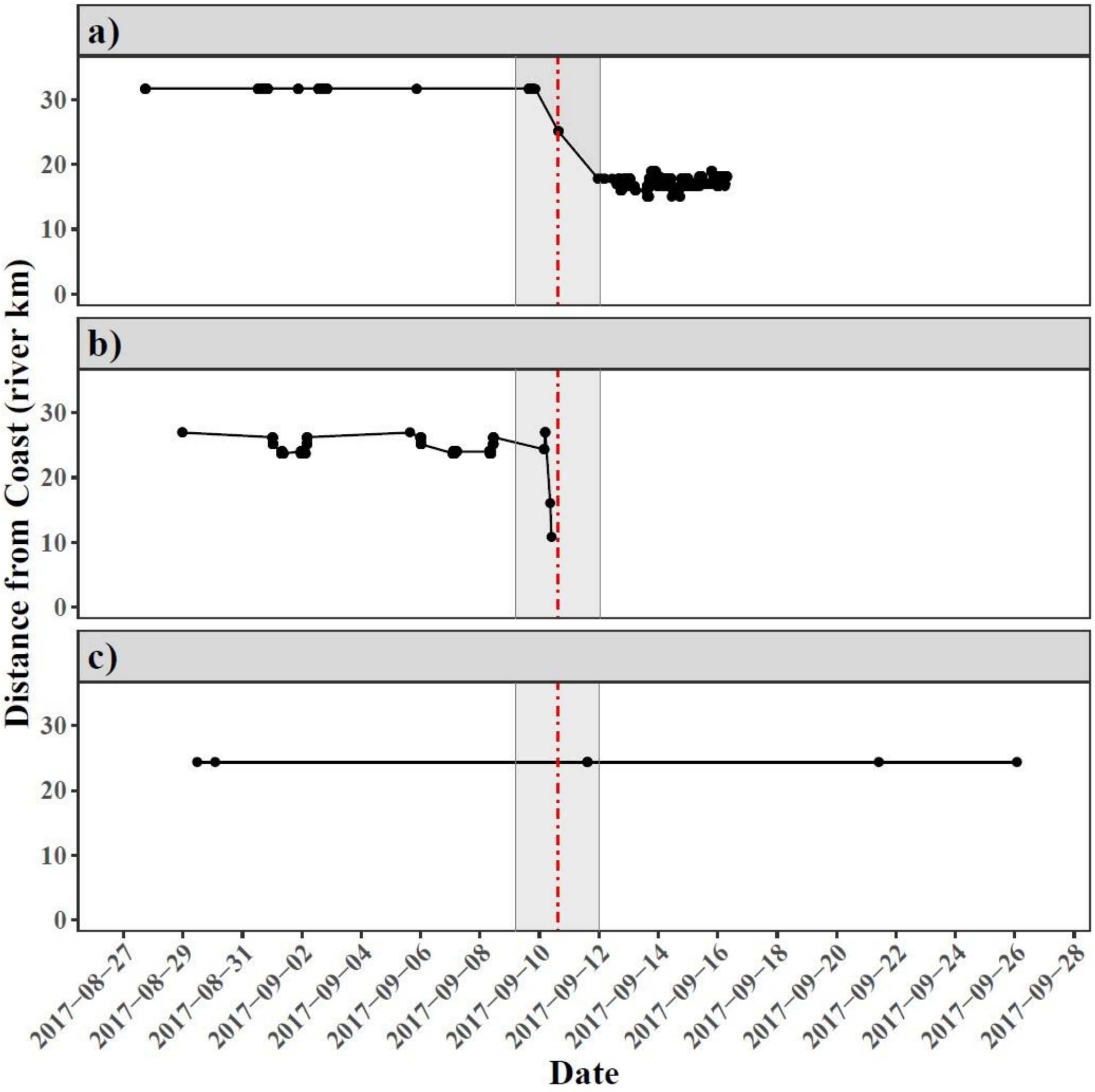


Fig. 3 Examples of acoustic receiver detection data for tagged common snook in the two weeks leading up to and following Hurricane Irma (timing of Shark River hurricane passage indicated by vertical dotted line). Movement paths show three observed patterns of movement: a) fish that moved from the upper river to Tarpon Bay, b) fish that moved from the upper river and were last detected on downstream-most receivers of the acoustic array, possibly depicting an exit of the river to the coast, and c) fish that did not move and continued to be detected in the upper river. The fish depicted in panel a) was not re-detected as of receiver downloads in June of 2018, indicating a possible mortality. The fish in panel b) was detected on a re-deployed coastal receiver on 14 December 2017 (beyond period depicted here); corroborating that it exited the system and had not returned to the river post-hurricane.

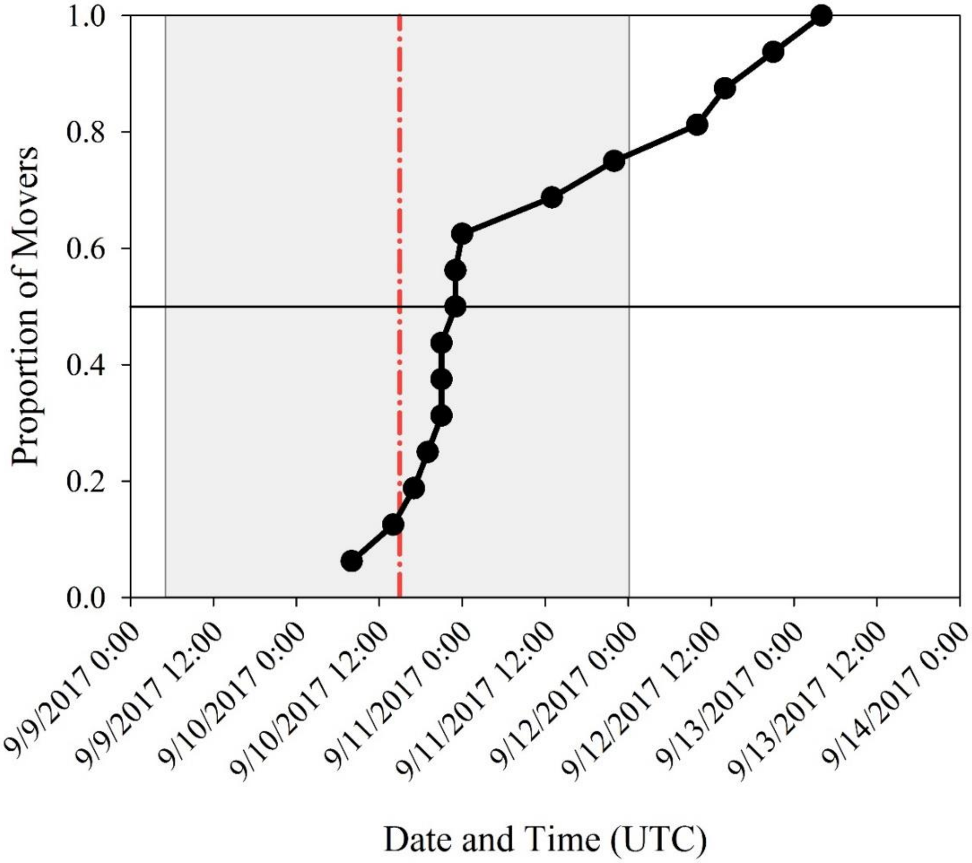


Fig. 4 Timing of common snook movement responses for the 16 fish that moved among river zones during Hurricane Irma, illustrating how 50% of zone changes (marked by black horizontal line) occurring by 23:00 UTC on 10 September, 8 hours after the storm passed the Shark River. The shaded box indicates the duration of the hurricane window, and the vertical dotted line marks Shark River passage (see Fig. 2).

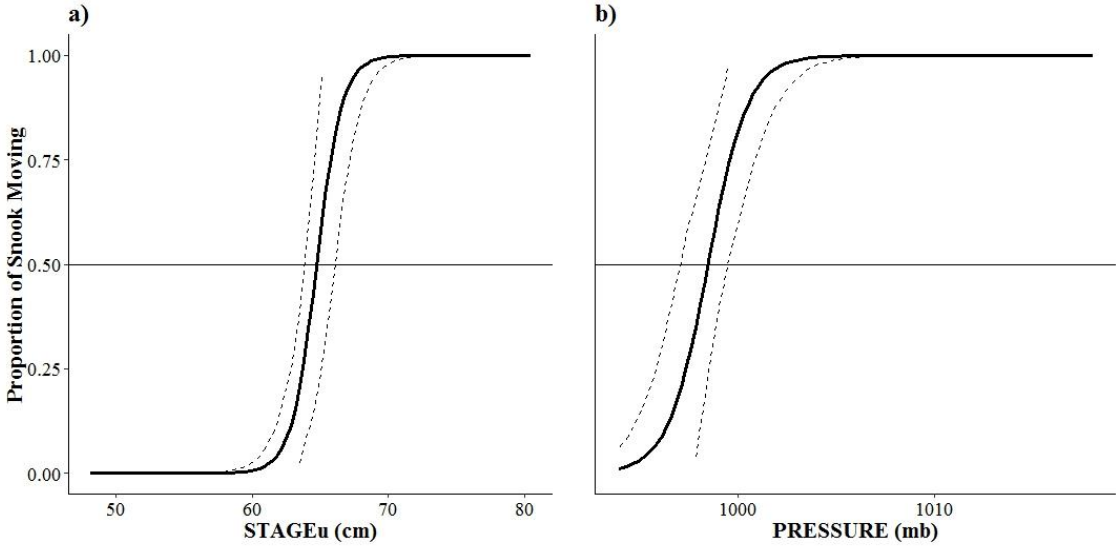


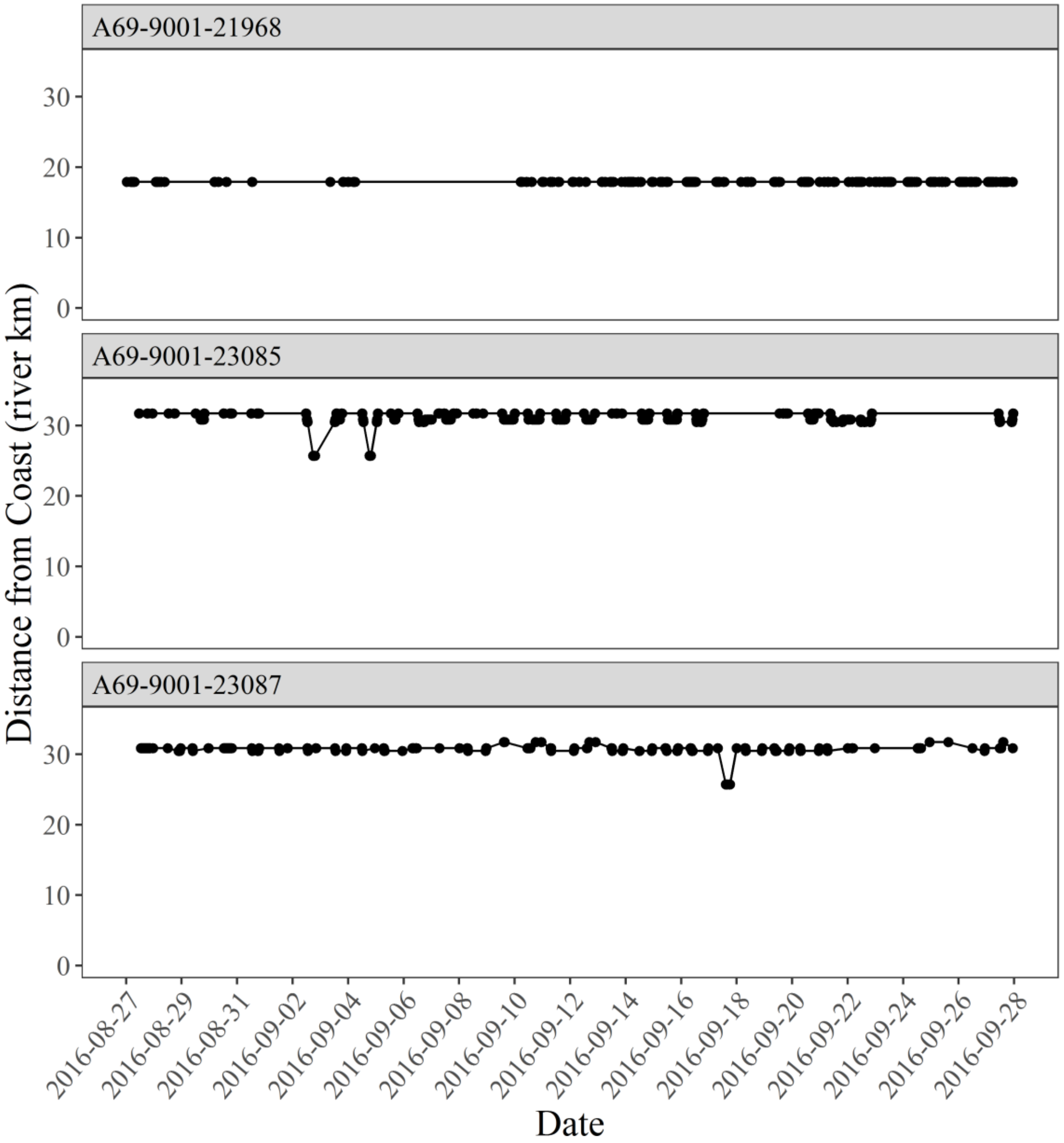
Fig. 5 Plotted variables in the best fitting logistic regression model (PRESSURE + STAGE$_U$) for common snook movement during Hurricane Irma. Variable effects are isolated by holding one variable at a fixed mean value in each plot, and black horizontal line marks the point where 50% of fish initiate movement between river zones. a) Fitted line for STAGE$_U$ with PRESSURE at a mean value of 1004 millibars (50% moved at 64.5 cm). b) Fitted line for PRESSURE, with STAGE$_U$ at the mean value of 69.82 cm (50% moved at pressures below 998 millibars). Dotted line denotes a 95% confidence interval.

Table 1 Fish details and tagging records for the 22 common snook detected in the Shark River during Hurricane Irma. Table shows unique tag code (Fish ID) for each individual, date the acoustic transmitter was implanted, fish size at time of tagging (Standard Length), and the number of unique detections on the acoustic array for each fish. Total number of detections are shown for both the duration of the study period (6 months before to 6 months after hurricane window, used to examine long-term movement patterns), as well as the time period during peak storm conditions used to make inference on hurricane-driven movements (Hurricane Detections). Hurricane movement indicates whether the fish moved among river zones during the hurricane (Yes or No), or if movement patterns could not be determined (Inconclusive) due to lack of pre or post-storm detections.

Fish ID	Date Tagged	Standard Length (cm)	Study Period Detections	Hurricane Detections	Hurricane Movement
32904	1/21/2014	55.2	983	3	No
21968	12/16/2015	67.0	2326	32	Inconclusive
21970	5/13/2016	62.7	9131	699	Yes
56006	5/14/2016	49.6	20796	263	Yes
56011	5/17/2016	42.2	6687	64	Inconclusive
56014	5/17/2016	43.5	14966	283	Yes
18367	5/17/2016	63.0	18269	79	Inconclusive
51640	12/13/2016	51.5	2165	429	Yes
51644	12/13/2016	50.5	16962	404	Yes
51645	12/13/2016	48.5	8437	61	Yes
51638	12/15/2016	47.0	9641	440	Yes
51652	2/26/2017	49.3	11065	181	Yes
51653	2/26/2017	45.7	39444	839	Yes
18370	2/27/2017	57.5	6074	383	Yes
51877	4/24/2017	64.5	1014	559	Yes
21959	4/24/2017	55.0	4090	74	Yes
18373	4/25/2017	60.5	5017	97	Inconclusive
18379	4/25/2017	65.5	8763	308	Yes
21960	4/25/2017	63.5	5259	63	Yes
18351	5/31/2017	58.2	8155	734	Yes
18382	5/31/2017	69.9	1170	15	Yes
21969	5/31/2017	54.5	1386	105	No

Table 2: Logistic regression model (GLM) output for the three hypotheses on movement cues investigated; 1) hurricane movements are explained by hurricane conditions, 2) movements are best explained by riverine conditions, 3) movements are best explained by a combination of hurricane and riverine factors. The best fitting overall model (i) is shown in bold text. PRESSURE$_{\Delta}$ is the change in barometric pressure between hourly intervals in the SR, and PRESSURE is the modeled pressure estimate (in millibars). STAGE$_{\Delta L}$ and STAGE$_{\Delta U}$ are the hourly changes in river stage (in cm) in the lower and upper river respectively, STAGE$_{L}$ is the measured lower river stage representing the storm surge, and STAGE$_{U}$ is measured stage in the upper river reflecting rainfall driven water levels. For output provided, k = number of model parameters, df = model degrees of freedom (number of estimated parameters), ΔAICc = is the difference in AICc score between the listed model and best fitting model, *w*AICc = AICc weight, Res Dev = Residual Deviance, LL = Log Likelihood, D^2 = the (adjusted) amount of deviance accounted for by the model. Probability of snook movement fit to 138 observations with 178.32 null deviance.

Model		Variable(s)	k	df	ΔAICc	*w*AICc	Res Dev	LL	D^2
Hurricane Effects	a.	PRESSURE$_{\Delta}$	1	2	141.2	<0.001	171.0	-85.05	0.04
	b.	PRESSURE	1	2	72.2	<0.001	102.1	-51.03	0.43
Riverine Effects	c.	STAGE$_{\Delta L}$	1	2	146.3	<0.001	176.1	-88.06	0.01
	d.	STAGE$_{\Delta U}$	1	2	137.5	<0.001	167.3	-83.66	0.06
	e.	STAGE$_{L}$	1	2	64.0	<0.001	93.9	-46.94	0.47
	f.	STAGE$_{U}$	1	2	9.4	0.007	39.3	-19.64	0.78
	g.	STAGE$_{U}$ + STAGE$_{L}$	2	3	7.6	0.016	35.3	-17.67	0.80
Combined Effects	h.	PRESSURE + STAGE$_{U}$ + STAGE$_{L}$	3	4	2.1	0.252	27.8	-13.88	0.84
	i.	**PRESSURE + STAGE$_{U}$**	**2**	**3**	**0**	**0.725**	**27.8**	**-13.88**	**0.84**



Online Resource 1: Movement paths from acoustic telemetry detections for three individual common snook in 2016, one year prior to the hurricane window. Each of the three panels depicts localized foraging behavior (as opposed to large-scale synchronous downstream movement) in the time period corresponding to the 2017 hurricane window described in the manuscript. Black circles indicate detections on an acoustic receiver, and each plot is labeled with the unique tag number of the individual fish.

CHAPTER IV

WHEN THE TIMING IS RIGHT: LINKING A SEASONAL PREY SUBSIDY TO THE BODY CONDITION OF COMMON SNOOK IN A COASTAL EVERGLADES RIVER

ABSTRACT

Seasonal movements of fishes among habitats often correspond to shifting resource availability and can occur in response to fluctuating freshwater inflows in coastal river systems. Seasonal availability of high-quality prey subsidies can provide resources that increase fitness, yet hydrologic variability can influence the movements of both consumers and their prey. Shifts in the timing and magnitude of prey availability driven by climate and water management may lead to a mismatch of resources, carrying consequences for the growth, survival, and reproduction of economically and ecologically valuable fish species. The objective of this study was to examine how seasonal/interannual variation in the timing and magnitude of key prey subsidies (sunfishes, *Lepomis* spp.) which concentrate into river channels from adjacent freshwater marshes during the dry season affect the body condition of Common Snook (*Centropomus undecimalis*). Further, we investigate how body condition relates to hydrologic variation, which influences both the movements of Snook into foraging areas, and prey availability. We addressed the study objectives by analyzing long-term abundance sampling data (2004-2021) from the Shark River in the Florida Coastal Everglades. We used generalized linear mixed models (GLMMs) to model Snook condition in relation to the prey subsidy (sunfish biomass at time of sampling), hydrologic conditions (water level, temperature, timing of marsh drydown), Snook size, and sampling year. Our results indicate that Snook body condition is best explained by a combination of these factors, with body condition increasing with higher sunfish biomass, lower water levels, during the transition between wet/dry seasons, and fish size, with notable variation among sampling years. Everglades National Park is the focus of

large-scale restoration efforts that seek to restore freshwater flows that have been reduced by land use change. Research examining the environmental conditions that maximize interactions between consumers and key prey subsidies and increase fitness can help inform water management decisions which benefit economically important recreational fish species.

INTRODUCTION

Animal populations depend on the availability of high-quality food resources to provide the energy and nutrients required for growth, survival, and reproduction. Often, consumers ranging from small birds, to freshwater fishes, to large marine mammals depend on resources that vary in both space and time (Abrahms et al. 2021; Abrahms et al. 2019; Cooke et al. 2016; Cotton 2007). Spatiotemporally discrete food resources can disproportionately contribute to the growth and condition of individuals, provide surplus energy that maximizes reproductive success, and increase the survival of offspring (Drent 1978; Merkle et al. 2016; Middleton et al. 2018; Van der Graaf et al. 2006). Consumers move among habitats to take advantage of these resources, and these movements often represent adaptive behaviors that match the timing of favorable habitat conditions and resource availability (Abrahms et al. 2021; Avgar et al. 2014; Lytle and Poff 2004; Middleton et al. 2018). Climate change, anthropogenic habitat alterations, and differential species responses to these changes may alter the timing and magnitude of resource availability in the future, and the ability to track temporal shifts may lead to matches or mismatches among consumers and critical resources, carrying implications for long-term population trends (Deacy et al. 2018; Post and Forchhammer 2007; Schindler et al. 2013; Sergeant et al. 2015; Thackeray et al. 2016).

For riverine fishes, the magnitude, frequency, duration, timing, and rate of change of freshwater flows can influence the availability/abundance of prey resources, and thus the movements of consumers into profitable foraging areas (Palmer and Ruhi 2019; Poff et al. 1997). In seasonally fluctuating systems, connectivity between river channels and floodplains serves as a vector for the transport of nutrients, organic matter, and organisms that enhance productivity and can provide consumers with access to prey subsidies (Garcia et al. 2017; Junk et al. 1989; Winemiller and Jepsen 1998). Past research has illustrated how fish species in diverse regions benefit from floodplain-derived subsidies, including for Northern Pike (*Esox lucius*) and Yellow Perch (*Perca flavescens*) in the temperate St. Lawrence River, Canada (Farly et al. 2019; Farly et al. 2021), Cichlids (*Cichla* spp.) in Venezuela's tropical Cinaruco River (Hoeinghaus et al. 2006; Winemiller and Jepsen 2004), and Barramundi (*Lates calcarifer*) and catfishes (*Neoarius* spp.) in multiple rivers of Australia (Crook et al. 2020; Jardine et al. 2012a; Jardine et al. 2012b). Body condition has been correlated with access to floodplain subsidies, and is a useful metric for assessing the fitness of fishes that has been linked to health, immune responses, survival, and reproduction (Abujanra et al. 2009; Brosset et al. 2016; Brosset et al. 2015; Farly et al. 2021; Luz-Agostinho et al. 2009; Stevenson and Woods Jr 2006). While past research has described how environmental conditions affect body condition (Abujanra et al. 2009; Blewett et al. 2017; Brosset et al. 2015; Luz-Agostinho et al. 2009), relatively few studies have explicitly linked variation in the availability and magnitude of floodplain prey subsidies to the body condition of riverine fish, partly due to a lack of high spatial/temporal frequency long-term community datasets that are able to quantify this variation (Cooke et al. 2016).

Common Snook (*Centropomus undecimalis*, hereafter Snook) are a widely distributed tropical euryhaline fish species that are well-suited for investigating how spatiotemporally patchy prey subsidies affect fish body condition. Snook are found in rivers, estuaries, and coastal waters of the western Atlantic, Caribbean Sea, and Gulf of Mexico, with their range extending from Brazil to Cedar Key on Florida's east coast and Cape Canaveral on Florida's west coast (Blewett et al. 2017; Munyandorero et al. 2020; Purtlebaugh et al. 2020). Snook are marine-obligate spawners requiring high salinities for successful reproduction (Ager et al. 1978; Chapman et al. 1978; Tucker Jr 1987), and form spawning aggregations in the lower estuaries, marine inlets, and coastal waters during the wet season (Boucek et al. 2017a; Lowerre-Barbieri et al. 2014; Massie et al. 2022; Young et al. 2016; Young et al. 2014). A migratory contingent of the Snook population moves into freshwater rivers after spawning which provides both refuge from lethal water temperatures (< ~10 °C) in the winter months at their northernmost range extent (Howells et al. 1990; Purtlebaugh et al. 2020), and enhanced foraging opportunities on freshwater prey during the dry season (Blewett et al. 2017; Boucek et al. 2017b; Boucek and Rehage 2013; Rehage et al. 2022; Rehage and Loftus 2007). Snook are protandrous hermaphrodites, and their transition from male to female has been reported to occur outside of the spawning season (Taylor et al. 2000; Young et al. 2020). Energy acquisition outside of the spawning season can be important for not only sex transitioning, but also for the maturation and the development of oocytes, and spawning migrations in the following year (Young et al. 2020).

Past research has linked energy flow from floodplain habitats to the diet of Snook found in upper river habitats (Rezek et al. 2020). In Florida rivers where Snook occur, freshwater prey subsidies are concentrated into river channels as water levels recede in adjacent floodplains marshes during the dry season, and serve as a key resource for Snook in the months before/after spawning (Blewett et al. 2017; Boucek et al. 2017b; Boucek and Rehage 2013; Rehage et al. 2022; Rehage and Loftus 2007). A study of Snook in the Peace River indicated that body condition was positively correlated with longer floodplain inundation, with condition increasing between high and low water levels, and stomach contents from gastric lavage consisted of large numbers of floodplain species (e.g., crayfishes, *Procambarus* spp., Brown Hoplo, *Hoplosternum littorale*, sunfishes, *Lepomis* spp.), illustrating the importance of floodplain prey concentration (Blewett et al. 2017). However, the magnitude and species identity of these prey subsidies can vary widely from year-to-year based on hydrologic conditions (e.g., length of floodplain inundation, temperature; Rezek et al. In Revision; Boucek et al 2016). Thus, there remains a need for research that quantifies how seasonal and interannual variation in the availability of freshwater prey and associated hydrological conditions that drive prey production and concentration affect body condition.

In this study, we use a long-term electrofishing dataset (2004 -2021) of fish communities in the Shark River, Everglades National Park (ENP), to examine how the magnitude of a freshwater prey subsidy (sunfishes, *Lepomis* spp.) and hydrologic variation affected variation in the body condition of Snook. Our primary research questions are twofold: Q1) How is Snook body condition affected by the timing and magnitude of the sunfish prey subsidy? and Q2) Does seasonal and annual variation in hydrologic conditions (namely water level, temperature, and floodplain inundation) also influence Snook body condition? We hypothesized that: H1) Seasonal increases in the sunfish prey subsidy will result in higher body condition, H2) Low water levels will result in higher Snook condition, due to prey concentration in the river channels, and H3) Snook condition is highest when the marshes dry below a critical threshold and prey first become available in the river channels. To test our hypotheses, we modeled Snook body condition in relation to sunfish biomass calculated from long-term sampling data and our selected hydrologic variables.

METHODS

Study Site

The Shark River is a low-gradient coastal river system in the southwestern region of Everglades National Park, with river channels that extend approximately 32 km inland from the coast and a drainage area of roughly 1700 km^2 (Fig. 1). The hydrologic regime is shaped by the regional subtropical climate, and seasonal peaks in precipitation, with more than 75% of the system’s rainfall occurring during the wet season in May-October (Abiy et al. 2019b; McIvor et al. 1994; Price et al. 2008; Saha et al. 2012). The magnitude and timing of freshwater flow is influenced by atmospheric teleconnections at both long and short timescales (El Niño Southern Oscillation, Atlantic Multidecadal Oscillation), which results in a high degree of interannual variability in seasonal water levels including droughts and prolonged flooding (Fig. 2, Abiy et al. 2019a; McIvor et al. 1994; Saha et al. 2012). Throughout the twentieth century, drastic alterations to the region’s hydrology resulting from intensive water management for urban and agricultural development have reduced the amount of freshwater flows by more than half (Marshall et al. 2020; Marshall et al. 2014).

The Shark River consists of distinct habitat zones, with freshwater creeks and marshes in the upper river that transition into mangrove forests, with progressively larger and more saline channels that flow into the Gulf of Mexico (Boucek et al. 2017b; Fry and Smith 2002; Massie et al. 2022; Matich et al. 2017; Rosenblatt and Heithaus 2011). The oligohaline upper river (Fig. 1b) consists of narrow shallow channels bordered by a combination of mangroves and freshwater marshes containing a mix of sawgrass (*Cladium* spp.) and freshwater woody plant species, with limited tidal influence in the wet season (Boucek and Rehage 2013; Boucek and Rehage 2014; Chen and Twilley 1999; Childers et al. 2006). Upper river water levels are closely tied to precipitation and conditions in the adjacent marshes, and as water levels drop throughout the dry season (November – April), floodplain species move from the drying marshes into the river channels seeking refuge (Boucek et al. 2017b; Boucek and Rehage 2013; Rehage et al. 2022; Rehage and Loftus 2007). Midriver, a mesohaline central embayment (Tarpon Bay) is marked by a transition from a predominantly freshwater fish community to one primarily consisting of estuarine and marine species, with shallow open habitats and more pronounced tidal fluctuations (Boucek and Rehage 2013; Rehage and Loftus 2007; Rosenblatt and Heithaus 2011).

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 2022). Sampling was conducted throughout the year, with three primary sampling events each year. The first sampling event was performed following the end of the wet season when marsh water levels were near their annual peak

(November-December). A second sampling event was conducted during the early dry season as water levels recede (January-March). A third sampling event occurred when water levels neared their minimum in the late dry season (April-May). Sampling consisted of boat-based electrofishing at 15 fixed sites in the upper and middle river (Boucek and Rehage 2013; Rehage and Loftus 2007). Each site consists of three replicate transects, for a total of 45 transects shocked per seasonal sampling event (Fig. 1b). In many years of study (2010-2014, 2016-2021), additional monthly samples events were conducted in-between these three primary sampling events at five upper river sites (15 transects-shown in blue in Fig 1b) to better track the timing and size of the seasonal increase of freshwater prey entering ecotonal creeks from drying marshes. These additional samples provided a higher degree of temporal resolution on how Snook abundance and prey landscapes change seasonally, as marsh water levels recede, and freshwater prey become concentrated in the river channels. Sampling at these headwater sites occurred between two and eight times per sampling year over the course of the study (mean = 5 headwater sampling events/year).

Following standardized methods, fish were captured using a boat-mounted GPP 9.0 electrofisher (Smith Root, Vancouver, WA, USA, Boucek and Rehage 2013; Rehage and 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 300 seconds of shock time to standardize sampling effort (see Boucek and Rehage 2013 for additional details). Two netters were stationed on the bow of the boat, and once immobilized, fish were netted and immediately transferred to an on-board aerated livewell. Approximately 100 m of shoreline was sampled for each transect, with the total distance sampled (meters) measured by a boat-mounted GPS unit and recorded at the end of each transect in order to accurately calculate sunfish and Snook abundance and sunfish biomass per 100 m of shoreline for use in statistical models. For all samples, captured sunfish and Snook were identified to the species level, measured (standard length in cm, SL), weighed (grams), and released live after being allowed to recuperate in ambient water.

Statistical Analyses

Snook Condition

To examine how seasonal/interannual variation in the magnitude of the freshwater prey subsidy and hydrologic conditions affect Snook body condition, we calculated a relative condition factor for the Shark River Snook population based on all individuals captured during long-term sampling where length and weight data were available. Relative condition (K_n) was selected as our condition metric, which uses a length-weight regression relationship specific to the study population (Anderson 1996). These methods are consistent with previous studies examining the body condition of fishes (Abujanra et al. 2009; Blewett et al. 2017; Brosset et al. 2015; Hoeinghaus et al. 2006; Luiz et al. 2019; Luz-Agostinho et al. 2009; Pope 2007). For each Snook where length and weight were measured, relative condition was calculated as W/W’, where W is the measured weight of the fish and W’ is the estimated mean weight-at-length for the entire study population. To estimate the mean weight-at-length relationship for the population, we first $\log_{10}$-transformed fish length (L = standard length in cm) and weight (W = weight in grams), and used a linear regression relationship to produce a value representing the average year-round body condition of Shark River Snook: $\log_{10}(W) = \alpha + \beta(\log_{10}L)$, where β is the slope and α is the intercept. To reduce the influence of outliers and instances where field measurement error was suspected, we removed records that were greater/less than two standard deviations of the weight-at-length regression residuals when calculating the mean weight-at-length relationship (detailed in Klassen et al. 2014). W' was then calculated using regression coefficients, where $W' = \alpha L^{\beta}$, and a relative condition factor value of K_n was calculated for each fish in the dataset ($K_n = W/W'$). Finally, we selected K_n estimates for use in our statistical models for fish that were captured at the five uppermost river sites (Fig. 1b). These sites were selected because they received the most frequent sampling effort over the long-term dataset, and they are in close proximity to the freshwater marshes and thus experience a higher contribution from freshwater prey subsidies (Boucek and Rehage 2013; Rehage and Loftus 2007).

Sunfish Biomass

To quantify the magnitude of the marsh prey subsidy available to Snook where and when they were captured, biomass was calculated from long-term sampling data for sunfishes (*Lepomis* spp.) at each transect/sampling event for the five upper river sites (Fig. 1b). We chose sunfishes to represent the seasonal marsh prey subsidy because the abundance of these prey species in the river channels has been shown to fluctuate in response to seasonal marsh water levels in the Shark River, and a reported 80% of prey items found in Snook stomach contents during the transition between the wet and dry season consisted of sunfish species (Boucek et al. 2017b; Boucek and Rehage 2013; Rehage and Loftus 2007; Rezek et al. In Revision).

Sunfish biomass was standardized across each transect, site and seasonal sampling event, and calculated as the weight (wet weight, grams) per 100 m of shoreline (summed weight of all sunfish captured in a transect / total distance sampled in meters x 100). In some cases, weight was only recorded for a subset of sunfishes captured, and for these we followed Klassen et al. (2014) and estimated species-specific wet biomass using the equation $W = aL^b$, consistent with our weight calculations for Snook K_n (described above). Length-weight relationships were derived from linear regression models built for each sunfish species that included all recorded field measurements collected over the course of our study (2004-2021), where W = wet weight biomass in grams, a = the intercept, and b = the SL coefficient (slope) from the regression models. Sunfish biomass was first calculated for each transect, site, and sampling event, and the mean sunfish biomass for each sampling event/site (averaging the biomass among the 3 transects at each site) was then calculated to represent the prey subsidy available to Snook on the date and at the sample site where they were captured. Because Snook are mobile predators that can take advantage of prey resources beyond their precise capture location (i.e., the ~100 m electrofishing transect), using the mean sunfish biomass for the three transects at each site allowed us to capture spatial differences among sample sites while also accounting for fine-scale differences in prey availability.

Statistical Models of Snook Condition

We used Generalized Linear Mixed Models (GLMMs) with a Gaussian error distribution and sample site as a random effect to investigate how the magnitude of the sunfish prey subsidy and seasonal/interannual environmental variation affect Snook body condition. The response variable for our models was the estimated relative body condition (K_n, described above) for each Snook captured, weighed, and measured at the five upper Shark River sites over course of our study. Analyses were performed using R statistical software and the glmmTMB package (Magnusson et al. 2017; Team 2022).

Modeling consisted of a four-step process where we first examined all independent variables for collinearity. Second, if collinearity was found, we selected the best fitting variable based on the lowest Akaike's information criterion (AIC, Akaike 1998) by comparing univariate models for each term. Third, we combined all selected variables into a global model. Finally, we reduced the global model using backward selection using the step() function from the stats package in R (Team 2022). For all models, we calculated R-squared values with the Performance package in R (Lüdecke et al. 2021), in order to show the amount of model variance explained, and selected a final best fitting model based on the lowest AIC score (Anderson 2007; Burnham and Anderson 2003; Johnson and Omland 2004; Symonds and Moussalli 2011). We also inspected model residuals to verify that all modeling assumptions were met and evaluate variance inflation factors (VIF) to ensure that results were not influenced by multi-collinearity using the DHARMa and Performance packages in R (Hartig 2022; Lüdecke et al. 2021).

To test hypothesis 1, that seasonal increases in the sunfish prey subsidy available to Snook in the river channels will result in higher K_n, we used mean sunfish biomass corresponding to the date and site where each individual Snook with a calculated K_n was captured. Exploratory models examined whether sunfish abundance (# of sunfish captured per 100 m) may better predict K_n relative to biomass. However, a comparison of univariate models indicated better performance with biomass (AIC > 2 points lower). Additionally, we considered a lagged variable representing sunfish biomass for the site where each Snook was captured during the previous sampling event for that year. However, this variable for lagged biomass was not statistically significant ($p = 0.37$, R squared < 0.01). Thus, mean site biomass at the time of sampling and without a lag was selected in the final models described here.

To test hypothesis 2, that lower water levels will result in higher Snook K_n, due to prey concentration in the river channels, we used a variable for daily mean water level relative to The North American Vertical Datum of 1988 (NAVD88) obtained from the Everglades Depth Estimation Network (EDEN, https://sofia.usgs.gov/eden/). Water level data were queried for a monitoring station located in the freshwater marsh just upstream from our sample sites (Fig. 1b, station MO215) and we then subtracted the ground surface elevation to determine the water depth at that station (average ground elevation at MO215 = -9.75 cm). Further, to test hypothesis 3, that K_n is highest when the marshes dry below a critical threshold where prey become concentrated in the river channels, we calculated a metric for the number of days in the previous 180 days (6 months) that marsh water level dropped below 30 cm, a level that corresponds to marsh flood stage. The ground elevation difference between sawgrass ridges and lower wet-prairie marsh sloughs in the Everglades ranges between approximately 10 and 25 cm (Trexler et al. 2005), and a water level > 30 cm should indicate inundation of most, if not all, habitat in the marshes adjacent to the river channels. Wet season water levels above 30 cm have also been reported to correspond to increases in sunfish biomass in the following dry season (Rezek et al. In Revision; Boucek et al. 2016). The six-month prior time-period was selected for two reasons. First, the dry season in South Florida extends from November to April. While marsh drying generally occurs in the later part of this time-period, hydrologic conditions vary from year-to-year based on differences in the amount of annual precipitation (Fig. 2). A window of 6 months allows us to capture marsh drydown timing across the entire long-term dataset. As the number of days below the drydown threshold increases, the abundance of freshwater prey that have moved into the river channels for refuge may have already been reduced due to consumption by predators. Second, the prior 6-month window also indicates the extent of marsh flooding in the previous wet season, a time-period particularly important for freshwater marsh production, and which can affect the overall abundance of freshwater prey each year (Chick et al. 2004; Trexler and Goss 2009; Trexler et al. 2002). High values for days < 30 cm in the prior six months indicate overall lower water levels in the previous wet season, a likely earlier annual drydown, and a likely longer dry season duration. To evaluate the efficacy this 30 cm threshold, or whether prey concentration/flood duration may be better represented by other water levels, we also calculated the number of days < 20 cm marsh water level, and number of days < 10 cm water level. When univariate models were compared using AIC, the 30 cm threshold consistently resulted in better model performance (lowest AIC) and was therefore selected for final models.

In addition to our hypothesized drivers, we included water temperature in our model based on observation that temperature influences body condition in other fish species, and affects marsh prey community structure in the Everglades (Brosset et al. 2015; Latour et al. 2017; Rezek et al. In Revision). Daily mean temperature data were obtained from the United States Geological Survey time-series for Bottle Creek (Station 022908295) located just upstream of our sample sites via the South Florida Water Management District’s environmental database (DBHYDRO, https://www.sfwmd.gov/science-data/dbhydro). We also included fish size (SL) as a model variable, because lager fish may be better able to capitalize on large-bodied prey species (Hoeinghaus et al. 2006; Luiz et al. 2019), and larger migratory Snook moving into headwater habitats to exploit the freshwater prey subsidy may benefit from increased prey availability relative to the greater population. Further, we included a factor variable for the sampling year to provide further evidence for the role of interannual variability in Snook condition and capture additional model variance not captured by our other variables.

RESULTS

Fish Sampling

Between November 2004 and June 2021, 2,994 individual Snook were captured during standardized electrofishing across all sites in the Shark River. Snook ranged in size from 2.8 to 79.5 cm SL (mean 38.8 +/- 13.7 cm SD), and weights from 5.6 to 7,880.0 g (mean 854.4 +/- 940.6 g). Snook weights were not recorded in three of the early sampling years (November 2006 – May 2009), and 487 fish that were missing length or weight data were therefore excluded from K_n estimates and statistical models. The 2,507 fish with data on both length and weight were captured at 73 unique sampling events. When these fish were included in linear regression models to generate mean weight-at-length relationship for the population, 111 individuals (less than 5%) had greater or less than two times the standard deviation of the residuals suggesting field measurement errors and were excluded from further estimates of K_n. In total, 2,396 individuals served as the basis for mean weight-at-length relationship used to calculate K_n. Of these fish, 1,492 Snook (62%) were captured at the five upper river sites (Fig. 1b) between 2004 and 2021, and these fish served as the basis for our statistical models.

Snook Condition

The $\log_{10}$ transformed linear regression equation we derived to estimate the mean weight-at-length relationship and estimate K_n for Snook in the Shark River, $\log_{10}(W) = -1.90 + 3.00(\log_{10}L)$, was highly significant ($p < 0.01$, R-squared = 0.99). When calculated for all Shark River fish, K_n varied both annually (Fig. 3, Table 1) and seasonally (Fig. 4, Table 2), and ranged from 0.70 to 1.29 (mean 1.00 +/- 0.09). K_n was similar when considering separately the 1,492 captured in the upper river sites, K_n ranged from 0.74 to 1.28 (mean 1.00 +/- 0.09). The highest annual K_n observed across individuals occurred in the 2010/2011 sampling season (mean 1.05 +/- 0.10), peaking in March/April (mean 1.06 +/- 0.07), and the lowest annual mean was observed in both 2015/2016 and 2020/2021 (mean = 0.93 +/- 0.08) with the lowest K_n observed in February of both sampling years (means of 0.91 and 0.89 respectively).

Sunfish Biomass

In total, 5,674 individual sunfish representing six species (Bluegill, *Lepomis macrochirus,* Redear Sunfish, *Lepomis microlophus*, Spotted Sunfish, *Lepomis punctatus*, Dollar Sunfish, *Lepomis marginatus*, Warmouth, *Lepomis gulosus*, and Bluespotted Sunfish, *Enneacanthus gloriosus*) were captured during the 17 years of electrofishing at the upper river sites, and served as the basis for our biomass calculations. Sunfish biomass was highly variable over time, ranging from a mean of zero sunfish captured (occurring at 6 different sampling events) to 987.83 +/- 392.63 g/100m in April 2013 (Tables 1 and 2). The highest mean annual biomass was recorded in the 2014/2015 sampling season (mean = 515.51 +/- 385.52 g/100m). The lowest mean biomass was recorded during the 2015/2016 sampling season with a mean catch across all sites/sample dates of 70.68 +/- 63.21 g/100m, also corresponding to one of two years where mean K_n was lowest.

Factors Affecting Snook Condition

We modeled Snook K_n in relation to variables both representing the magnitude of the sunfish prey subsidy and variation in environmental conditions (Table 3). Three candidate metrics for a marsh drydown threshold representing the timing of freshwater prey concentration and extent of wet season flooding (days marsh water level < 10, 20, 30 cm) were highly collinear (Pearson's correlation > 0.9), and we selected days < 30 cm based on the lowest AIC and highest R^2 value. High collinearity (Pearson's correlation > 0.6) was not detected for any other variable pairings, and six variables were included in the global model: Marsh water level, number of days marsh water level < 30 cm, water temperature, sunfish biomass, Snook size (SL), and sampling year. The global model was reduced using backward selection, and only temperature was removed. Thus, our final model consisted of five variables (Marsh water level, days marsh water level < 30 cm, sunfish biomass, fish size, and sampling year). This model captured 24% of the variance in Snook K_n (Table 3).

We examined the individual contributions of each of the variables in our best model and plotted the isolated effects of each variable (Table 4, Fig. 5). All model variables were statistically significant ($p < 0.01$). Sampling year had the highest contribution to explaining model variance (marginal $R^2 = 0.12$), followed by water level (marginal $R^2 = 0.06$), sunfish biomass (marginal $R^2 = 0.04$), fish size (marginal $R^2 =$

0.04), and the number of days the marsh level was < 30 cm (marginal $R^2 = 0.1$). K_n showed a positive relationship with both sunfish biomass and fish size. K_n had a negative relationship with water level, and the number of days marsh water levels was below 30 cm (Fig. 5).

DISCUSSION

In this study, we examined how the magnitude of a freshwater prey subsidy, and the seasonal/interannual variation in water level that drives the timing and size of the prey subsidy, affects the body condition of the economically important and popular recreational fish species, Common Snook (Fedler 2009; Munyandorero et al. 2020). The quantity and quality of food resources, and favorable environmental conditions that promote trophic linkages, are critical to the long-term performance of animal populations. This can be particularly important when resources fluctuate in space and time, and seasonal/interannual variation that affects resource availability can carry consequences for the growth, survival, and the reproductive success of individuals and populations (Farly et al. 2021; Isaac et al. 2016; Middleton et al. 2018; Roberts et al. 2019). Body condition can serve as an indicator for environmental change, and in assessing ecosystem restoration goals. For example, body condition has been used as a performance metric for American alligators (*Alligator mississippiensis*) and American crocodiles (*Crocodylus acutus*) in the Everglades (Brandt et al. 2016; Briggs-Gonzalez et al. 2021; Strickland et al. 2022).

Many riverine fishes exploit seasonal prey subsidies maintained by fluctuations in the natural flow regime that provide connectivity between river channels and floodplain productivity (Bunn and Arthington 2002; Castello et al. 2015; Crook et al. 2020; Farly et al. 2019; Hoeinghaus et al. 2006; Poff et al. 1997). Anthropogenic alterations to the landscape, climate change, and management of a limited freshwater supply for multiple uses can impact the magnitude and timing of floodplain resources (Palmer and Ruhi 2019; Poff 2018). Our results show significant relationships among sunfish biomass, water level, fish size, and interannual variation that account for 24% of the variance in Snook body condition across a 14-year dataset.

Our models indicate a positive correlation between sunfish biomass and Snook condition. These results provide additional evidence to past research describing the seasonal importance of marsh sunfishes to Snook foraging (Boucek et al. 2017b; Boucek and Rehage 2013; Rehage and Loftus 2007). Boucek and Rehage (2013) conducted gastric lavage sampling in the Shark River, and found that Snook preferentially feed on sunfishes, constituting 80% of prey items present in stomach contents during early marsh drydown. Additionally, Rezek et al. (2020) used stable isotope analysis coupled with acoustic telemetry, and reported a 69% dietary contribution from freshwater prey for Snook whose distributions were primarily in the upper river. Similar dependencies on specific prey species have been reported for fish in other systems. In Venezuela, 45% of the diet of the piscivorous *Cichla temensis* consisted of Pellegrin (*Semaprochilodus kneri*) during falling water levels, corresponding to an increase in body condition (Hoeinghaus et al. 2006; Winemiller and Jepsen 2004). Farley et al. (2021) reported positive correlations between floodplain prey and the body condition of multiple fish species in a large fluvial lake in Quebec, Canada, and that condition was related to flooding duration and magnitude (i.e., the cumulative annual area of the floodplain that was inundated with water). Further, Barramundi in Australia that migrated into freshwater rivers and thus accessed floodplain prey subsides grew 25% faster in the year following migration than non-migratory individuals who remained in the estuary (Roberts et al. 2019).

A large annual sunfish prey subsidy in the dry season may be particularly important for Snook, because the dry season precedes annual reproductive migrations that begin with the onset of the wet season (Lowerre-Barbieri et al. 2014; Massie et al. 2022; Young et al. 2016; Young et al. 2014). Previous histological studies of female Snook have shown how the dry season corresponds to the development and regeneration of oocytes, and high hepato-somatic indices indicate that this time-period is also where sex transition and maturation occurs (Young et al. 2020). Energy acquired during the dry season can therefore be allocated to sexual maturation, sex transition, downstream spawning migrations, and ultimately reproduction (Massie et al. 2022; Young et al. 2020). In five of the seven years (71%) where annual mean K_n was > 1.0, peak sunfish biomass occurred in March and April, just prior to the beginning of the spawning season and corresponding to the dry season period, and where past acoustic telemetry studies in the Shark River have reported the greatest upper river habitat use by tagged fish (up to 70% of acoustic detections recorded in upper river, Rehage et al. 2022).

Our results showed a strong correlation between decreasing marsh water levels and Snook condition, illustrating the importance of prey concentration during the dry season. Falling water levels typically correspond to the highest fish density in floodplain river food webs, and an increase in predator-prey interactions (Pereira et al. 2017; Winemiller 2004). For example, the feeding activity of multiple cichlid species (*Cichla temensis, Cichla intermedia*) in the Cinaruco River, Venezuela, were highest during falling water levels, also corresponding to the highest mean body condition (Jepsen et al. 1999; Jepsen et al. 1997). Further, an investigation of piscivorous fishes in Upper Paraná River, Brazil, found a negative relationship between prolonged flooding and body condition (Luz-Agostinho et al. 2009). Correlations between fluctuating water level and body condition have also been reported for Snook. In a study in the Peace River, Blewett et al. (2017) used eight years of sampling data to show how Snook consumed high numbers of prey originating from river floodplains, and that there was a 1.2-fold increase in body condition as water levels receded at onset of the dry season. The importance of seasonal prey concentration has also been described for other consumers in the Everglades. Nesting and foraging success of Everglades wading birds has been linked to seasonal water level fluctuations in the freshwater marshes, particularly falling water levels which concentrate prey and increase accessibility for consumers (Beerens et al. 2011; Botson et al. 2016).

Our models also indicate a weak but significant negative relationship between the number of days that marsh water levels dropped below 30 cm in the six months prior to capture and Snook body condition. K_n progressively dropped below the mean with increasing time from this 30 cm water level threshold, which corresponds to the beginning of prey concentration in the Shark River (Rezek et al. In Revision). Other studies have reported similar findings where body condition is highest during the early stages of drydown. In the St. Lawrence River, Canada, the contribution of floodplain prey to the diets of juvenile fish in Lake Saint-Pierre was highest early in the growing season and when floodplain production was highest (Farly et al. 2019).

Fish size was positively related to Snook condition, suggesting that larger Snook in the upper Shark River may be better able to capitalize on the marsh prey subsidy. Larger migratory Snook move into headwater habitats from marine/estuarine habitats in the dry season to exploit freshwater prey subsidies (Blewett et al. 2017; Boucek et al. 2017b; Boucek and Rehage 2013; Rehage et al. 2022), and we hypothesize that larger migrants may gain additional benefit from consuming larger-bodied prey above the gape-limitations of smaller resident fish. Higher condition in larger fish has also been reported for other fish species. For example, the condition of large Barramundi which feed on inundated floodplains in Australian rivers were higher relative to smaller fish, which was attributed to gape limitation and the ability to consume a wider range of prey sizes (Luiz et al. 2019). The condition of large-gaped Barramundi remained higher in the months when floodplains were no longer accessible, suggesting that individuals able to capitalize on floodplain prey can offset weight loss during times of lower prey availability with energy gained from a seasonal subsidy (Luiz et al. 2019). Similarly, the condition of large *Cichla temensis* (> 30 cm) which feed on migratory prey during falling water levels was significantly higher than smaller individuals of the same species, which was partially attributed to gape-limitation and the ability to consume large prey species, specifically Pellegrin (Hoeinghaus et al. 2006). Further, Cargnelli et al. (1997) found that the condition of Bluegill in a Canadian lake was higher in larger fish following the winter months, indicating that resources acquired months earlier can help sustain fish through harsher conditions. Future research able to make comparisons between movement patterns, energy needs as a function of size, and body condition among smaller resident and larger migratory Snook would offer valuable additional insight.

Our results demonstrate that interannual variability has a large impact on Snook body condition, and sampling year explained 12% of model variance. Year-to-year variability in condition has been observed in other fishes. For example, in a 14-year study of 16 fish species in Chesapeake Bay, Latour et al. (2017) found substantial variation in condition among years, and suggested that variation might be explained by interannual differences in primary productivity. In South Florida, the timing and magnitude of seasonal precipitation varies dramatically from year-to-year (Abiy et al. 2019a; Abiy et al. 2019b), and periodic droughts or prolonged flooding can have a large effect on water levels, marsh inundation, and marsh prey production, all of which can in turn affect Snook condition. For example, water levels were exceptionally high throughout the sampling seasons where annual Snook condition was the lowest across our dataset (2015/2016 and 2020/2021, mean $K_n = 0.93$ both years). In these years, dry season marsh water levels did not drop below 30 cm at all in the 2015/2016 dry season, and did not reach this level until mid-May in 2020/2021, reducing the prey concentration effect throughout much of the dry season. Further, 2015/2016 corresponded to the lowest annual sunfish biomass observed in our study (70.7 g/100m, 75 % lower than the 14-year average), and in 2020/2021, peak biomass was not reached until May when water level dropped below 30 cm in the marsh. Conversely, the sampling year with the highest Snook condition (2010/2011, mean $K_n = 1.05$) followed a wet season in 2009 where water levels were above the long-term average, and incidentally, following a cold spell in January 2010 which resulted in 80% declines in Snook CPUE (Boucek et al. 2022; Boucek et al. 2017b; Stevens et al. 2016), which may have reduced competition for prey due to decreases in the relative abundance of Snook. Blewett et al. (2017) reported similar findings for Snook in the Peace River, with the highest body condition in years with average or above annual water levels, which would result in higher prey production.

CONCLUSION

We examined how the body condition of Snook is influenced by the magnitude of a freshwater prey subsidy (sunfishes, *Lepomis* spp.) which originates in the freshwater marshes and is concentrated in river channels during falling water levels in the dry season. Further, we investigated how seasonal and interannual environmental variations which can influence both floodplain productivity and the accessibility to these prey resources is related to Snook body condition. Using statistical models, we illustrate how a combination of these factors interact and result in both seasonal and interannual variations in condition. Our results suggest not only that the body condition increases with the magnitude of the sunfish prey subsidy, but also that condition increases during falling water levels and is of most benefit to individuals present near floodplain habitats when prey first become available and can fully capitalize on this resource. Body condition can have implications for performance of both individuals and populations, and may be an informative management metric that provides additional insight on population health and habitat quality not reflected by relative abundance alone. Population health is not typically included as a management end point, although quantifying condition is straightforward and cost effective, can be calculated from existing sampling data. Incorporating bioindicators for multiple species into monitoring and assessment could aid in evaluating the efficacy of water management/restoration efforts. Findings from the present study provide additional insight into the importance of a key prey resource for a valued fishery, and the environmental conditions that maintain access to this resource.

This information can be useful when considering freshwater management decisions in a highly managed landscape. Research which describes how resource availability fluctuates over time as a factor of environmental variation, and how this affects the body condition of consumer populations, can help inform management decisions aimed at the conservation of ecologically, economically, and socially important species.

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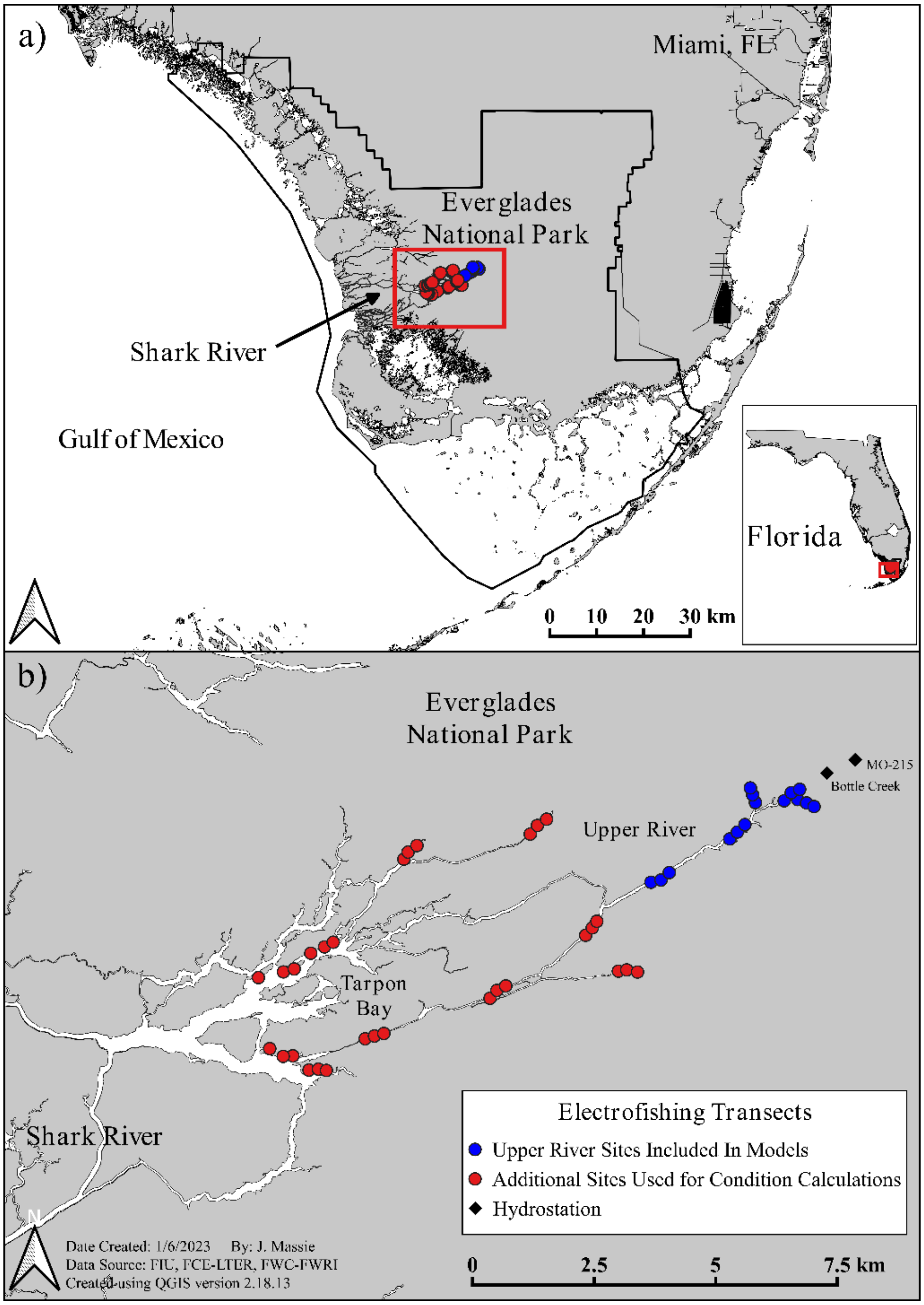

Figure 1: Map of the study area in Everglades National Park where fish community sampling was conducted between 2004 and 2021. Panel a) shows the location of the Shark River in SW Florida, and panel b) depicts the 15 electrofishing sites (three transects/site) where fish were captured. Blue dots denote the five upper river sites used to model how sunfish biomass and hydrologic variation affect Snook K_n, and red dots indicate additional sites/transects throughout the river where fish length/weights were used to calculate the mean population average body condition (K_n, calculated for all sites, blue and red dots). Black diamonds show the location of hydrologic monitoring stations where environmental conditions (water level, temperature, salinity) were measured.

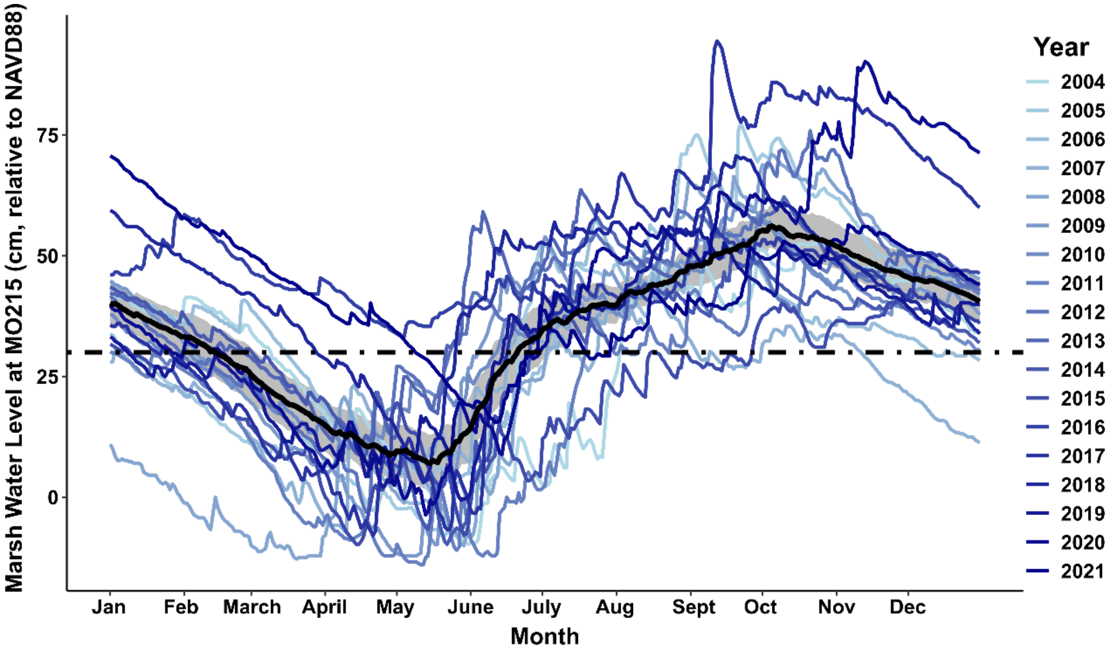

Figure 2: Hydrographs of water level in the freshwater marsh of the upper Shark River at station MO215 (see Fig. 1b) for each year of the study (2004-2021). Individual color-coded lines correspond to each sampling year and illustrate the high degree of interannual variability in both the timing and magnitude of freshwater flows. The solid black line represents the long-term mean daily water level for the full period that MO215 has been recording data (1996-present) with the shaded area indicating standard error in water level across the dataset. The horizontal hashed line denotes the 30 cm threshold that corresponds to the beginning of marsh prey concentration in the river channels during falling water levels.

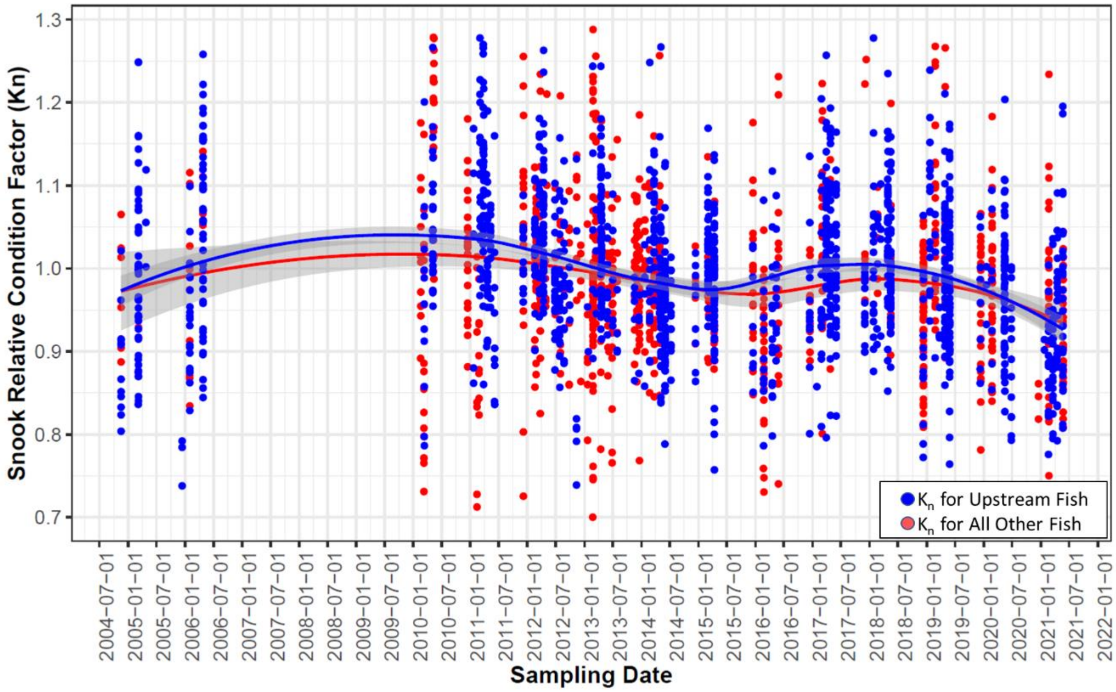

Figure 3: Plot depicting the relative body condition (K_n) of Common Snook for all individuals captured over the course of the study (2004-2021) where length and weight data were available. Blue dots depict fish from 5 the upper river sites most frequently sampled over time and adjacent to freshwater marshes which were used in statistical models predicting how sunfish biomass and water level affect K_n. Red dots show fish captured lower in the river and in Tarpon Bay which were included in the calculations of the average K_n for the entire Shark River Snook population. Solid lines show local regression fitting (loess) curves depicting trends over time for both the modeled upper river fish (blue), and all additional individuals captured over the course of the study (red). Note: Snook weights were not recorded during sampling events which occurred between November 2006 and May 2009, and K_n was not calculated for these sampling events.

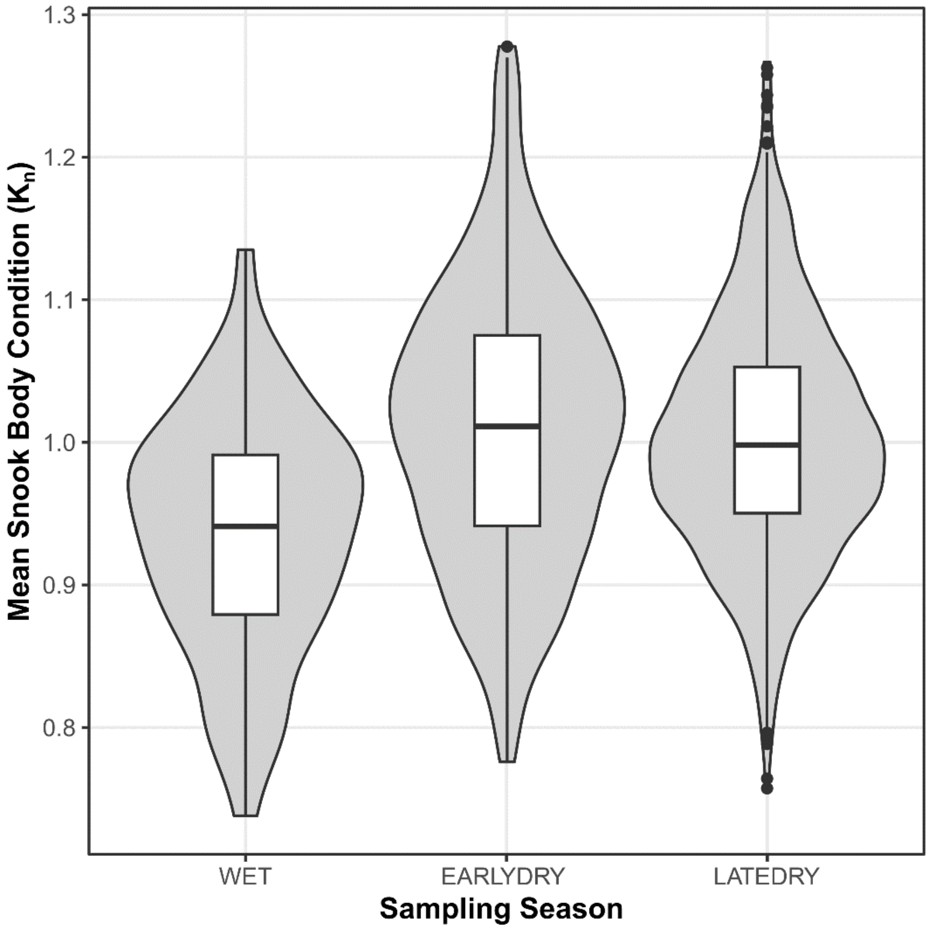

Figure 4: Violin plots depicting the seasonal variation in the relative body condition of Common Snook (K_n) captured at the five uppermost sites in the Shark River adjacent to the freshwater marshes. Wet season sampling (WET) was conducted in November/December following annual water levels maximums, EARLYDRY samples are collected as water levels recede during the dry season (January – March), and LATEDRY sampling occurred at the end of the dry season (April/May) when water levels approach the seasonal minimum.

Table 1: Summary of Common Snook body condition (K_n) for each sampling year showing the number of sampling events each year (# Events), the number of fish captured (n), mean body condition (K_n), standard deviation (SD), and standard error (SE) for both the subset of fish included in statistical models (captured at 5 upper river sites, Fig 1b), and for all fish captured at all sites over the course of the study (2004 – 2021). Mean sunfish biomass across sites each year with SD and SE are also shown.

		K_n: Upper River Snook (Model Fish Only)				K_n: All Snook Captured in Shark River				Sunfish Biomass (g/100m)		
Sampling Year	# Events	n	mean	SD	SE	n	mean	SD	SE	mean	SD	SE
2004-2005	3	61	0.98	0.11	0.01	70	0.98	0.10	0.01	340.29	384.40	221.93
2005-2006	3	73	1.01	0.12	0.01	88	1.01	0.11	0.01	150.37	156.57	90.40
2009-2010	2	40	1.03	0.10	0.02	88	1.03	0.13	0.01	305.59	187.63	132.67
2010-2011	6	105	1.05	0.10	0.01	143	1.03	0.11	0.01	407.35	421.03	171.88
2011-2012	8	164	1.02	0.07	0.01	273	1.02	0.08	0.00	169.57	143.56	50.76
2012-2013	8	102	1.02	0.09	0.01	254	1.00	0.10	0.01	454.86	428.40	151.46
2013-2014	8	177	0.97	0.07	0.01	299	0.98	0.07	0.00	395.59	496.29	175.46
2014-2015	3	109	0.99	0.07	0.01	147	0.98	0.06	0.01	515.51	385.52	222.58
2015-2016	4	46	0.93	0.08	0.01	107	0.94	0.09	0.01	70.68	63.21	31.60
2016-2017	6	150	1.01	0.08	0.01	186	1.01	0.09	0.01	183.90	193.68	79.07
2017-2018	6	130	1.01	0.08	0.01	151	1.02	0.08	0.01	270.86	216.54	88.40
2018-2019	6	153	0.99	0.09	0.01	243	0.99	0.09	0.01	223.61	183.12	74.76
2019-2020	5	95	0.96	0.08	0.01	154	0.96	0.08	0.01	235.24	268.18	119.93
2020-2021	5	87	0.93	0.08	0.01	193	0.94	0.08	0.01	347.50	288.17	128.87

Table 2: Summary of Common Snook relative body condition (K_n) for each sampling event showing the date sampling occurred, the number of fish sampled (n), mean body condition (K_n), standard deviation (SD), and standard error (SE) for both the fish included in statistical models (captured at 5 upper river sites, Fig 1b), and for all fish captured at all sites over the course of the study (2004 – 2021). Mean sunfish biomass with SD and SE are also shown.

		K_n: Upper River Snook (Model Fish Only)				K_n All Snook Caught in Shark River				Sunfish Biomass (g/100m)		
Sampling Year	Sample Date	n	mean	SD	SE	n	mean	SD	SE	mean	SD	SE
2004-2005	11/15/2004	12	0.89	0.06	0.02	18	0.92	0.08	0.02	0.00	NA	NA
2004-2005	3/7/2005	46	1.00	0.10	0.02	49	0.99	0.10	0.01	505.33	370.48	111.70
2004-2005	4/25/2005	3	1.06	0.06	0.03	3	1.06	0.06	0.03	10.21	14.44	10.21
2005-2006	12/12/2005	3	0.77	0.03	0.02	3	0.77	0.03	0.02	0.00	NA	NA
2005-2006	1/30/2006	21	0.94	0.07	0.01	32	0.95	0.08	0.01	87.73	77.78	27.50
2005-2006	4/24/2006	49	1.06	0.11	0.02	53	1.06	0.10	0.01	304.91	170.35	64.39
2009-2010	3/9/2010	12	0.97	0.12	0.03	30	0.93	0.12	0.02	248.62	201.31	100.65
2009-2010	5/5/2010	28	1.06	0.07	0.01	48	1.10	0.10	0.01	348.32	194.20	73.40
2010-2011	1/22/2011	5	1.01	0.14	0.06	5	1.01	0.14	0.06	191.64	71.64	41.36
2010-2011	2/13/2011	19	1.10	0.09	0.02	34	1.00	0.14	0.02	734.26	603.44	269.87
2010-2011	3/24/2011	35	1.10	0.09	0.02	35	1.10	0.09	0.02	758.24	444.49	140.56
2010-2011	4/15/2011	25	1.01	0.07	0.01	25	1.01	0.07	0.01	331.76	163.42	61.77
2010-2011	5/4/2011	12	1.03	0.04	0.01	12	1.03	0.04	0.01	110.45	50.84	22.74
2010-2011	6/5/2011	9	0.94	0.10	0.03	9	0.94	0.10	0.03	66.87	48.59	19.84
2011-2012	12/5/2011	12	1.02	0.04	0.01	34	1.04	0.10	0.02	61.32	86.73	61.32
2011-2012	2/18/2012	19	1.03	0.05	0.01	55	1.02	0.06	0.01	301.17	21.86	15.46
2011-2012	3/18/2012	19	1.06	0.07	0.02	40	1.04	0.09	0.01	238.06	169.44	56.48
2011-2012	4/13/2012	44	1.06	0.07	0.01	53	1.05	0.07	0.01	271.03	89.46	26.97
2011-2012	6/26/2012	25	0.99	0.05	0.01	28	0.99	0.05	0.01	20.84	32.74	10.91
2011-2012	7/26/2012	23	0.98	0.07	0.02	31	0.98	0.08	0.02	0.00	NA	NA
2011-2012	8/22/2012	17	0.99	0.07	0.02	18	0.99	0.07	0.02	5.37	7.60	3.40
2011-2012	9/25/2012	5	0.97	0.02	0.01	14	0.98	0.07	0.02	38.71	9.21	5.32
2012-2013	11/11/2012	7	0.88	0.15	0.06	13	0.97	0.15	0.04	63.97	7.99	4.61
2012-2013	1/20/2013	2	0.93	0.04	0.03	8	0.91	0.08	0.03	442.53	531.32	375.70
2012-2013	2/22/2013	5	1.06	0.14	0.06	62	1.00	0.13	0.02	837.18	234.75	135.53
2012-2013	3/14/2013	4	1.00	0.06	0.03	27	1.04	0.08	0.02	502.49	345.82	199.66
2012-2013	4/15/2013	66	1.05	0.07	0.01	83	1.04	0.07	0.01	987.83	392.63	130.88
2012-2013	5/28/2013	9	0.99	0.06	0.02	17	0.98	0.07	0.02	318.97	182.42	91.21
2012-2013	6/26/2013	5	1.00	0.07	0.03	30	0.96	0.08	0.01	26.05	34.80	20.09
2012-2013	7/23/2013	4	0.92	0.03	0.02	9	0.98	0.09	0.03	25.97	36.72	25.97
2013-2014	11/17/2013	6	0.95	0.04	0.02	13	0.97	0.06	0.02	96.69	16.55	9.55
2013-2014	12/15/2013	4	0.93	0.04	0.02	27	0.97	0.08	0.01	197.99	280.00	197.99
2013-2014	1/21/2014	5	0.97	0.06	0.03	13	0.99	0.06	0.02	28.84	40.09	28.35
2013-2014	2/22/2014	14	1.00	0.10	0.03	27	0.98	0.09	0.02	248.76	134.22	60.02

Table 2 cont.

		K_n: Upper River Snook				K_n: All Snook				Sunfish Biomass		
Year	Date	n	mean	SD	SE	n	mean	SD	SE	mean	SD	SE
2013-2014	3/22/2014	22	1.06	0.05	0.01	45	1.01	0.07	0.01	458.02	303.88	124.06
2013-2014	4/27/2014	57	0.96	0.07	0.01	81	0.98	0.08	0.01	977.41	696.79	220.35
2013-2014	5/31/2014	56	0.95	0.06	0.01	56	0.95	0.06	0.01	101.19	88.04	27.84
2013-2014	7/9/2014	13	0.94	0.04	0.01	13	0.94	0.04	0.01	46.71	43.81	19.59
2014-2015	12/11/2014	9	0.95	0.06	0.02	14	0.96	0.05	0.01	0.00	NA	NA
2014-2015	3/2/2015	37	1.02	0.05	0.01	51	1.01	0.06	0.01	799.99	316.83	112.02
2014-2015	4/11/2015	63	0.98	0.07	0.01	82	0.97	0.07	0.01	288.78	141.52	42.67
2015-2016	12/14/2015	8	0.94	0.07	0.02	24	0.97	0.09	0.02	22.05	31.19	18.01
2015-2016	2/21/2016	10	0.91	0.08	0.03	37	0.90	0.08	0.01	36.69	NA	NA
2015-2016	4/17/2016	16	0.92	0.08	0.02	16	0.92	0.08	0.02	92.22	130.42	75.30
2015-2016	5/12/2016	12	0.97	0.06	0.02	30	0.97	0.10	0.02	52.95	45.99	18.77
2016-2017	12/12/2016	13	0.96	0.08	0.02	23	0.95	0.07	0.01	33.72	43.45	19.43
2016-2017	1/27/2017	1	0.86	NA	NA	1	0.86	NA	NA	137.94	NA	NA
2016-2017	2/26/2017	17	0.97	0.09	0.02	39	1.01	0.10	0.02	253.22	128.14	73.98
2016-2017	3/27/2017	49	1.05	0.07	0.01	49	1.05	0.07	0.01	384.82	282.68	115.40
2016-2017	4/24/2017	36	1.02	0.08	0.01	40	1.02	0.09	0.01	113.74	81.82	28.93
2016-2017	5/31/2017	34	1.00	0.07	0.01	34	1.00	0.07	0.01	110.67	79.24	25.06
2017-2018	12/1/2017	14	0.95	0.04	0.01	21	0.99	0.09	0.02	253.77	255.63	180.76
2017-2018	1/26/2018	19	1.01	0.10	0.02	19	1.01	0.10	0.02	433.78	292.50	168.88
2017-2018	2/16/2018	6	1.00	0.07	0.03	11	1.02	0.06	0.02	157.07	151.27	75.64
2017-2018	3/13/2018	4	1.03	0.08	0.04	4	1.03	0.08	0.04	69.13	35.78	20.66
2017-2018	4/27/2018	44	1.05	0.07	0.01	44	1.05	0.07	0.01	346.08	252.29	79.78
2017-2018	5/15/2018	43	1.00	0.07	0.01	52	1.00	0.07	0.01	294.02	177.71	56.20
2018-2019	12/10/2018	14	0.91	0.09	0.02	67	0.94	0.07	0.01	147.23	152.11	68.03
2018-2019	1/21/2019	17	1.08	0.08	0.02	17	1.08	0.08	0.02	125.91	114.63	57.31
2018-2019	2/24/2019	5	1.00	0.07	0.03	34	1.05	0.09	0.02	142.52	113.97	50.97
2018-2019	3/24/2019	4	0.93	0.02	0.01	4	0.93	0.02	0.01	226.01	122.39	86.54
2018-2019	4/28/2019	51	1.00	0.07	0.01	59	1.01	0.08	0.01	236.29	192.18	64.06
2018-2019	5/28/2019	62	0.99	0.09	0.01	62	0.99	0.09	0.01	317.55	283.63	81.88
2019-2020	12/10/2019	8	0.96	0.07	0.03	32	0.96	0.07	0.01	116.42	132.09	66.05
2019-2020	1/19/2020	3	0.97	0.04	0.02	3	0.97	0.04	0.02	17.38	21.96	15.53
2019-2020	2/22/2020	7	0.97	0.09	0.03	42	0.97	0.08	0.01	391.09	315.39	141.05
2019-2020	5/13/2020	63	0.98	0.07	0.01	63	0.98	0.07	0.01	214.53	290.05	91.72
2019-2020	6/26/2020	14	0.90	0.07	0.02	14	0.90	0.07	0.02	0.00	NA	NA
2020-2021	1/23/2021	2	0.91	0.01	0.01	2	0.91	0.01	0.01	0.00	NA	NA
2020-2021	2/19/2021	16	0.89	0.06	0.02	49	0.93	0.10	0.01	271.25	221.67	99.13
2020-2021	3/19/2021	24	0.90	0.06	0.01	24	0.90	0.06	0.01	235.03	105.33	47.10
2020-2021	4/16/2021	19	0.94	0.08	0.02	19	0.94	0.08	0.02	181.81	147.17	60.08
2020-2021	5/22/2021	26	0.97	0.10	0.02	53	0.94	0.09	0.01	671.42	331.61	110.54

Table 3: Model selection results from GLMMs examining how the magnitude of the sunfish prey pulse, hydrologic variation, fish size, and sampling year affect the relative body condition (K_n) of Common Snook. Univariate model results for each variable included in the final model are also shown for comparison and to illustrate the contribution to variance explained.

	Model Variables	**AIC**	**ΔAIC**	**Cond. R^2**	**Marg. R^2**	**p-value**
Global Model	Marsh Water Level + Days Marsh < 30cm + Temperature + Sunfish Biomass + Fish Size (SL) + Year	-3300.0	1.4	0.24	0.22	
Best Model	*Marsh Water Level + Days Marsh < 30cm + Sunfish Biomass + Fish Size (SL) + Year*	*-3301.4*	*0.0*	*0.24*	*0.22*	
Univariate Models	Marsh Water Level	-3081.3	220.1	0.11	0.06	< 0.01
	Days Marsh < 30cm	-2971.4	330.0	0.04	0.01	< 0.01
	Temperature	-2982.4	319.0	0.04	< 0.01	0.85
	Sunfish Biomass	-3034.7	266.7	0.06	0.04	< 0.01
	Fish Size (SL)	-3050.9	250.5	0.08	0.04	< 0.01
	Year	-3148.0	153.4	0.15	0.12	< 0.01

Table 4: Summary statistics for the best GLMM model (see Table 3) predicting the relative body condition (K_n) of Common Snook in relation to sunfish biomass, hydrologic variation, fish size, and sampling year. Results show a positive significant relationship between higher K_n and magnitude of sunfish biomass, and fish size, and a negative relationship with water level and the number of days the freshwater marsh has dropped below 30 cm when prey become concentrated in the river channels.

Variable	Beta	SE	z-value	p-value
(Intercept)	9.55E-01	1.66E-02	57.53	< 0.01
Water Level	-1.38E-03	1.66E-04	-8.3	< 0.01
Days Marsh < 30 cm	-3.76E-04	7.33E-05	-5.14	< 0.01
Sunfish Biomass	2.76E-05	6.73E-06	4.1	< 0.01
Fish Size (SL)	1.57E-03	2.03E-04	7.73	< 0.01
Year 2	2.09E-02	1.48E-02	1.41	0.16
Year 6	5.25E-02	1.71E-02	3.07	< 0.01
Year 7	4.57E-02	1.38E-02	3.31	< 0.01
Year 8	7.13E-02	1.35E-02	5.3	< 0.01
Year 9	2.20E-02	1.44E-02	1.53	0.13
Year 10	-1.86E-02	1.29E-02	-1.44	0.15
Year 11	-6.86E-03	1.36E-02	-0.5	0.61
Year 12	-1.46E-02	1.69E-02	-0.86	0.39
Year 13	2.44E-02	1.29E-02	1.89	0.06
Year 14	3.51E-02	1.35E-02	2.6	< 0.01
Year 15	2.87E-02	1.33E-02	2.16	0.03
Year 16	-2.00E-02	1.40E-02	-1.43	0.15
Year 17	-4.41E-02	1.48E-02	4.571	< 0.01

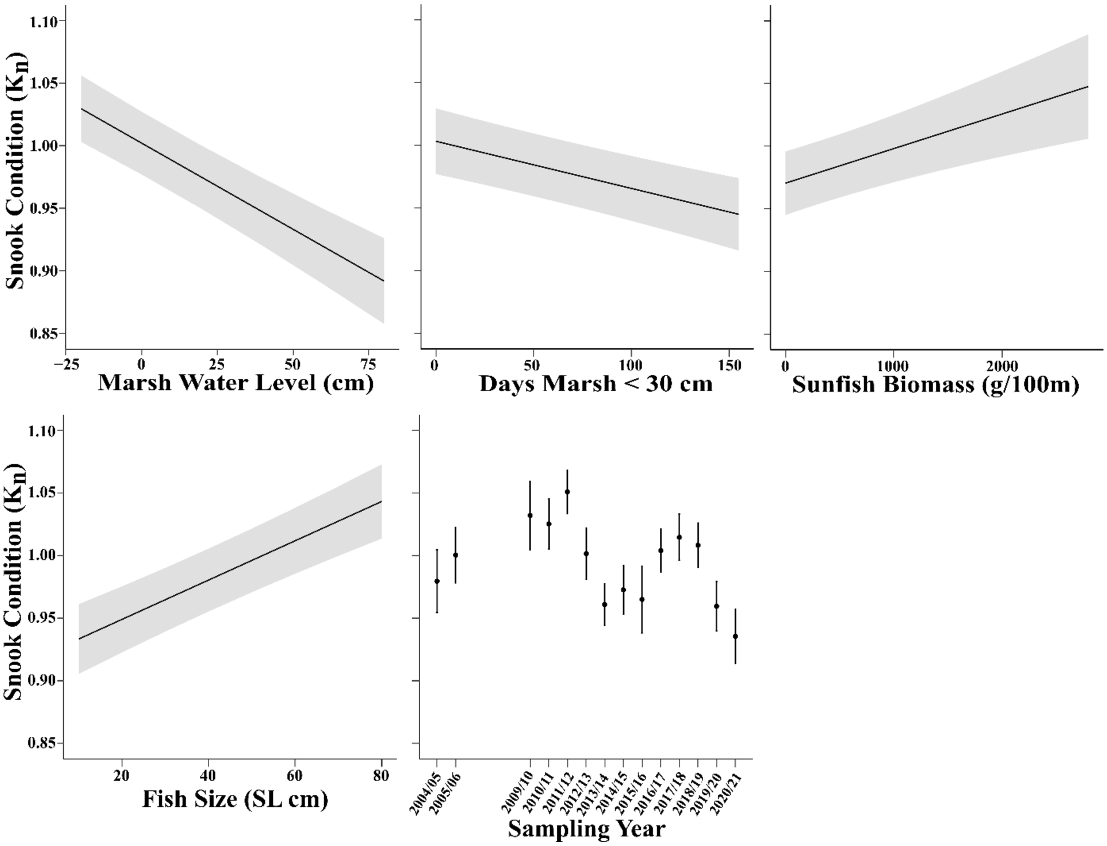

Figure 5: Plotted variables for the best-fitting GLMM model for the relative body condition (K_n) of Common Snook in the Shark River bounded by a 95% confidence interval. Individual effects of each variable kept in the best model in Table 3 are assessed by holding the other variables at a fixed mean value. Together these variables explain 24% of the long-term variability in K_n between 2004 and 2021. Note: Snook weights were not recorded during sampling events which occurred between November 2006 and May 2009, and K_n was not calculated for these sampling events.

CHAPTER V

LONG-TERM PATTERNS IN ENVIRONMENTAL CONDITIONS AND THE RELATIVE ABUNDANCE OF COMMON SNOOK IN A SUBTROPICAL COASTAL RIVER

ABSTRACT

Over past decades, aquatic systems have experienced accelerating shifts in environmental conditions as a factor of climate change, which has altered temperature and precipitation regimes, and resulted in unprecedented rates of modern sea-level rise. Further, aquatic habitat conditions have also been affected by anthropogenic alterations to the landscape, water management decisions, and ecosystem restoration. Environmental variability can result in fluctuations in the abundance and distribution of fish populations from year-to-year, with either negative or positive impacts depending on species-specific behavioral and physiological requirements, and the ability to adapt to changing conditions. In this study, our objective was to better understand how environmental variation over time has affected the relative abundance of riverine fish in freshwater/estuarine habitats by relating long-term fish sampling data to long-term datasets of environmental conditions. To address this objective, we analyzed 17 years of electrofishing data (2004-2021) for Common Snook (*Centropomus undecimalis*) in the Shark River, Everglades National Park, and long-term time-series of environmental conditions (water level, temperature, salinity, precipitation). We used Seasonal and Trend decomposition using Loess (STL) to isolates the effect of seasonality and identify non-linear trends in both environmental time-series and Snook abundance, and Mann-Kendal Trend Tests to identify monotonic and directional (increasing or decreasing) trends over time. Further, to identify the environmental factors which best explain seasonal/interannual variation in Snook abundance, we used generalized linear models (GLM) to relate variations in Snook relative abundance among years/seasons to environmental covariates. We found significant long-term trends of gradually increasing water level and temperature, and decreasing salinity. Results showed that the long-term trend in Snook abundance over the 17 years of sampling was relatively stable. However, increases/decreases in Snook relative abundance corresponded to both seasonal changes in water level, and the periodic occurrence of extreme environmental conditions (e.g., cold spells, droughts, prolonged dry-season flooding). GLMs indicated that Snook relative abundance had a negative relationship with water level and positive relationship with temperature. Understanding how past environmental change has affected animal populations can provide insight into how they may respond to shifting future conditions, which can help inform conservation and management efforts.

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 and Poff 2004; Palmer and 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 resources required for growth, survival, and reproduction, and have been linked to fisheries productivity (Correa and Winemiller 2018; Gillson 2011; Junk et al. 1989; Massie et al. 2022; Winemiller and 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. 2019a; Robins et al. 2005). Further, systems with alterations to 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; Ruhí 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 impacts are predicted to only increase in the future (Dessu et al. 2018; Flower et al. 2017; Keellings and Hernández Ayala 2019; Milly et al. 2008; Welcomme and 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 impacts 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 level 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 impacts on long-term population trajectories (Feyrer et al. 2015). Further, 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 that 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 distribution 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 Bearing Sea (Spies et al. 2020), coral reef fishes in South East Australia (Booth et al. 2018), warm-water fishes in the rivers of France (Daufresne and Boet 2007), Common Snook (*Centropomus undecimalis*) in the Suwanee River, Florida (Purtlebaugh et al. 2020), and multiple temperate fish species in Tasmania (Last et al. 2011). In order to anticipate how aquatic 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.

Common Snook (hereafter Snook) are a widely distributed tropical/subtropical fish species that are ideal for examining how environmental change in river systems affect 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 et al. 2017a; Lowerre-Barbieri et al. 2014; Young et al. 2016), with juveniles moving inland to nursery habitats in small oligohaline creeks and freshwater marshes (Gilmore et al. 1983; Peters et al. 1998; Wilson et al. 2022). Ontogenetic habitat shifts occur at two and three 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 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 seasonal increases in freshwater prey concentrated in river channels during the dry season

(Blewett et al. 2017; Boucek et al. 2017b; Boucek and 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 (Chapter II of this dissertation, Massie et al. 2022). Disturbances introduced by extreme climate events, such as tropical storms and hurricanes can also affect the movement patterns and Snook distribution within coastal riverscapes, and can have either positive or negative long-term impacts on the population depending on the timing and scale of movements in relation to key life-history events, and resource availably (Chapter III of this dissertation, Massie et al. 2020). Further, seasonal and interannual variations in water level can dictate access to key prey subsidies in freshwater habitats and carry implications for the health and fitness of Snook (Massie, Chapter IV of this dissertation; Rezek et al. In Revision).

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, Everglades National Park. Our research questions are twofold, 1) What are the long-term trends in environmental conditions in freshwater/estuarine habitats of the Shark River? and 2) Do long-term trends in environmental conditions correspond to changes in the relative abundance of Snook over time? Based on past research, we hypothesize that H1) Long-term trends in environmental conditions correspond to long-term patterns of abundance for the Snook population in freshwater/estuarine habitats, H2) The relative abundance of Snook from year-to-year is a factor of annual environmental conditions (namely water level, temperature, salinity, and precipitation), and H3) Annual variation in the timing and magnitude of freshwater flows differentially affects seasonal trends in Snook abundance in freshwater/estuarine habitats (i.e., trends in wet season abundance vs. dry season abundance). To test our hypotheses, we used time-series data of environmental conditions and of Snook abundance in a coastal Everglades river, examined trends in each timeseries, and used statistical models to relate variations in Snook relative abundance among years/seasons to environmental covariates.

METHODS

Study Site

The Shark River is an extensive coastal river system in the southwestern region of ENP (Fig. 1). The hydrologic regime is shaped by tidal cycles, the regional subtropical climate, and freshwater flows which are driven by seasonal rainfall patterns influenced by atmospheric teleconnections (Abiy et al. 2019a; McIvor et al. 1994; Saha et al. 2012). The Shark River extends inland approximately 32 km from the coast, with a drainage area of roughly 1700 km^2, 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 Mexico (Fry and Smith 2002; McIvor et al. 1994; Saha et al. 2012). Throughout the twentieth 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. 2020; Marshall et al. 2014). 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 et al. 2019b; 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 2022). 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 (Fig. 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-December), a second monthly event during the transitional period of decreasing flow (between January-March), and a third monthly sample when water levels neared a dry season minimum (between April-May).

Fish were captured by boat-based electrofishing using a GPP 9.0 electrofisher (Smith Root, Vancouver, WA, USA) following standardized methods (Boucek and Rehage 2013; Rehage and 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 300 seconds 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 on-board aerated livewell. The distance sampled at each transect was recorded at the end of each transect using GPS in order to calculate catch-per-unit-effort (CPUE). Each transect sampled approximately 100 meters of shoreline, but sample distances varied based on fish catches and sampling conditions. Captured fish were measured (standard length in cm, SL), weighed (grams), 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 100m of shoreline (total # snook captured in a transect / total distance sampled in meters x 100). The mean CPUE for each of the three seasonal sampling events (wet, early dry, late dry) was then calculated to estimate overall seasonal/annual abundance, and related to environmental variables using statistical models.

Between 2004 and 2021, 51 seasonal sampling events were performed corresponding to wet, early dry, and late dry season conditions (Supplementary Table 1). In total, across the 51 samples and nine sites (three transects/site), 1,286 estimates of Snook abundance (CPUE) were calculated and used in the analysis. For each sampling event, the specific sampling timing was based on annual hydrologic conditions (Fig. 2), and thus sampling dates varied across the study (Supplementary Table 1). In total 1,420 individual Snook were captured, ranging in size from 5.0 to 77.5 cm SL (mean 39.5 cm +/- 11.3 SD).

Environmental Data

Time-series data for environmental conditions in the Shark River (water level, water temperature, salinity, precipitation) were obtained for the entire common time-period where data were available for all variables (Oct 2003-Feb 2023). Daily water level (cm relative to NAVD 88) and precipitation (cm) were queried from the Everglades Depth Estimation Network (EDEN, https://sofia.usgs.gov/eden/) for two monitoring stations (Fig. 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 (degrees C) for Bottle Creek (Station 022908295), and salinity (PSU) measurements for Bottle Creek and Canepatch (Station ENPCN) were obtained from the United States Geological Survey via the South Florida Water Management District’s environmental database (DBHYDRO, https://www.sfwmd.gov/science-data/dbhydro). Time-series data contained instances where daily observations were not recorded for water level (182 of 7006 observations, 2.5% of data), water temperature (157 of 7006 observations, 2.2% of data), and salinity (53 of 7006 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 Supplementary Figs. 1-3, Moritz and Bartz-Beielstein 2017; Team 2022). This method isolates the seasonal component from time-series data, imputes missing values into the de-seasonalized data, and then re-introduces the seasonal component. We then calculated mean monthly values for water level, temperature, and salinity, and total monthly precipitation to match the temporal resolution of our Snook relative abundance data (monthly CPUE), and for use in time-series trend analyses and statistical models. Monthly climate indices were obtained from the National Oceanic and Atmospheric Administration (NOAA), with data for the El Niño/Southern Oscillation Index (ENSO) queried from the National Centers for Environmental Information (https://www.ncei.noaa.gov/access/monitoring/enso/soi), and data for the Atlantic Multidecadal Oscillation Index (AMO) 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 non-linear 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) respectively using R statistical software (Team 2022). First, we used Seasonal and Trend decomposition using Loess (STL) to isolate the effect of seasonality and determine whether non-linear long-term trends were present in the data (Cleveland et al. 1990; Hartmann et al. 2018). STL is an efficient and robust nonparametric technique that uses generalized additive modeling to identify non-linear 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 STL models were able to extract the seasonal and trend components from the time-series, we examined the residuals (remainder) of the time-series after removing the seasonal and trend components for normality using quantile-quantile plots (QQ-plots), with a normal distribution of the residuals indicating that seasonal decomposition was able to extract a real trend and residuals consist 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-Kendal Trend Test on both observed data (monthly values calculated from raw data) and the seasonally corrected trends using the Kendall library in R (Hipel and McLeod 1994; McLeod and McLeod 2015). This technique has been used previously to detect trends in environmental data (Abiy et al. 2019b; Aditya et al. 2021). For Snook CPUE, multiple Mann-Kendal Trend Tests were performed to examine the entire dataset (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 (Sens's slope) for monotonic trends identified by the Mann-Kendal test using the Trend package in R (Pohlert 2020).

To identify the environmental factors which contribute to variation in Snook abundance over time, we then used generalized linear models (GLMs) with a Gaussian error distribution. The response variable was the mean Snook CPUE at each monthly sampling event. We selected environmental variables that influence habitat conditions in the Shark River, and which vary both seasonally and annually, as well as climatic indices to consider whether atmospheric teleconnections correlate with CPUE. For 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 climate indices we included AMO and ENSO due to their influence on climatic and hydrologic conditions on both long and short timescales (Abiy et al. 2019a). A variable for sampling year was also included to help explain additional model variance not captured by our other metrics. Modeling was performed using a 4-step process where we first examined all individual variables for collinearity. Second, if collinear variables were identified, we selected a best fitting variable using AICc (Akaike 1998). Third, all 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 AICc score (Anderson 2007; Burnham and Anderson 2003; Johnson and Omland 2004; Symonds and Moussalli 2011).

RESULTS

Fish Sampling and CPUE

CPUE was highly variable among years and seasons (Fig. 3). The highest number of Snook captured at a single sampling event was 91 individuals, occurring during a late dry 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 meters of mangrove shoreline (mean 1.3 +/- 0.1 SE), with catches lowest in the wet season and highest in the late dry season. Mean CPUE ranged from 0.0 to 1.3 Snook/100m (mean 0.5 +/- 0.1) in the wet season, 0.1 to 2.6 in the early dry season (mean 1.0 +/- 0.1), and from 0.2 to 6.3 in the late dry season (mean 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 (Fig. 4). Evaluation of the residuals indicated that the distribution followed a predominantly normal distribution for water level, temperature, and to a lesser extent for precipitation (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 dataset. Remainder residuals for salinity showed large deviations from a normal distribution, indicating that the seasonally decomposed trends were less effective at extracting the non-linear trends and seasonal components from the time-series data. Snook CPUE also showed a strong seasonal component to these data (Fig. 5a), and the remainder residuals indicated a normal distribution, indicating that the STL model was able to isolate the long-term trend from seasonality.

Mann-Kendal trend tests indicated the presence of significant monotonic trends in environmental data for both monthly observed (measured) data and for seasonally adjusted data (Fig. 6, Table 1). Water level showed a significant positive trend over time for both observed and seasonally adjusted data ($p < 0.001$). The trend in water temperature was not significant for observed data ($p = 0.219$) but showed a significant positive trend for seasonally adjusted data ($p < 0.001$). Salinity had a significant negative trend for both observed ($p = 0.042$) and seasonally adjusted data ($p < 0.001$). No significant trend was found for either observed ($p < 0.387$) or seasonally adjusted precipitation ($p < 0.866$). A significant monotonic trend was not found for Snook CPUE using the Mann-Kendall trend tests (Fig. 5, Table 1) for either observed or seasonally adjusted data ($p = 0.733$ and 0.961 respectively), or when the wet, early dry, and late dry seasons were examined independently ($p = 0.967$, 0.266, and 0.303 respectively, Fig. 3).

Relating Environmental Conditions to Snook Abundance

After making pairwise comparisons of each variable combination for water level, temperature, salinity, precipitation, and climate indices (AMO, ENSO), we found high collinearity between water levels at Bottle Creek and MO215 (Pearson’s correlation >0.9), between salinity at Bottle Creek and Canepatch (Pearson’s correlation >0.7), and between Bottle Creek temperature and precipitation (Pearson’s correlation >0.7). We selected Bottle Creek water level and temperature for our global model to best represent conditions experienced by Snook in the river channels. Further, we selected salinity at

Canepatch because it experiences more seasonal variation in salinity relative to Bottle Creek (Bottle Creek salinities are < 1.0 PSU for much of the year), allowing us to better detect salinity trends over time. After removal of collinear variables, our global model consisted of six variables (Table 2; water level, water temperature, salinity, AMO index, ENSO index, and sampling year). When reduced using backward selection, we selected a model containing only two variables, Bottle Creek water level and water temperature based on the lowest AICc (Table 3). A more complex model also containing the AMO index performed comparably. However, this more complex model was within 2 AICc points. Thus, 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 (Fig. 7). Examination of univariate models for variables remaining in the best model suggests an equal contribution of both water level and temperature in explaining 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 significant 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. While no clear monotonic trend was found in the Snook population over our 17-year study, statistical models show the influence of both water level and temperature on the relative abundance of Snook, accounting for 46% of the seasonal/annual variance in CPUE. A high degree of both seasonal and interannual variation was observed for Snook CPUE, and annual abundance oscillated over the long-term dataset. 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 impacts on annual relative abundance.

Our results show a negative correlation between water level and Snook CPUE in the Shark River, and we observed a statistically significant trend of increasing water levels over time. Water level is a key process shaping the behavior and distribution of riverine fishes, and fluctuations in water level can affect both seasonal patterns in 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 (Massie, Chapter IV of this dissertation; Blewett et al. 2017; Boucek et al. 2017b; Boucek and Rehage 2013; Boucek et al. 2016; Rehage et al. 2022; Rehage and 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 utilize freshwater prey that migrate from floodplain habitats into the river channels during falling water levels (Hoeinghaus et al. 2006; Winemiller and Jepsen 2004). Further, the abundance of Barramundi (*Lates calcarifer*) and catfishes (Neoarius spp.) in Australia increase seasonally in freshwater habitats, correspond to changing water levels and access to floodplain prey resources (Crook et al. 2020; Jardine et al. 2012a; Jardine et al. 2012b; Roberts et al. 2019b).

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 Snook abundance, which we hypothesize 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 water level among the wet and dry seasons. This corresponded to one of the lowest late dry season Snook CPUE estimates in our study, which was observed in May of 2016 (75% lower than long-term seasonal mean). Further, in the early dry season of 2018, persistent high water levels associated with heavy rainfalls 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 Snook 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 which 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 (Massie, Chapter IV of this dissertation; Rezek et al. In Revision). Further, the lowest late dry season CPUE occurred in April 2005 (92% less than 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 which includes wet season flooding that enhances prey production.

We found a significant positive relationship between Snook CPUE and water temperature, and time-series analysis indicated the presence of an increasing monotonic trend for temperature in the Shark River over time. Snook are a tropical species, and because Florida populations exist at the northern extend of their geographic range, increasing temperature could have a positive effect on abundance (Blewett et al. 2017; McMichael et al. 1989; Munyandorero et al. 2020; Purtlebaugh et al. 2020). The upper thermal tolerance of Snook has been reported at approximately 35–42 C, with thermal preferences ranging from 26 to 29 C (Paschke et al. 2018; Regil et al. 2015), well within the range of temperatures 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 Snook mortality throughout Florida (Boucek et al. 2022; Boucek et al. 2017b; Stevens et al. 2016), with water temperatures dropping below 10 C for a period of three days 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 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 South East Australia, and found that while 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 establishment of a permanent population may be limited to species with higher cold-tolerance (e.g., *Abudefduf* spp.). Leriorato et al. (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. Further, Matich 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, and it was five to seven years before CPUE returned to levels observed prior to the cold spell. These results, combined with findings from the present study, illustrate how physiological limitations to low temperatures can affect long-term population trends, and suggest that continued warming and a reduction of future extreme cold events may have positive long-term impacts on thermally constrained species.

The second highest CPUE in our study occurred following the COVID-19 lockdown (hereafter COVID) in May 2020, which greatly reduced recreational angling near our study site. While we did not collect data on recreation fishing effort, and cannot explicitly link fishing pressure to Snook CPUE, it is possible that reduced fishing pressure contributed to our observations of temporarily higher Snook abundance. Other studies have explored how COVID influenced angler behavior and fishing pressure. For example, Phillip et al. (2023) reported how a reduction in recreational fishing during COVID increased the reproductive success of Black Bass (*Micropterus* spp.) in Ontario, Canada due to reduced angling pressure during the spawning season, resulting in increased levels of annual recruitment. However, other studies note how positive effects on fish abundance due to reduced fishing pressure during COVID may be only temporary due to a subsequent increase in fishing activity when restrictions eased, and interest in outdoor socially distanced activities increased. Bunt and Jacobson (2022) found that angler exploitation rates for Rainbow Trout (*Oncorhynchus mykiss*) in a tributary river to Lake Huron decreased by half during the early part of COVID in the spring of 2020, but that there was more than a fourfold increase in harvest rate once travel restrictions were lifted. Further, Trudeau et al. (2022) reported that sales for first-time fishing license purchasers in Wisconsin increased by 71% in the summer of 2020, which may have increased harvest pressure on easily accessibly inland lakes. While our data are not able to make explicit linkages between recreational fishing and Snook abundance, future studies that investigate on how fishing pressure relates to long-term variation in abundance of recreational fish species would offer additional insight.

Water management, restoration efforts, and climate change are all predicted to contribute to hydrologic changes in the future (Abiy et al. 2019b; Dessu et al. 2021; Dessu et al. 2018; 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. Analysis of long-term precipitation records suggest an overall shortening of the wet season in South Florida, and the historic bi-modal rainfall patterns during the summer months may become unimodal (Abiy et al. 2019b). 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. 2021; Dessu et al. 2018), which could both increase the abundance freshwater prey and decrease access to this resource if dry season water levels are not sufficiently low 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 et al. 2019a; Boucek et al. 2016; Flower et al. 2017).

CONCLUSION

We quantified long-term trends in environmental conditions using hydrologic time-series and described progressively wetter and warmer conditions in the Shark River, with increasing trends in water level and water temperature, and a decreasing trend in salinity corresponding to higher levels of freshwater flow. No significant positive or negative trend was found in Snook abundance over our 17-year dataset, suggesting a relative long-term stability of the population and the ability of Snook to adapt to changing environmental conditions. However, significant pulsed extreme climate events (cold spells, droughts, prolonged flooding), which occurred periodically over the course of the study and relate to physiological constraints and foraging success for Snook, corresponded to wide variation in annual relative abundance and resulted in oscillating Snook abundance over time. Further, we found a strong negative correlation between water level and Snook abundance, and a positive correlation with water temperature. While examination of Snook abundance trends for each sampling season (wet, early dry, late dry) were not statistically significant, our data contained suggestive evidence for decreasing abundance in the wet/early dry seasons with higher water levels over time, and increasing abundance in the late dry season. Future efforts will continue to monitor Snook populations and seasonal abundance trends in relation to gradually changing environmental conditions due to climate change and water management.

We illustrate the importance of collecting long-term data which can provide a better understanding of linkages between environmental variation and changes in animal populations over time. Water management, restoration efforts, and climate change are all predicted to contribute to future hydrologic changes in the future, and understanding the long-term trends of the past is key to making predictions about expected changes in the future. Relatively few studies have maintained long-term datasets on higher-order biota, and efforts to maintain long-term monitoring programs should be prioritized to help inform natural resource management. As environmental conditions continue to gradually change, long-term data able to quantify population responses can assist in conservation efforts for ecologically and economically important species.

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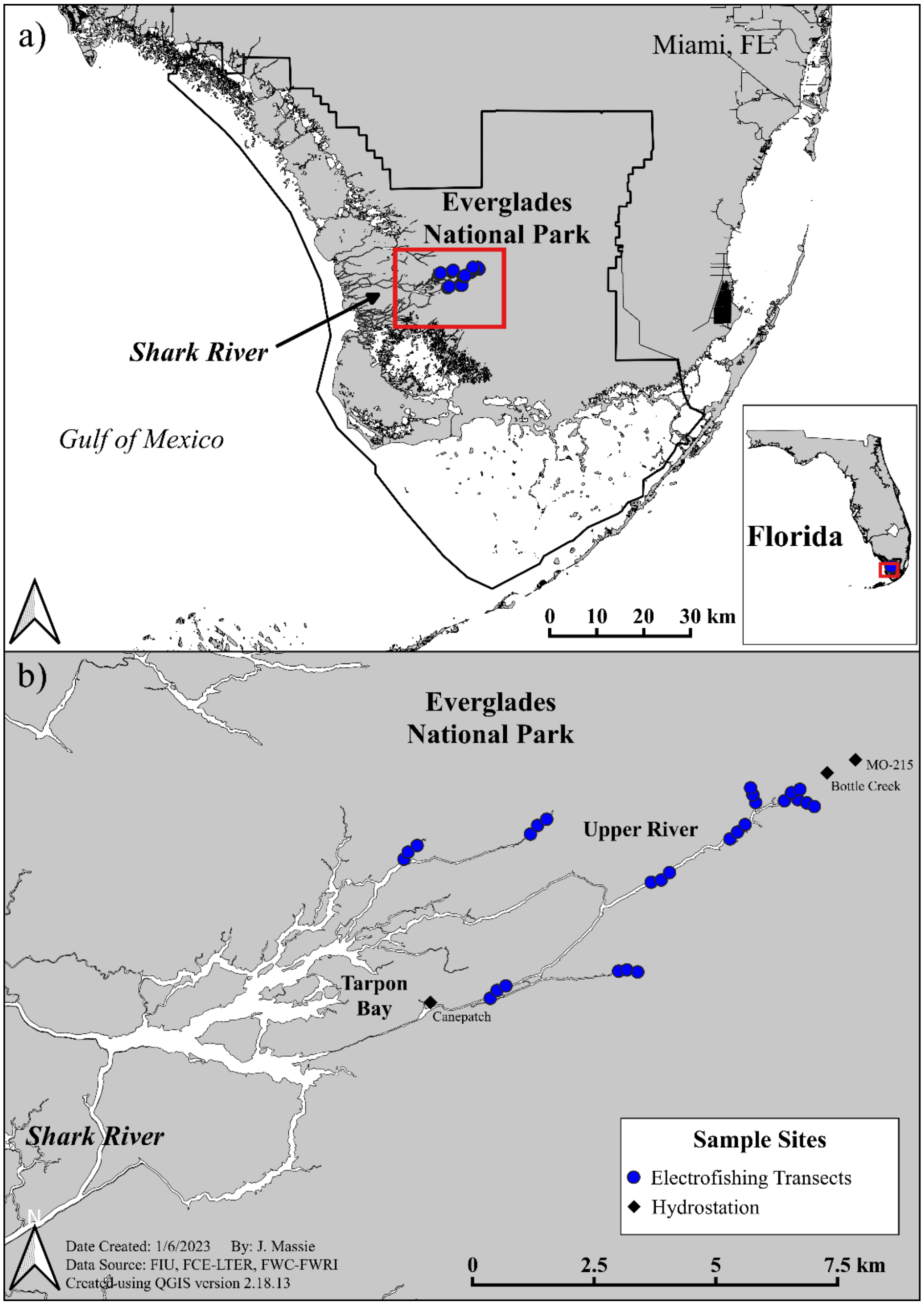

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Figure 1: Map of the study area in Everglades National Park where seasonal fish community sampling was conducted between 2004 and 2021. Panel a) shows the location of the Shark River in SW Florida, and panel b) depicts the nine electrofishing sites (three transects/site) where fish were captured (27 transects total). Black diamonds show the location of hydrologic monitoring stations where environmental conditions (water level, temperature, salinity, precipitation) were measured.

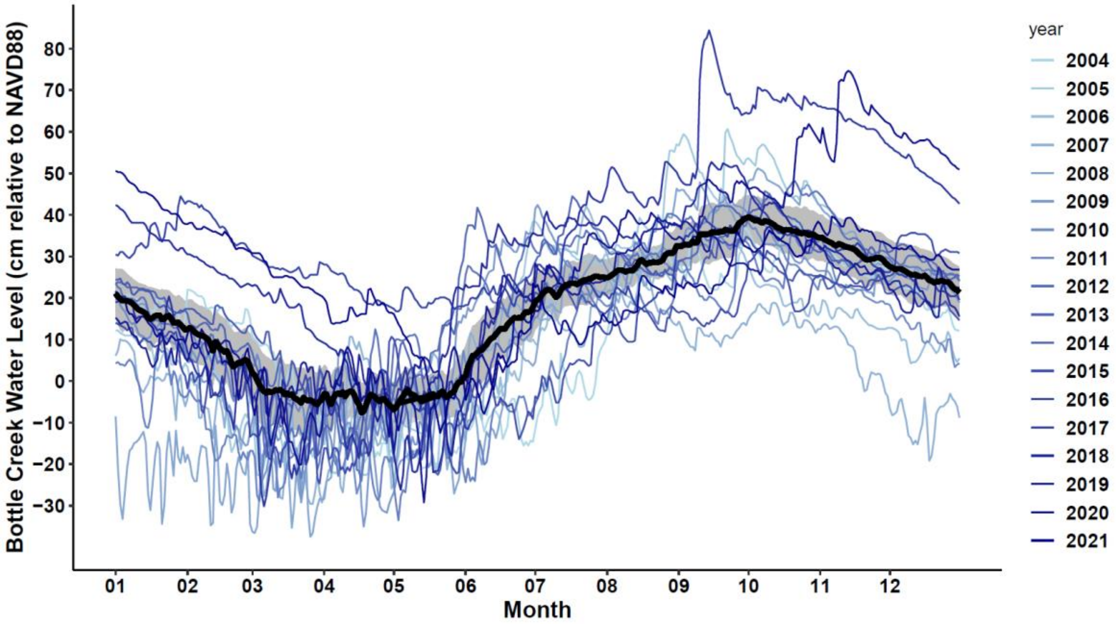


Figure 2: Hydrographs of water level in the upper Shark River at the Bottle Creek hydrostation (see Fig. 1b) for each year of the study (2004-2021). Individual color-coded lines correspond to sampling year and illustrate the high degree of interannual variability in both the timing and magnitude of freshwater 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 dataset.

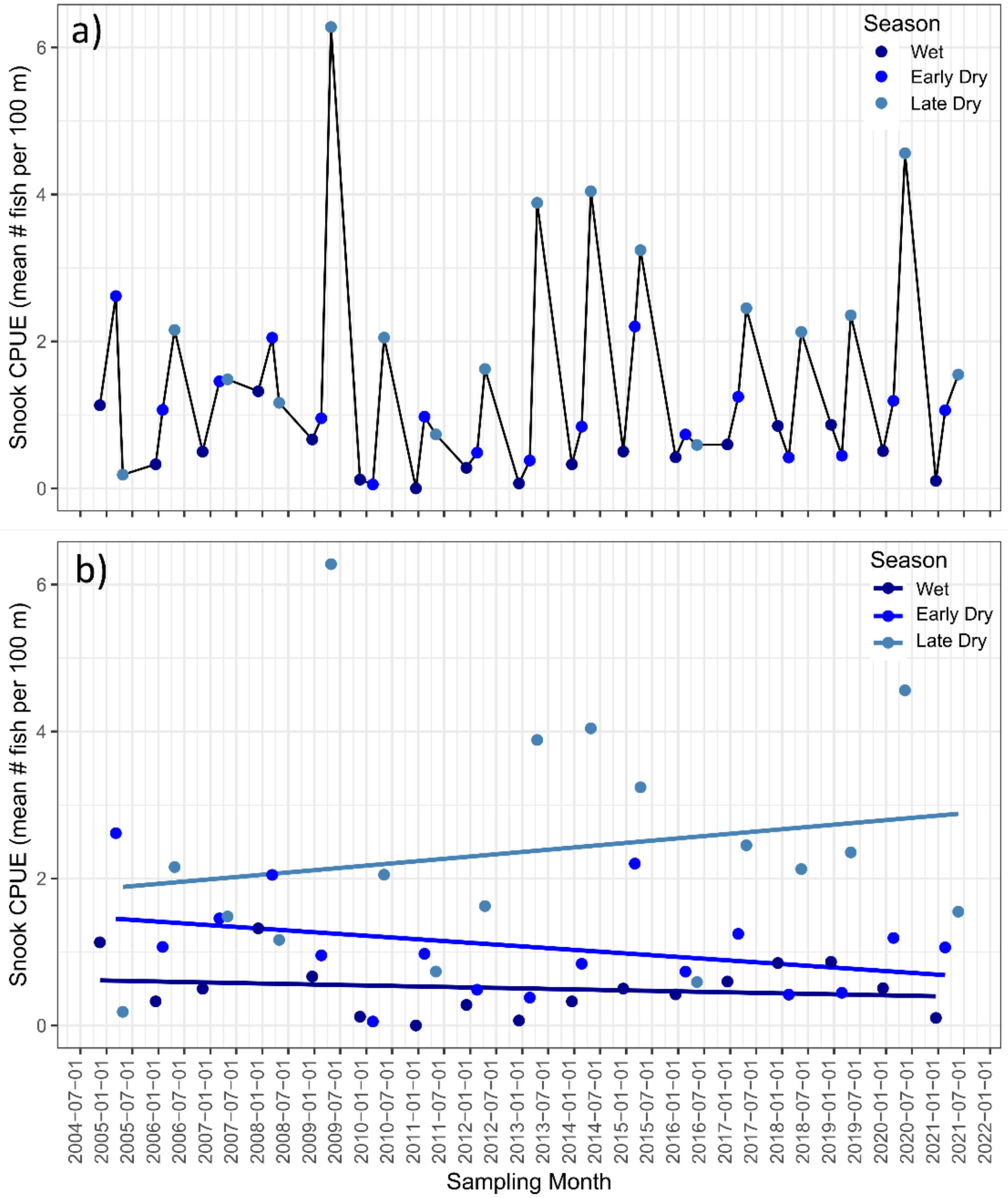


Figure 3: Catch-per-unit-effort (CPUE) for Common Snook from seasonal electrofishing sampling at nine sites in the Shark River between November 2004 and May 2021. Individual points reflect the mean CPUE for each of the 51 monthly sampling events, color coded by season. A monthly wet season sample was collected between November and December, an early dry season sample between January and March, and a late dry season sample between April and May. Month of sampling varied by year based on annual hydrologic conditions. Panel a) shows CPUE for each sampling event connected by a straight line to visualize change in abundance over time. Panel b) includes points indicating CPUE for each sampling event, with solid lines showing a fitted linear regression trendline, and suggests a decrease in wet and early dry season Snook catches over time, and an increase in late dry season catches.

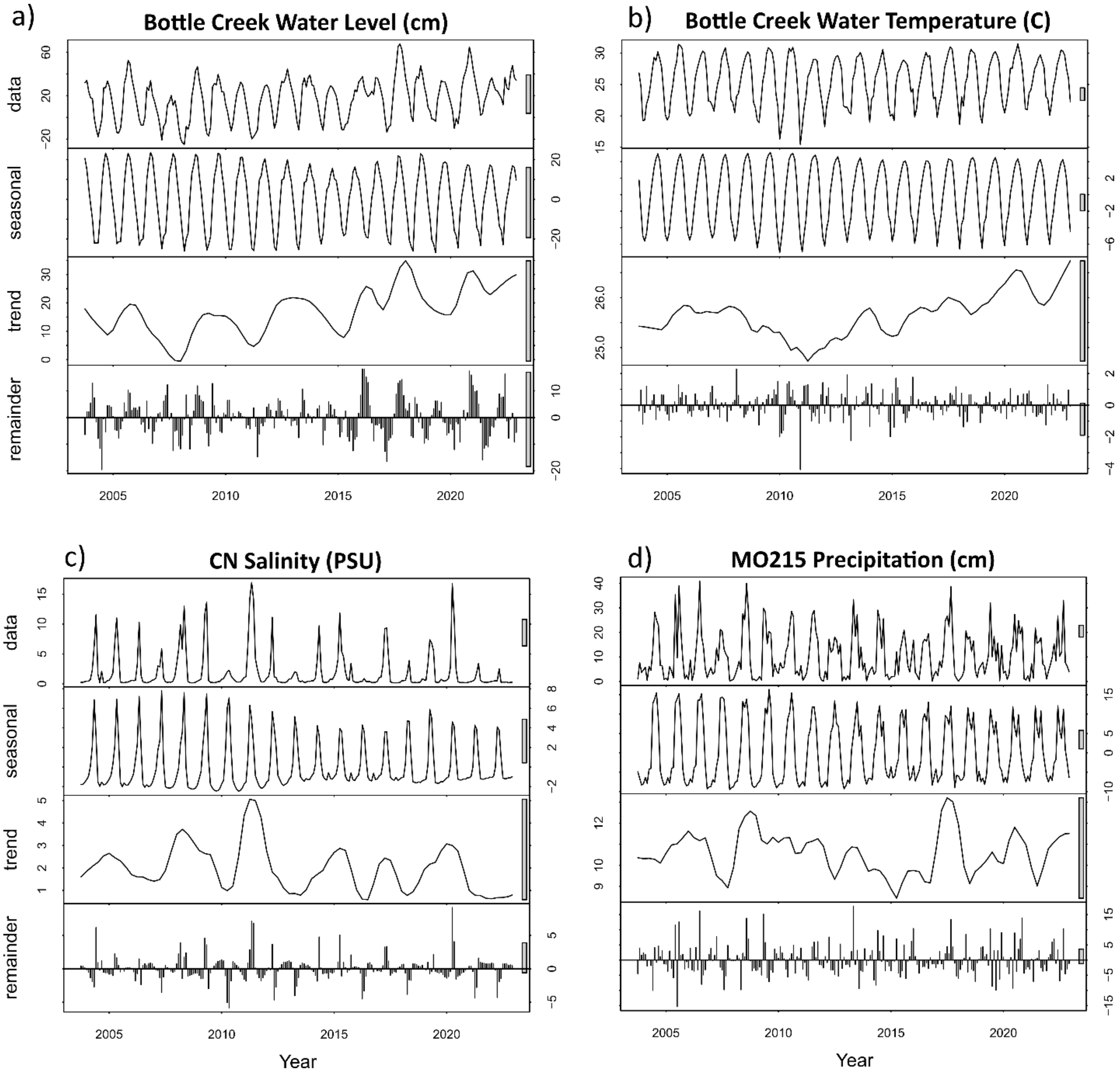


Figure 4: Results from Seasonal and Trend decomposition using Loess (STL) models used to identify non-linear long-term environmental trends over time for the entire common time-period where data were available for all variables (Oct 2003-Feb 2023). Each panel shows the measured data (data), the isolated seasonal component from the time-series (seasonal), the non-linear trend identified (trend), and the unquantified error isolated from the time-series once seasonal and trend components have been removed (remainder). Time series trends based on monthly data are shown for a) water level in the upper river at the Bottle Creek hydrostation, b) water temperature at the Bottle Creek, c) salinity at the Canepatch hydrostation, and d) precipitation at the MO215 hydrostation.

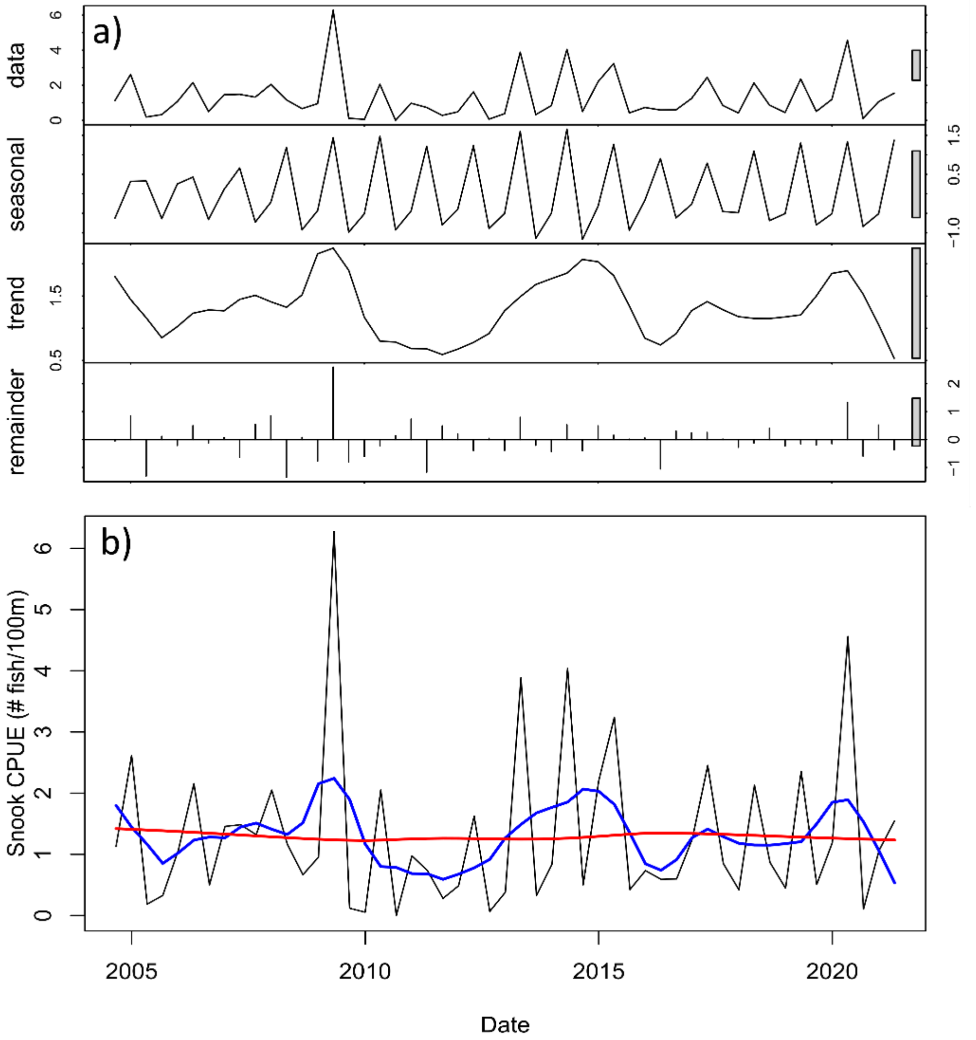


Figure 5: Trend estimates for Snook catch-per-unit-effort (CPUE) data identified by Seasonal and Trend decomposition using Loess (STL) models used to identify non-linear long-term environmental trends over time (panel a), and Mann-Kendall trend tests for monotonic trends in both raw and seasonally corrected data (panel b). Panel a) shows the raw CPUE data (data), the isolated seasonal component from the time-series (seasonal), the non-linear trend identified (trend), and the noise isolated from the time-series once seasonal and trend components have been removed (remainder). In panel b), the black line shows estimated seasonal CPUE, the blue line indicates the seasonally adjusted non-linear trend, and the red line shows the fitted monotonic trend line for seasonally corrected CPUE. The monotonic trend from the Mann-Kendall trend test was not statistically significant.

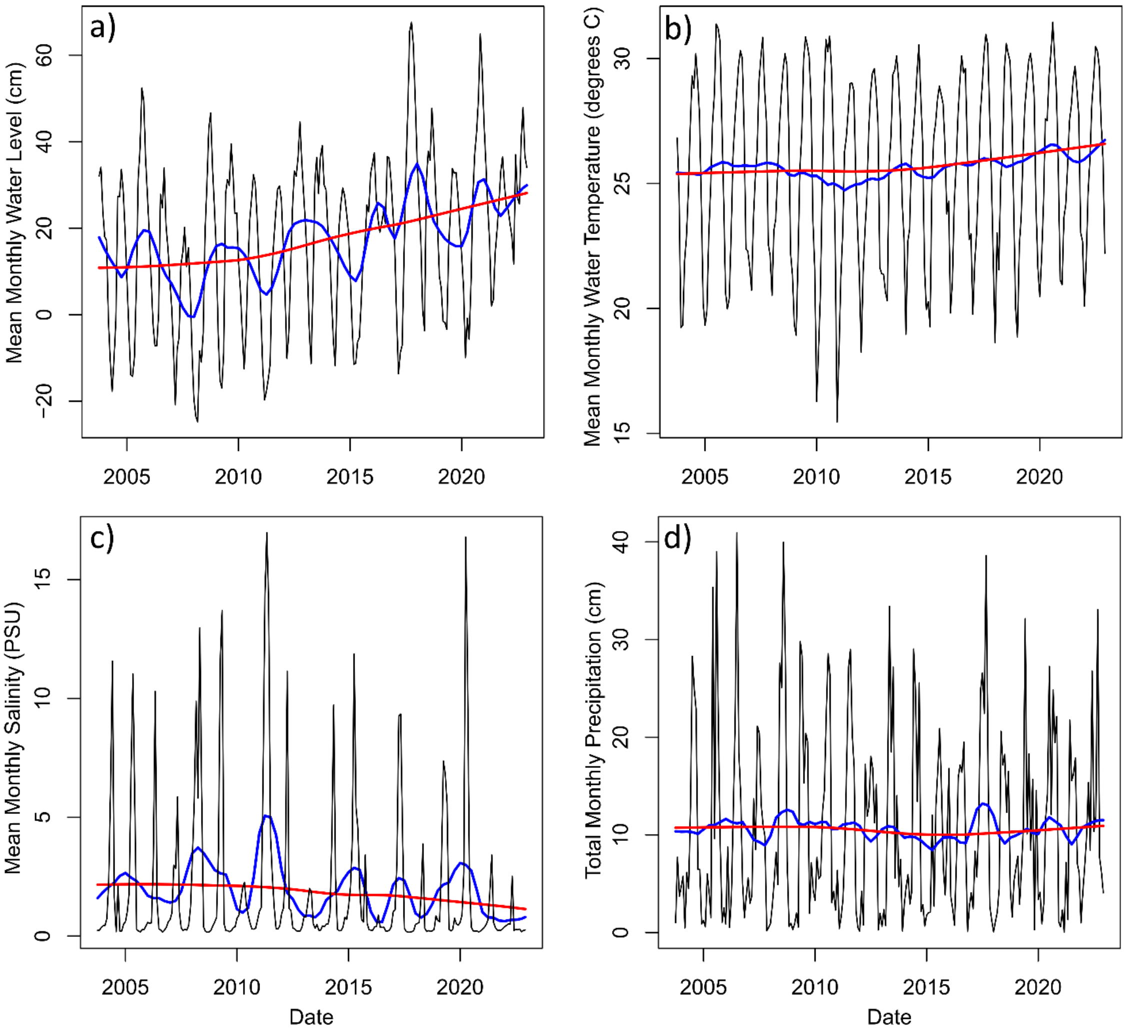


Figure 6: Trends in environmental data identified by Mann-Kendall trend and Sen's slope tests for both observed (measured) and seasonally corrected data for the entire period where data were available for all variables (Oct 2003-Feb 2023). Black lines indicate measured environmental variables, blue lines indicate the seasonally adjusted data, and the red line shows the fitted monotonic trend line for seasonally corrected data for a) mean monthly water level at the Bottle Creek hydrostation, b) mean monthly water temperature at Bottle Creek, c) mean monthly salinity at the Canepatch hydrostation, and d) total monthly precipitation at the MO215 hydrostation. Significant monotonic trends were found in the measured environmental data for water level and salinity. For seasonally corrected data, water level, temperature, and salinity had significant trends. A monotonic trend was not found for total monthly precipitation in either measured or seasonally corrected data.

Table 1: Results from the Mann-Kendall trend and Sen's slope tests used to identify monotonic trends in environmental data and Snook catch-per-unit-effort (CPUE). Results are shown for both observed data (measured mean monthly water level, temperature, salinity, and total monthly precipitation) and seasonally adjusted data. For Snook CPUE, trend tests were also performed independently by season. Statistically significant trends are shown in bold.

		Mann-Kendall Trend Test		Sen's Slope				
Mann-Kendall Trend Test	Variable	tau	p-value	Slope	Lower 95% CI	Upper 95% CI	z-value	p-value
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
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

Table 2: Model selection results based on lowest AICc value from GLM models examining the environmental variables affecting the relative abundance Common Snook in the Shark River among 51 sampling events between November 2004 and 2021. The response variable for models is the mean seasonal catch-per-unit-effort each year (wet, early dry, and late dry CPUE) across 17 years of electrofishing.

Model Variables	df †	AICc	ΔAICc ‡	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

† Model degrees of freedom; ‡ Difference in AICc score between each model and lowest AICc model

Table 3: Summary statistics for the best GLM model (see Table 2) examining the environmental variables affecting the relative abundance of Common Snook in the Shark River among 51 seasonal sampling events between November 2004 and May 2021. Results show a significant negative relationship between catch-per-unit-effort (CPUE) and water level, and a positive relationship with CPUE and water temperature.

Variable	Beta	SE	z-value	p-value
(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

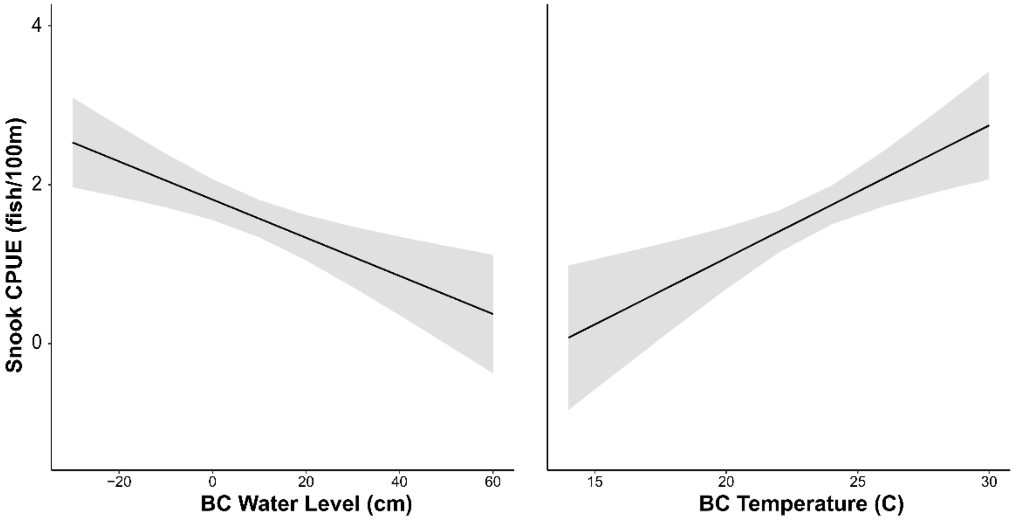
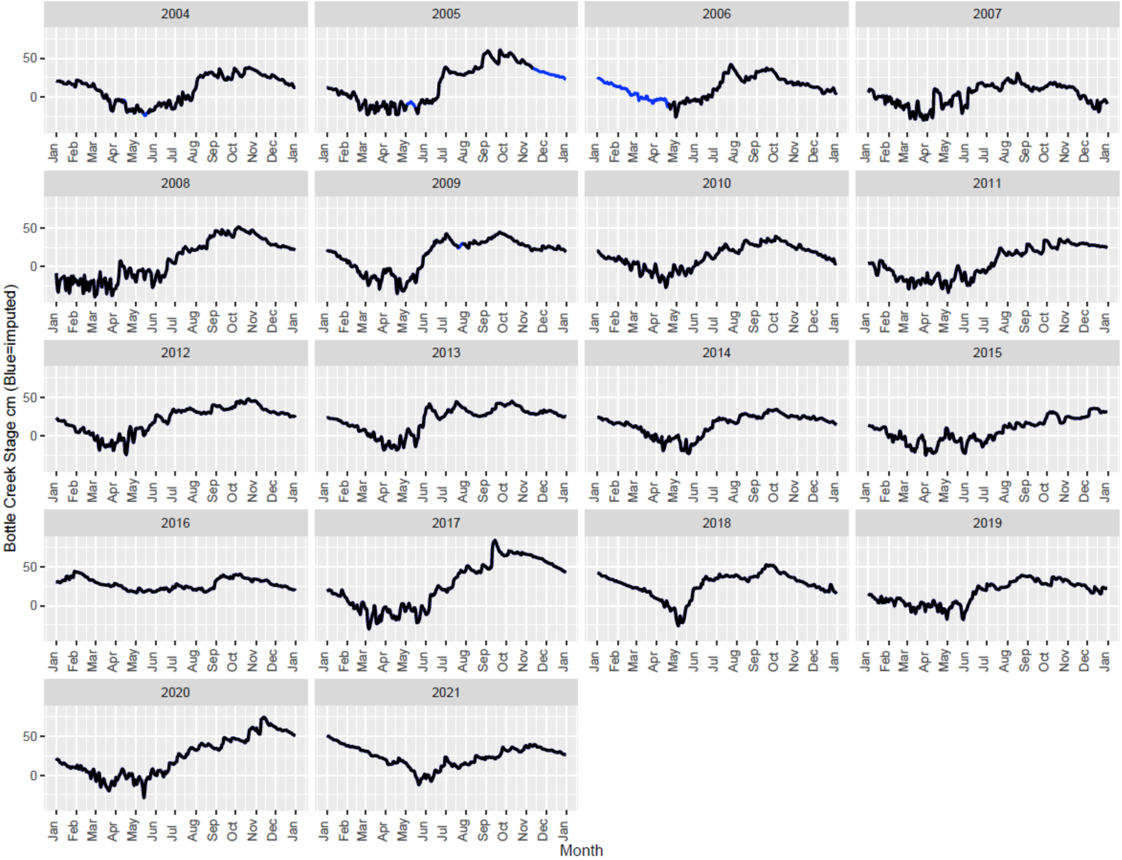
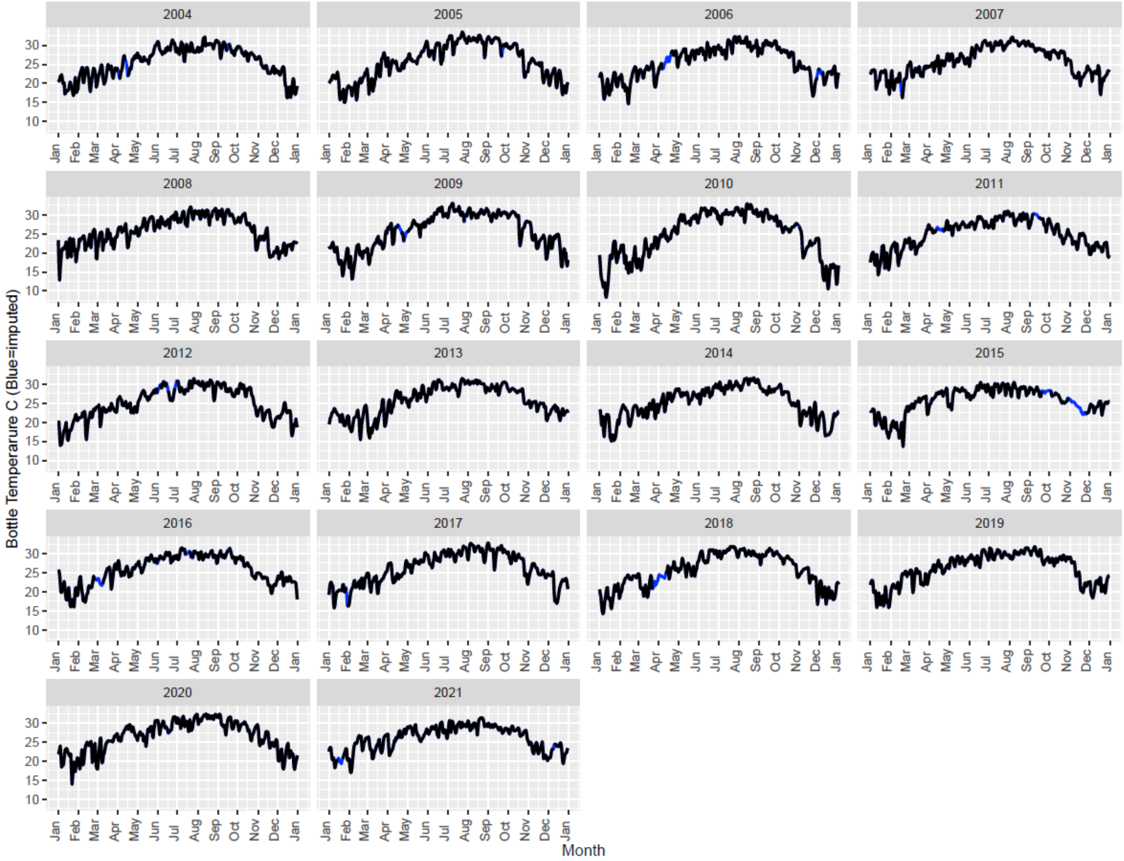


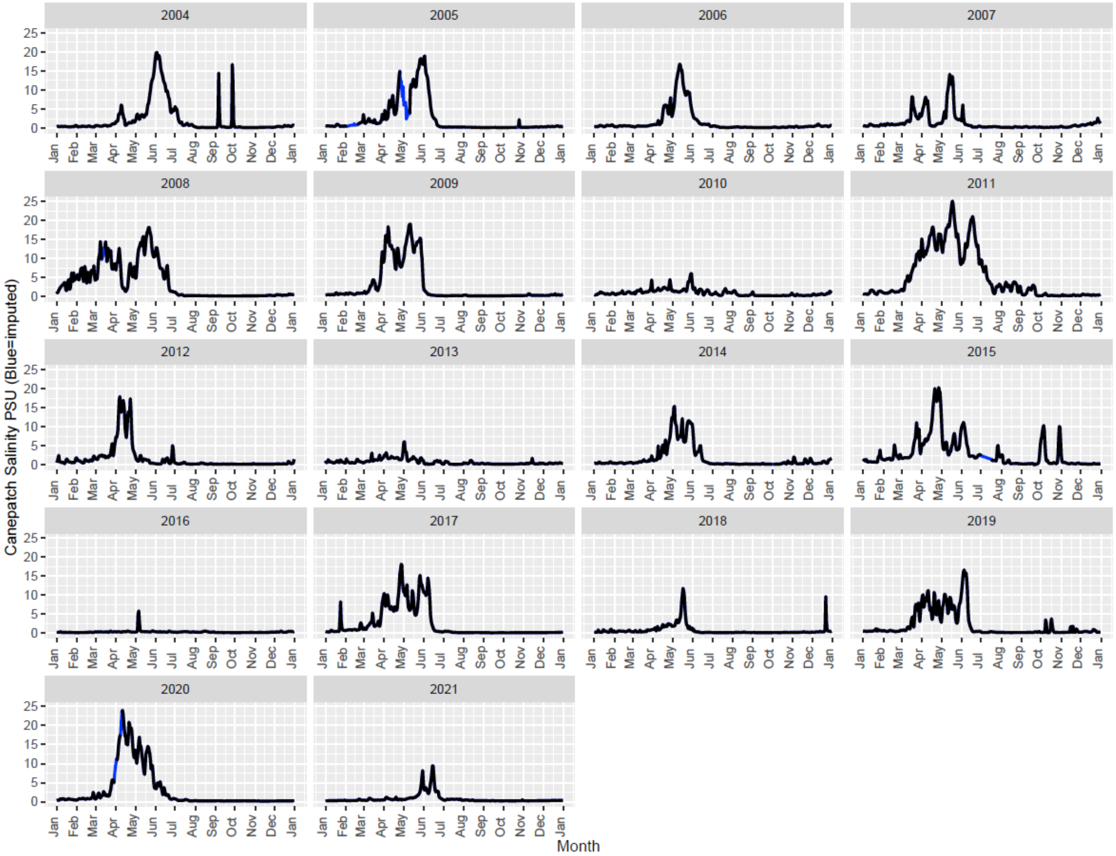
Figure 7: Plotted variables for the best-fitting GLM model for the relative abundance of Common Snook in the Shark River (catch-per-unit-effort, CPUE) bounded by a 95% confidence interval. Individual effects of each variable kept in the best model are assessed by holding the other variables at a fixed mean value. Together these variables explain 46% of the long-term variability in CPUE.



Supplementary Figure 1: Results from seasonally decomposed missing value imputation used to compute complete time-series for water level (cm) at the Bottle Creek hydrostation (see Fig. 1b). Black areas of the curve indicate measured daily observations, and blue portions show where estimated values were imputed (182 of 7006 observations, 2.5% of data).



Supplementary Figure 2: Results from seasonally decomposed missing value imputation used to compute complete time-series for temperature (degrees C) at the Bottle Creek hydrostation (see Fig. 1b). Black areas of the curve indicate measured daily observations, and blue portions show where estimated values were imputed (157 of 7006 observations, 2.2% of data).



Supplementary Figure 3: Results from seasonally decomposed missing value imputation used to compute complete time-series for salinity (PSU) at the Canepatch hydrostation (see Fig. 1b). Black areas of the curve indicate measured daily observations, and blue portions show where estimated values were imputed (53 of 7006 observations, 0.7% of data).

Supplementary Table 1: Common Snook catch-per-unit-effort (CPUE) by sampling year and season from 17 years of electrofishing sampling in the Shark River (2004-2021), showing a high degree of both seasonal and interannual variation. The total number of transects sampled (n) and total number of Snook captured are noted. Mean CPUE across sample sites is shown for each sampling event with standard deviation (SD) and standard error (SE). Mean fish size (standard length, SL) is also shown with SD and SE.

Sample Year	Season	Month	n	Total # Snook	Mean CPUE	SD CPUE	SE CPUE	Mean SL	SD SL	SE SL
2004-2005	Wet	Nov	18	19	1.1	2.7	0.6	40.1	10.8	2.5
2004-2005	Early Dry	Mar	18	50	2.6	2.7	0.6	40.5	11.6	1.6
2004-2005	Late Dry	April	18	4	0.2	0.5	0.1	49.8	15.0	7.5
2005-2006	Wet	Dec	17	6	0.3	0.7	0.2	41.8	6.3	2.6
2005-2006	Early Dry	Jan	24	33	1.1	1.9	0.4	38.1	11.9	2.1
2005-2006	Late Dry	April	26	69	2.2	3.2	0.6	41.9	9.6	1.2
2006-2007	Wet	Nov	27	14	0.5	0.8	0.2	34.2	15.2	4.1
2006-2007	Early Dry	Mar	27	37	1.5	2.1	0.4	42.5	14.4	2.4
2006-2007	Late Dry	May	27	42	1.5	3.0	0.6	28.9	10.0	1.5
2007-2008	Wet	Dec	27	37	1.3	1.7	0.3	35.9	12.5	2.1
2007-2008	Early Dry	Mar	27	51	2.0	3.0	0.6	39.4	15.0	2.1
2007-2008	Late Dry	April	27	31	1.2	2.9	0.6	37.2	13.7	2.5
2008-2009	Wet	Dec	27	16	0.7	1.8	0.3	34.3	3.2	0.8
2008-2009	Early Dry	Feb	27	20	1.0	2.1	0.4	44.8	14.6	3.3
2008-2009	Late Dry	April	27	91	6.3	9.4	1.8	37.6	7.9	0.8
2009-2010	Wet	Nov	27	3	0.1	0.4	0.1	43.0	2.5	1.4
2009-2010	Early Dry	Feb	25	1	0.1	0.3	0.1	46.5	NA	NA
2009-2010	Late Dry	May	27	48	2.1	3.6	0.7	45.9	7.9	1.1
2010-2011	Wet	Dec	27	0	0.0	0.0	0.0	0.0	NA	NA
2010-2011	Early Dry	Feb	27	32	1.0	1.7	0.3	47.8	10.0	1.8
2010-2011	Late Dry	May	18	13	0.7	1.4	0.3	37.6	12.5	3.5
2011-2012	Wet	Dec	27	8	0.3	0.8	0.2	40.0	5.0	1.8
2011-2012	Early Dry	Feb	27	14	0.5	1.1	0.2	42.7	8.4	2.3
2011-2012	Late Dry	April	27	40	1.6	2.0	0.4	38.7	10.3	1.6
2012-2013	Wet	Dec	27	1	0.1	0.3	0.1	30.5	NA	NA
2012-2013	Early Dry	Feb	27	9	0.4	1.1	0.2	44.1	8.7	2.9
2012-2013	Late Dry	April	27	68	3.9	9.7	1.9	39.7	8.9	1.1
2013-2014	Wet	Dec	27	6	0.3	1.5	0.3	38.8	6.3	2.6
2013-2014	Early Dry	Feb	27	20	0.8	2.6	0.5	37.0	8.5	1.9
2013-2014	Late Dry	April	27	80	4.0	7.3	1.4	39.8	10.9	1.2
2014-2015	Wet	Dec	27	11	0.5	2.2	0.4	45.7	12.8	3.9

Supplementary
Table 1 cont.

Sample Year	Season	Month	n	Total # Snook	Mean CPUE	SD CPUE	SE CPUE	Mean SL	SD SL	SE SL
2014-2015	Early Dry	Mar	27	39	2.2	4.9	0.9	40.8	8.2	1.3
2014-2015	Late Dry	April	27	66	3.2	6.4	1.2	43.1	9.9	1.2
2015-2016	Wet	Dec	27	10	0.4	1.1	0.2	39.6	11.2	3.5
2015-2016	Early Dry	Feb	27	19	0.7	2.1	0.4	39.8	8.0	1.8
2015-2016	Late Dry	May	27	16	0.6	1.1	0.2	38.6	8.0	2.0
2016-2017	Wet	Dec	27	16	0.6	1.4	0.3	38.2	7.5	1.9
2016-2017	Early Dry	Feb	27	20	1.2	5.2	1.0	37.7	8.8	2.0
2016-2017	Late Dry	April	18	39	2.5	3.2	0.7	41.1	10.6	1.7
2017-2018	Wet	Dec	27	20	0.8	2.3	0.4	34.3	6.7	1.5
2017-2018	Early Dry	Feb	27	11	0.4	1.0	0.2	42.8	9.9	3.0
2017-2018	Late Dry	May	27	49	2.1	3.8	0.7	38.1	11.5	1.6
2018-2019	Wet	Dec	27	20	0.9	1.8	0.3	41.8	8.6	1.9
2018-2019	Early Dry	Feb	27	12	0.4	1.2	0.2	38.6	15.3	4.4
2018-2019	Late Dry	April	27	54	2.4	5.0	1.0	35.2	11.9	1.6
2019-2020	Wet	Dec	27	9	0.5	1.6	0.3	37.3	11.6	3.9
2019-2020	Early Dry	Feb	27	22	1.2	2.8	0.5	43.5	17.9	3.8
2019-2020	Late Dry	May	15	65	4.6	11.5	3.0	40.0	13.7	1.7
2020-2021	Wet	Dec	27	3	0.1	0.5	0.1	50.3	7.6	4.4
2020-2021	Early Dry	Feb	27	21	1.1	2.7	0.5	35.8	6.6	1.4
2020-2021	Late Dry	May	27	35	1.5	2.5	0.5	37.3	11.8	2.0

CHAPTER VI

CONCLUSION

Understanding where, when, and why animals move is a central theme in ecology (Nathan et al. 2008; Nathan et al. 2022). Movement patterns offer insight into how animals experience their environment, and how environmental variation and disturbance may alter the timing/extent of movement, which can affect ecological interactions and carry consequences for individuals, populations, and ecosystems (Abrahms et al. 2021; Earl and Zollner 2017; Rezek et al. 2020). In riverine systems, coastal fishes are a beacon of environmental change, and can serve as indicator to both inform and assess management/restoration actions (Crossin et al. 2017; Wilson et al. 2022). Further, quantitative research which describes the causes and consequences of movement can enhance conservation efforts by providing natural resource managers with information which can guide the scale/type of management, and help identify/evaluate management actions (Allen and Singh 2016; Cooke et al. 2016; Hussey et al. 2015; Schmutz and Sendzimir 2018). Through my dissertation chapters, I provided additional evidence that the freshwater flow regime and river/floodplain dynamics are a central factor in the behavior and ecology of fishes in riverine systems, affecting both movement patterns and the timing/extent of seasonal resource availability (Abrahms et al. 2021; Lytle and Poff 2004; Palmer and Ruhi 2019; Poff et al. 1997; Poff 2018).

In Chapter II (Massie et al. 2022), I investigated how both seasonal and interannual variation in environmental conditions interact to shape the migratory patterns of an economically important and popular recreational fish species (Munyandorero et al. 2020), Common Snook (*Centropomus undecimalis*, hereafter Snook) in the Shark River, Everglades National Park. I found that the proportion of tagged Snook migrating each year was positively related to the extent of freshwater marsh drydown preceding the spawning season, which is indicative of prey concentration and foraging potential, can increase available energy, and thus be allocated to maturation, migration, and reproduction. Further, I found that high water levels and positive daily rates of change in water level serve as important cues that trigger the timing of migration within the spawning season. In chapter III (Massie et al. 2020), I described how the large-scale downstream movements of Snook during Hurricane Irma corresponded to drops in barometric pressure, and to rainfall-driven increases in water level. Disturbance-driven movements by Snook in response to changes in water level are also consistent with the environmental cues which elicit reproductive migrations during the spawning season (Massie et al. 2022). In Chapter IV, I illustrated how receding dry season water levels in freshwater marshes, and corresponding increases in the biomass of a freshwater prey subsidy in the river channels, correlate with increases in Snook body condition. The timing of marsh drawdown and seasonal availability of freshwater prey correspond to critical times in Snook life-history (e.g., maturation, sex transition), and should be an important consideration for water management. Finally, in Chapter V, I found significant long-term trends of gradually increasing water level and temperature in the upper Shark River, and decreases in salinity. Further, results showed that the long-term trend in Snook abundance over 17 years of sampling was relatively stable. However, increases/decreases in relative abundance corresponded to both seasonal changes in water level, abundance was highest in the dry season, and the periodic occurrence of extreme environmental conditions (e.g., cold spells, droughts, prolonged dry-season flooding).

My research has provided new information which quantitatively describes the environmental conditions that shape animal movement patterns, maintain access to key prey subsidies, and promote long-term stability of coastal species. These findings, which were built upon a foundation of past research, can in turn help guide future research. Specifically, I suggest several promising avenues for future research:

- Future efforts could provide additional insight on the spawning migrations of coastal fishes by further investigating the role of individual energy status, social cues, and density dependence on migratory decisions.
- To enhance our understanding of the consequences of disturbance-driven movements, future work could compare the immediate responses and long-term consequences of movements driven by extreme climate events (ECE) such as hurricanes across multiple events. Further, research investigating whether behavioral responses might be predictable based on behaviors expressed before the occurrence of ECE may be particularly insightful.
- Research able to link fish body condition to individual movement patterns using high-resolution tracking data (i.e., acoustic telemetry), energy needs as a function of size, and make explicit comparisons of body condition among smaller resident and larger migratory Snook would offer valuable additional insight.

In summary, my dissertation has addressed outstanding research gaps by quantifying the environmental dependencies for a migratory riverine species in a highly managed, impact prone coastal region. I illustrated the importance of freshwater flow in different aspects of Snook life-history (e.g., migration, habitat-use, foraging), and offer three key findings relevant to natural resource management. First, variation in water level is critical, including both wet season increases, and dry season decreases that reflect the natural flow regime. Fluctuations in water level presents important migratory cues associated with reproduction, can increase the number of fish migrating each year, and affect both marsh productivity and access to freshwater prey. Second, the health and fitness of riverine consumers are tied to seasonal prey subsidies and river/floodplain connectivity. Hydrologic variation can maximize trophic linkages, and therefore body condition, and incorporating bioindicators into management and assessment can provide valuable information not reflected by abundance alone. Finally, environmental conditions in aquatic systems are gradually changing as a factor of climate, water management, and restoration. Maintaining long-term datasets is required to understand how animal populations have responded to environmental change, and can inform future management decisions. Water management can mitigate potential climate impacts. As conditions shift under climatic change, understanding how these changes will affect animal movement, migration, foraging, and the consequences for population trends, can inform conservation efforts aimed at preserving ecologically and economically important species, such as the Common Snook.

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APPENDICES

I. Permission emails

A. Springer Nature (CHAPTER II)

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

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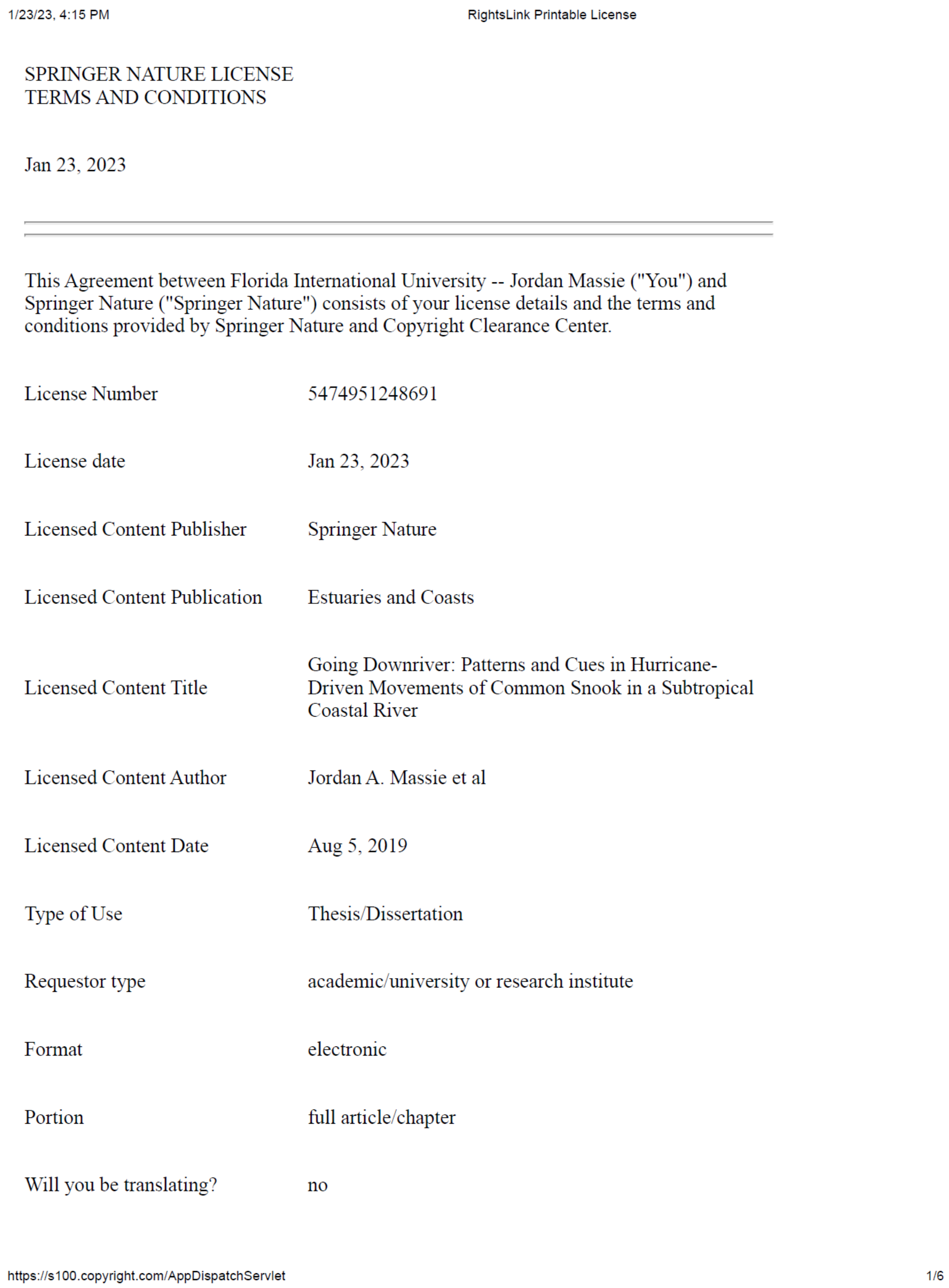

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PUBLICATIONS AND PRESENTATIONS

Boucek, R., A. Trotter, D. Blewett, J. Ritch, R. Santos, P. Stevens, J. Massie, and J. Rehage. 2019. Contrasting river migrations of Common Snook between two Florida rivers using acoustic telemetry. *Fisheries Research* 213: 219-225.

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