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# Going Downriver: Patterns and Cues in 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.

**Keywords** Hurricanes · Extreme climate events · Common snook · *Centropomus undecimalis* · Animal movement · Acoustic telemetry

## 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).

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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. 2019, *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 h), and into deeper offshore areas that may increase survival (Heupel et al. 2003; Liu et al. 2010; Udyawer et al. 2013; Strickland et al. 2019, *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; and (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 1700 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

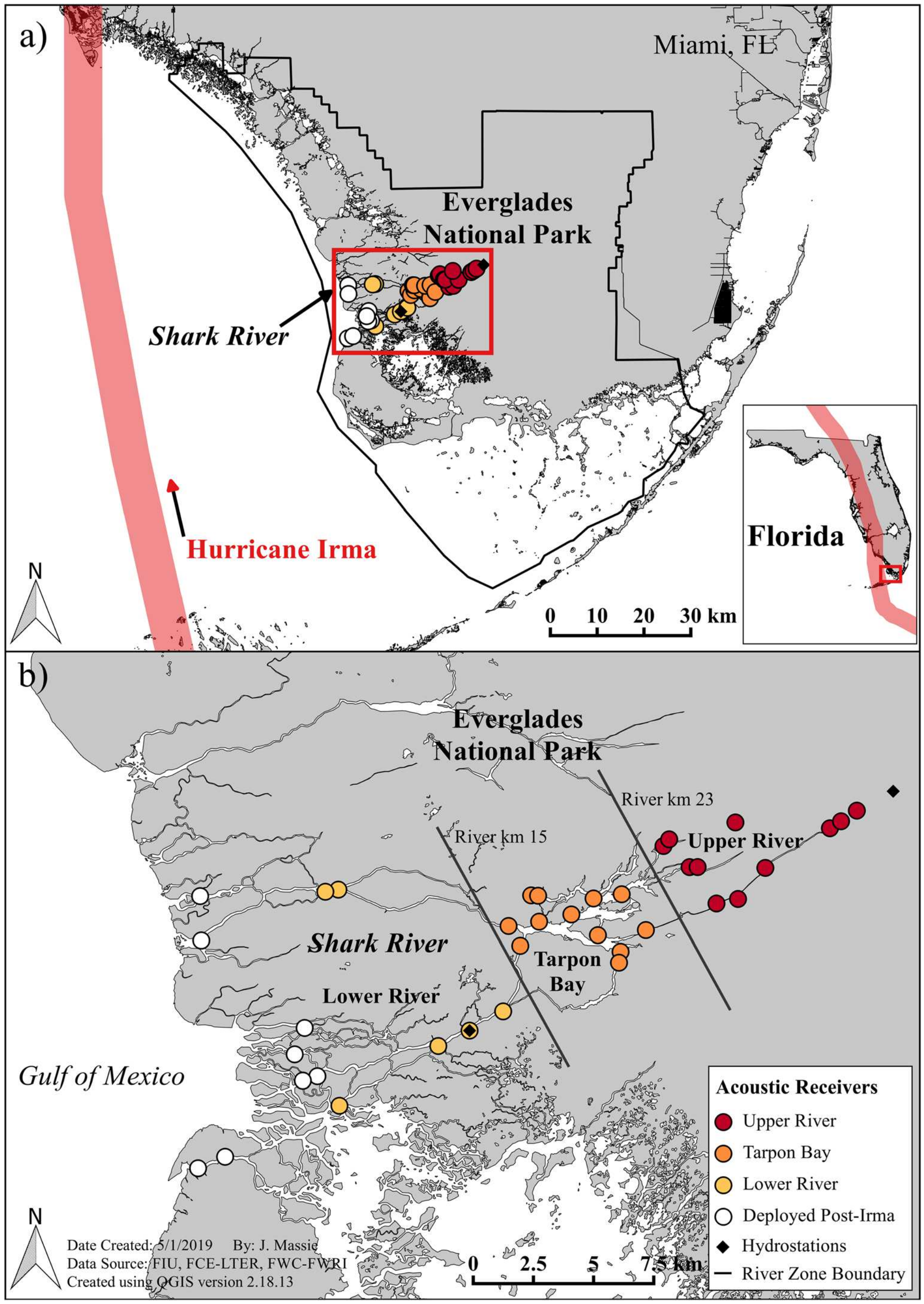


**Fig. 1** Maps of the study area in Everglades National Park. **a** Location of the acoustic array in the Shark River (red box) and the storm path of Hurricane Irma from south to north (indicated by the red band). **b** Details of acoustic receiver and hydrostation placement within the river system. 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

combination of mangrove and freshwater marshes containing a mix of sawgrass (*Cladium* sp.) and freshwater woody plant species, with depths ranging from 1 to 3 m, rocky/mud bottoms, and limited tidal influence (Chen and Twilley 1999; Childers 2006; Boucek and Rehage 2013, 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 to 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 the 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 2 to 3 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, 2019; Matich et al. 2017). 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 min 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 (69 kHz 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 s, 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 h, 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.

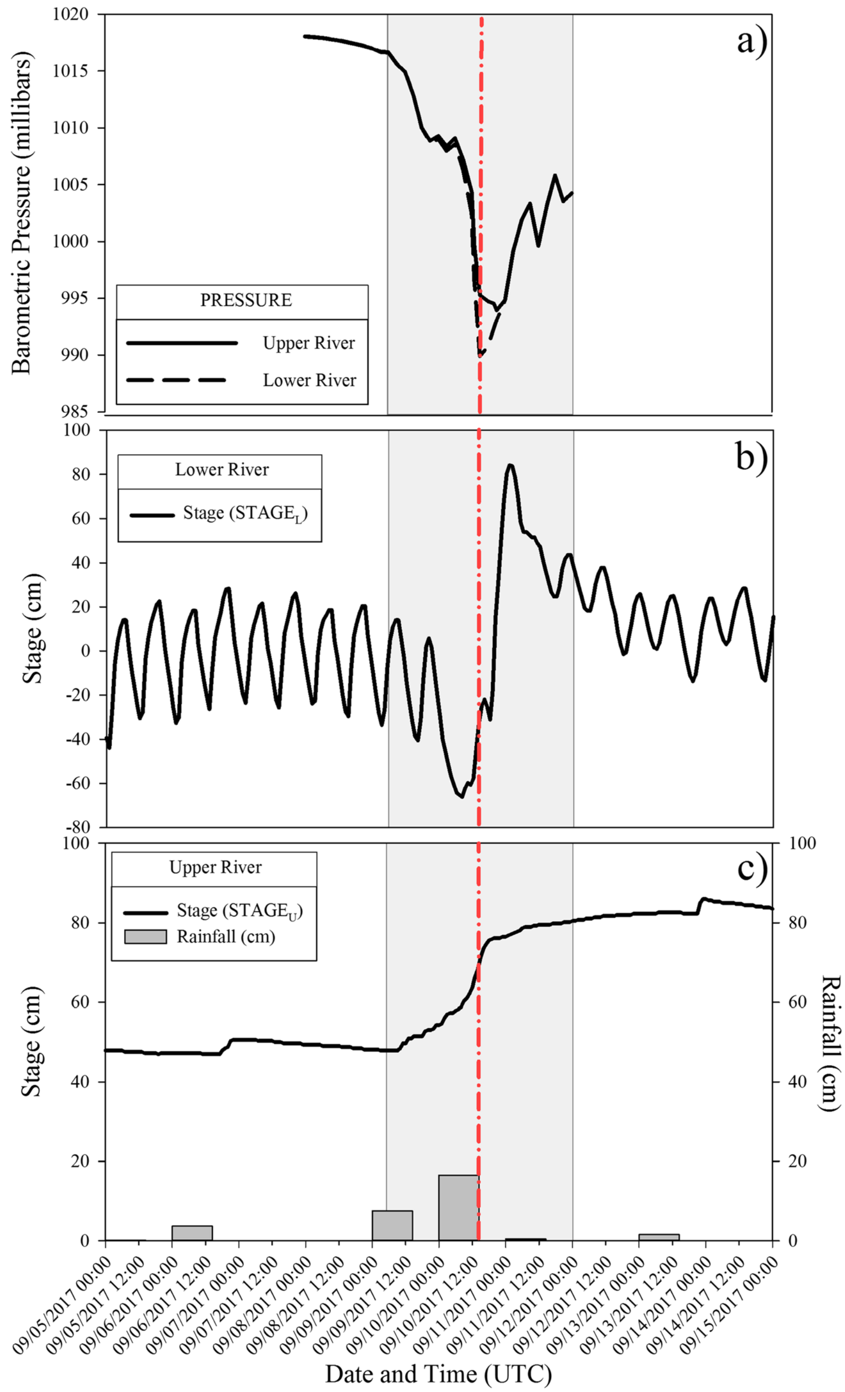


**Fig. 2** Environmental conditions in the Shark River for the 10 days surrounding the passage of Hurricane Irma (15:00 UTC on 10 September 2017, red dotted line). Shading in all three panels shows the 67-h hurricane window denoted by changes in hurricane (barometric pressure) and riverine conditions (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

**Table 1** Fish details and tagging records for the 22 common snook detected in the Shark River during Hurricane Irma

| Fish ID | Date tagged | Standard length (cm) | Study period detections | Hurricane detections | Hurricane movement |
|---|---|---|---|---|---|
| 32904 | 21 January 2014 | 55.2 | 983 | 3 | No |
| 21968 | 16 December 2015 | 67.0 | 2326 | 32 | Inconclusive |
| 21970 | 13 May 2016 | 62.7 | 9131 | 699 | Yes |
| 56006 | 14 May 2016 | 49.6 | 20,796 | 263 | Yes |
| 56011 | 17 May 2016 | 42.2 | 6687 | 64 | Inconclusive |
| 56014 | 17 May 2016 | 43.5 | 14,966 | 283 | Yes |
| 18367 | 17 May 2016 | 63.0 | 18,269 | 79 | Inconclusive |
| 51640 | 13 December 2016 | 51.5 | 2165 | 429 | Yes |
| 51644 | 13 December 2016 | 50.5 | 16,962 | 404 | Yes |
| 51645 | 13 December 2016 | 48.5 | 8437 | 61 | Yes |
| 51638 | 15 December 2016 | 47.0 | 9641 | 440 | Yes |
| 51652 | 26 February 2017 | 49.3 | 11,065 | 181 | Yes |
| 51653 | 26 February 2017 | 45.7 | 39,444 | 839 | Yes |
| 18370 | 27 February 2017 | 57.5 | 6074 | 383 | Yes |
| 51877 | 24 April 2017 | 64.5 | 1014 | 559 | Yes |
| 21959 | 24 April 2017 | 55.0 | 4090 | 74 | Yes |
| 18373 | 25 April 2017 | 60.5 | 5017 | 97 | Inconclusive |
| 18379 | 25 April 2017 | 65.5 | 8763 | 308 | Yes |
| 21960 | 25 April 2017 | 63.5 | 5259 | 63 | Yes |
| 18351 | 31 May 2017 | 58.2 | 8155 | 734 | Yes |
| 18382 | 31 May 2017 | 69.9 | 1170 | 15 | Yes |
| 21969 | 31 May 2017 | 54.5 | 1386 | 105 | No |

The 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 is 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

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 (discussed 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/h), 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 6 months leading up to and the 6 months following Hurricane Irma. This 6-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 the 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 ($STAGE_{\Delta U}$ and $STAGE_{\Delta L}$).

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 6-h 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 1; 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 nonstorm conditions, SR populations are subject to daily changes in salinity due to tidal influences. Thus, stage was selected for use in the final analyses reported here.

## 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 $PRESSURE_{\Delta}$. 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 $STAGE_{\Delta U}$ to represent the rain-driven increase in upper river water levels, models with $STAGE_L$ or $STAGE_{\Delta L}$ 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 $PRESSURE_{\Delta}$) 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. 2016; 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 6 months before and 6 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 nonindependence of observations within each time period. For the 6-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 mbar, until a rapid decline on 9 September, marking the beginning of our hurricane window, and reached a minimum of 994 mbar in the upper river at 21:00 UTC on 10 September, 6 h 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 mbar 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: 12 of the 22 fish (55%) moved from the upper river to Tarpon Bay (Fig. 3a),

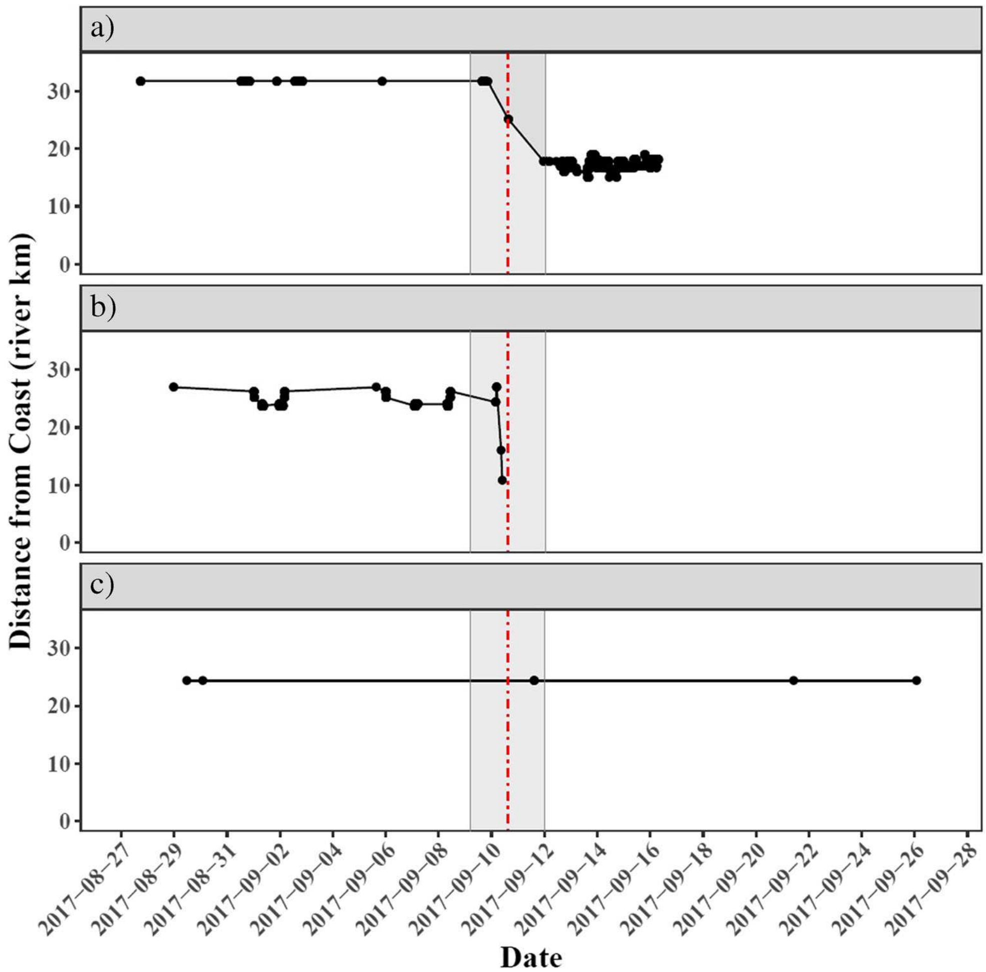


**Fig. 3** Examples of acoustic receiver detection data for tagged common snook in the 2 weeks leading up to and following Hurricane Irma (timing of Shark River hurricane passage indicated by vertical dotted line). Movement paths show three observed patterns of movement: **a** fish that moved from the 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 **a** was not redetected as of receiver downloads in June of 2018, indicating a possible mortality. The fish in **b** was detected on a redeployed coastal receiver on 14 December 2017 (beyond the period depicted here), corroborating that it exited the system and had not returned to the river post-hurricane

and four fish moved rapidly from the upper river to the lower river (18%) and were not redetected 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, 8 h after the eye of the hurricane passed the SR, and while PRESSURE remained near the minimum of 994 mbar (Fig. 4). The first fish moved downstream at 8:00 UTC on 10 September, 7 h before SR passage, and the last detected movement occurred a few days after the storm at 4:00 UTC on 13 September (61 h 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 6 months prior to the hurricane window, during the hurricane window, and 6 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 6 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 6-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

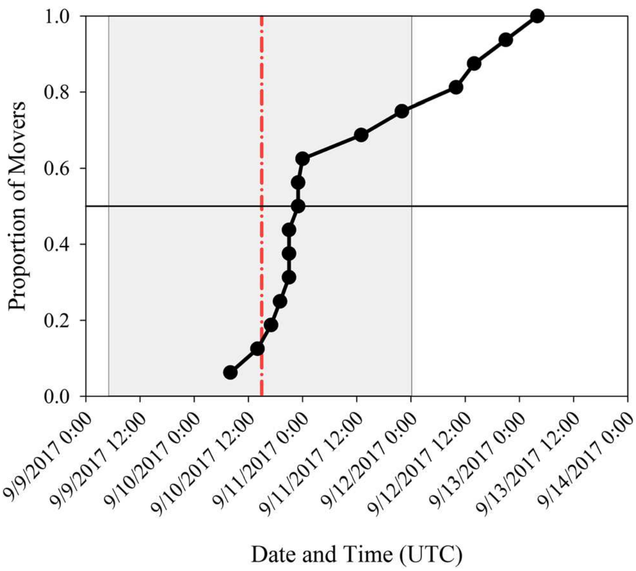


**Fig. 4** Timing of common snook movement responses for the 16 fish that moved among river zones during Hurricane Irma, illustrating how 50% of zone changes (marked by black horizontal line) occurred by 23:00 UTC on 10 September, 8 h after the storm passed the Shark River. The shaded box indicates the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

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 redetected, suggesting either mortality or undetected outmigration. In total, 11 of the 16 fish that relocated during the hurricane window were subsequently redetected 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 $PRESSURE_{\Delta}$ (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 ($STAGE_{\Delta L}$ $D^2$ 0.01, $STAGE_{\Delta U}$ $D^2$ 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.

**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, and (3) movements are best explained by a combination of hurricane and riverine factors

| 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* |

The best-fitting overall model (i) is shown in italics. $PRESSURE_{\Delta}$ is the change in barometric pressure between hourly intervals in the Shark River, 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 common snook movement fit to 138 observations with 178.32 null deviance

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 mbar (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 mbar, three fish moved as this minimum PRESSURE persisted (lasting until about 9 h after SR passage), and the remaining six fish initiated movement as PRESSURE returned to 1004 mbar. 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.

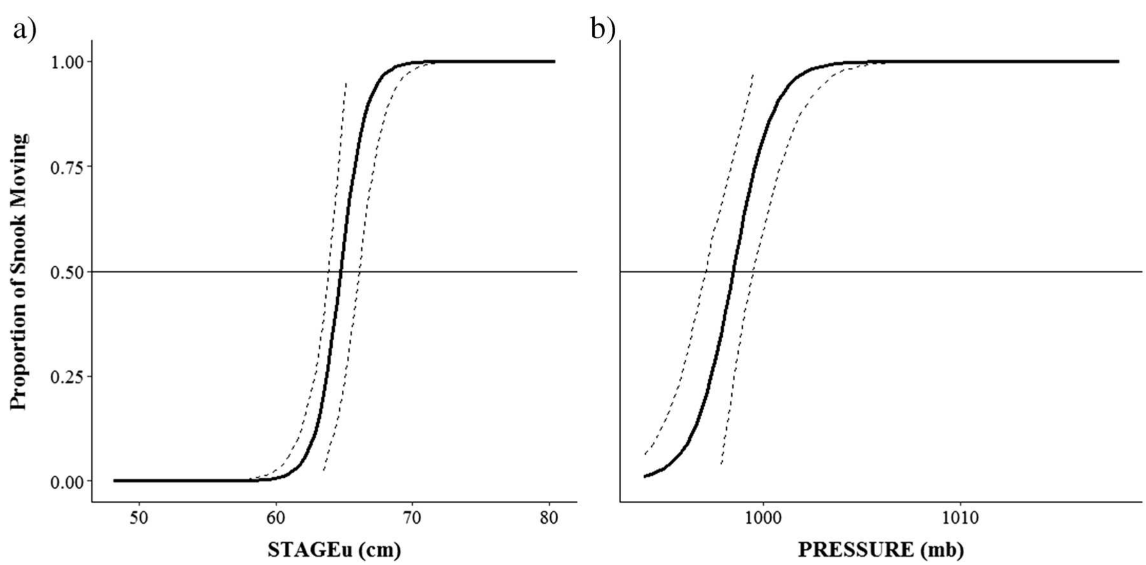


**Fig. 5** Plotted variables in the best-fitting logistic regression model (PRESSURE + $STAGE_U$) for common snook movement during Hurricane Irma. Variable effects are isolated by holding one variable at a fixed mean value in each plot, and black horizontal line marks the point where 50% of fish initiate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

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 5 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 redetected 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 the 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 6 h 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 7 h 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 h 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), intra-population 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/h 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. 2019, *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 10 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 redetected 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 7 h before to 6 h after SR passage. Two of these fish reappeared on the array on 24 October and 31 October 2017, a third individual on 14 December 2017, and the fourth fish was redetected on 11 April 2018, nearly 7 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 redetected as of 10 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, 1 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 subpopulations 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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