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# Poleward expansion of common snook *Centropomus undecimalis* in the northeastern Gulf of Mexico and future research needs

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# Abstract

Globally, rising temperatures have resulted in numerous examples of poleward shifts in species distribution patterns with accompanying changes in community structure and ecosystem processes. In the Gulf of Mexico, higher mean temperatures and less frequent winter freezes have led to the expansion of tropics-associated marine organisms. Our objectives were to quantify changing environmental conditions and the poleward expansion of the common snook Centropomus undecimalis into the Cedar Keys area of Florida, USA (29 deg N). The snook is an economically and recreationally important sport fish found from southern Brazil to south Florida. Cedar Key and the Lower Suwannee River are north of the snook's historically documented range, likely due to lethal water temperatures during winter. Using data from a long-term monitoring program, we report an increase in catches of snook in this area since 2007. The spatial and temporal expansion of the species began with adult fish in 2007. By 2018, snook of all sizes were found in the region, and we found strong evidence of local reproduction during 2016–2018. The locations of nursery habitat and winter thermal refuges (e.g., freshwater springs) need to be identified and have implications for land-use policy and minimum-flow regulations for rivers. The arrival of the snook in the northern Gulf of Mexico could affect food web ecology and habitat interactions among estuarine predators, and future studies should evaluate snook's food habits and competitive interactions with resident fishes in this expanded range. Our study provides an example of how species range expansions due to changing temperatures should result in new research priorities to evaluate impacts of climate change on coastal systems.

# Introduction

Increases in temperature have influenced the physiology, phenology, and geographic ranges of organisms [1,2] and, with models predicting an additional increase of 2.4–6.4 °C over the next

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100 years [3], is expected to continue. These changes can therefore influence spatial habitat use and trophic dynamic processes in food webs [4-6], and rising temperatures have been implicated in the northward spread of a variety of organisms in the Gulf of Mexico (hereafter referred to as Gulf). The lack of heavy frosts has allowed a number of tropical/subtropical species to extend into and persist in the northernmost reaches of the Gulf. For example, black mangrove Avicennia germinans have become common throughout the Gulf [7-10], including Texas [11], Louisiana [12], Mississippi [13], and Florida [14]. Both red and white mangroves (Rhizophora mangle and Languncularia racemosa, respectively) are now common in Florida's Big Bend region near Cedar Key (author's, personal observation). Warmwater corals not previously observed in the northern Gulf, such as Acropora palmata, have been observed [15], and green turtles (Chelonia mydas) have become more abundant in the northeastern Gulf [16]. Satellite telemetry and long-term data from sighting networks also indicate that the West Indian manatee *Trichechus manatus* has increased in prevalence along northern Gulf states [17,18]. Comparisons of seagrass-associated fishes in Louisiana, Mississippi, Alabama, and northwest Florida from the 1970s to 2006-2007 indicated increased abundance of tropical and subtropical fishes (e.g., yellowtail snapper Ocyurus chrysurus; sergeant major Abudefduf saxatilis; and stoplight and emerald parrotfishes Sparisoma viride and Nicholsina usta, respectively), among others [19].

Quantifying the spatial and temporal expansion of organisms into higher latitudes is important in understanding how climate change is affecting food webs and fisheries. Here, we describe the northward range expansion of common snook (*Centropomus undecimalis*, hereafter referred to as snook) into the Cedar Key and Lower Suwannee River region (Fig 1). Snook are prized game fish and support an economically important recreational fishery [20,21] in southern Gulf waters. Snook are stenothermic and highly sensitive to cold temperatures; the first sign of cold stress is the cessation of feeding, followed by loss of equilibrium and death [22–25]. We hypothesize that the combination of milder winters and warmer summers has promoted the expansion of a Florida snook population into northerneastern Gulf waters. A recent study shows a similar range expansion for snook in the western Gulf [26]. We sought to quantify the changes in snook catches using a long-term standardized sampling program, to explore the spatial extent and temporal changes in size structure, assess evidence for local reproduction, and identify future research needs for an expanding range of a subtropical apex predator in the Gulf.

## Methods

#### Ethics statement

No specific permission for sampling was required, as sampling was conducted by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute. However, every effort was made to reduce stress and not harm captured fish, before releasing. No protected species were sampled.

## Study site

The Suwannee River lies in the northern region of the Florida Gulf Coast and is one of the largest undammed rivers in the eastern United States (Fig 1). At its mouth lies the Cedar Keys National Wildlife Refuge and the Big Bend Seagrass Aquatic Preserve. This area of Florida, known as the Nature Coast, has received high priority for conservation in the northern Gulf based on the presence of imperiled species and their habitats [27]. The region around the Suwannee River estuary also represents an ecotone between poleward-shifting mangroves and temperate salt marshes [8,14] and in recent years has seen an increase in occurrence of tropical species such as red mangrove, roseate spoonbill *Platalea ajaja*, and snook, the focus of this





study. The study area contains a diverse mix of estuarine, river, and tidal creek habitats which includes extensive seagrass beds, oyster reefs, mangroves, salt marshes, and unvegetated bottom that support valuable recreational and commercial fisheries.

#### **Environmental conditions**

To evaluate temperature changes in the region, we used a publicly available data set from a stationary weather instrument maintained and located in Cedar Key (National Oceanic and Atmospheric Administration (NOAA) gauge CDRF1, <u>http://www.ndbc.noaa.gov/station\_page.php?station=cdrf1</u>). We attempted to obtain a long-term time series of water temperature data, but data gaps precluded use of water temperatures. Therefore, we used air temperature data from NOAA gauge CDRF-1 instead of water temperature because the use of fixed measurements taken at a stationary location reduces variability and facilitates more consistent comparisons, and data from the site had fewer missing points than data from other sources. Finally, because the water in the larger sampling region is so shallow (<2m), water and air temperatures are likely to be similar [14,28]. We analyzed air temperature for instances of warm weather conditions by using linear regression to assess the relationship between the number of days in each year that temperature reached < 12 °C (the lower lethal limit for snook [22,24]). We included 18 years of data in this analysis, dating back to 2000, when the first snook in the area was documented by fishery-independent monitoring.

#### **Field sampling**

The Florida Fish and Wildlife Conservation Commission's Fisheries Independent Monitoring program conducted monthly standardized stratified-random sampling in the Suwannee River estuary during 1997-2018 (Fig 2). This program uses multiple gear types, including a 183-m haul seine, a 21.3-m seine, and a 6.1-m otter trawl, to collect data on various life-history stages of fishes and selected invertebrates from a variety of habitats. Detailed descriptions of site selection and standardized sampling techniques can be found in two peer-reviewed journals and a program data summary report [29-31]. In summary, the estuary was divided into geographic and logistical zones. Zones were further divided into a cartographic grid of cells measuring 1-min latitude  $\times$  1-min longitude; cells were randomly selected for sampling. Sampling cells were stratified by habitat and depth, thereby identifying the gear type and deployment technique best suited in those areas. The 21.3-m seine and the 6.1-m otter trawl targeted primarily age-0 and juvenile fishes from different depths; the 21.3-m seine sampled shallow water  $(\leq 1.8 \text{ m})$  along shorelines and in open-water habitat  $(\leq 1.5 \text{ m})$ , whereas a 6.1-m otter trawl sampled relatively deep water (1.8-7.6 m). The 183-m haul seine targeted subadult and adult fish along shorelines in water depths  $\leq$ 2.5 m [30]. All gear types and associated techniques were standardized with regard to amount of area fished, by following standardized sampling procedures. Effort among gear types and deployment techniques was roughly proportional to the available habitat. Sampling gear and effort are summarized in Table 1.

## Data analysis

During 1997–2018, sampling effort and locations remained nearly constant. Thus, we combined catches from all gear types each year to quantify the spatial and temporal expansion of snook. Before 2002, changes were made regarding effort and sampling location (Table 1); for example, the Lower Suwannee River was added to the sampling universe in 2001. These changes in effort and location, however, were made before snook appeared in our data, except for one snook captured in a 183-m haul seine in 2000. Sampling effort for all gear types did not change during 2002–2018. Further, >97% of all snook catches occurred in the 183-m haul



Fig 2. Map of study area, showing all randomly selected sample sites, 1997–2018. The grid system represents the Fisheries Independent Monitoring program's universe.

seine set along shorelines, and total fishing effort using the haul seine was constant during 1999–2018. Therefore, we amalgamated all the catches of snook to evaluate temporal trends in snook catches through the time series.

We evaluated the evidence for increasing temporal trends in snook catches using Akaike information criterion (AIC) model selection [32]. The time series of snook catches was fitted to an exponential model  $C = a \times exp^{b^*(Year)}$  using maximum likelihood and a lognormal distribution, where *a* is the intercept parameter and *b* is the exponent parameter. The exponential

model was compared to an intercept-only model fitted with a lognormal distribution, and AIC model selection was used to evaluate the relative credibility of each model [32]. The delta AIC values were computed between the two candidate models, and values greater than 10 are considered to have negligible credibility relative to the lowest AIC model [32].

We characterized changes in spatial distribution and quantified temporal extent of snook catches, changes in size distribution over time, evidence that snook were reproducing locally, and assessed seasonality. The spatial distribution of snook catches was plotted using GPS locations at each sample site. We then assessed the spatial location of catches through time to quantify the spatial expansion in the catches. The size structure of snook was plotted across time to quantify changes in the length distribution, show how size distribution changed throughout the time series, including presense of age-0 fish (<100 mm standard length [SL]) and subsequent juvenile fish (100 to 300 mm SL). Mean monthly catches, all years combined, were plotted with mean water temperature taken during each net deployment by month to evaluate seasonal patterns.

We used the same 22 years of data to assess trends in the frequency of occurrence of snook, black mangrove, and red mangrove. Occurrence of mangroves was recorded at each seine haul, allowing us to quantify the frequency of occurrence through time. Only data from the 183-m haul seine were used for this analysis, which sampled only shoreline areas and captured the majority (>97%) of snook in this study. We also plotted the frequency of occurrence of shore types coded as black mangroves or red mangroves during 183-m haul sampling, since mangroves have been shown to be important habitat for snook [29] and the climatic factors affecting both snook and mangroves appear to be similar [8, 33].

Gear	Location	Years	Effort (hauls yr <sup>-1</sup> )	No. fish	% Total snook catch	Min. SL	Max. SL
183 × 2.5-m haul seine	bay	1997	95	0	0		
		1998	120	0	0		
		1999-2018	192	610	97.6	105	885
			Subtotal	610	97.6		
21.3 x 1.8-m seine	bay	1997	216	0	0		
		1998-2018	252	1	0.2	220	220
	tidal creeks	1997	72	0	0		
		1998-2018	108	10	1.6	53	133
	Suwannee River	2001	55	0	0		
		2002-2018	60	3	0.5	187	376
			Subtotal	14	2.3		
6.1-m otter trawl	bay	1997	230	0	0		
		1998-2000	0	0	0		
		2001	110	0	0		
		2002-2018	120	0	0		
	Suwannee River	2001	55	0	0		
		2002-2018	60	1	0.2	331	331
			Subtotal	1	0.2		

#### Table 1. Summary of snook collected by gear type, location, and effort in the Suwannee River estuary, Florida. Standard length = SL.

Location included the estuary (bay), tidal creeks, and Lower Suwannee River (Suwannee River).

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Fig 3. Air temperature data from the Cedar Key NOAA buoy (CDRF1) indicate rising temperatures since 2000, in terms of declining number of days <12°C.

#### Results

#### **Environmental conditions**

Clear increases in air temperature were documented at the CDRF1 gauge (Fig 3). Regression analysis indicated the number of days below the lethal limit of snook has significantly ( $F_{1,17} = 5.72$ , P<0.05) declined since 2000 (Fig 3).

#### Field sampling

In total, 625 snook, ranging in SL from 53 mm to 885 mm, were collected during combined fish sampling from the Suwannee River estuary. Snook were captured primarily along shorelines in open estuarine areas with the 183-m haul seine (98% of total snook catch); the 21.3-m seine and 6.1-m otter trawl comprised only 2% of the total catch. Snook captured by these two gear types were almost exclusively (93%) from tidal creek and river habitat (Table 1).

In 2000, the first snook (703 mm SL) was captured near the Cedar Key islands during monthly stratified random sampling (Figs 4–6), documenting the northernmost extent of its range. Another snook was not captured again until 2007, when yearly occurrences of snook began to appear during sampling. From 2012 through 2018, there was an exponential increase in snook catches. Total catches in 2017 (N = 163) tripled catches from the previous year (N = 56). In 2018, catches increased to N = 231 and was the highest of all years of sampling (Fig 4).

The exponential model provided a substantially more credible fit to the data than a constant temporal catches model. The delta AIC value for the intercept-only model was 188, indicating that the constant catch through time model had near zero credibility relative to the exponential model. Therefore, the exponential model was selected as the preferred model, indicating sharply increasing catches in recent years (Fig 4).



Fig 4. Yearly catches of snook collected in 183-m haul seines, 21.3-m seines, and 6.1-m otter trawls in the Suwannee River estuary, Florida. Data (symbols) and the fitted exponential model (line) are shown. Data represent total snook catches of all gear types combined.

Expansion in spatial distribution and size composition of snook was evident through time in the Suwannee River estuary (Figs 5 and 6). During the early years of expansion, captured snook were almost exclusively larger, older individuals. We hypothesize that these individuals likely immigrated to the Suwannee River estuary from southern estuaries. Early captured (2007–2011) snook were collected primarily around the Cedar Key islands (Fig 5). During 2012–2015, the spatial distribution of snook expanded around the Cedar Key islands and to the north toward the Suwannee River. Catches of snook continued to increase and spatial distribution continued to expand into areas north of the Suwannee River in 2016–2018. Areas in which snook were captured also expanded into the river and tidal creek areas, with four snook captured in the Suwannee River and 10 captured in tidal creeks (Table 1). As catches and distribution of Snook increased during 2012–2018, the size structure changed from primarily large individuals to individuals of all sizes, including age-0 fish that had likely hatched locally. By 2018, we found a population that appeared fully established with presumed local reproduction ongoing with fish less than 100 mm SL (Fig 6).

Snook were captured across all months during this study but were least abundant (N = 5) during late winter (January and February), when water temperatures averaged 14.4 °C and 15.8 °C, respectively (Fig 7). Catches increased in March and April (N = 90) as water temperatures approached 20 °C and decreased in May (N = 25). Catches continued to increase (N = 207) through the summer (June–August) as water temperatures peaked. The largest catches (N = 210) were made during a two-month period in late summer and early fall (September and October), as water temperatures started to decrease. Catches during November and December (N = 88) were similar to early spring catches, as water temperature decreased towards 20°C. We did collect snook during relatively low temperatures, including a cold event in December 2017, when water temperature dropped below 12°C. During this event, two snook were captured in water at 11.9°C, below the reported lethal low temperature of 12.5°C,

and five snook were captured in water at 13.5 °C. In December 2018, another 19 snook were captured in water at 13.9 °C.

Since 2000, when the first snook was captured at its northernmost extent, there was an increase in the frequency of occurrence of black mangrove through 2018 (Fig 8). Frequency of occurrence of snook and red mangrove started to increase after 2007, as well as total snook catch per year and continued to increase throughout the study period (Figs 4 and 8). However,



Fig 5. Locations of snook catches in the Suwannee River estuary, Florida, with all sampling gear combined. Panels represent blocks of data collected, 1997–2018. Grid system represents the Fisheries Independent Monitoring universe.

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**Fig 6. Length frequency distributions of snook collected in the Suwannee River estuary, Florida, with all sampling gear combined.** Combined years align with years in Fig 5. Total number of fishes captured (N) is represented.

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red mangrove, black mangrove, and snook all showed a substantial decrease in frequency of occurrence during a hard freeze in 2010, but slightly rebounded the following year and continued to increase through our study. These data support that the exponential increase in snook catches during 2016–2018 reflected an expansion in spatial distribution over time and did not result from several large catches from a few sampled areas (Figs 4 and 8).

## Discussion

The poleward expansion of snook in the northern Gulf of Mexico likely resulted from increasing water temperatures and less frequent winter freezes. The Suwannee River estuary experienced clear evidence of warming waters, in terms of temperatures above the lethal limit for snook, a trend that may have facilitated the expansion of the subtropical snook. The last extended cold event that extensively killed mangroves in this area was 1989 (author's personal observation), and while a general trend of warming temperatures is present, it is possible that less frequent, but more intense cold events could occur via atmospheric instability in the polar regions creating stochastic events such as polar vortexes [34].

Poleward shifts in the biogeographic distributions of marine organisms have been well documented (reviewed in [1, 35,36]). These distribution changes have been documented for primary producers such as phytoplankton [37], algae [38], and emergent plants [39], and for invertebrates such as fouling organisms [40], bivalves [41], gastropods [42], squids [43], amphipods [44], and crabs [45,46]. Mobile aquatic organisms such as fishes can quickly migrate to follow optimal environmental conditions, and fish distribution patterns exhibit similar changes. For example, southern species have begun replacing northern species in



Fig 7. Combined monthly catches (1997–2018) of snook collected in the Suwannee River estuary, Florida, with all sampling gear combined. Monthly mean water temperatures, calculated from all sample sites during the study period whether or not a snook was caught, are represented by the black line.

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Fig 8. Yearly frequency of occurrence of snook, black mangrove, and red mangrove observed at 183-m haul seine sites in the Suwannee River estuary, Florida. The vertical dotted line indicates the 2010 winter freeze.

California reef fish assemblages [47], and Perry et al. [48] documented similar changes in North Sea fishes, with around half of the species ranges expanding northward. In all these instances, rising temperatures have been hypothesized as the mechanism driving the range shift.

Along with poleward expansion of snook in the Gulf of Mexico (this study, [26]), there has been substantial expansion in both red mangrove and black mangrove, which provide important habitat for both juvenile and adult snook [29, 49,50]. It is unclear whether the mangrove expansion northward is a mechanism for snook expansion, but clearly the habitats are shifting from salt marsh to mangroves in this region [8, 14], which will further improve habitat for snook. Snook commonly use mangrove habitat in southern estuaries, however are habitat generalists and use habitats in proportion to their relative availability [51]. Therefore, we predict as mangroves expand northward, snook are likely to utilize those habitats.

Our observation of expanding mangrove habitat is consistent with Cavanaugh et al. [33], who reported a doubling of spatial extent of mangroves along the east coast of Florida, between latitudes 29°N and 29.75°N, which directly corresponded to our study area (29°4′ N–29°20′ N) along the west coast of Florida. Cavanaugh et al. [14] found that decreases in the frequency of cold events, rather than increases in mean air temperature, facilitated the expansion of mangroves. Daily minimum temperature has increased faster than daily maximum or mean temperature, resulting in a warming trend over the past 50 years [2, 8, 33]. Thus, the expansion of snook in this region was likely correlated with increased temperatures overall.

The sustainability of a snook population in the Suwannee River estuary may depend on the availability of thermal refugia or the ability of the species to adapt to colder climate. This newly established population is still likely to be exposed to cold events greater in magnitude or duration than events in their historical range. Snook in Florida experienced extensive mortality events during the extremely cold winters of 1989–1990, 2000–2001, and 2009–2010. Thus, we expect that snook in the Suwannee River estuary will still experience setbacks due to cold kills.

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The winter of 2010, for example, caused an extreme cold kill of snook that extended as far south as the Everglades and substantially altered abundance and catch by anglers [25, 52]. Recovery of snook following this cold kill took as long as four years, depending on location [53]. Snook catches in our study area were noticeably reduced by the 2010 cold kill, but fully recovered within three years.

Since 2010, winters have been relatively mild, and it is during this time that the snook population expanded substantially northward, beyond the Suwannee River. However, snook in the Suwannee River estuary survived minor cold events in 2017 and 2018, which suggests that snook at this latitude may have developed local behavioral adaptations by finding thermal refuge in the Suwannee River, tidal creeks, or areas with warm groundwater springs, common throughout the region. During these cold events in our study, snook were captured near the mouth of the Suwannee River. Movement patterns of snook can affect their vulnerability to extreme cold events [28, 53]. Snook in their historic range are known to migrate into rivers, creeks, and channels post-spawning to endure cold events [53]. Catches in our study were greatest during the presumed post-spawning season (September and October). Snook may have been congregating before migrating to the Suwannee River or tidal creek habitat to endure the winter.

A key uncertainty is the degree to which thermal refugia in the form of groundwater springs may provide resilience to this snook population and allow individuals to withstand cold kill events. We expect snook in the Suwannee River estuary to adapt a behavioral strategy that takes advantage of thermal refuges during winter; that is, they will seek groundwater springs by moving into rivers and creeks as winter sets in, returning to the open estuary as water temperatures warm again. The geology in the region is karst porous limestone with extensive springs and groundwater seeps [54]. Natural springs provide constant water temperature throughout the year, and, because spring water is warmer than ambient water temperature in winter, the coastal springs provide thermal refugia for cold-intolerant fishes and marine mammals [55]. Groundwater flow rates are strongly influenced by precipitation patterns and water levels in the Lower Suwannee River [56,57]. Thus, changes in freshwater flow patterns could influence the availability of thermal refugia during winter, and understanding this relationship is a key future research need.

Research is also needed to determine whether the biology of snook differs at a more northern latitude, particularly regarding differences in spawning and growth, which may influence the persistence of snook and its impact on fishery management strategies. Cold weather in northern latitudes begins earlier and ends later than in areas farther south. Therefore, we expect the snook spawning season, which has been correlated to water temperature during summer months in southern latitudes [58,59], to be shorter in more northern areas. A species at the northern extent of its range also tends to grow faster than those at lower latitudes. This is thought to be a compensatory response to a shorter growing season, known as the counter gradient hypothesis [60]; when the species has the opportunity to grow, it does so quickly before cold temperatures slow their growth again [61]. Thus, we expect snook growth rates in the Suwannee River estuary to be faster than in their historic range. Similarly, fish natural mortality is affected by both growth rate and temperature [62], and future research should explore whether growth and mortality differ in the northern expansion of the snook's range, which could alter optimal management plans (e.g., bag or size limits).

We found evidence for local reproduction of snook, with age-0 fish first occurring in 2010 followed by juvenile fish captured in subsequent years. The shoreline of the Suwannee River estuary is characterized by an expansive network of coastal tidal creeks that provide ideal habitat for age-0 and juvenile snook. Beginning in 2016, age-0 and juvenile snook were commonly observed within tidal creeks, further suggesting self-recruitment. However, the variability of

recruitment and level of survival are not clear and warrant further investigation. Additional evidence of local reproduction is that island habitats and channels around Cedar Key are consistent with descriptions of spawning sites for snook farther south [59]. Summer water temperatures are warm enough for spawning at the Cedar Keys, which in southern estuaries typically begins in April or May, when water temperatures reach approximately 22°C [63,64]. In our study, catches decreased at that time, which may have been attributed to snook moving to potential spawning aggregations, such as deep channels around barrier islands or offshore wrecks and reefs, where they were not vulnerable to our sampling gear [59].

Identification of snook nursery habitat should be a high priority if resource managers wish to encourage a sustainable recreational snook fishery in the Suwannee River estuary. Age-0 snook typically recruit to areas well into the land margin such as river backwaters, the headwaters of tidal creeks and high-marsh ponds [65–67]. These habitats often lie at the interface with coastal development and urbanization and so are particularly vulnerable to anthropogenic impacts. Quantifying the habitat use of coastal wetlands by a recreationally important species may help raise awareness of their value. Possible nursery habitats can be identified by expanding fisheries monitoring into remote tidal creeks and marsh ponds, where snook are known to reside. Then it may be possible to assess the relative importance of each nursery (those that support the highest growth rates and condition [68,69]) and its contribution to the adult population [70].

Changes in species distributions could have trophic impacts for historically native predators and prey fish populations [1]. Snook support important fisheries and are prized by anglers, but its spatial expansion and the resulting competition for resources could negatively impact historically dominant inshore sport fish in the northern Gulf, particularly red drum *Sciaenops ocellatus* and spotted seatrout *Cynoscion nebulosus*. Snook exhibit a high degree of diet overlap with red drum in South Florida, where both species historically occur [71]. Red drum, snook, and spotted seatrout are all mid-trophic-level predators that consume a range of demersal fishes and invertebrates [71,72]. Red drum populations increased sharply in South Florida following an extreme statewide cold kill of snook in 2010, suggesting that release from competition with or predation by snook could have allowed an increase in red drum abundance [52]. The expansion of snook into the Suwannee River estuary could influence abundance of prey populations and growth rates for red drum and spotted seatrout, ultimately influencing sustainable harvest strategies for these species. Thus, future research should explore habitat and diet overlap among historically native and novel predators, as well as prey population responses to expanding predator populations like snook.

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#### References

- Scheffers BR, Pecl G. Persecuting, protecting or ignoring biodiversity under climate change. Nat Clim Change. 2019; 9: 581–586.
- 2. Intergovernmental Panel on Climate Change. Climate change 2007: synthesis report. 2007.
- Jones PD, New M, Parker DE, Martin S, Rigor IG. Surface air temperature and its changes over the past 150 years. Rev Geophys. 1999; 37(2): 173–199.
- 4. McCarty JP. Ecological consequences of recent climate change. Conserv Biol. 2001; 15(2): 320–331.
- Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 2003; 421(6918): 37–42. https://doi.org/10.1038/nature01286 PMID: 12511946
- Marshak AR, Heck KL. Interactions between range-expanding tropical fishes and the northern Gulf of Mexico Red Snapper Lutjanus campechanus. J Fish Biol. 2017; 91(4): 1139–1165. https://doi.org/10. 1111/jfb.13406 PMID: 28905373
- McMillan C, Sherrod CL. The chilling tolerance of Black Mangrove, *Avicennia germinans*, from the Gulf of Mexico coast of Texas, Louisiana and Florida. Contrib Mar Sci. 1986; 29: 9–16.
- Osland MJ, Enwright N, Day RH, Doyle TW. Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. Global Change Biology 2013; 19: 1482–1494. https://doi.org/10.1111/gcb.12126 PMID: 23504931
- Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW. Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob Change Biol. 2014; 20(1): 147–157.
- Osland MJ, Hartmann AM, Day RH, Ross MS, Hall CT, Feher LC, Vervaeke WC. Microclimate influences mangrove freeze damage: implications for range expansion in response to changing macroclimate. Estuaries and Coasts 2019; https://doi.org/10.1007/s12237-019-00533-1.
- Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, et al. Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. Est Coast Shelf S. 2013; 119: 7–16.
- 12. Perry CL, Mendelssohn IA. Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. Wetlands. 2009; 29(1): 396–406.
- Macy A, Sharma S, Sparks E, Goff J, Heck KL, Johnson MW, Cebrian J. Tropicalization of the barrier islands of the northern Gulf of Mexico: a comparison of herbivory and decomposition rates between Smooth Cordgrass (*Spartina alterniflora*) and Black Mangrove (*Avicennia germinans*). PLoS ONE. 2019; 14(1), e0210144. https://doi.org/10.1371/journal.pone.0210144 PMID: 30615652
- 14. Stevens PW, Fox SL, Montague CL. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetl Ecol Manag. 2006; 14(5): 435–444.
- Precht WF, Aronson RB. Death and resurrection of Caribbean coral reefs: a palaeoecological perspective. Conservation Biology Series-Cambridge. 2006; 13: 40.
- Avens L, Goshe LR, Harms CA, Anderson ET, Hall AG, Cluse W, et al. Population characteristics, age structure, and growth dynamics of neritic juvenile Green Turtles in the northeastern Gulf of Mexico. Mar Ecol Prog Ser. 2012; 458: 213–229.

- Fertl D. Dolphins, whales, and manatees of Florida: a guide to sharing their world. J Mammal. 2004; 85 (4): 816–816.
- Aven A, Carmichael RH, Hieb EE, Ross M. West Indian Manatee movements reveal novel occupancy and distribution patterns in the northern Gulf of Mexico. 2016; <u>https://doi.org/10.7287/peerj.preprints.</u> 2072
- Fodrie F, Heck KL, Powers SP, Graham WM, Robinson KL. Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. Glob Change Biol. 2010; 16(1): 48–59.
- Ley JA, Allen MS. Modeling marine protected area value in a catch-and-release dominated estuarine fishery. Fish Res. 2013; 144: 60–73.
- Muller RG, Trotter AA, Stevens PW. The 2015 stock assessment update of Common Snook, *Centropomus undecimalis*. In House Report No. 2015–004. St. Petersburg, Florida: Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission. 2015.
- Shafland PL, Foote KJ. A lower lethal temperature for fingerling Snook, *Centropomus undecimalis*. Northeast Gulf Sci. 1983; 6(2): 175–177.
- 23. Howells RG, Sonski AJ, Shafland PL, Hilton BD. Lower temperature tolerance of Snook, *Centropomus undecimalis*. Northeast Gulf Science. 1990; 11(2): 155–158.
- Adams AJ, Hill JE, Kurth BN, Barbour AB. Effects of a severe cold event on the subtropical, estuarine dependent Common Snook, *Centropomus undecimalis*. Gulf and Caribbean Research. 2012; 24(1): 13–21.
- 25. Blewett DA, Stevens PW. Temperature variability in a subtropical estuary and implications for Common Snook *Centropomus undecimalis*, a cold-sensitive fish. Gulf of Mexico Science. 2014; 32(1): https://doi.org/10.18785/goms.3201.04.
- Anderson J, Williford D, González A, Chapa C, Martinez-Andrade F, Overath RD. Demographic, Taxonomic, and Genetic Charicterization of the Snook Species Complex (*Centropomus* spp.) along the Leading Edge of Its Range in the Northwestern Gulf of Mexico. N American J of Fisheries Man. 2020; 40(1): 190–208.
- Beck MW, Odaya M. Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. Aquatic Conservations: Marine and Freshwater Ecoystems 2001; 11: 235–342.
- Boucek RE, Heithaus MR, Santos R, Stevens PW, Rehage JS. Can animal habitat use patterns influence their vulnerability to extreme climate events? An estuarine sportfish case study. Global Change Biol. 2017; 00: 1–13. Available from https://doi.org/10.1111/gcb.13761.31.
- Winner BL, Blewett DA, McMichael RH, Guenther CB. Relative abundance and distribution of Common Snook along shoreline habitats of Florida estuaries. Transactions of the American Fisheries Society. 2010; 139: 62–79.
- Purtlebaugh CH, Rogers KR. Recruitment and essential habitat of juvenile sand seatrout (*Cynoscion arenarius*) in four estuaries along the west coast of Florida. Gulf of Mexico Science. 2007; 1: 15–32.
- Fish and Wildlife Research Institute. 2018. Fisheries-independent monitoring program 2018 annual data summary report. Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida. 2018.
- Anderson DR. Model based inference in the life sciences: a primer on evidence. 1<sup>st</sup> ed. New York: Springer; 2008.
- Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, et al. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. PNAS. 2014; 111(2): 723–727. https://doi.org/10.1073/pnas.1315800111 PMID: 24379379
- Francis JA, Vavrus SJ, Cohen J. Amplified Arctic warming and mid-latitude weather: new perspectives on emerging connections. Wiley Interdisciplinary Reviews: Climate Change. 2017; 8(5): e474.
- Sorte CJ, Williams SL, Carlton JT. Marine range shifts and species introductions: comparative spread rates and community impacts. Glob Ecol Biogeogr. 2010; 19(3): 303–316.
- Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. Marine taxa track local climate velocities. Science. 2013; 341(6151): 1239–1242. https://doi.org/10.1126/science.1239352 PMID: 24031017
- Nehring S. Establishment of thermophilic phytoplankton species in the North Sea: Biological indicators of climatic changes? ICES J Mar Sci. 1998; 55(4): 818–823.
- Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, Santos AM. Do distributional shifts of northern and southern species of algae match the warming pattern? Glob Change Biol. 2007; 13(12): 2592–2604.
- Zomlefer WB, Judd WS, Giannasi DE. Northernmost limit of *Rhizophora mangle* (Red Mangrove; Rhizophoraceae) in St. Johns County, Florida. Castanea. 2006; 71(3): 239–244.

- Barry JP, Baxter CH, Sagarin RD, Gilman SE. Climate-related, long-term faunal changes in a California rocky intertidal community. Science. 1995; 267(5198): 672. https://doi.org/10.1126/science.267.5198. 672 PMID: 17745845
- Berge J, Johnsen G, Nilsen F, Gulliksen B, Slagstad D. Ocean temperature oscillations enable reappearance of Blue Mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar Ecol Prog Ser. 2005; 303: 167 Svalbard after a 1000 year absence 175.
- 42. Mieszkowska N, Leaper R, Moore P, Kendall MA, Burrows MT, Lear D, et al. Marine biodiversity and climate change: assessing and predicting the influence of climatic change using intertidal rocky shore biota. Marine Biological Association Occasional Publications. 2005; 20: 43.
- Brodeur RD, Ralston S, Emmett RL, Trudel M, Auth TD, Phillips AJ, et al. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. Geophys Res Lett. 2006; 33(22). https://doi.org/10.1029/2006gl027800
- 44. Foster JM, Thoma BP, Heard RW. Range extensions and review of the caprellid amphipods (Crustacea: Amphipoda: Caprellidae) from the shallow, coastal waters from the Suwannee River, Florida, to Port Aransas, Texas, with an illustrated key. Gulf Caribb Res. 2004; 16: 161–175.
- Spivak ED, Luppi TA. Southern range extension of two western Atlantic intertidal mud crabs: *Panopeus meridionalis* Williams, 1984 and *Eurypanopeus depressus* Smith, 1869 (Crustacea: Brachyura: Panopeidae) in Argentinian waters. P Biol Soc Wash. 2005; 118: 551–557.
- Hollebone AL, Hay ME. Population dynamics of the non-native crab *Petrolisthes armatus* invading the South Atlantic Bight at densities of thousands m<sup>-2</sup>. Mar Ecol Prog Ser. 2007; 336: 211–223.
- 47. Holbrook SJ, Schmitt RJ, Stephens JS. Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecol Appl. 1997; 7(4): 1299–1310.
- Perry AL, Low PJ, Ellis JR, Reynolds JD. Climate change and distribution shifts in marine fishes. Science. 2005; 308(5730): 1912–1915. https://doi.org/10.1126/science.1111322 PMID: 15890845
- Aliaume C, Zerbi A, Miller J. Nursery habitat and diet of juvenile *Centropomus* species in Puerto Rico estuaries. Gulf of Mexico Science. 1997; 15. https://doi.org/10.18785/goms.1502.03
- Adams AJ, Murchie KJ. Recreational fisheries as conservation tools for mangrove habitats. American Fisheries Society Symposium. 2015; 83: 43–56.
- Stevens PW, Dutka-Gianelli J, Nagid EJ, Trotter AA, Johnson KG, Tuten T, et al. Niche partitioning among snook (Pisces: Centropomidae) in rivers of southeastern Florida and implications for species range limits. Estuaries and Coasts. 2019; 43: 438–439.
- Santos RO, Reghage JS, Boucek R, Osborne J. Shift in recreational fishing catches as a function of an extreme cold event. Ecosphere. 2016. https://doi.org/10.1002/ecs2.1335
- Stevens PW, Blewett DA, Boucek RE, Rehage JS, Winner BL, Young JM, et al. Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida. Ecosphere. 2016; 7(8): e01400. https://doi.org/10.1002/ecs2.1400
- Raabe EA, Bialkowska-Jelinska E. Thermal imaging of the Waccasassa Bay Preserve: image acquisition and processing. U.S. Geological Survey Open File Report. 2010; <u>https://doi.org/10.3133/ofr20101120</u>
- Florida Fish and Wildlife Conservation Commission. Springs Coast Fish Community Assessment Project. Final Report. Brooksville, Florida: Southwest Florida Water Management District, Brooksville. 2019.
- Katz BG, DeHan RS, Hirten JJ, Catches JS. Interactions between ground water and surface water in the Suwannee River Basin, Florida. Journal of the American Water Resources Association. 1997; 33: 1237–1254.
- Crandall CA, Katz BG, Hirten JJ. Hydrochemical evidence for mixing of river water and groundwater during high-flow conditions, lower Suwannee River basin, Florida, USA. Hydrogeology Journal. 1999; 7: 4544671.
- Perera-García MA, Mendoza-Carranza M, Contreras-Sánchez M, Huerta-Ortíz M, Pérez-Sánchez E. Reproductive biology of common snook *Centropomus undecimalis* (Perciformes: Centropomidae) in two tropical habitats. Revista de Biología Tropical. 2011; 59(2): 669–681. PMID: 21717854
- 59. Taylor R, Grier H, Whittington J. Spawning rhythm of Common Snook in Florida. J Fish Biol. 1998; 53: 502–520.
- Conover DO. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Transactions of the American Fisheries Society. 1990; 119: 416–430.
- Conover D, Teresa MC. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic Silversides from different latitudes. Oecologia. 1990; 83: 316–324. <u>https:// doi.org/10.1007/BF00317554</u> PMID: 28313001

- **62.** Pauly D. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Science 1980; 39: 175–192.
- **63.** Tucker JW, Campbell SW. Spawning season of Common Snook along the east central Florida coast. Florida Scientist. 1988; 1–6.
- **64.** Young JM, Yeiser BG, Whittington JA. Spatiotemporal dynamics of spawning aggregations of Common Snook on the east coast of Florida. Marine Ecology Progress Series. 2014; 505: 227–240.
- Peters KM, Matheson RE, Taylor RG. Reproduction and early life history of Common Snook, *Centropomus undecimalis* (Bloch), in Florida. Bulletin of Marine Science. 1998; 62(2): 509–529.
- Stevens PW, Blewett DA, Poulakis GR. Variable habitat use by juvenile Common Snook, *Centropomus undecimalis* (Pisces: Centropomidae): applying a life-history model in a southwest Florida estuary. Bulletin of Marine Science. 2007; 80(1): 93–108.
- Barbour AB, Adams AJ, Lorenzen K. Size-based, seasonal, and multidirectional movements of an estuarine fish species in a habitat mosaic. Marine Ecology Progress Series 2014; 507: 263–276.
- Brame AB, McIvor CC, Peebles EB, Hollander DJ. Site fidelity and condition metrics suggest sequential habitat use by juvenile Common Snook. Mar Ecol Prog Ser. 2014; 509: 255–269.
- **69.** Schulz K. Assessment of coastal habitat restoration using fish community metrics and juvenile sportfish condition. M.S. Thesis. University of Florida. 2019.
- **70.** Ley JA, Rolls HJ. 2Using otolith microchemistry to assess nursery habitat contribution and function at a fine spatial scale. Marine Ecology Progress Series. 2018; 606: 151–173.
- Malinowski C, Cavin J, Chasar L, Coleman F, Koenig C. Trophic relationships and niche partitioning of Red Drum *Sciaenops ocellatus* and Common Snook *Centropomus undecimalis* in coastal estuaries of South Florida. Estuaries and Coasts. 2019. https://doi.org/10.1007/s12237-018-00512 -y
- Llanso RJ, Bell SS, Vose FE. Food habits of Red Drum and Spotted Seatrout in a restored mangrove impoundment. Estuaries. 1998; 21: 294–306.