

8-18-2016

Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida

P. W. Stevens

Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission

D. A. Blewett

Charlotte Harbor Field Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission

Ross E. Boucek

Department of Biology, Southeast Environmental Research Center, Florida International University, rboucek@fiu.edu

Jennifer S. Rehage

Department of Biology, Florida International University, rehagej@fiu.edu

B. L. Winner

Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission

See next page for additional authors

Follow this and additional works at: https://digitalcommons.fiu.edu/fce_lter_journal_articles



Part of the [Life Sciences Commons](#)

Recommended Citation

Stevens, P. W.; Blewett, D. A.; Boucek, Ross E.; Rehage, Jennifer S.; Winner, B. L.; Young, J. M.; Whittington, J. A.; and Paperno, R., "Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida" (2016). *FCE LTER Journal Articles*. 410.

https://digitalcommons.fiu.edu/fce_lter_journal_articles/410

This material is based upon work supported by the National Science Foundation through the Florida Coastal Everglades Long-Term Ecological Research program under Cooperative Agreements #DBI-0620409 and #DEB-9910514. Any opinions, findings, conclusions, or recommendations expressed in the material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

This work is brought to you for free and open access by the FCE LTER at FIU Digital Commons. It has been accepted for inclusion in FCE LTER Journal Articles by an authorized administrator of FIU Digital Commons. For more information, please contact dcc@fiu.edu, jkrefft@fiu.edu.

Authors

P. W. Stevens, D. A. Blewett, Ross E. Boucek, Jennifer S. Rehage, B. L. Winner, J. M. Young, J. A. Whittington, and R. Paperno

Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida

P. W. STEVENS,^{1,†} D. A. BLEWETT,² R. E. BOUCEK,³ J. S. REHAGE,³ B. L. WINNER,¹ J. M. YOUNG,⁴
J. A. WHITTINGTON,⁴ AND R. PAPERNO⁵

¹Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 100 8th Avenue Southeast, St. Petersburg, Florida 33701 USA

²Charlotte Harbor Field Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 585 Prineville Street, Port Charlotte, Florida 33954 USA

³Department of Biology, Florida International University, 11200 SW 8th Street, Miami, Florida 33199 USA

⁴Tequesta Field Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 19100 Southeast Federal Highway, Tequesta, Florida 33469 USA

⁵Indian River Field Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 1220 Prospect Avenue, Suite 285, Melbourne, Florida 32901 USA

Citation: Stevens, P. W., D. A. Blewett, R. E. Boucek, J. S. Rehage, B. L. Winner, J. M. Young, J. A. Whittington, and R. Paperno. 2016. Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida. *Ecosphere* 7(8):e01400. 10.1002/ecs2.1400

Abstract. For species that are closely managed, understanding population resilience to environmental and anthropogenic disturbances (i.e., recovery trajectories across broad spatial areas) can guide which suite of management actions are available to mitigate any impacts. During January 2010, an extreme cold event in south Florida caused widespread mortality of common snook, *Centropomus undecimalis*, a popular sport fish. Interpretation of trends using fishery-independent monitoring data in five south Florida estuaries showed that changes in catch rates of adult snook (>500 mm standard length) varied between no effects postevent to large effects and 4-yr recoveries. The reasons for the variation across estuaries are unknown, but are likely related to differences in estuary geomorphology and habitat availability (e.g., extent of deep rivers and canals) and differences in the proportions of behavior contingents (i.e., segments of the population that use divergent movement tactics) that place snook in different areas of the estuary during winter. Emerging awareness of the presence of behavior contingents, identification of overwintering sites, and improvements of abundance indices in remote nursery habitats should provide a better understanding of population resilience to disturbance events for snook. Given that changes in the frequency of short-lived, severe cold events are currently unknown, the findings and management actions described here for a tropical species living at the edge of its distribution should be useful to scientists forecasting the effects of climate change.

Key words: *Centropomus undecimalis*; coastal areas; common snook; disturbance; fishes; Special Feature: Extreme Cold Spells.

Received 22 October 2015; revised 18 April 2016; accepted 5 May 2016. Corresponding Editor: H. Liu.

Copyright: © 2016 Stevens et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** Philip.Stevens@MyFWC.com

INTRODUCTION

Extreme events can strongly affect population and community structure by causing physiological stress in affected species, mass mortality events, and reordering of species dominance (Jentsch et al. 2007, Smith 2011, Boucek and Rehage 2014a, Hoover et al. 2014). In coastal regions, common extreme events include severe storms (Greenwood et al. 2006), algal blooms (Flaherty and Landsberg 2011), and anthropogenic disturbances such as chemical spills (Rooker et al. 2013). The severity of these events is a function of the characteristics of the disturbance and the response of the species affected (Smith 2011). If effects to water and habitat conditions are short-lived, recoveries of communities or populations to pre-event conditions can be relatively rapid, ranging from weeks to a few years (Stevens et al. 2006b, Flaherty and Landsberg 2011). For communities or species that are closely managed, understanding both the initial effects (resistance) and recovery rates (resilience) after a disturbance can guide the suite of management actions that are best suited to mitigate any impacts (see options in McEachron et al. 1994).

Stochastic cold events can have deleterious effects on fish populations in coastal areas, especially for tropical species that are living at the edge of their distribution (Gilmore et al. 1978, Boucek et al., *in press*). Severe cold events have been shown to influence forest and seascape structure (Precht and Aronson 2004, Ross et al. 2009, Kemp et al. 2016), drive faunal community composition in predictable ways (Boucek and Rehage 2014a, b, 2015), and reset poleward range expansions of tropical species (Stevens et al. 2006a). The timing (rate of change and duration), spatial extent, minimum temperature, and local conditions (e.g., tidal stage, wind speed, depth) are all important factors in determining the severity of cold events in subtropical coastal systems (Storey and Gudger 1936, Blewett and Stevens 2014). Fishes are adapted to survive unfavorable environmental conditions to some degree by altering behavior and movement. The spatial heterogeneity of cold events provides opportunities for fish to migrate from the most affected areas or seek thermal refuge to increase survival (Harvey et al. 1999). Refuge in close proximity to the area of disturbance aids in population recovery by

reducing mortality of those physically fit enough to migrate (Weber et al. 2013) and by providing a source of recolonization back into usual residential habitats (Hoffsten 2003).

In Florida, Common Snook *Centropomus undecimalis* is a tropical species that supports a substantial recreational fishery (2.1 million fish caught per year, 90% of which are released; Muller and Taylor 2012); however, the species is sensitive to severe cold events (Gilmore et al. 1978, Blewett and Stevens 2014), which adds to the challenge of managing the fishery. While a few individuals can occur as far north as Cedar Key on Florida's west coast and Jacksonville on the east coast, the primary distribution of snook in Florida is limited to coastlines south of the temperate to subtropical transition, which spans roughly from Tarpon Springs on Florida's west coast to Cape Canaveral on the east coast (Gilmore et al. 1983, Rivas 1986). During January 2010, a severe cold event extended southward throughout south Florida, dropping inshore water temperatures to below the minimum temperature tolerance of snook ($\sim 10^{\circ}\text{C}$; Howells et al. 1990) for a period of at least 2 d (Adams et al. 2012, Blewett and Stevens 2014, Boucek et al., *in press*) causing mass mortality of snook throughout their range in Florida. To reduce any additional mortality and to allow long-term monitoring programs to gauge impacts, resource managers immediately closed the recreational snook fishery (<http://myfwc.com/fishing/saltwater/recreational/fish-kills/>).

Given the geographic scale of the extreme cold event, information was needed on population recovery rates of snook from representative locations throughout south Florida. The objective of this study was to examine long-term trends in snook populations from fishery-independent monitoring data sets to (1) gauge the initial effect of the 2010 cold event to the snook population (resistance) and (2) determine the postevent recovery of the snook population (resilience) across five Florida estuaries. Although our current estimate of the event's scale suggests it is very infrequent (Boucek et al., *in press*), there are many uncertainties associated with future climate change (Vavrus et al. 2006). Climate models indicate overall warming trends, but changes in the frequency of short-lived, severe cold events are just beginning to be considered (Kodra et al. 2011). Despite the gravity of cold events in

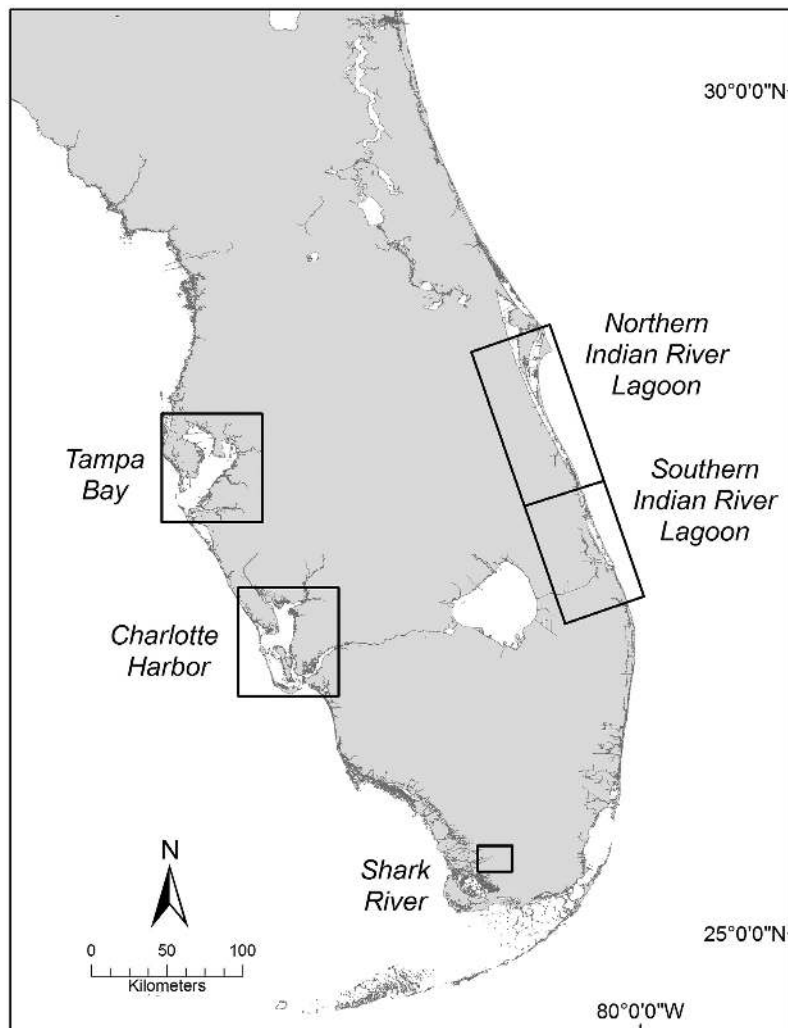


Fig. 1. Locations of fishery-independent monitoring within the core range of snook in Florida.

structuring the fauna of the subtropics, population and community responses to such events remain understudied. Understanding the factors that contribute to variation in recovery across multiple estuaries for a representative tropical species should allow for improvements in the understanding of the vulnerability of different populations to extreme events and ultimately enable resource managers to better account for these environmental events in their management plans.

METHODS

Resistance and resilience of snook across estuaries

The effects of the 2010 cold event on snook, and subsequent recovery, were determined from

fishery-independent monitoring data sets available for five Florida estuaries. Trends in catch per unit effort (CPUE) from standardized programs were generated for adult snook (snook are mature by 500 mm standard length [SL], Peters et al. 1998). Trends in snook CPUE in Tampa Bay, Charlotte Harbor, Northern Indian River Lagoon, and Southern Indian River Lagoon (Fig. 1) were generated from catch data (1997–2014) collected by a large haul seine (183 × 3 m, 37.5-mm stretch mesh), as part of the Florida Fish and Wildlife Conservation Commission (FWC), Fish and Wildlife Research Institute's Fisheries-Independent Monitoring program (Kupschus and Tremain 2001, Winner et al. 2010). Monthly stratified-random sampling was conducted (approximately 12–19

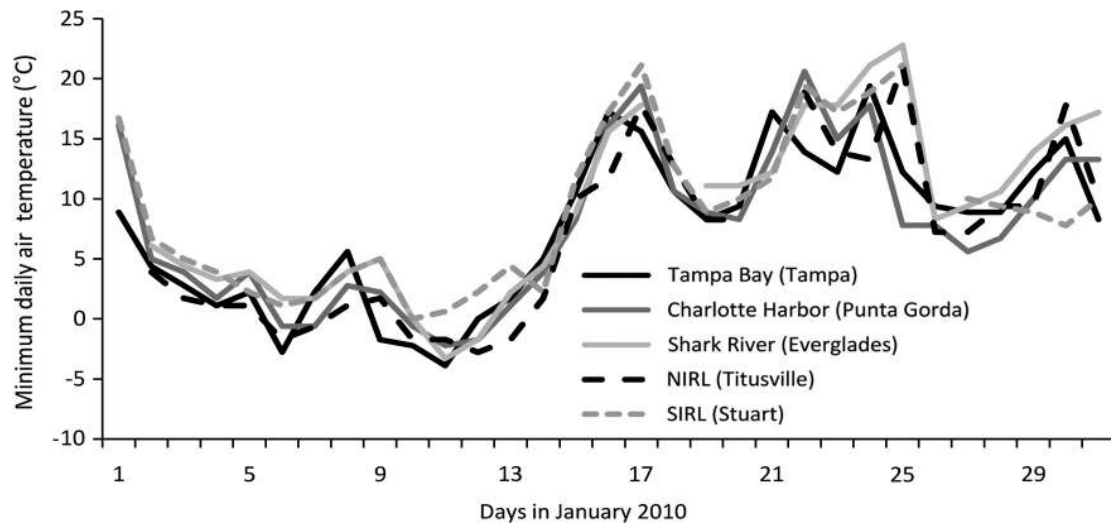


Fig. 2. Minimum daily air temperatures during January 2010 in five estuaries within the core range of snook (Tampa Bay, Charlotte Harbor, Northern Indian River Lagoon [NIRL], Southern Indian River Lagoon [SIRL], and Shark River). The specific station (city) within each estuary is indicated in parentheses.

samples per month in each estuary \times 18 yr = 216–342 samples per estuary). The seine was deployed by boat in a rectangular shape (40 \times 103 m) along shorelines and on offshore flats inside the estuary and retrieved by hand. All fishes were identified to the lowest possible taxon, counted, and measured to the nearest millimeter (SL). CPUE of snook was calculated as fish per set (each set encompassed 4120 m² or \sim 100 m of shoreline).

Trends in snook CPUE in the oligohaline portion of the Shark River estuary, in Everglades National Park (Fig. 1), were generated from electrofishing data collected between 2005 and 2014 at six fixed sites located at the headwaters (for details on the sampling program, see Boucek and Rehage 2013). Fish communities were sampled at these sites three times per year using a boat-mounted, generator-powered electrofisher (two-anode, one-cathode Smith-Root 9.0 unit, Smith-Root, Vancouver, Washington, USA). Three replicate electrofishing samples were conducted at fixed locations in each site, each 200 m apart (6 sites \times 3 samples \times 3 seasons \times 8 yr = 432 electrofishing samples). For each sample, we ran the boat at idle speed at a randomly selected creek shoreline and applied 5 min of pedal time (Rehage and Loftus 2007). Power output was standardized to 1500 W, given temperature and conductance

conditions measured at the beginning of each sample (Burkhardt and Gutreuter 1995). We recorded the distance travelled during each sample using a GPS. Electrofishing CPUE is reported as the number of fish caught or shocked per 100 m of shoreline ($[\text{CPUE}/\text{distance travelled}] \times 100 \text{ m}$). After collecting the sample, we measured and weighed all snook caught and then release them at the point of collection.

Data analyses of cold effects

To gauge the relative effects of the cold event across estuaries, air temperatures were plotted. Minimum daily air temperatures were acquired from a widely available data set for the month of January 2010 (www.usclimatedata.com), except Shark River which was obtained from Everglades National Park. An attempt was made to compare available water temperature data (e.g., monitoring stations, weather buoys). However, the process of selecting a site to represent an estuary proved difficult. For example, data from a deep ocean port in the Northern Indian River Lagoon had a minimum water temperature during the cold event that was 8°C warmer than in a shallow portion of the estuary (E. Reyier, unpublished data). Without an understanding of the meteorological and oceanographic factors affecting each site, a

comparison of water temperatures among estuaries could be misleading (see also Blewett and Stevens 2014).

Fisheries-independent monitoring data were analyzed to assess both resistance and resilience of the snook population to the cold event. The CPUE of snook (mean and SE) was plotted over the available time series for each estuary after performing natural log-transformations on the raw data. To analyze CPUE data with respect to the cold event, each sample was standardized to the mean precold event (1997–2009) CPUE measured in the estuary from which the sample was taken (standardized CPUE = [CPUE/precold event average]). Effects to the snook population (initial effects in 2010 and length of recovery) were determined by comparing standardized CPUEs between the pre-event period (before 2010) and the samples postevent (2010, 2011, 2012, 2013, and 2014) in each estuary. Because data were not normally distributed, differences were determined by calculating 95% confidence intervals (CIs) for pre- and postcold event means from a bootstrapped distribution with 1000 iterations. If CIs of pre-event and 2010 standardized CPUE overlapped, fish populations were considered resistant to the cold event. Recovery was determined as the number of years needed for the CIs around the standardized CPUE to overlap with their respective pre-event CI.

Movement and mortality from acoustic telemetry

To supplement results from fishery-independent monitoring in the Indian River Lagoon and to better understand the effect of the cold event on snook behavior as well as survival, an acoustic monitoring data set was analyzed to estimate survival of tagged fish after the 2010 cold event. Adult snook ($n = 223$; range: 441–932 mm SL, Vemco, Bedford, Nova Scotia, Canada) tagged with Vemco V-16 ultrasonic passive acoustic tags were monitored within a collaborative array of over 200 receivers spanning >300 km of coastline including river, estuary, nearshore, and offshore habitat in the Indian River Lagoon (Young et al. 2014). A total of 87 tagged fish were detected during the time of the 2010 cold event (17 December 2009–27 January 2010). To estimate survivorship, the time frame was divided into three groups, before (17–31 December), during (1–12 January), and after (13–27 January), and

the number of tagged snook detected after the cold event was calculated. Generalized linear models were used to model survival as a function of sex, total length, and location (latitude and longitude) before and during the cold event. To determine if any broad scale movements occurred during the cold event, the distance and bearing between daily locations of tagged fish was calculated. Generalized linear models were used to model mean location (latitude and longitude), and distance and bearing between daily locations, of tagged snook as a function of time (i.e., before, during, and after the cold event).

RESULTS

Resistance to cold event across estuaries

The cold event extended through the core range of snook (Fig. 2). Minimum daily air temperatures fell to near or below the freezing point during 5–7 and 10–14 January. Air temperatures in the northern estuaries were about 3°C colder than those in the farthest south.

The initial effects of the January 2010 cold event on snook CPUE varied among the estuaries (Fig. 3). Along the west coast (Tampa Bay, Charlotte Harbor, Shark River), snook CPUE fluctuated without trend in each estuary through 2009, reached lowest levels after the January 2010 cold event (2010 and 2011), and had an increasing trend thereafter. In the Northern Indian River Lagoon, the CPUE immediately after the 2010 cold event was similar to the CPUE in other years (e.g., 1998) and later decreased to all-time lows (2011–2014). In the Southern Indian River Lagoon, trends in CPUE fluctuated without trend through 2009 and did not change following the cold event.

A closer examination of standardized snook CPUE after the cold event helped to quantify the initial effects to the snook population in each estuary (Fig. 4). Standardized CPUEs in the affected estuaries of the west coast decreased by 52% (Tampa Bay), 76% (Charlotte Harbor), and 94% (Shark River) in 2010 compared to the precold event CPUEs. In each case, the CI between the precold event CPUE and the 2010 CPUE did not overlap, indicating a lack of resistance. In contrast to the west coast estuaries, the CIs of standardized CPUEs in 2010 overlap with those of the pre-event CPUEs indicating resistance to the event in both Northern and Southern Indian River Lagoon.

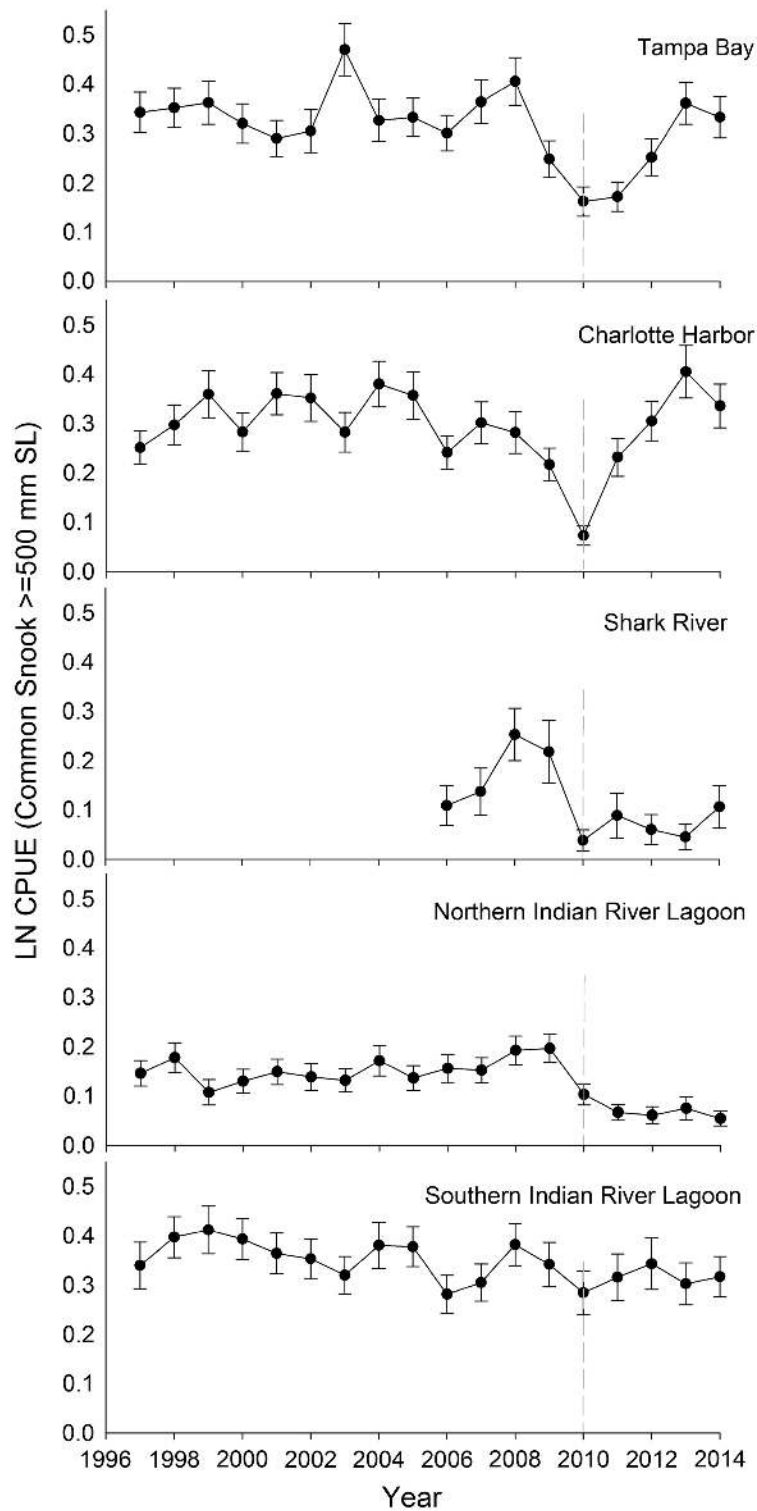


Fig. 3. Catch per unit effort (CPUE; natural log-transformed; mean \pm SE) of snook captured using 183-m haul seines (Tampa Bay, Charlotte Harbor, Northern Indian River Lagoon, and Southern Indian River Lagoon) and electrofishing (Shark River). Dashed line indicates year of cold event (2010).

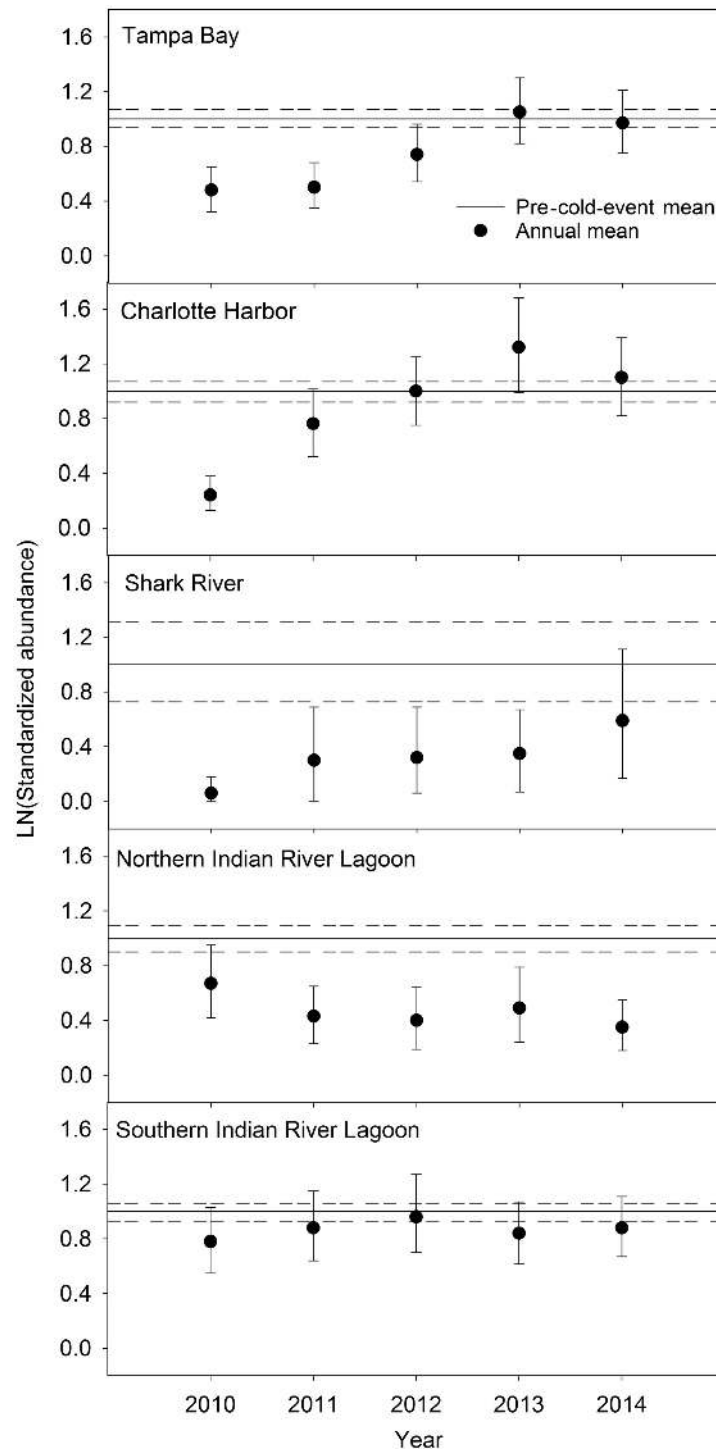


Fig. 4. Standardized snook CPUE (mean \pm 95% confidence intervals [CI]) in Tampa Bay, Charlotte Harbor, Shark River, Northern Indian River Lagoon, and Southern Indian River Lagoon before the severe cold event (lines) and in each year following the cold event (circles). For 2010, overlap in 95% CI between precold event and 2010 indicates resistance (no effect of the cold event). For snook in affected estuaries, resilience or recovery period is defined as the number of years between the cold event and the year in which 95% CI overlap.

Resilience to cold event across estuaries

The recovery of the snook population varied across the west coast estuaries, and lagged effects occurred in the Northern Indian River Lagoon. Along the west coast where snook CPUE decreased substantially after the cold event, the CIs of standardized CPUE overlapped with those of the pre-event CPUE between 1 and 4 yr later. Recovery from the cold event occurred in 2011 in Charlotte Harbor, 2012 in Tampa Bay, and 2014 in Shark River. In the Northern Indian River Lagoon, the CIs of standardized CPUE no longer overlapped with those of the pre-event CPUE starting in 2011, indicating either a lagged effect of the cold event or other circumstances that affected the snook population. By the end of the study period, standardized CPUE in the Northern Indian River Lagoon still remained 65% below its precold event mean. In contrast, the 95% CIs of standardized CPUE in the Southern Indian River Lagoon overlapped with those of the pre-event CPUE in each of the years after the event, indicating resistance during the entire study period.

Movement and mortality from acoustic telemetry

The estimate of snook survival through the 2010 cold event was high in the Indian River Lagoon system. Of the 86 snook that were detected at the start of the cold event, 90% of tagged fish ($n = 77$) survived the cold event, 74 were detected within the first two weeks following the cold event, and three more fish were detected in the following months (Fig. 5). Nine fish (10%) were last detected between 1 and 11 January, which is within the time period associated with the cold event. There did not appear to be any major differences in mortality between geographic areas of the Lagoon (e.g., four of the nine presumed mortalities were in the Northern Indian River Lagoon); thus, acoustic data were combined for further analysis. Sex, total length, and mean location before and during the cold event had no significant effect on survival.

Acoustic tracking data did not indicate any movement associated with the event at the scale of the tagged population; however, a closer examination of snook movements does reveal some response to the cold event for a few individuals. No significant change in the latitude ($F_2 = 1.07$, $P = 0.3450$) or longitude ($F_2 = 1.63$, $P = 0.1988$) of

snook was found for the three time periods (before, during, and after), and bearing estimates (mean) between daily locations did not vary among before (north 34°), during (southeast 165°), and after (north 336°) periods ($F_2 = 1.59$, $P = 0.2177$). However, further analysis of individual snook tracks showed a general movement trend toward inlets for fish that were in estuarine habitats before the cold event and no movement for fish in rivers (Fig. 5). For example, 10 of 25 snook found in an estuary habitat before the cold event quickly moved to inlets during the cold event. Also, four of 18 snook found at inlets before the cold event moved to another inlet further south. Of 31 snook detected in rivers before the cold event, none left the rivers they were detected in. Overall, detection in inlets was highest and in rivers lowest during the cold period than the periods before or after. However, with all data pooled, there was no significant difference between distance travelled (mean \pm SE) before (0.48 ± 0.08 km), during (0.75 ± 0.22 km), or after (0.75 ± 0.14 km) the cold event ($F_2 = 0.65$, $P = 0.5255$).

DISCUSSION

As expected for a tropical species at the edge of its distribution (Boucek et al., *in press*), the extreme 2010 cold event had a negative effect on tropical snook in southern Florida. However, both resistance and resilience varied among systems. On the west coast, the snook population was greatly affected by the cold event. Standardized snook CPUEs were reduced by an average of 74% across the three Florida west coast estuaries (Everglades, Charlotte Harbor, and Tampa Bay). Numerous fish kills (tens of thousands of individuals) reported to the Florida Fish and Wildlife Conservation Commission (e.g., Blewett and Stevens 2014) suggested that these declines in CPUE were a result of mortality. On the east coast, fewer fish kills were reported, survivorship of tagged snook was high (>90%), and snook CPUE in both the Northern and Southern Indian River Lagoon did not decline in 2010. The CPUE of snook in the Northern Indian River Lagoon declined later (2011–2014), but these declines do not seem to be directly associated with the 2010 cold event (see below). Resilience also varied across affected populations. On the west coast, time to recovery to precold

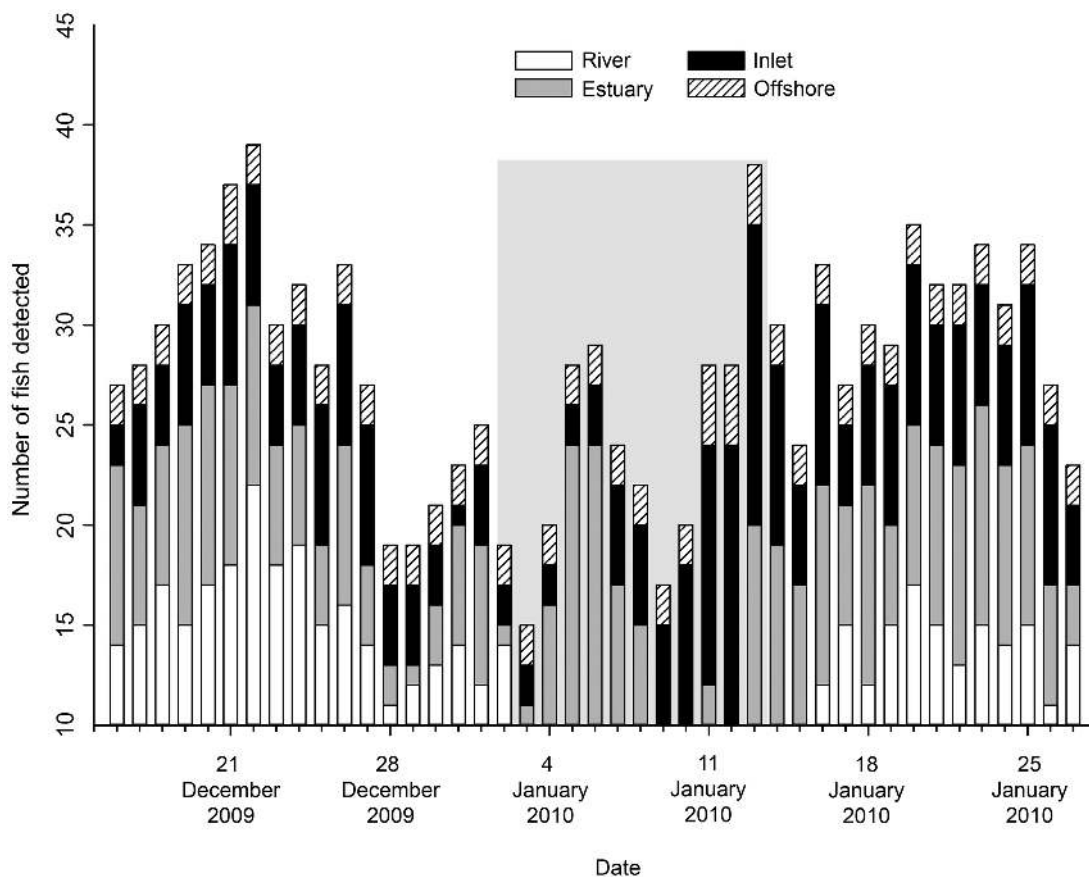


Fig. 5. Number of tagged snook detected in acoustic monitoring array in Indian River Lagoon before and after the 2010 cold event. Dates of cold event (1–12 January) are highlighted in gray.

event abundances varied spatially, with the fastest recovery in Charlotte Harbor (1 yr), intermediate recovery in Tampa Bay (2 yr), and slow recovery in the Shark River (4 yr). These findings illustrate substantial variation in both the effect and recovery of a valuable recreational fishery to an extreme event and highlight the importance of monitoring populations across broad spatial scales.

Resistance to cold event across estuaries

The effects of latitude did not explain the variation in resistance to the cold event across snook populations. Despite a pattern of colder air temperatures at the northern end of the study area during the cold event, the effects to snook populations did not follow this trend. Survivorship of tagged snook in the Indian River Lagoon exceeded 90% for fish present at both the southern and northern ends of the estuary. The proximity of the Indian River Lagoon to

the Gulf Stream current is known to moderate the climate and influence the ichthyofauna (Gilmore 1995). On Florida's west coast, the estuary farthest south, Shark River, had the greatest decline in snook CPUE. One factor contributing to the lack of resistance in the Shark River may be local adaptation. Species at warm latitudes experience cold events less often over the long run and may lack traits (behavioral or physiological) that enable them to better cope with cold stress (e.g., Cook-Patton et al. 2015). The 2010 cold event in the Everglades was the most severe on record in the past 100 yr (Boucek and Rehage 2014a); however, in west coast estuaries farther north, low air temperatures were consistent with a one in 8-yr cold event (Stevens et al. 2006a). These differences in event frequency may help explain why snook at the most southerly latitudes were less resistant to the cold event than areas farther north.

Other factors that likely influence the variable resistance to the cold event across estuaries are differences in habitat availability (e.g., extent of deep rivers and canals) and estuary geomorphology (e.g., proximity of habitats to one another). The ability of a fish to move to warmer microhabitats during a cold event may be as important as latitude. During a 3-yr study in Charlotte Harbor, water temperatures across snook habitats (river, canal, and estuary) were remarkably similar ($<1^{\circ}\text{C}$), except just after major cold fronts (~ 3 d) when temperatures in rivers and canals were about 2°C warmer than in the estuary (Blewett and Stevens 2014). The short amount of time that habitats exhibited any differences in water temperatures, and the distribution of snook kill locations thought to represent relatively warmer sites (e.g., deep, wind-protected shorelines), supported a hypothesis of small-scale winter habitat selection, similar to that reported for other species (Harvey et al. 1999, Weber et al. 2013). That is, as water temperatures dropped, snook moved to the nearest warm water site they could reach within ~ 1 d. Such movements may explain why snook CPUE did not decrease, at least initially, in the Indian River Lagoon. A conspicuous feature of this narrow estuary is the proximity of snook habitats—major rivers, open estuarine shorelines, and several inlets—to one another. Given the short time constraints that snook have in responding to cold events, this proximity (as little as 5 km) provides more opportunities to move into a different habitat than in the larger, more expansive estuaries. Acoustic data showed that several snook moved toward ocean inlets at the onset of the cold event, which may represent a movement toward a warm water site. Other small-scale movements likely not detected by the acoustic array, such as movement into nearby deepwater habitats (canals, marinas, bridge pilings, river bends), are possible within a very short time frame (<1 d) from any point in the estuarine system. In the relatively shallow and undeveloped Shark River, in contrast, deep sites along shorelines are few. Although the geomorphology of the Shark River differs from the larger estuaries in this study, it is representative of estuarine systems in the Everglades. To determine the importance of deepwater sites to snook responding to cold events, acoustic telemetry could prove helpful. The placement of receivers

in suspected thermal refuge sites (deep, wind-protected shorelines) within large-scale arrays could provide data on the behavioral response of this species to low temperatures and help to discern the importance of these microhabitat movements to enhancing survival.

Resilience to cold event across estuaries

The presence of behavior contingents (i.e., segments of the population that use divergent movement tactics) that place snook in different areas of the estuary during winter could have influenced population resilience to the cold event, particularly for Charlotte Harbor where recovery was quickest. An understanding of behavioral contingents in the snook population, similar to that gained in other species (Rosenblatt and Heithaus 2011, Sih et al. 2012), is just beginning to emerge (Blewett et al. 2009, Lowerre-Barbieri et al. 2014). Acoustic monitoring in a large river found that a portion of the tagged population resided in the river year after year, except for a seasonal movement out of the river during the summer spawning season (Trotter et al. 2012). An estuary contingent was evident in an acoustic monitoring study that tracked spawning-related movements near passes and in the interior of a large estuary (Lowerre-Barbieri et al. 2014). A portion of the tagged population remained in the estuary year-round and did not exhibit catadromy. Similar patterns are evident from recent telemetry data in the Shark River (R. Boucek et al., *unpublished data*). Variation in seasonal, annual, and cross-system catadromy that place snook in different areas of the estuary during winter can be an important factor during cold events because water temperatures in these habitats (rivers vs. estuary) vary enough (2°C) to influence survivorship when temperatures drop near the snook lethal limit. In Charlotte Harbor, snook that occupied rivers and canals during the cold event were thought to exhibit greater survivorship than those in the open estuary where extensive kills were reported (Blewett and Stevens 2014). If large portions of the snook population survived the cold event in habitats outside of the estuary proper, these contingents may have provided a later source of recruitment to the estuary population for which trends in CPUE were presented. Movements of snook from rivers to

fill vacant niches left by the estuary contingent could explain why snook CPUE in Charlotte Harbor recovered only 1 yr after the freeze.

The effects of multiple stressors on a population are important when gauging the effects of a stochastic event (Boucek and Rehage 2014a). In the Northern Indian River Lagoon, snook initially resisted the cold event, but in subsequent years, CPUE was lower than the precold event mean implying a delayed effect or other circumstances contributed to the decline. The behavior contingent resident to the Northern Indian River Lagoon (see Young et al. 2014), and any settlement of juveniles, were likely affected by a series of environmental events. Subsequent to the cold event, the Northern Indian River Lagoon experienced an extended algal bloom that was actually two blooms (separate in space, but overlapping in time) that persisted through much of 2010 and resulted in a 40% loss of seagrass biomass and a 95% loss of macroalgal biomass (Phlips et al. 2015). These conditions may have led to an overall movement of fish into alternative habitats or areas farther south that were unaffected by the bloom. The low CPUE in the Northern Indian River Lagoon postcold event could be the result of emigration from the area and also a lack of new recruitment into the suboptimal habitat created by the algal bloom, but the 2010 cold event does not appear to have resulted in an immediate mortality event as in the west coast estuaries.

In the Florida west coast estuaries where snook CPUE was greatly affected, recovery rates were generally on the order of 2–4 yr, which suggests population recovery was dependent on annual juvenile recruitment (dependent on survival of spawning age fish after the cold event). Growth of juvenile snook to adults is known to be highly variable, but a 2- to 4-yr time frame is of the appropriate scale (McMichael et al. 1989, Taylor et al. 2000). Unfortunately, trends in juvenile snook abundance from nursery habitats were not available at a broad spatial scale. This has been identified as a major data gap in stock assessments attempting to gauge population resilience and demographics (Muller and Taylor 2012). Understanding year-class strength of juveniles would provide for better assessments of the population recovery rates that could occur after a cold event. Also, an increase in reproductive potential of remaining adults, and fast growth of juveniles, is

a population response to stochastic events documented for other fishes (Rose et al. 2001, Yatsu et al. 2008). Knowledge of the year-class strength of juveniles could shorten closures of the fishery if strong recruitment into the adult population was imminent. To meet this data need, fisheries-independent monitoring programs are being expanded into juvenile snook habitat.

Management implications

The spatial variation in both resistance and resilience across estuaries in Florida was an important factor with respect to species management. Scientists and managers tracking the adult snook population were informed of the initial effects and recovery associated with the cold event from monitoring programs covering an appropriate spatial scale. Following reports of extensive fish kills in January 2010, the snook fishery was closed to harvest to allow researchers associated with fishery-independent monitoring programs to assess the effects of the event. Management of the snook fishery is divided into east and west coast components, because they have been shown to be two different stocks (Muller and Taylor 2012). Based on the assessment of acoustic tracking and fisheries-independent monitoring in the Indian River Lagoon, the east coast snook fishery (centered in the Southern Indian River Lagoon) was reopened on 17 September 2010 (<http://myfwc.com/fishing/saltwater/recreational/fish-kills/>). The west coast fishery remained closed until 1 September 2013 to allow the stock more time to recover. Given the resolution of data available for snook in Florida, it may be possible to implement a place-based management strategy for this species (Lorenzen et al. 2010). Such a strategy would be useful in responding to stochastic events with variable effects across estuaries (e.g., cold event, slow recovery in Shark River) or multiple stressors with localized effects (e.g., cold event followed by algal blooms, Northern Indian River Lagoon).

ACKNOWLEDGMENTS

We thank the dedicated field staff that assisted with these expansive sampling efforts across the state of Florida. This project was supported with funds collected from the State of Florida Saltwater

Fishing License sales, Department of the Interior, US Fish and Wildlife Service, Federal Aid for Sport Fish Restoration Grant Number F-43 to the Florida Fish and Wildlife Commission, and RECOVER (REstoration COordination & VERification under the Comprehensive Everglades Restoration Plan (CERP). Everglades data were additionally supported by NSF WSC-1204762 and the Florida Coastal Everglades Long-Term Ecological Research program under Grant No. DBI-0620409. We appreciate the comments of several anonymous reviewers and the editorial suggestions of Janet Ley and Bland Crowder.

LITERATURE CITED

- Adams, A. J., J. E. Hill, B. N. Kurth, and A. B. Barbour. 2012. Effects of a severe cold event on the subtropical, estuarine-dependent common snook, *Centropomus undecimalis*. *Gulf and Caribbean Research* 24:13–21.
- Blewett, D. A., and P. W. Stevens. 2014. Temperature variability in a subtropical estuary and implications for common snook *Centropomus undecimalis*, a cold-sensitive fish. *Gulf of Mexico Science* 32:44–54.
- Blewett, D. A., P. W. Stevens, T. R. Champeau, and R. G. Taylor. 2009. Use of rivers by common snook *Centropomus undecimalis* in southwest Florida: a first step in addressing the overwintering paradigm. *Florida Scientist* 72:310–324.
- Boucek, R. E., and J. S. Rehage. 2013. No free lunch: displaced marsh consumers regulate a prey subsidy to an estuarine consumer. *Oikos* 122:1453–1464.
- Boucek, R. E., and J. S. Rehage. 2014a. Climate extremes drive changes in functional community structure. *Global Change Biology* 20:1821–1831.
- Boucek, R. E., and J. S. Rehage. 2014b. Examining the effectiveness of consumer diet sampling as a nonnative detection tool in a subtropical estuary. *Transactions of the American Fisheries Society* 143:489–494.
- Boucek, R. E., and J. S. Rehage. 2015. A tale of two fishes: using recreational angler records to examine the link between fish catches and floodplain connections in a subtropical coastal river. *Estuaries and Coasts* 38:124–135.
- Boucek, R. E., E. E. Gaiser, H. Liu, and J. Rehage. *In press*. A review of sub-tropical community resistance and resilience to extreme cold spells. *Ecosphere*.
- Burkhardt, R. W., and S. Gutreuter. 1995. Improving electrofishing catch consistency by standardizing power. *North American Journal of Fisheries Management* 15:375–381.
- Cook-Patton, S. C., M. Lehmann, and J. D. Parker. 2015. Convergence of three mangrove species towards freeze-tolerant phenotypes at an expanding range edge. *Functional Ecology* 29:1332–1340.
- Flaherty, K. E., and J. H. Landsberg. 2011. Effects of a persistent red tide (*Karenia brevis*) bloom on community structure and species-specific relative abundance of nekton in a Gulf of Mexico estuary. *Estuaries and Coasts* 34:417–439.
- Gilmore, G. R. 1995. Environmental and biogeographic factors influencing ichthyofaunal diversity: Indian River Lagoon. *Bulletin of Marine Science* 57:153–170.
- Gilmore, R. G., L. H. Bullock, and F. H. Berry. 1978. Hypothermal mortality in marine fishes of south-central Florida, January 1977. *Northeast Gulf Science* 2:77–97.
- Gilmore, R. G., C. J. Donahoe, and D. W. Cooke. 1983. Observations on the distribution and biology of the common snook, *Centropomus undecimalis* (Bloch). *Florida Scientist* 46:313–336.
- Greenwood, M. F. D., P. W. Stevens, and R. E. Matheson Jr. 2006. Effects of the 2004 hurricanes on the fish assemblages in two proximate southwest Florida estuaries: change in the context of multi-annual variability. *Estuaries and Coasts* 29:985–996.
- Harvey, B. C., R. J. Nakamoto, and J. L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Oncorhynchus clarki*) during fall and winter. *Canadian Journal of Fisheries and Aquatic Sciences* 56:2161–2166.
- Hoffsten, P. O. 2003. Effects of an extraordinarily harsh winter on macroinvertebrates and fish in boreal streams. *Archiv für Hydrobiologie* 157:505–523.
- Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. Contrasting sensitivities of two dominant C4 grasses to heat waves and drought. *Plant Ecology* 215:721–731.
- Howells, R. G., A. J. Sonski, P. L. Shafland, and B. D. Hilton. 1990. Lower temperature tolerance of snook, *Centropomus undecimalis*. *Northeast Gulf Science* 11:155–158.
- Jentsch, A., J. Sonski, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5:365–374.
- Kemp, D., M. A. Colella, L. A. Bartlett, R. R. Ruzicka, J. W. Porter, and W. K. Fitt. 2016. Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys. *Ecosphere* 7(6): e01373. <http://dx.doi.org/10.1002/ecs2.1373>
- Kodra, E., K. Steinhäuser, and A. R. Ganguly. 2011. Persisting cold extremes under 21st century warming scenarios. *Geophysical Research Letters* 38:1–5.
- Kupschus, S., and D. Tremain. 2001. Associations between fish assemblages and environmental factors in nearshore habitats of a subtropical estuary. *Journal of Fish Biology* 58:881–889.

- Lorenzen, K., R. S. Steneck, R. R. Warner, A. M. Parma, F. C. Coleman, and K. M. Leber. 2010. The spatial dimensions of fisheries: putting it all in place. *Bulletin of Marine Science* 86:169–177.
- Lowerre-Barbieri, S., D. Villegas-Rios, S. Walters, J. Bickford, W. Cooper, R. Muller, and A. Trotter. 2014. Spawning site selection and contingent behavior in common snook, *Centropomus undecimalis*. *PLoS ONE* 9:1–16.
- McEachron, L. W., G. C. Matlock, C. E. Bryan, P. Unger, T. J. Cody, and J. H. Martin. 1994. Winter mass mortality of animals in Texas bays. *Northeast Gulf Science* 13:121–138.
- McMichael, R. H., Jr., K. M. Peters, and G. R. Parsons. 1989. Early life history of the snook, *Centropomus undecimalis*, in Tampa Bay, Florida. *Northeast Gulf Science* 10:112–125.
- Muller, R. G., and R. G. Taylor. 2012. The 2012 stock assessment update of common snook, *Centropomus undecimalis*. In-House Report IHR2012-002. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, Florida, USA.
- Peters, K. M., R. E. Matheson Jr., and R. G. Taylor. 1998. Reproduction and early life history of common snook, *Centropomus undecimalis* (Bloch), in Florida. *Bulletin of Marine Science* 62:509–529.
- Phlips, E. J., et al. 2015. From red tides to green and brown tides: bloom dynamics in a restricted subtropical lagoon under shifting climatic conditions. *Estuaries and Coasts* 38:886–904.
- Precht, W. F., and R. B. Aronson. 2004. Climate flickers and range shifts of reef corals. *Frontiers in Ecology and the Environment* 2:307–314.
- Rehage, J. S., and W. F. Loftus. 2007. Seasonal fish community variation in headwater mangrove creeks in the southwestern Everglades: an examination of their role as dry-down refuges. *Bulletin of Marine Science* 80:625–645.
- Rivas, L. R. 1986. Systematic review of the perciform fishes of the genus *Centropomus*. *Copeia* 1986:579–611.
- Rooker, J. R., L. L. Kitchens, M. A. Dance, R. D. Wells, B. Falterman, and M. Cornic. 2013. Spatial, temporal, and habitat-related variation in abundance of pelagic fishes in the Gulf of Mexico: potential implications of the Deepwater Horizon oil spill. *PLoS ONE* 8:e76080.
- Rose, K. A., J. H. Cowan, K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2:293–327.
- Rosenblatt, A. E., and M. R. Heithaus. 2011. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *Journal of Animal Ecology* 80:786–798.
- Ross, M. S., P. L. Ruiz, J. P. Sah, and E. J. Hanan. 2009. Chilling damage in a changing climate in coastal landscapes of the subtropical zone: a case study from south Florida. *Global Change Biology* 15:1817–1832.
- Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. *Ecology Letters* 15:278–289.
- Smith, M. D. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology* 99:656–663.
- Stevens, P. W., S. Fox, and C. L. Montague. 2006a. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management* 14:435–444.
- Stevens, P. W., D. A. Blewett, and J. P. Casey. 2006b. Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of Hurricane Charley. *Estuaries and Coasts* 29:994–1003.
- Storey, M., and E. W. Gudger. 1936. Mortality of fishes due to cold at Sanibel Island, Florida, 1886–1936. *Ecology* 17:640–648.
- Taylor, R. G., J. A. Whittington, H. J. Grier, and R. E. Crabtree. 2000. Age, growth, maturation, and protandric sex reversal in common snook, *Centropomus undecimalis*, from the east and west coasts of South Florida. *Fishery Bulletin* 98:612–624.
- Trotter, A. A., D. A. Blewett, R. G. Taylor, and P. W. Stevens. 2012. Migrations of common snook from a tidal river with implications for skipped spawning. *Transactions of the American Fisheries Society* 141:1016–1025.
- Vavrus, S., J. E. Walsh, W. L. Chapman, and D. Portis. 2006. The behavior of extreme cold air outbreaks under greenhouse warming. *International Journal of Climatology* 26:1133–1147.
- Weber, C., C. Nilsson, L. Lind, K. T. Alfredsen, and L. E. Polvi. 2013. Winter disturbances and riverine fish in temperate and cold regions. *BioScience* 63:199–210.
- Winner, B. L., D. A. Blewett, R. H. McMichael Jr., and C. B. Guenther. 2010. Relative abundance and distribution of Common Snook along shoreline habitats of Florida estuaries. *Transactions of the American Fisheries Society* 139:62–79.
- Yatsu, A., K. Y. Aydin, J. R. King, G. A. McFarlane, S. Chiba, K. Tadokoro, M. Kaeriyama, and Y. Watanabe. 2008. Elucidating dynamic responses of North Pacific fish populations to climatic forcing: influence of life-history strategy. *Progress in Oceanography* 77:252–268.
- Young, J. M., B. G. Yeiser, and J. A. Whittington. 2014. Spatiotemporal dynamics of spawning aggregations of common snook on the east coast of Florida. *Marine Ecology Progress Series* 505:227–240.