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Temperature Variability in a Subtropical Estuary and Implications for Common Snook *Centropomus undecimalis*, a Cold-Sensitive Fish

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Variability in winter water temperature was compared among three habitat types (estuary, river, canal) in a subtropical estuarine system to explore how it might affect site selection and survival of a cold-sensitive fish, Common Snook *Centropomus undecimalis.* The study was conducted during three winters (2008–2010); a rapid cooling event occurred during the first winter, mild temperatures the second, and an extreme cold event in the third (an 80-yr event). During the extreme cold event in January 2010, catastrophic fish mortality occurred throughout the region that resulted in the emergency closure of the Common Snook recreational fishery. Over the entire studied estuarine system, dead Common Snook were reported at 43 sites; 26 of the sites were large fish kills consisting of 100–2,000 individuals. The distribution of mortality sites was widespread, although most were located in the estuary proper (n = 39), with only several in rivers and canals (n = 4). Temperature loggers recorded similar water temperatures among habitat types (estuary, river, canal), except during short periods (~3 d; up to 2°C) after cold fronts; this indicates that fish have distinct time constraints if searching for warmer water sites. During the short periods after cold fronts, canal water temperatures were the warmest and most stable, whereas the river and estuary temperature rankings varied.

Introduction

Winter mortality of fishes occurs from subarctic regions to the lower subtropical latitudes throughout the oceans and estuaries and in a variety of freshwater lakes, rivers, and reservoirs (Hurst, 2007). Causes of mortality include thermal stress, starvation, predation, and disease, sometimes in combination, and can vary with species, climate, and system (i.e., marine, estuarine, freshwater). In the subtropics, where the average winter temperatures are warm, unpredictable and infrequent cold events can cause mass mortality of fishes, which has been well documented in the coastal areas of Florida and Texas (e.g., Moore, 1976, Gilmore et al., 1978). Cold stress from these events can kill a wide variety of fish species. Typically, fishes that die are in the northern portion of their range (e.g., Tarpon *Megalops atlanticus*). Even species not at the northern extreme of their range can be killed by sudden cold events because they lack the time to acclimate to the temperature change (e.g., Spotted Seatrout *Cynoscion nebulosus*, Red Drum *Sciaenops ocellatus*; Storey and Gudger, 1936).

Observations on winter mortality of fishes have prompted investigations into their use of habitats in winter, particularly habitats that allow fish to survive the cold. As reviewed by Hurst (2007), winter habitat use by fish has been studied principally in freshwater systems (Raibley et al., 1997, Huusko et al., 2007). Estuarine fishes may have winter habitat requirements similar to those of freshwater species, which exhibit small-scale habitat selection that let them avoid low oxygen levels, minimize energy expenditures, take advantage of small changes in temperature, or find refuge from predators (Magnuson et al., 1985, Knights et al., 1995); however, this possibility has rarely been addressed for marine and estuarine fishes, so their winter microhabitats are still largely unknown.

In the estuaries of southern Florida, recreationally important fishes include subtropical species that are sensitive to cold water temperatures, especially sudden decreases in water temperature. For example, Tarpon, Striped Mojarra *Eugerres plumieri*, Crevalle Jack *Caranx hippos*, Ladyfish *Elops saurus*, and Permit *Trachonotus falcatus* have been reported dead in great numbers after a major freeze (Gilmore et al., 1978), but perhaps the fish most recognized as being adversely affected by extreme cold weather events is Common Snook *Centropomus undecimalis.* This popular iconic species is large bodied and widely known by the public, making reports of kills of this species more reliable than those of less recognizable species.

Snook range from the U.S. Mid-Atlantic coast to southern Brazil, including the insular and mainland margins of the Gulf of Mexico and the Caribbean Sea (Rivas, 1986). Because of low temperature tolerance their true northern range is limited to the 15°C isotherm (Shafland and Foote, 1983), and collections to the north of that isotherm have been attributed to isolated pelagic larval transport or extended adult migrations during the warmer months (Merriner et al., 1970). The lower lethal temperature of adult Snook has been determined in the laboratory at 7–9°C (Howells et al., 1990), but extensive physiological and metabolic studies related to temperature requirements of Snook have not been conducted as they have for other species (e.g., striped bass, *Morone saxatilis*; Jones and Sidell, 2005). In addition, the lower lethal temperature for Snook has not been corroborated in their natural environment.

In Florida, Snook are abundant in tropical and subtropical estuarine systems along the east coast from Cape Canaveral southward around the peninsula to Tarpon Springs. They use a variety of shoreline habitats such as barrier islands and mangrove forests (Winner et al., 2010), as well as man-made canal systems and large inland stretches of freshwater rivers (Blewett and Stevens, 2013, Blewett et al., 2013). During winter, it is thought that Snook seek deeper shoreline areas in the rivers, canals, and even in the estuary to provide warmer water during cold periods (Volpe, 1959, Blewett et al., 2009, Winner et al., 2010). Small sections of spring-fed rivers along the Gulf coast of central and northern Florida have been shown to provide considerably warmer water (up to 12°C greater than estuary) during winter, which has enabled some tropical organisms (i.e., tropical fishes and manatee) to extend their northern range (Sorice et al., 2006). In the southern regions of Florida, where most of the Snook population resides, the rivers are not spring fed and any temperature moderation provided by deep waters associated with rivers, canals, or estuary shorelines is unknown. Understanding temperature variability among estuarine habitat types (i.e., estuary proper, river, canal) is an initial step that could help classify the value of deepwater habitats as thermal refuge for Snook. In addition, these findings may be applicable for other subtropical species and on greater geographical scales (e.g., southern Gulf of Mexico, Caribbean Sea).

For this study, water temperatures during three consecutive winters (2008–2010) were monitored at hourly intervals throughout the Charlotte Harbor estuarine system in southwest Florida (Fig. 1). During this period, two winter (cold-water) fish mortality events occurred. The second event (January 2010), the most severe in Florida in last 80 yrs (Boucek and Rehage, 2014), was massive and widespread, affected estuaries throughout Central and South Florida, and resulted in the emergency closure of the recreational Snook fishery in Florida. The objectives of this paper are 1) to compare average water temperatures among three general habitat types (estuary proper, river, and canal) of the Charlotte Harbor estuarine system, 2) to identify important winter habitat sites for Snook within this system by documenting the spatial extent and severity of mortality from a catastrophic cold event, and 3) to document Snook mortality and associated water temperatures in the field.

Materials and Methods

Temperature data.—From 15 Nov. to 31 Jan. during three consecutive years (2007/08, 2008/09, 2009/10), 10 temperature loggers (Onset HOBO® Water Temp Pro v2, accuracy of 0.2°C) were deployed within three general habitat types (estuary, river, canal) of Charlotte Harbor (Fig. 1). Temperature loggers were placed approximately 0.5 m from the bottom at each site, and water temperature was recorded every hour. Loggers were deployed (number sites, depth range in meters at mean low water) in the estuary proper (4, 0.7–2.0), the main stems of rivers (4, 1.1–2.2), and canals (2, 0.8–1.1). All the sites selected in the three habitat types represented relatively deep areas near the shoreline. The rivers and canals are predominantly deep along the shoreline (>1 m water depth), and the temperature logger sites reflect the average water depths found in these two systems. The estuary proper, however, has predominantly shallow water along the shoreline (<1 m mean low water), and thus the logger sites selected within this habitat type were distinctly deeper than average. For analysis, hourly water temperatures during the last week of December through January were averaged for each day among sites within a habitat type. A 3-d average of water temperatures (°C) for each habitat type (estuary, river, canal) before (pre) and after (post) the passage of a cold front in each winter were compared using ANOVA; any significant differences were further analyzed using Tukey multiple comparison test. Pre- and postcold front dates (separated by a backslash) used in analysis: 2008 = 29–31 Dec. 2007/3–5 Jan. 2008; 2009 = 11–13 Jan. 2009/16–18 Jan. 2009; 2010 = 30–31 Dec. 2009 and 1 Jan. 2010/4–6 Jan. 2010. In addition, we used the same postcold front data to calculate the coefficient of variation (CV) for each habitat type and year to determine the stability of water temperatures in each habitat type after a cold front.

Episodic winter mortality of Common Snook.—Detailed information from cold-event mortality of Snook at multiple sites during 3–8 Jan. 2008 and

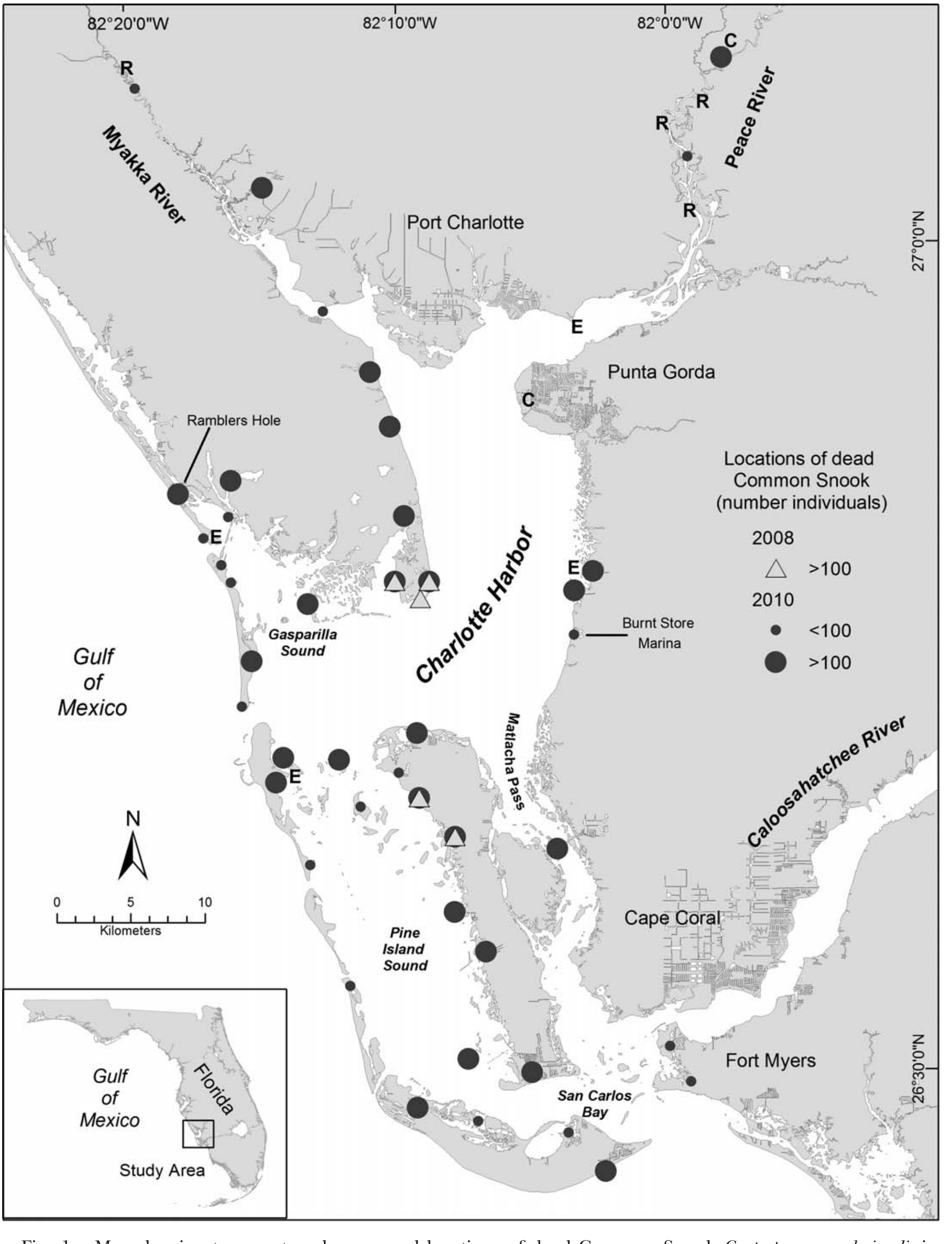

Fig. 1. Map showing temperature loggers and locations of dead Common Snook *Centropomus undecimalis* in the Charlotte Harbor estuary, Florida. The locations of temperature loggers deployed in each of three winters (2008–2010) are indicated by the letters E, R, and C (estuary, river, and canal). During winter 2010 water temperatures were also monitored at Rambler's Hole and Burnt Store Marina. The locations where dead Common Snook were observed during the cold event in 2008 are indicated by gray triangles (≥100 individuals), and those observed during 2010 are indicated by black circles (<100 individuals and ≥100 individuals).

7–21 Jan. 2010 was obtained by collecting reports from the public (i.e., anglers, boaters, people living on waterways), fishing charter captains, law-enforcement officers, cooperating scientists, and biologists conducting ongoing monthly monitoring and research. Most initial reports were made to the Florida Fish and Wildlife Conservation Commission's (FWC) fish-kill hotline or reported directly to biological or environmental field laboratories in the Charlotte Harbor area. For this project each report received by phone or e-mail was followed up with an interview, which included a series of questions focusing on the number of dead Snook [>1 ft. long, 300 mm total length (TL)] and an exact description of the location. In addition, an independent search for dead Snook in the estuary and major rivers was conducted in conjunction with four separate long-term intensive biological monitoring programs in the area: 1) fisheries sampling of the Charlotte Harbor estuary and lower Myakka and Peace rivers (Poulakis et al.. 2003), 2) freshwater fisheries sampling of the Peace River (Blewett et al., 2013), 3) wildlife survey of the Myakka River, and 4) Smalltooth Sawfish *Pristis pectinata* sampling of the lower Caloosahatchee River (Poulakis et al., 2013). Because the number of dead Snook reported at each site was not determined using standardized techniques, raw mortality count data for each site were grouped into four categories: <100, 100–499, 500–999, and 1,000–2,000 dead individuals, and then plotted on a map to show the spatial distribution. Those sites with ≥100 dead individual Snook were considered to be major mortality sites and were the primary focus for the results.

Documentation of Common Snook mortality and associated water temperatures in the field.—During the winter of 2010 two additional temperature loggers were deployed in the estuary at depths of 0.7 and 1.2 m and were helpful in documenting lower lethal water temperatures for Snook in the wild (Fig. 1). Both of these loggers were fortuitously placed in locations where large numbers of Snook gathered during the extreme winter mortality event. Both areas are embayments protected from the wind and adjacent to the open estuary. The first, Rambler's Hole, is a natural area approximately 0.7 km^2 in area with an average depth of 1.8 m and an equal area of adjacent shallow flats (<1 m deep); the other, Burnt Store Marina, is a man-made basin approximately 4.9 km^2 in area with an average depth of 2.5 m. At Rambler's Hole, a fishing charter captain estimated the number of live and dead fish on three consecutive days during the mortality event (10–12 Jan. 2010). On his third day of observations, the authors joined him and counted dead Snook (all could be seen on the bottom) and measured TL of randomly selected individuals. Also that same afternoon (12 Jan.), the authors investigated two other sites within 5 km of Rambler's Hole (both man-made basins), and counted the numbers of live Snook near the surface. In the afternoon of 13 Jan. a local fishing guide and FWC volunteer investigated all of Burnt Store Marina and counted the number of live Snook near the surface. Dead Snook could not be seen on the bottom at this site so numbers were recorded by marina staff as they removed dead floating Snook from the basin between the days of 13 and 29 Jan.

Results

Temperature data.—Winter water temperatures varied greatly, from a high of 25.3°C to a low of 8.4°C (Fig. 2). The effects of cold fronts were apparent, with a reduction in water temperature (~2–4°C) occurring the first 3 d after their passage. Two cold-weather events occurred that caused fish mortalities in South Florida. The first occurred during 1–3 Jan. 2008 and lowered estuarine water temperatures from 24°C to 13°C in less than 60 hr. The second occurred over an extended period in Jan. 2010. Water temperatures fell below 14°C and remained there for 2 wk (3–17 Jan.), with the lowest temperatures <10°C occurring during 11–12 Jan.

Minimum water temperatures were different between the three habitat types after cold fronts (Fig. 3). For example, during the week of 7 Jan. 2008, water temperatures in all habitat types were nearly identical, but during the week of 14 Jan., after passage of a cold front, temperatures dropped in all but differed as much as 2°C among the habitats. Closer examination of water temperatures using data for 3 d before and 3 d after cold fronts further illustrates differences between the habitats (Fig. 4). Before passage of cold fronts, differences between the habitat types were minimal (≤0.5°C), but after passage of cold fronts, they differed from 1.2°C to 1.8°C. During the first 2 yr after passage of cold fronts, the canal habitat was the warmest, followed by the river, and then the estuary; the third year, the canal habitat again was the warmest, but followed by the estuary, and then the river (P values < 0.01; Tukey multiple comparison test). With regard to water temperature stability among the habitat types, the temperatures in the river fluctuated the least after the passage of a cold front, followed by the canal, and then the estuary in the first 2 yr (2008 CV = 0.057, 0.063, 0.084;

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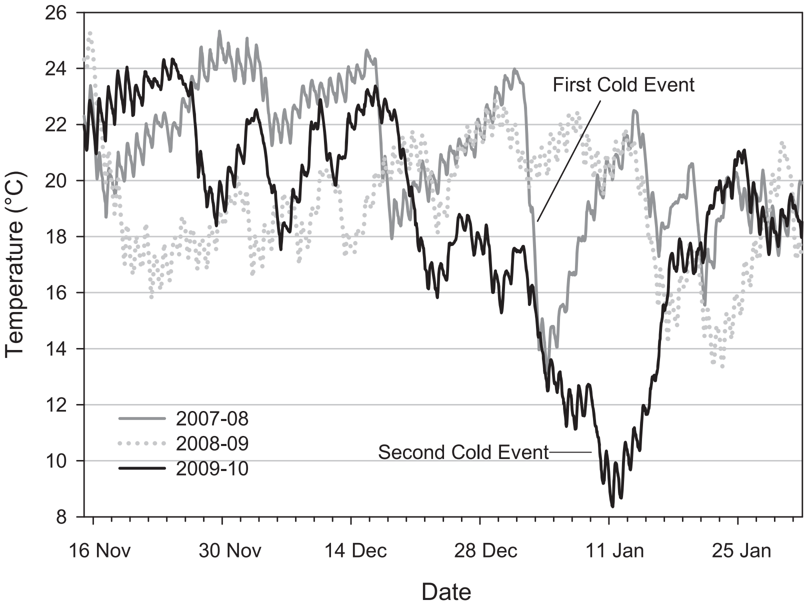

Fig. 2. Average hourly water temperature (°C) of the Charlotte Harbor estuarine system from 16 Nov. through 31 Jan. each year (all temperature logger data combined).

2009 CV = 0.039, 0.045, 0.060). During the third year, the canal was the most stable, followed by the estuary, and then the river (2010 CV = 0.038, 0.049, 0.057).

Episodic winter mortality of Common Snook.—After the 2008 cold event, Snook kills were identified during 3–8 Jan. at five sites within the Charlotte Harbor estuary (Fig. 1). The sites occurred in western Charlotte Harbor and eastern Pine Island Sound and each had more than 100 reported dead Snook. Two of the five sites were investigated by fisheries biologists and had a total of 1,127 dead Snook measuring 282–909 mm TL.

After the 2010 cold event, fish kills reported during 7–21 Jan. were large and widespread throughout the estuarine system, found at 43 sites (Fig. 1). Of these, 26 were major kills (≥100 dead individuals), of which 24 were located in the estuary proper and two adjacent to the main stems of rivers (Myakka River tributary and Peace River canal). No major kills were noted in the Caloosahatchee River or its adjacent canal system (Cape Coral) or in either of the two major canal systems adjacent to the upper estuary (Port Charlotte and Punta Gorda). Major kills were observed primarily in Pine Island Sound (11 sites; 4,200–10,492 dead individuals), followed by western Charlotte Harbor (five sites; 3,200–6,998), Gasparilla Sound (four sites; 800–2,496), eastern Charlotte Harbor (two sites; 200–998), and Matlacha Pass (one site; 100–499). Eight of the 43 reported sites were investigated by fisheries biologists, and 3,454 dead Snook were counted ranging from 138 to 1,070 mm TL.

Documentation of Common Snook mortality and associated water temperatures in the field.—During the coldest 3 d of the 2010 cold event, daily observations of Snook at Rambler's Hole documented a progression of water temperatures that resulted in a major fish kill (Fig. 5). At 1400 hr on 10 Jan., an estimated 300 Snook were observed congregating in a relatively small area along the shoreline; no dead fish were observed. The water temperature was 10.1°C and had been below 10°C for approximately 5 of the previous 24 hr, with a low of 9.6°C. Twenty-four hours later (11 Jan.) approximately half of the Snook had died, whereas the rest were observed alive. The water temperature was 9.3°C and had been below 10°C for approximately 16 of the previous 24 hr, with a low of 8.5°C. Forty-eight hours after the first observation (12 Jan.), all the Snook in this area had died (n = 479, 330–762 mm SL). The water temperature was 9.2°C and had been below 10°C for the previous 24 hr, with a low of 8.3°C. On the same day, at 1400 hr, two large man-made basins (marinas) within 5 km of Rambler's Hole were visited; both areas contained live Snook (approximately 350 individuals total), and no dead fish were observed. In addition, on 13 Jan., at 1200 hr, in another large man-made basin (Burnt Store Marina), no dead Snook were observed and 272 live fish were

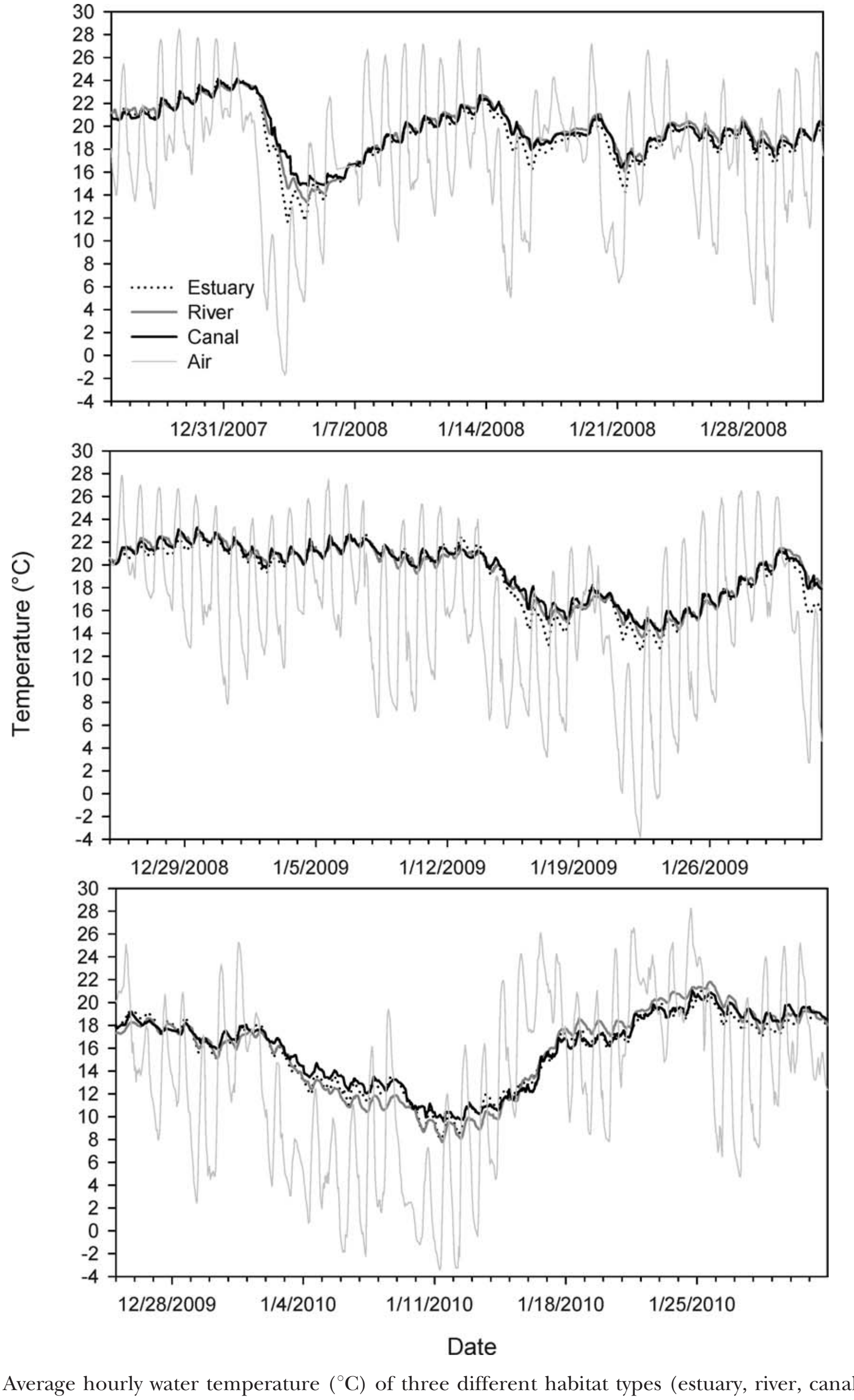

Fig. 3. Average hourly water temperature (°C) of three different habitat types (estuary, river, canal) and air temperature (°C) at Peace River Water Facility during the last week of Dec. through Jan. each year.

counted. During the next 16 d, 91 dead Snook were removed from this basin by marina staff. Water temperature readings taken in the marina showed that temperatures fell below 10°C for only 6 hr during the entire event.

Discussion

Winter water temperatures were monitored during 3 yr (2008, rapid cooling event; 2009, mild temperatures; and 2010, extreme cold

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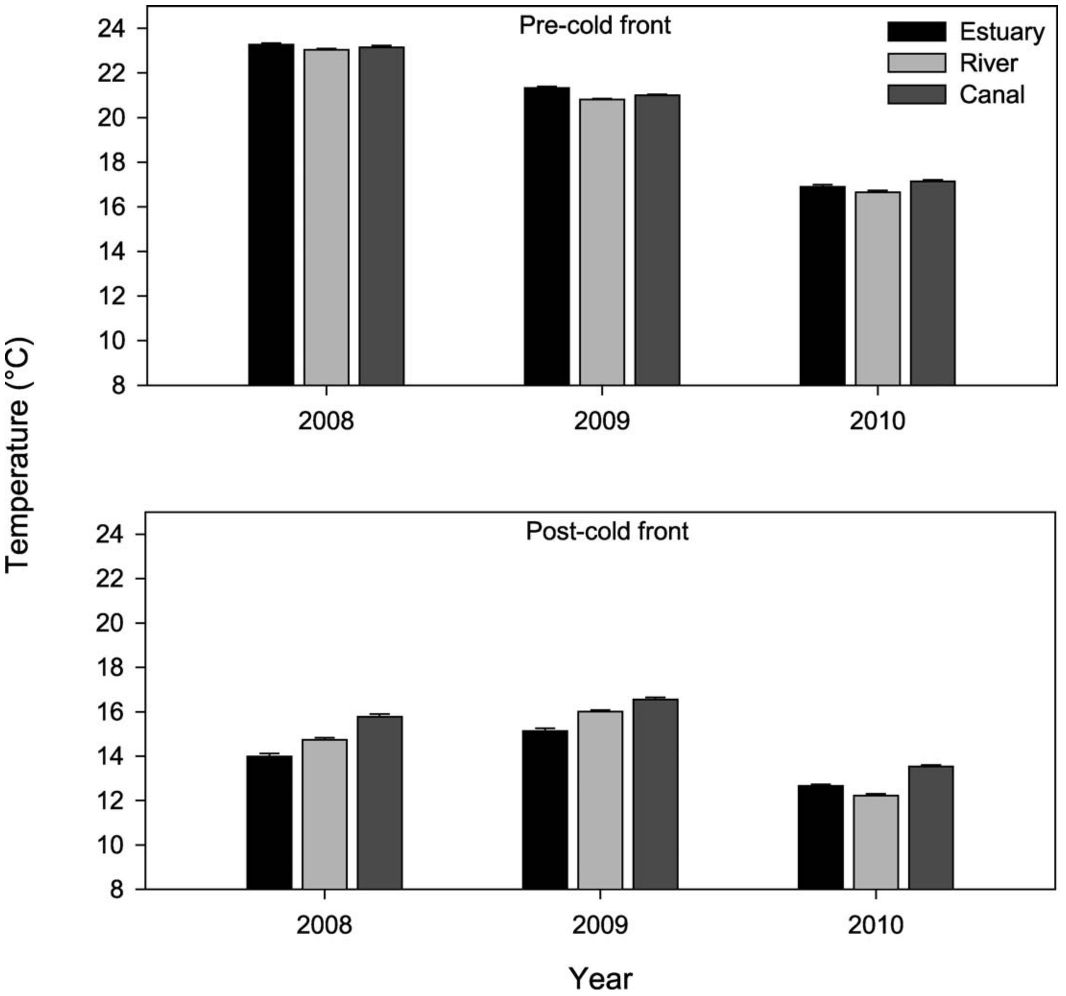

Fig. 4. Three-day average of water temperatures (°C) for each habitat type (estuary, river, canal) before (pre) and after (post) the passage of a cold front in each winter. Pre- and postcold front dates (separated by a backslash): 2008 = 29–31 Dec. 2007/3–5 Jan. 2008; 2009 = 11–13 Jan. 2009/16–18 Jan. 2009; 2010 = 30–31 Dec. 2009 and 1 Jan. 2010/4–6 Jan. 2010.

event), which helped explain how different winter water temperature scenarios affect Snook survival in the subtropics. The 2008 cold event was the result of a strong cold front preceded by relatively warm winter temperatures. Water temperatures reached an average low of only 13°C, but the temperature change was abrupt (11°C over 1 d). During this event, Snook mortalities were not widespread, but rather clustered at several sites in two small regions of Gasparilla and Pine Island sounds, and compared with the 2010 cold event, there were very few sites with dead fish. The habitat was similar for all five Snook mortality sites in 2008; each site encompassed a small area of moderate depth (1.0–1.3 m) near extensive shallow flats (<1.0 m) that were adjacent to large open embayments.

Differences in water temperatures among the major habitat types (estuary, river, canal) occurred during short periods of time (~3 d) after the passage of a cold front. During these short periods in the first 2 yr of the study, water temperatures along deep shorelines (>1.2 m) in the estuary dropped the fastest and were the coldest and most unstable among the three habitat types. After a cold front, the deep estuary sites in this study likely retained less heat than the river and canal sites because of their connectivity, via tides and wind, to extensive nearby shallow-water flats (<1.0 m). In contrast, there is little shallow water in or adjacent to the lower freshwater portions of the rivers and in the canals. In addition, the effects of cold winds blowing across water and mixing of water layers

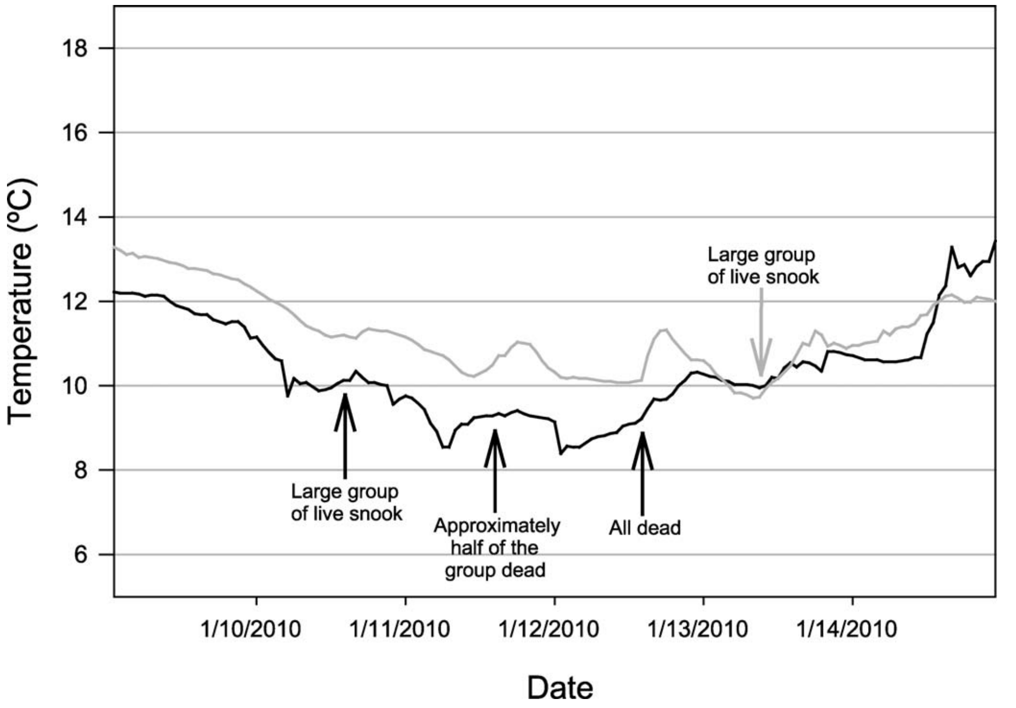

Fig. 5. Hourly water temperatures (°C) at two locations where Common Snook *Centropomus undecimalis* congregated during the coldest 6 d of the 2010 cold event (black line = Rambler's Hole; gray line = Burnt Store Marina). Arrows mark the time of day that site observations were made (arrow color corresponds with the line color for each site).

are much greater in a large, open estuary than in a narrow river or canal (Shafland, 1995, Hamilton et al., 2001). A study in the Everglades National Park also showed how sudden drops in air temperature relate to water temperatures in different aquatic habitats; canal habitat was more thermally stable than marsh, pond, or solution hole habitats (Schofield et al., 2010). In the present study, these differences in water temperature between habitat types, which occur for only short periods, highlight time and search constraints that Snook might confront when seeking warmer sites or habitats. For example, after the onset of a cold front, Snook have only about 1 d to find warmer water, so it seems unlikely that they could travel from the lower estuary to a river or canal (a distance of 20–40 km) under stressful conditions in enough time to benefit from the brief period of warmer water that those habitats may offer.

The 2010 cold event was much larger in scale and caused widespread mass mortality of Snook and many other species throughout the estuary. This unusual winter event occurred after the passage of consecutive cold fronts, which resulted in a week of low water temperatures and two consecutive days of water temperatures less than 10°C (average temperature logger readings). Widespread freezes that affect terrestrial crops in Florida occur about every 8 yr (Miller and Downtown, 1992). Freezes that affect fish populations are even less frequent, occurring approximately every 20 yr (Gilmore et al., 1978, Snelson and Bradley, 1978). The FWC fisheries monitoring program, established in the region in 1990, had never documented widespread winter fish mortality at the scale of the one that occurred in 2010. The sites where Snook mortality occurred are likely representative of places where Snook seek refuge during cold fronts. All the sites were relatively small, deep, protected from wind, and close to the shoreline. Several studies have shown that Snook use shallow mangrove shoreline areas in the estuary year round (Blewett et al., 2006, 2009; Winner et al., 2010). The behavior of using small, deep sites during cold fronts and adjacent shallow flats between fronts could be described as small-scale winter habitat selection, similar to the behavior of centrarchids in freshwater systems, in which they take advantage of small temperature differences by making short movements to adjacent areas (Knights et al., 1995). Small-scale winter habitat selection by Snook (movement to the nearest deep site at the onset

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of a cold front), rather than large-scale movements to a specific habitat, could help explain why Snook are distributed widely throughout the estuary during winter.

Because of the severity of the 2010 cold event and the fortuitous placement of temperature loggers in two areas closely monitored by fishing guides, we had the unique opportunity to estimate a lethal lower temperature for Snook in the wild. To date, only two laboratory experiments have been conducted on this species to determine its lower lethal temperature, and only one used adult fish (Shafland and Foote, 1983, Howells et al., 1990). In the laboratory, young adult Snook (n = 14, 265–380 mm) acclimated to 25°C had a lethal temperature of 8.9°C, and those acclimated to 15°C had a lethal temperature of 7.6°C. The findings from our field study were similar and showed that Snook can withstand several days of temperatures between 10°C and 12°C and even as much as 20 hr at temperatures just below 10°C in the wild; however, since we observed Snook near the surface in the afternoon at both sites (presumably in an effort to warm up in the direct sun), a vertical profile of temperatures would have been ideal for understanding the different exposure levels of these fish. In addition to an estimated lower lethal temperature for Snook, we were able to demonstrate that a slight difference in temperature, as little as 1°C, between sites can be crucial to the survival of this species during extreme cold events in South Florida. Slightly warmer waters at Burnt Store Marina resulted in much lower Snook mortality than at Rambler's Hole. Differences in physical characteristics between the two sites help explain the temperature differences; the marina site had darker water and substrate, a larger area of deep water (50% greater), and less tidal flushing than the natural embayment.

The number of mortality sites in each of the habitats seems to correspond to results of long-term fisheries sampling. Rivers and canals, for example, contain large numbers of Snook (Blewett et al., 2009, 2013), yet only two sites were found with mass mortalities (>100 Snook) in these habitats. An electrofishing study, ongoing in the lower freshwater portion of the Peace River, showed that Snook abundance rebounded quickly (1 to 4 mo) after the cold event (Blewett and Stevens, 2013). In the estuary where 24 mortality sites occurred, Snook abundance decreased dramatically after the freeze (Adams et al., 2012) and remained low for 2 yr on the basis of State fisheries monitoring data (Muller and Taylor, 2012).

The lower, brackish areas of rivers could be an important site for Snook during cold events. A temporary movement of Snook from the freshwater portion of rivers into deep, brackish areas could explain why Snook abundance in the river rebounded so quickly as recorded by the electrofishing study (Blewett and Stevens, 2013). Salinity is dynamic in the area where the Peace River and the estuary meet (McPherson and Hammett, 1991). Haloclines commonly form in such areas because of the strong convergence of freshwater, flowing downstream against saline estuarine tides (Ibanez et al., 1997). During cold periods, haloclines can provide thermal refuge, because denser saline water gets trapped near the bottom and does not mix with fresher surface waters (Stith et al., 2010). In these areas, large fishes cannot be sampled effectively because the waters are too saline for electrofishing and typically too deep and laden with snags for large seines; thus abundance estimates for Snook within this moving section of the river are currently lacking and their use of this habitat during cold weather is unknown. Now that this area has been identified as a possible refuge, novel methods (e.g., side-scan sonar, acoustic tagging studies) could be used to test this hypothesis.

Annual variations in weather patterns can negate otherwise beneficial features (i.e., narrow and deep waterways) that protect sites from cold wind and allow water to retain heat longer. This may have been the case in the third year of the study when the estuary habitat had warmer average water temperatures than the river habitat, which was a reversal from the two prior years. A close examination of river flow during the study showed that winter 2010 flows were four times as great as those in 2008 and 2009 (U.S. Geological Survey stream flow gauge data Peace River Arcadia #02296750). In the Peace River most flow originates from far inland and upstream, where water temperatures throughout winter can be 1.0–3.5°C colder than at locations farther downstream (Blewett et al., 2013). The increase in river flow in 2010 could have been a factor responsible for lowering downstream river water temperatures and may have pushed Snook into the lower, brackish regions of the river during the event.

The results and interpretations of the temperature logger data presented in this study must be viewed with caution because of the small number of loggers (n = 10) deployed in such a large estuarine system. The temperature data presented here can be built upon by more sophisticated studies in the future. Developing a model with greater spatial coverage and vertical profiling of temperature loggers that can account for site-specific variables such as tidal and river flow patterns, depth, adjacent depths, fetch, and amount of wind protection will eventually provide greater insights into the overall temperature dynamics of this system and relative values of habitats as thermal refuge.

In summary, we documented for a subtropical estuary precise locations where mass mortalities of Snook occurred during extreme cold events. We suggest that these are sites that Snook use during brief periods of cold weather (~3–5 d postfreeze), a hypothesis that could be tested by sampling the sites regularly during winter or through acoustic tagging studies. However, during a rare cold event (80-yr event) these sites were not sufficient for their survival because of the severity of the event. The warmest locations where Snook survived the 2010 event remain for the most part unknown, but our observations suggest that fish residing in rivers and canals had greater survival than those residing in the estuary. We based this on a lack of reported Snook mortalities from these two habitat types and from trends in Snook abundance in the Peace River and in the estuary (Blewett and Stevens, 2013). Because weather patterns (i.e., cold-front intensity and duration, rainfall) are so dynamic, Snook mortality in different habitat types may vary from one cold event to the next, especially in rivers, where flows and levels can change dramatically from year to year. In addition, we found that differences in water temperature between habitat types were only discernible for a few days after the passage of cold fronts. The magnitude of temperature differences was relatively small (up to 2°C), and far less than has been documented for spring-fed rivers and other known thermal refuges (up to 12°C). It is unlikely that the temperatures in the studied rivers and canals are warm enough and of long-enough duration to prompt large-scale, seasonal movements by tropical species for the purpose of overwintering. Nevertheless, the 2°C difference in water temperature found among habitats during this study can be important for survival of tropical species during infrequent cold events that decrease temperatures right at their lethal limit.

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