Vol. 563: 211–218, 2017
doi: 10.3354/meps11960

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 20

Ecological effects of river flooding on abundance and body condition of a large, euryhaline fish

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ABSTRACT: The extraordinary productivity of fish and invertebrates on the floodplains of tropical rivers has been well documented, and large predatory fishes are known to take advantage of prey moving into river channels during falling-water periods. To quantify relationships between river flow and the abundance and body condition (weight relative to length) of a representative predator, electrofishing sampling for common snook *Centropomus undecimalis* was conducted in the Peace River, Florida, USA, during 2005 and 2007–2013. In years with at least average flows or higher, snook abundance increased up to 3-fold and body condition increased 1.2-fold from summer (high-water) to fall (falling-water). Snook consumed large numbers of fish species whose life histories are tied to inundated floodplains. During a year of severe drought, when floodplain inundation was minor, snook diet was comprised primarily of one small-bodied species, and snook abundance and body condition did not increase between sampling periods. Over the 8 yr record, mean annual abundance and body condition of snook were positively related to mean annual river flow (R^2 = 0.88) and the number of days that river level exceeded a specific threshold (R^2 = 0.70), respectively. A portion of the snook population moves from the estuary into rivers to take advantage of abundant food resources derived from riverine habitats. These results demonstrate a connection between riverine prey production and the body condition and movement patterns of a euryhaline predator and highlight a pathway for energy transfer from freshwater floodplains to estuarine and marine habitats.

KEY WORDS: Euryhaline species · Charlotte Harbor estuary · Floodplain river · Peace River · *Centropomus undecimalis* · Diet · Environmental flow

INTRODUCTION

The extraordinary productivity of small-bodied fishes and invertebrates on the floodplains of tropical rivers is correlated with patterns of river flow and flooding (Moses 1987, Junk et al. 1989, Agostinho & Zalewksi 1995). In addition, large predatory fishes take advantage of seasonal prey productivity associated with tropical floodplains (Winemiller & Jepsen 1998, Hoeinghaus et al. 2006). For some species, high flow and floodplain inundation allow access to permanent freshwater lagoons where prey production is high. This access can result in increased survival and growth rates for predators, as is the case for juvenile barramundi *Lates calcarifer* in Australia (Robins et al. 2006), a euryhaline species that moves between riverine and marine food webs (Milton et al. 2008, Jardine et al. 2012). The large and economically important freshwater catfishes of South America, such as *Pseudoplatystoma fasciatum* and *Pseudoplatystoma trigrinum* (Reid 1983, Winemiller & Jepsen 1998), use floodplain and channel habitats to feed on abundant prey, while the freshwater African tigerfish *Hydrocynus vittatus* primarily uses river channel habitat

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and intercepts floodplain prey as they move from drying floodplains to permanent channels (Winemiller & Kelso-Winemiller 1994).

The importance of river flow and flooding for large predatory fishes has been recognized for the remote tropics of Australia, South America, and Africa (Winemiller & Kelso-Winemiller 1994, Winemiller & Jepsen 1998, Robins et al. 2006). Large rivers in some subtropical regions have a similar climate (i.e. warm rainy season) and geomorphology (i.e. large floodplain) to those in the tropics (Bayley 1995, Kelly & Gore 2008); therefore, we expect that river flow and flooding are also important for large predators in the subtropics. Quantifying such relationships would be particularly useful to water managers, who work to ensure that rivers and estuaries receive the appropriate water deliveries to maintain productive ecosystems (Sklar & Browder 1998, Estevez 2002, Flannery et al. 2002).

Long-term sampling of common snook *Centropomus undecimalis* in a large subtropical river in Florida provides an opportunity to examine the effects of river flow and flooding on a large-bodied euryhaline fish species inhabiting riverine systems. The species inhabits tropical and subtropical coastal, estuarine, and riverine systems of the western Atlantic, the Gulf of Mexico, and the Caribbean Sea (Rivas 1986) and is valuable either commercially or recreationally throughout its range. It is an obligate marine spawner (Peters et al. 1998, Taylor et al. 1998) but is known to occupy rivers for extended periods (Trotter et al. 2012). Seasonal movements of snook between marine and freshwater habitats have been documented, but the cues for the onset of those movements are not well understood (Blewett et al. 2009, 2013). The objective of this study is to examine abundance, condition, and diet of large snook (primarily adults 350 to 1000 mm total length [TL]) over an 8 yr period in a lower river system. Specifically, we test the hypothesis that snook abundance and body condition are related to river flow and water level, and make inferences about their movements between the estuary and river.

MATERIALS AND METHODS

Study area

The Peace River is a coastal, subtropical river located in southwest Florida USA (Fig. 1) that flows into the Charlotte Harbor estuary (700 km^2). The river is 182 km long, with an average annual discharge of 32.7 m^3 s^{-1}. The highest river flows typically occur

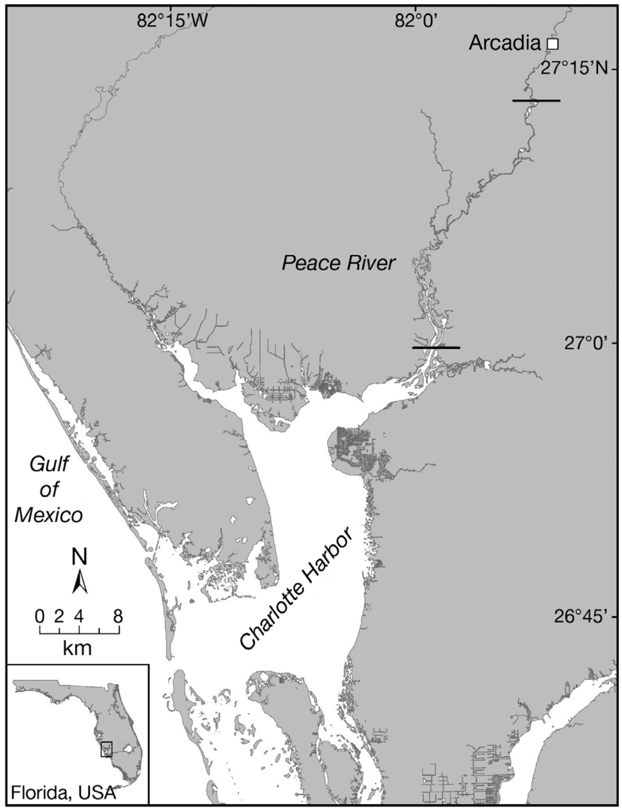

Fig. 1. Peace River, Florida, USA. Solid lines denote the stretch of river that was sampled

from July through September and coincide with the summer rainy season (Kelly & Gore 2008). Water levels rapidly draw down from October through December as the dry season approaches. Strip mines, agriculture, and urban development in the Peace River watershed have altered its hydrology and water quality (PBS&J 2007), but its course and that of most of its main tributaries remain unaltered and unimpounded. The river's banks have primarily been left undeveloped, and there are still extensive floodplains, backwater sloughs, wetlands, and forested corridors throughout its course (PBS&J 2007).

A 30 river km reach of the lower Peace River was sampled between 20 and 50 river km upstream of the mouth. This portion of the river hosts the greatest abundance of snook (Blewett et al. 2013). The river's width ranges from 40 m at the upstream boundary of the sampling area to 160 m at the downstream boundary. The sampling area is freshwater, though during the latter portion of the dry season (spring) a portion (ca. 7 km) becomes brackish (to a salinity of 25) (Stevens et al. 2013). In this reach, shorelines are dominated by red mangrove *Rhizophora* spp., bulrushes *Scirpus* spp., and leather fern *Acrostichum* *danaeifolium*, transitioning to large overhanging trees (i.e. southern live oak *Quercus virginiana*, bald cypress *Taxodium distichum*, and coastalplain willow *Salix caroliniana*), shrubs, and snags (i.e. dead trees).

Fish sampling

Snook and other large predatory fish species were sampled using electrofishing during summer (high-water period, 21 June to 20 September) and fall (falling-water period, 21 September to 20 December). A stratified-random sampling design was used to sample fish. To ensure that samples were spread evenly along the river, random sites were selected from points spaced 0.1 km apart along the center line of the river within subzones that were created for site selection purposes only. Effort during each sampling event (summer and fall) varied over the course of the study: n = 6 to 12 in 2005, n = 7 to 8 in 2007, n = 12 in 2008–2009, and n = 16 in 2010–2013. During 2005, a 5 min transect was completed at each site, and the distance traveled was measured in meters (average transect length = 150 m). Starting in 2007, all transects were standardized at 200 m. All transects were run along the shoreline in water depths ranging from 1.0 to 4.0 m. Depth was recorded at the beginning and end of each transect, and all sampling was completed between 08:00 and 18:00 h eastern standard time (EST). At each electrofishing transect, stunned snook were collected from the water with dip nets and placed in a large holding tank. After the completion of each transect, all fish were measured to the nearest mm TL, weighed to the nearest 0.1 g, and released.

Snook collected from each transect were sampled for diet (up to 10 ind. per transect). Contents of stomachs were removed by gastric lavage and then inspected with clear acrylic tubes for any remaining prey items before releasing the snook alive (procedure described by Stevens et al. 2010). Stomach contents were placed into a plastic bag, immediately immersed in ice, and frozen upon return to the laboratory. Once thawed, contents were sorted and identified to the lowest possible taxon. Pieces of prey items were counted as one, unless countable parts such as otoliths or claws were found. The abundance of important prey taxa in common snook *Centropomus undecimalis* diet each year (combining summer and fall) were plotted. The important prey taxa were defined as the top 4 distinguishing prey as reported by Blewett et al. (2013), and *Oreochromis* spp., which was a common prey item during the study period.

Statistical procedures

Metrics were calculated and plotted for visual interpretation. Snook abundance data are presented as the number of fish per 100 m of shoreline, and body condition is reported as relative condition (K_n). Relative condition K_n is calculated for each fish as W/W', where W is the weight of the individual and W' is the length-specific mean weight for fish in the population under study as predicted by a weight–length equation (Anderson & Neumann 1996). To establish a standard weight–length model for estimating K_n of snook from this region, we compiled a large data set of snook (n = 2558) from fishery monitoring in the Charlotte Harbor estuary from 2001 through 2010 (see Winner et al. 2010 for sampling details). The size distribution of snook in the estuary was the same as for those in the river (Blewett et al. 2009). Weight–length data were $\log_{10}$-transformed, and a linear regression ($y = 3.24x - 5.79$) was derived to represent a fit of K_n that equaled 1.00, representing the average year-round body condition of snook from the estuary. Snook abundance and body condition were calculated for each sampling event and plotted against river flow. For the purpose of comparing river flow values ($m^3\ s^{-1}$) during the study with historical flow values, median river flow and 25th- and 75th-percentile flows were calculated from 1932–2011 data and plotted. Any differences in snook abundance and body condition that occurred within a year (summer vs. fall sampling events) were tested with Mann-Whitney rank sum tests ($p < 0.05$).

We used linear regression to test the hypothesis that snook abundance and body condition were related to river flow ($m^3\ s^{-1}$). Data were ln-transformed prior to analysis, and the assumptions for the linear regressions were verified. The regressions were performed on data combining summer and fall sampling events for each year and mean annual river flow. Performing regressions using summer and fall sampling events separately would require major assumptions in assigning corresponding flow data. The approach of evaluating data at the annual scale allowed us to integrate data over a time scale appropriate to our question (i.e. are abundance and body condition of a predator in a given year related to freshwater inflow?).

We also tested the hypothesis that snook abundance and body condition were related to the duration of river floodplain inundation. Using continuous river flow data alone may not answer this question because there may be specific thresholds that inundate floodplain habitats and anabranch connections. How long these habitats are flooded may influence prey production on the river floodplain, and in turn influence predator abundance and body condition. Extensive information on river flow or water level, and the types of habitats that get flooded, were not available for the Peace River. To provide for a continuum, regressions were performed on electrofishing data combining summer and fall sampling events and the number of days the river water level exceeded a stage of 0.6, 1.2, 1.8, 2.4, or 3.0 m during each year (R^2 values reported). Data were ln-transformed prior to analysis, and the assumptions for the linear regressions were verified. Water level data were taken from the U.S. Geological Survey (USGS) stream flow gauge data (Peace River Arcadia, gauge #02296750). A reading of zero on the gauge (surveyed at 1.8 m above National Geodetic Vertical Datum of 1929) roughly corresponds to the river bottom and the term 'stage' represents the water level above this benchmark.

RESULTS

Freshwater inflows in the Peace River varied dramatically over the course of the study. The first and last years of the study (2005 and 2013, hereafter referred to as flood years) had high river flowsthat ranked slightly above the 75th percentile, whereas the second year of sampling (2007) was a drought year and had flows well below the 25th percentile (Fig. 2). From 2008 through 2012, the river had varying degrees of annual flow, all close to the historic median, except in 2011, when flows only slightly exceeded the 25th percentile.

In general, abundance and body condition of snook increased between the summer and fall sampling events within each year (Fig. 2b,c). Snook abundances during fall sampling events were significantly greater than those in summer for 2005, 2009, and 2013 (Mann-Whitney rank sum tests, $p < 0.05$). The magnitude of these differences was greatest during the flood years (2005 and 2013), when snook abundance more than tripled from summer to fall. The body condition of snook also increased from summer to fall, 8% on average. Body condition during fall sampling events were significantly greater than those in summer, except during 2005 and 2007 (Mann-Whitney rank sum tests, $p < 0.05$).

Over the long term, linear regression revealed that abundance and body condition of snook were closely related to river flow. Annual abundance of snook over the study period (combined summer and fall sampling events for each year) showed a strong and positive relationship with river flow ($R^2 = 0.88$; Fig. 3). Annual body condition had a positive, but weaker, relationship with river flow ($R^2 = 0.52$). The annual body condition of snook and the duration of floodplain inundation produced a stronger fit; the regression with the highest R^2 value occurred for the annual number of days the river exceeded a water

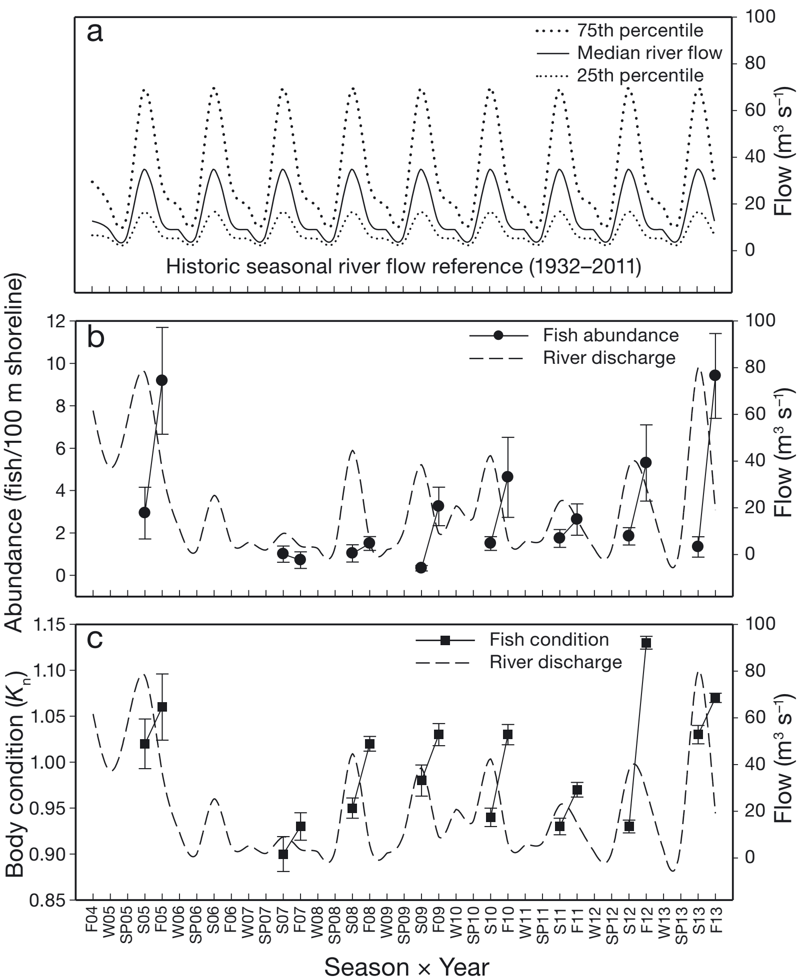

Fig. 2. (a) Median, 25th-percentile, and 75th-percentile flows in the Peace River, Florida calculated from 79 yr of flow data (1932–2011); note that values are the same for each year and are provided as a reference to compare to flow data in other panels. (b,c) Summer and fall abundance (fish per 100 m of shoreline) and body condition (K_n) of common snook *Centropomus undecimalis* in the Peace River (black dots with standard error bars) in relation to flow (dashed line) from summer (S) 2005 through fall (F) 2013 (SP: spring; W: winter). Seasons and years are shown in the *x*-axis labels

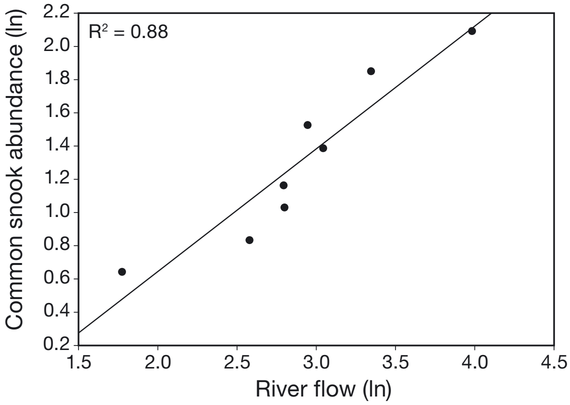

Fig. 3. Regression of mean summer and fall common snook *Centropomus undecimalis* abundance versus mean annual river flow (all data ln-transformed; $R^2 = 0.88$)

Table 1. Reported R^2 values from linear regressions of mean common snook *Centropomus undecimalis* annual abundance (fish per 100 m shoreline) and body condition (K_n) versus mean annual river flow and number of days that the river level exceeds specific stages (0.6 m increments). River level data were taken from the U.S. Geological Survey stream flow gauge data (Peace River Arcadia #02296750). Highest R^2 values are in **bold**

River flow and flooding duration	R^2 Abundance (fish/100 m shoreline)	R^2 Body condition (K_n)
River flow	**0.88**	0.52
Flooding duration when river stage exceeded		
0.6 m	0.44	0.04
1.2 m	0.60	0.61
1.8 m	0.67	**0.70**
2.4 m	0.82	0.64
3.0 m	0.82	0.40

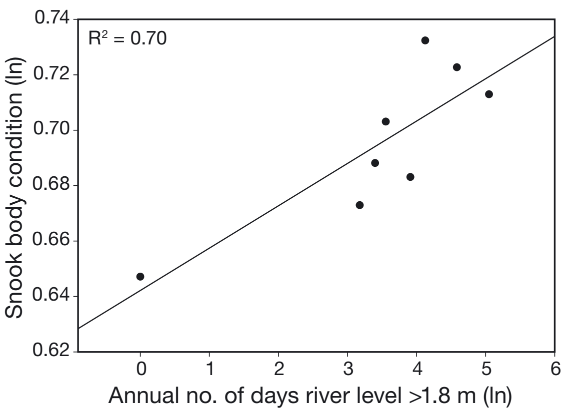

Fig. 4. Regression of mean summer and fall common snook *Centropomus undecimalis* body condition (K_n) versus annual number of days that river level exceeded a stage of 1.8 m (all data ln-transformed; $R^2 = 0.70$)

level of 1.8 m ($R^2 = 0.70$; Table 1, Fig. 4). Annual abundance of snook also had a strong and positive relationship with the number of days the river exceeded water levels of 2.4 and 3.0 m ($R^2 = 0.82$; Table 1).

The diet of snook varied over the course of the study (Fig. 5). The most important prey items were typically crayfishes *Procambarus* spp. and brown hoplo *Hoplosternum littorale*. During 2007, however, snook ate mostly grass shrimp *Palaemonetes* spp.

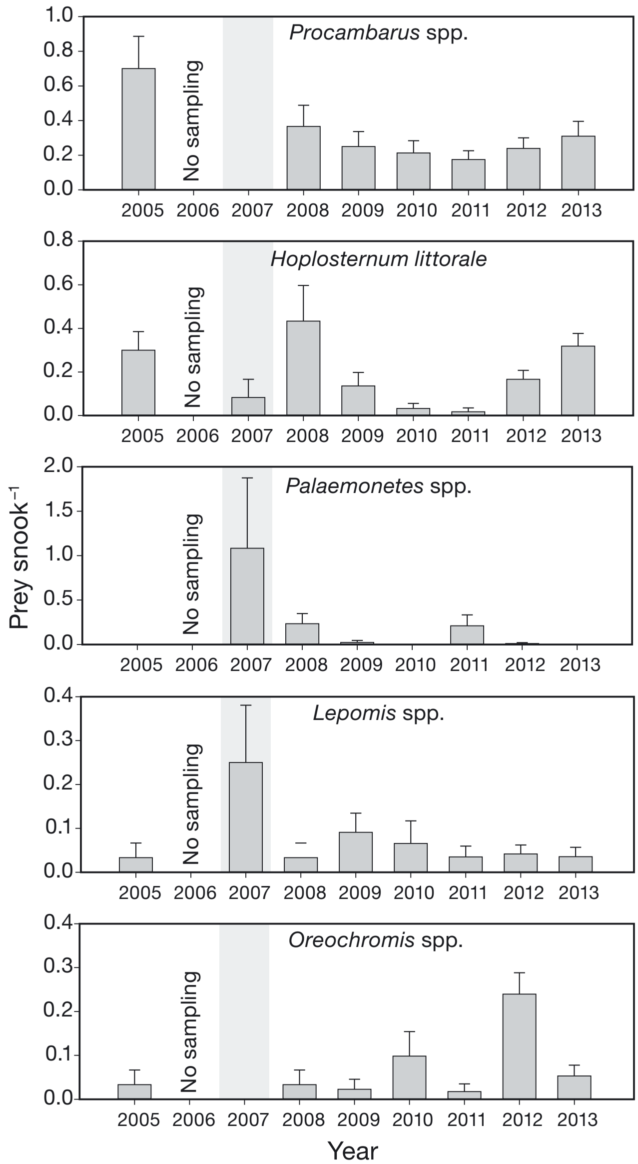

Fig. 5. Abundance (±1 SE) of important prey taxa found in the stomachs of common snook *Centropomus undecimalis* each year (combining summer and fall; top 4 distinguishing prey taxa as reported by Blewett et al. 2013, and *Oreochromis* spp.). High flows occurred in 2005 and 2013 (flood years), and the lowest flows occurred during a drought in 2007 (shaded in gray)

and sunfishes *Lepomis* spp. During 2012, snook consumed large amounts of tilapia *Oreochromis* spp., an exotic species in the Peace River.

DISCUSSION

The strong positive relationship between river flow and snook abundance implies that a portion of the population moves from the estuary into rivers when river flow is high. In central and southern Florida, the end of spawning season for snook (late summer/early fall; Taylor et al. 1998) coincides with the end of the rainy season, when rivers are typically flooded but begin to recede rapidly (Kelly & Gore 2008). During this time, snook that leave the spawning grounds and move to flooded rivers have access to prey residing in floodplain habitats (e.g. sloughs) and in the river channel. As waters recede, prey are forced off of the drying floodplain and become concentrated in the river channel. This movement of large quantities of prey from the floodplain to the main river channel over a short period of time can provide for important subsidies to the diet of large, riverine predators (Jepsen et al. 1997, Hoeinghaus et al. 2006, Boucek & Rehage 2013). For snook in this study, movement into rivers to take advantage of this abundant prey resulted in increases in body condition. During high-flow years, snook that occupied rivers had up to 7% greater body condition (i.e. were much heavier with respect to length) than snook in the estuary.

The increased body condition of snook is likely driven by changes in prey availability. Annual variations in rainfall, resulting in different water levels, can greatly affect fish and invertebrate production in rivers (Rogers et al. 2005, Fernandes et al. 2009). Years with high flow (enlargement of the river and floodplain) and long durations of flow (allowing more time for reproduction and growth of prey) have greater production of river floodplain species than do low-flow years (Moses 1987, Junk et al. 1989, Fernandes et al. 2009). For snook, the most important prey items in rivers are crayfishes *Procambarus* spp. and brown hoplo *Hoplosternum littorale* (Stevens et al. 2010, Blewett et al. 2013); both require floodplain inundation for reproduction and survival of young (Mol 1996, Acosta & Perry 2000). During the drought year of 2007, few snook moved into the river, and those that were present had the lowest body condition documented during the study. Snook were relegated to eating mostly small grass shrimp *Palaemonetes* spp. (mean TL of 15 mm) and lesser amounts of sunfishes *Lepomis* spp. rather than the floodplain species that typically rank high in their diet (e.g. crayfishes and brown hoplo). In addition to river flow, factors not examined in this study might support high prey production and increased body condition of snook (flooding explained 70% of the variation in snook condition). For example, extreme population fluctuations of prey, of which exotic fish are a major component (Stevens et al. 2010, Blewett et al. 2013), may affect the condition of large predatory fish. In 2012, an average flow year, snook body condition reached the highest level reported in the study. This high level in body condition was most likely the result of snook consuming large amounts of tilapia *Oreochromis* spp., an exotic species in the Peace River (Champeau et al. 2009). The reasons behind seemingly sporadic peaks in abundance of exotic fishes requires further examination.

Results from this North American subtropical river study concur with those from the remote tropics (Winemiller & Jepsen 1998, Moses 2001, Robins et al. 2006): river flow is important for large predatory fishes and is related to their abundance and body condition. In the Peace River, the strong relationships between a representative predator and river flow suggest that prey resources become more abundant with higher flows and longer floodplain inundation. A portion of the snook population likely uses rivers opportunistically for foraging. Seasonal movements of snook into a large tributary to capitalize on concentrated prey have been found in the coastal Everglades (Boucek & Rehage 2013).

Enhancements to the study design could unravel the connections between river floodplains, prey, and large river predators in the subtropics. A concurrent study on the floodplain to sample prey could provide information related to the duration of floodplain inundation and prey production, as well as to the seemingly sporadic variation in exotic prey populations. Higher sampling resolution of predators in the river during the period of high flows and receding water levels would be useful. In this case, biweekly to monthly sampling effort between summer and fall is recommended. The timing of snook movements between the river and estuary may be important for understanding the cues that lead to seasonal differences in snook abundance. For example, olfaction could be important for snook in assessing organic river-water cues while in the estuary. The ability to use sensory cues to find rivers has been identified in several families of fish (e.g. salmon, lampreys, and shad) (Dodson & Leggett 1974, Døving & Stabell 2003, Vrieze et al. 2010). A lack of organic river-water cues during the 2007 drought could explain the low snook abundance that occurred during that year (i.e. snook stayed in the estuary rather than traveled to rivers). Another enhancement in the study design would be greater sampling effort in both river channel and backwater habitats along the river to allow for finer spatial resolution in the analysis. The abundance of snook may be greater at sites where sloughs drain into the main river channel. Such sites may serve as potential ambush points for snook to capture prey moving off the floodplain into the river. When evaluating abundance estimates, some consideration should also be given to the effect of variable water level/flow on sampling efficiency (as per Gwinn et al. 2016). Fortunately, increased flow (and depth and turbidity) will reduce snook catch, not increase it, so any bias associated with reduced efficiency during high flows will make the study more conservative.

The importance of floodplains to a large predator has important ecological implications for water management. Managing the Peace River to optimize floodplain inundation can directly enhance the river's use by an economically important species. The relationships quantified in this study can be incorporated into models that test outcomes of different management strategies. For example, calculating the amount of habitat flooded at different river-water levels and including the effects on floodplain biota (e.g. reproduction and growth) in relation to abundance and condition of common snook or other predators (e.g. largemouth bass *Micropterus salmoides* or gar *Lepisosteus* spp.) could be a useful approach. In the case of snook, movements from rivers to marine waters move floodplain resources to estuaries and coasts, and emphasize the need for managers to maintain connectivity between these systems (Polis et al. 1997, Layman et al. 2007). Spawning aggregations of snook in the lower estuary and beaches are subject to predation by even larger piscivores (e.g. sharks and dolphins). An apex predator along the coast that consumes a snook could be ingesting prey that are only 1 trophic level removed from freshwater crayfish and brown hoplo (for river to estuary movements, see Trotter et al. 2012). These results demonstrate a connection between riverine prey production and the body condition and movement patterns of a euryhaline predator, and highlight a pathway of energy transfer from freshwater floodplains to estuarine and marine habitats.

Acknowledgements. We thank the staff members of the Florida Fish and Wildlife Conservation Commission who assisted during this project and to the several reviewers who provided valuable comments on the manuscript. This study was supported by the Southwest Florida Water Management District (Numbers 08POSOW0490, 08POSOW1743, and 10POWOW0239), a Florida State Wildlife grant (T-13-R-1), funds collected from State of Florida Saltwater Fishing License sales, and the U.S. Department of the Interior, US Fish and Wildlife Service, Federal Aid for Sport Fish Restoration Grant Number F-43.

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Editorial responsibility: Konstantinos Stergiou, Thessaloniki, Greece

Submitted: March 24, 2016; Accepted: October 28, 2016
Proofs received from author(s): December 20, 2016