



# Illustrating the value of cross-site comparisons: Habitat use by a large, euryhaline fish differs along a latitudinal gradient

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## ABSTRACT

Plasticity in life-history traits and behaviors allows organisms to track spatial environmental variation, such as that resulting from a latitudinal gradient. In estuaries, hydrological patterns can vary greatly with latitude, causing variable habitat use patterns across a species' range. For Common Snook (*Centropomus undecimalis*) a large euryhaline fish, seasonal movements between the open estuary and freshwater reaches of rivers have been documented. We hypothesized that the timing of river use by Snook would be driven primarily by the magnitude of freshwater inflow, except at the northern limit of its range where lethal water temperatures may be a stronger influence. Data from electrofishing studies (2012–2016) conducted in rivers associated with four estuaries along a latitudinal gradient in western Florida were compared for seasonal differences in Snook abundance using negative binomial regression. In rivers of southwestern Florida (those in Everglades and Charlotte Harbor), Snook abundances increased three-fold during the time of year when surface waters inundating floodplains recede and force prey into the main stems of rivers. These hydrologically driven processes, and surges in Snook abundance, occurred during spring in the Everglades and fall in rivers of Charlotte Harbor. In Tampa Bay rivers, which have less freshwater inflow than the rivers farther south, Snook abundance differed little between seasons. In spring-fed rivers north of Tampa Bay, Snook abundances in fall and winter were twice those of spring and summer; stable water temperatures were thought to provide thermal refuge at the northernmost range of Snook. This work illustrates how the timing of habitat use by a species, and the underlying reasons, can differ greatly among sites. It also demonstrates the value of cross-site comparisons in providing for a more complete understanding of how a species uses available habitats across its range.

## 1. Introduction

Plasticity in the life-history traits and behaviors of marine fishes (e.g., age, growth, fecundity, diet, habitat use), whether driven by differences in genotype or phenotypic expression, allows for local and regional adaptations within a species (DeWitt et al., 1998; Davenport et al., 2006; Duputié et al., 2015). Such adaptations are particularly relevant along latitudinal gradients. For example, behavioral plasticity in habitat use, especially the use of thermal refugia, may allow a species to survive extreme cold events or expand its poleward range (Sunday et al., 2014). Although temperature is an obvious driver of variation in life-history traits and behaviors across latitudinal gradients, a suite of other factors such as system productivity and prey availability interact

and influence life-history variation across space (Houde, 1989; Present and Conover, 1992; Hoxmeier et al., 2004; Davenport et al., 2006).

In estuaries, hydrologic patterns and their influence on ecological processes can differ greatly with latitude, which in turn can affect habitat use and behaviors of predatory fishes. For example, in riverine systems of the southeastern USA, peak water levels and freshwater inflows occur during spring, whereas in tropical and sub-tropical rivers, freshwater inflows peak towards the end of the summer rainy season (e.g., Kelly and Gore, 2008). The hydrology of rivers influences prey availability to freshwater and euryhaline predators (Beesley et al., 2012). In the tropics, the seasonal recession of water from vast expanses of wetlands forces potential prey into the main stem of rivers (Winemiller and Jepsen, 1998; Hoetinghaus et al., 2006), and

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euryhaline predators may move upstream to consume those prey (Boucek and Rehage, 2013; Matich and Heithaus, 2014). The concentration of prey into tributaries and movement of predators upstream occurs during the period of receding water, the timing of which can differ by system. Thus, plasticity in habitat use (in this case use of rivers) by predators enables them to alter their behavior (movement patterns) to take advantage of prey that originate in other systems (floodplains). This concept is similar to the match/mismatch hypothesis proposed for early life history (Durant et al., 2007), which states that species' life-history traits often evolve to overlap with optimal availability of prey.

A species that illustrates the importance of both temperature and hydrologic drivers in shaping habitat use is Common Snook *Centropomus undecimalis*. Snook is a large euryhaline species that occupies a wide range of habitat (Winner et al., 2010) in tropical and subtropical waters of the Western Atlantic (Rivas, 1986). Susceptibility to cold (lower lethal limit is 7–9 °C; Shafland and Foote, 1983; Howells et al., 1990) is a major factor limiting Snook distribution in Florida (Stevens et al., 2016), similar to many species at the poleward extent of its range. Within an individual estuary, Snook distribution and movements can be driven by spawning (they are obligate marine spawners) or prey availability (Taylor et al., 1998; Trotter et al., 2012; Boucek and Rehage, 2013). Several behavioral patterns have been identified for Snook. In Tampa Bay, a segment of the Snook population remained close to their spawning sites year round, which were located in the lower estuary (Lowerre-Barbieri et al., 2014). In a large river of Charlotte Harbor, fish resided in the river most of the year, making short-duration migrations out of the river only during the summer spawning season (Trotter et al., 2012). In the Everglades, Snook moved between the estuarine and freshwater reaches of a large river to capitalize on prey that concentrated into main river channels as water receded from river floodplains (Boucek and Rehage, 2013; Blewett et al., 2017).

Plasticity in habitat use makes Snook an excellent focal species for the study of differences in habitat use across a latitudinal gradient, and the differences in hydrology and temperature that occur with latitude in Florida provide an ideal setting. The most likely drivers of habitat use by Snook in Florida are temperature and hydrology. Use of rivers by Snook along the southwestern coast of Florida has already been shown to be driven primarily by hydrology (see above; Boucek and Rehage, 2013; Blewett et al., 2017). In the present study, we used additional data sets from study areas farther north: the rivers leading into Tampa Bay and, still farther north, a series of spring-fed rivers leading into the Gulf of Mexico (Fig. 1). We hypothesize that the use of spring-fed rivers by Snook is driven primarily by temperature. Snook are at the northern limit of their range in the spring-fed rivers, and the warm, stable temperatures offered there by groundwater base flow (23 °C; Sorice et al., 2003) likely provide for overwintering habitat. Thus, we expect an increase in Snook abundance during winter as the spring-fed rivers are used as thermal refuge. The relative influences of temperature and hydrology on Snook abundance in Tampa Bay rivers are harder to predict, because Tampa Bay lies within a transition zone between more temperate climate to the north and tropical climate to the south (Stevens et al., 2006; Osland et al., 2013). The magnitudes of prey subsidies driven by hydrology will depend on freshwater inflows and the degree to which inundated floodplains trigger productivity of prey. The objective of this study was to test for seasonal changes in Snook abundance in rivers along a latitudinal gradient in Florida. In a species that exhibits great habitat plasticity, we seek to better understand to what degree this plasticity enables the species to adapt to local environmental conditions.

## 2. Materials and methods

Snook were sampled in a range of rivers along the Gulf of Mexico coast of Florida during 2012–2016. Use of rivers by Snook can vary considerably by year depending on broad-scale climatic conditions

(e.g., annual rainfall and freshwater inflow, cold events, droughts; Stevens et al., 2016; Boucek et al., 2016, 2017; Blewett et al., 2017), so it was important to compare data sets that were collected during the same time period to minimize climatic effects as much as possible and to focus on comparisons of seasonal habitat use along a latitudinal gradient (Table 1). The rivers sampled included 1) Shark River in the coastal Everglades; 2) Peace and Myakka rivers of Charlotte Harbor; 3) Hillsborough, Little Manatee, Manatee, and Alafia rivers of Tampa Bay; and 4) Homosassa, Chassahowitzka, and Crystal rivers, which represent the spring-fed rivers that lead to the Gulf of Mexico north of Tampa Bay.

Air temperature and freshwater inputs across the study areas were compared for at least a decade to elucidate differences as a function of latitude. Stations representative of each study area were chosen based on the availability of data maintained by the National Oceanic and Atmospheric Administration, the National Climatic Data Center (<https://www.ncdc.noaa.gov/>) and the U.S. Geological Survey (<https://waterdata.usgs.gov/nwis>). For air temperature (°C), the period 2001–2014 had data availability for the stations closest to representative rivers: Weeki Wachee (spring-fed rivers), Tampa Bay Forecast Center (Tampa Bay), Punta Gorda (Charlotte Harbor), and Everglades (Everglades). For freshwater inflows (m<sup>3</sup>/s), the period 2000–2016 had the greatest data availability on gauged river flow. Homosassa River (site 02310700; 2004–2016) was used to represent spring-fed rivers; Little Manatee River was used to represent Tampa Bay rivers (site 2300500; 2000–2016); Peace River (site 2296750; 2000–2016) was used to represent Charlotte Harbor rivers; and Shark River (sites 252230081021300 and 252551081050900; 2004–2016) was used for the Everglades. Data across the time record for each station were averaged by day of year (days 1–366).

Electrofishing was conducted in each study area. A boat-mounted, generator-powered electrofisher was used (a two-anode, one-cathode Smith-Root 9.0 unit). Power output was standardized to 1500 W, given temperature and conductance conditions measured at the beginning of each sample (Burkhardt and Gutreuter, 1995). For each of the rivers, stunned Snook were collected from the water with dip nets and placed in a large holding tank. After each transect was completed, Snook were measured to the nearest mm total length (TL). All sampling was conducted between 0800 and 1800 Eastern Standard Time. High salinity limited the sampling universe at times for some of the river systems because electrofishing is most effective in freshwater (Burkhardt and Gutreuter, 1995). If salinity at a site was as high as 10 PSU, the site was still sampled, provided the water was shallow enough to allow for effective electrofishing. If salinity exceeded 10–15 PSU, an alternative site was sampled farther upriver, chosen from a list of randomly selected alternate sites. For coastal Everglades and Charlotte Harbor, salinities were always less than 2 PSU.

In the coastal Everglades, electrofishing data for 2012–2015 were included for six fixed sites located at the headwaters of the Shark River (for details on the sampling program, see Boucek and Rehage, 2013). Fish communities were sampled at these sites 5–9 times per year (November–June). Previous research with more frequent sampling (i.e., monthly) found that the November–June period allowed adequate assessment of changes in Snook abundance during the year (Boucek et al., 2016). Three replicate electrofishing transects, 200 m apart, were conducted at fixed locations at each site (total n = 412). Along each transect, the boat was run at idle speed at a randomly selected creek shoreline and 5 min of electrofishing was conducted (Rehage and Loftus, 2007). The distance traveled during each transect was recorded using a GPS. Depth ranged from 0.5 to 3.0 m.

In the rivers of Charlotte Harbor, electrofishing data for 2012–2015 were included in the comparison. Fish were sampled during two calendar seasons: summer (21 June–20 September) and fall (21 September–20 December). Previous research with more frequent sampling (four seasonal sampling events) found that summer and fall sampling allowed adequate assessments of changes in Snook abundance during the year (Blewett et al., 2009; Blewett et al., 2013). For site

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