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# Atlantic Tarpon (*Megalops atlanticus)* exhibit upper estuarine habitat dependence followed by foraging system fidelity after ontogenetic habitat shifts

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ABSTRACT

Fish can have complex life histories and use multiple habitats and resources during different life stages. Consequently, their complete life histories are often poorly understood. Atlantic Tarpon (*Megalops atlanticus*) is an ecologically and economically important sport fish, yet little is known about its lifelong habitat and resource use. We used stable isotope analysis of eye lens $\delta^{13}C$ and $\delta^{15}N$ to explore patterns in trophic history and habitat use of 16 Atlantic Tarpon from west-central Florida and Louisiana. The stable isotope chronologies indicated dependence on upper estuarine habitats during the early life history, and an ontogenetic shift to coastal waters at approximately 10 years of age and 140 cm total length. During the coastal phase, Atlantic Tarpon displayed among-individual variability and within-individual consistency in basal-resource dependence. Our study highlights the importance of upper estuarine habitats to the early life stages of Atlantic Tarpon, as well as the possibility that adults show fidelity to coastal systems for feeding and growth.

## 1. Introduction

Many fish species have complex life histories that result in their use of multiple habitats and resources throughout their lifespans to maximize growth, survival, and reproduction (Whitfield, 1990; Able and Fahay, 1998; Able, 2005; Gillanders, 2005). Migration maximizes fitness by allowing the fish to seek optimal environments and resources throughout the year and during different life history stages (Dingle and Drake, 2007). Ecologically, these movements are important, as they result in a substantial movement of biomass, energy, and nutrients (Deegan, 1993).

There are different types of migrations fish species can exhibit. One form is ontogenetic migration, which entails habitat shifts made by individuals at various times during life. As fish grow larger, individuals may move across habitats in response to changes in predation risk or gape-related changes in diet (Werner and Gilliam, 1984; Werner and Hall, 1988). Another form is seasonal migration which often involves large-scale movements between areas used for feeding and reproduction (Barton, 2007). Natural selection favors individuals that occupy habitats that maximize the growth-to-mortality ratio, including those that occupy particular sequences of habitats to this effect (Dahlgren et al., 2006; Snover, 2008). Migration routes are often consistent over space and time, and species can exhibit fidelity to spawning and feeding grounds (Rosenberg et al., 2000; Hunter et al., 2003; Schofield et al., 2010). Understanding fish habitat use and migration is important for spatially explicit management and conservation (Hobson, 1999), yet improving this understanding is impeded by the limitations of conventional tagging and other methods used to investigate fish habitat use (Seeley and Walther, 2018).

Recent applications of natural, ecogeochemical tags to this problem have improved interpretations of habitat residency and resource use, avoiding some of the issues prevalent with conventional tagging (Thorrold et al., 2002; Begout et al., 2016; Schaefer and Fuller, 2016). In addition, stable isotope analysis (SIA) of body parts that function as chronological recorders allows re-creation of lifelong histories of diet and habitat use in individuals (Tzadik et al., 2017). Lifelong diet histories include information on the types of primary producers that support biomass at higher trophic levels (i.e., basal resources, *sensu* March and Pringle, 2003). By coupling knowledge of basal-resource isotope variation with knowledge of geographic variation in baseline isotopes (isoscapes), we can begin to make inferences about habitat use as well as migrations that may be occurring among habitats.

Identifying critical habitats and tracking movements among them by migrating species have remained major research challenges (Elsdon

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and Gillanders, 2003). Conventional external tags (e.g., dart tags, satellite tags) are useful in many applications but can also have logistical constraints such as tag loss, cost, inability to tag small juveniles, and low return rates (Robson and Regier, 1966; McFarlane et al., 1990). Natural tags such as otolith trace elements and SIA provide alternative means for investigating species movement. Natural tags are advantageous because they are incorporated at an early life stage, can provide continuous life history information (rather than punctuated observations), and cannot be lost (Elsdon et al., 2008). SIA of the eye lens is a novel natural tagging technique that has the potential to increase spatial and temporal resolution of movement and habitat use while minimizing the problems associated with conventional tags (Wallace et al., 2014; Tzadik et al., 2017; Quaeck-Davies et al., 2018). Internally recorded stable isotopes, specifically $\delta^{13}C$ and $\delta^{15}N$, can be used to recreate lifelong trends in animal diets, basal resource use, and movements (Post, 2002; Wallace et al., 2014).

Fish eye lenses have been recently shown to be an internal recorder of stable isotopes in fishes and are one of the only known sources of simultaneous $\delta^{13}C$ and $\delta^{15}N$ temporal records in bony fishes (Wallace et al., 2014; Quaeck-Davies et al., 2018). As a fish grows, the eye lens proportionally increases in size as new concentric layers grow at the outside of the eye lens (Nicol and Somiya, 1989; Horwitz, 2003). The cells in the completed layers undergo attenuated apoptosis, in which all organelles are removed, rendering future protein synthesis impossible. Therefore, each successive layer represents a distinct, conserved record of dietary stable isotopes at the time of apoptosis (Nicol and Somiya, 1989). These layers can be peeled away (delaminated) and analyzed individually, allowing re-creation of lifetime isotope histories.

$\delta^{15}N$ increases by approximately 3‰ per trophic step and is thus a strong indicator of trophic position (Minagawa and Wada, 1984; Peterson and Fry, 1987). In contrast, $\delta^{13}C$ has a relatively low trophic enrichment of about 1‰ per trophic step and is a weaker indicator of trophic position (DeNiro and Epstein, 1978; Peterson and Fry, 1987). However, in estuarine and other coastal environments, a number of interrelated, numerical guidelines exist for interpreting lifetime trends in $\delta^{13}C$ as these relate to basal-resource dependence.

The goal of the present study was to use SIA of a chronological isotope recorder, the eye lens, to examine the following questions regarding the life history and migration of a poorly understood marine fish, the Atlantic Tarpon (*Megalops atlanticus*), specifically: 1) what habitats and resources do juvenile and sub-adults use during their ontogeny?; 2) how do individuals transition from habitats associated with ontogeny to those associated with sexual maturity, and when does this occur?; and 3) what habitats and basal resources are used by adults during their seasonal/annual migrations?

## 2. Methods

### 2.1. Study species

Atlantic Tarpon, *Megalops atlanticus,* is a large, elopomorph fish found in coastal and inshore waters of the tropical and subtropical Atlantic Ocean (Wade, 1962). Atlantic Tarpon is a prized sportfish, and the recreational fishery generates billions of dollars and thousands of jobs annually in the United States alone (Crabtree et al., 1992; Ault et al., 2008; Seyoum et al., 2008). As a highly mobile mesopredator, Atlantic Tarpon use different habitats and resources throughout its life cycle, foraging on a wide variety of prey, and can be prey to several shark species (Ault et al., 2008; Hammerschlag et al., 2012). Despite the ecological and economic importance of this species, a complete understanding of its full life history is lacking. Most research has focused on development of the Atlantic Tarpon's leptocephalus larva (Wade, 1962; Crabtree et al., 1992; Shenker et al., 2002) as well as demographic aspects of larger individuals such as age, growth, and reproduction (Crabtree et al. 1992, 1995, 1997; Andrews et al., 2001). Recently, tagging and otolith microchemistry studies have begun to address questions concerning adult migration and habitat use (Brown and Severin, 2007; Luo et al., 2008; Woodcock and Walther, 2014; Rohtla and Vetemaa, 2016). Atlantic Tarpon is currently listed as vulnerable by the IUCN (Adams et al., 2012) due, in part, to regional exploitation, loss of natal habitat, poor water management, and offshore disturbances such as oil spills (Ault et al., 2008).

Research on Atlantic Tarpon habitat use has generally been limited to snapshot observations. Following their pelagic leptocephalus larval stage, Atlantic Tarpon typically recruit to upper estuarine habitats such as brackish lagoons, mangroves, and tidal creeks, where predation is thought to be low and food resources are widely available (Crabtree et al., 1995; Seymour et al., 2008). As juvenile Atlantic Tarpon approach maturity, they appear to become more dependent on deeper-water habitats such as rivers, sloughs, and canals that provide access for emigration into coastal waters (Ault et al., 2008); however, no definitive link between these habitats and the adult stage has been demonstrated. The juvenile/sub-adult stage is thought to last approximately seven to ten years, at which point individuals become sexually mature and undergo an ontogenetic migration to coastal waters, where they join the adult spawning stock; this migration may also involve changing food habits (Cyr, 1991; Crabtree et al. 1992, 1997). In general, the movement patterns and trophic relationships associated with this ontogenetic shift are poorly understood.

### 2.2. Specimen collection

Adult Atlantic Tarpon were collected opportunistically from fishing mortalities from West-Central Florida (FL, $n = 13$) and Louisiana (LA, $n = 3$) (Table 1.). Recreational fishing mortalities often result from

**Table 1**
Size, age, and collection information for Atlantic Tarpon specimens. Methods for age determination are presented in Section 2.4.

| Specimen ID | Collection date | Total length (mm) | Weight (estimated kg.) | Age (years) | Location |
|---|---|---|---|---|---|
| **T01** | 5/13/2014 | 1829 | 45 | 17 | Boca Grande Pass, FL |
| **T02** | 5/22/2014 | 1699 | 41 | 19 | Bean Point, Anna Maria Island, FL |
| **T03** | 6/10/2014 | 2210 | 91 | 22 | Bean Point, Anna Maria Island, FL |
| **T04** | 6/19/2014 | 1651 | 27 | 19 | Captiva Island, FL |
| **T05** | 6/25/2014 | 1626 | 41 | 15 | Anna Maria Island, FL |
| **T06** | 7/22/2014 | 1651 | 36 | 21 | Charlotte Harbor, FL |
| **T07** | 8/11/2014 | 1778 | 39 | 14 | Tampa Bay, FL |
| **T09** | 8/24/2014 | 1397 | 25 | 10 | Charlotte Harbor, FL |
| **T10** | 9/14/2014 | 1524 | 50 | 20 | Charlotte Harbor, FL |
| **T11** | 5/18/2015 | 1829 | 54 | 17 | Egmont Key, FL |
| **T12** | 7/01/2015 | 1880 | 61 | 14 | Anna Maria Island, FL |
| **T13** | 9/21/2015 | 2108 | 64 | 17 | Tampa Bay, FL |
| **T14** | 9/23/2015 | 1588 | 27 | 12 | Tampa Bay, FL |
| **T15** | 7/23/2015 | 2184 | 70 | 16 | Grand Isle, LA |
| **T16** | 7/23/2015 | 2134 | 75 | 19 | Grand Isle, LA |
| **T17** | 7/23/2015 | 2057 | 59 | 15 | Grand Isle, LA |

exhaustion during the fight or from shark attacks. The low sample size from Louisiana were not part of the original collection plan but were an opportunistic collection from a kill-tournament in Grand Isle, LA. Specimens were collected during the recreational fishing seasons (April through September) of 2014 and 2015. This time period reflects the months when large numbers of Atlantic Tarpon inhabit the coastal waters of each of the sampling regions. Individuals were kept in a large cooler on ice from time of collection to dissection. Storage on ice has been shown to prevent isotopic offsets in predatory fishes (Stallings et al., 2015). Biological sampling included eyes and eye lenses, sagittal otoliths, and muscle tissue.

### 2.3. *Sample preparation*

Left eye lenses of each specimen were delaminated according to Wallace et al. (2014). Whole eyes were removed by severing the sclera at its junction with the optic nerve and by severing the rectus (orbital) muscles near their junction with the sclera. Eyes were individually wrapped in aluminum foil, placed in plastic bags, and frozen upon return to the laboratory. Eyes were thawed before dissection. After thawing, a scalpel was used to create a flap in the cornea, which was then folded back to allow removal of the lens. Exterior tissue, including the lens capsule, and vitreous material were manually removed while rinsing with deionized water. The rinsed lens, which contains the lens nucleus, cortex, and lens epithelium together as one cohesive unit, was then placed in a glass Petri dish where successive layers of cortical laminae were separated using two pairs of fine-tip forceps under a dissecting stereomicroscope, until reaching the largely dehydrated core of the eye lens. The core is defined here as the central region of the lens that remains after manual delamination. The large eyes of adult Atlantic Tarpon have a hardened core region that is largely dehydrated and is difficult to delaminate. These dehydrated cores were approximately 5–6 mm in diameter and contained multiple lens laminae. Laminae from the hardened core were obtained by sectioning the core along the equatorial plane and through the nucleus using an Isomet low-speed saw equipped with two blades that were separated by a 0.75 mm spacer. The resulting section had readily identifiable laminae that were manually divided and removed under a dissecting stereomicroscope until reaching the central region of the eye lens (~1.0 mm in diameter). After each delamination, an ocular micrometer was used to measure the diameter at the equator to the nearest 0.1 mm. Drying of all laminae was rapid (< 1 h) and did not require heating. Dried lamina samples were stored in one-dram glass vials after being homogenized with a mortar and pestle.

### 2.4. *Stable isotope analysis*

Eye lens samples were analyzed for elemental carbon and nitrogen (C, N) and bulk stable isotope ratios ($\delta^{13}$C, $\delta^{15}$N). First, 400–1000 µg of each lens layer was collected and weighed on a Mettler-Toledo precision micro-balance, wrapped in tin capsules, and loaded into a Costech Technologies Zero-Blank Autosampler. Samples were combusted at 1050 °C in a Carlo-Erba NA2500 Series-II Elemental Analyzer coupled in continuous-flow mode to a Finnigan Delta Plus XL isotope ratio mass spectrometer. Isotopic measurements were normalized to the AT-Air and VPDB scales, respectively, using NIST 8573 and NIST 8574 L-glutamic acid standard reference materials. Measurements were expressed in per mil (‰) using δ notation, where $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$, and R is the isotopic ratio of interest (e.g., $^{13}$C:$^{12}$C). Analytical precision was estimated by replicate measurements of a working standard (NIST 1577b, bovine liver; E. Goddard, USF, pers. comm. To Ben Kurth, 2018).

### 2.5. *Age estimation*

Sagittal otoliths were independently aged by the Age and Growth Lab at Florida's Fish and Wildlife Research Institute (FWRI). The frequency of annulus formation in Atlantic Tarpon otoliths has been validated by comparing radiocarbon trends in the otolith with temporal trends in bomb-spike radiocarbon (Andrews et al., 2001). Using video photomicrography and measuring software, individual annuli were marked and the radial distance of each annulus from the core was measured at the sulcus. We recognized that eye-lens diameter is strongly proportionate to fish length, which allowed us to first relate otolith age to body length, and then relate age-at-length to lens diameter. The existence of strong proportionality between eye dimensions and body length has been observed in a multitude of vertebrates, including teleosts (Kroger and Fernald, 1994; Howland et al., 2004; Richardson et al., 2015). A third-order polynomial function was generated that estimated age as a function of annulus radial distance from the otolith core. All polynomial functions had $R^2$ values greater than or equal to 0.97. The polynomial function was then used to estimate the age and total length (TL) that each lamina represented. Since the outermost layer of the eye lens is well hydrated and is disproportionately thick compared to the other laminae, it was excluded from the generation of the polynomial function and estimation of eye-lens age. Likewise, the polynomial function did not include the marginal increment, assuming the marginal increment and hydrated outer layer of the eye lens represented approximately the same period of time and growth.

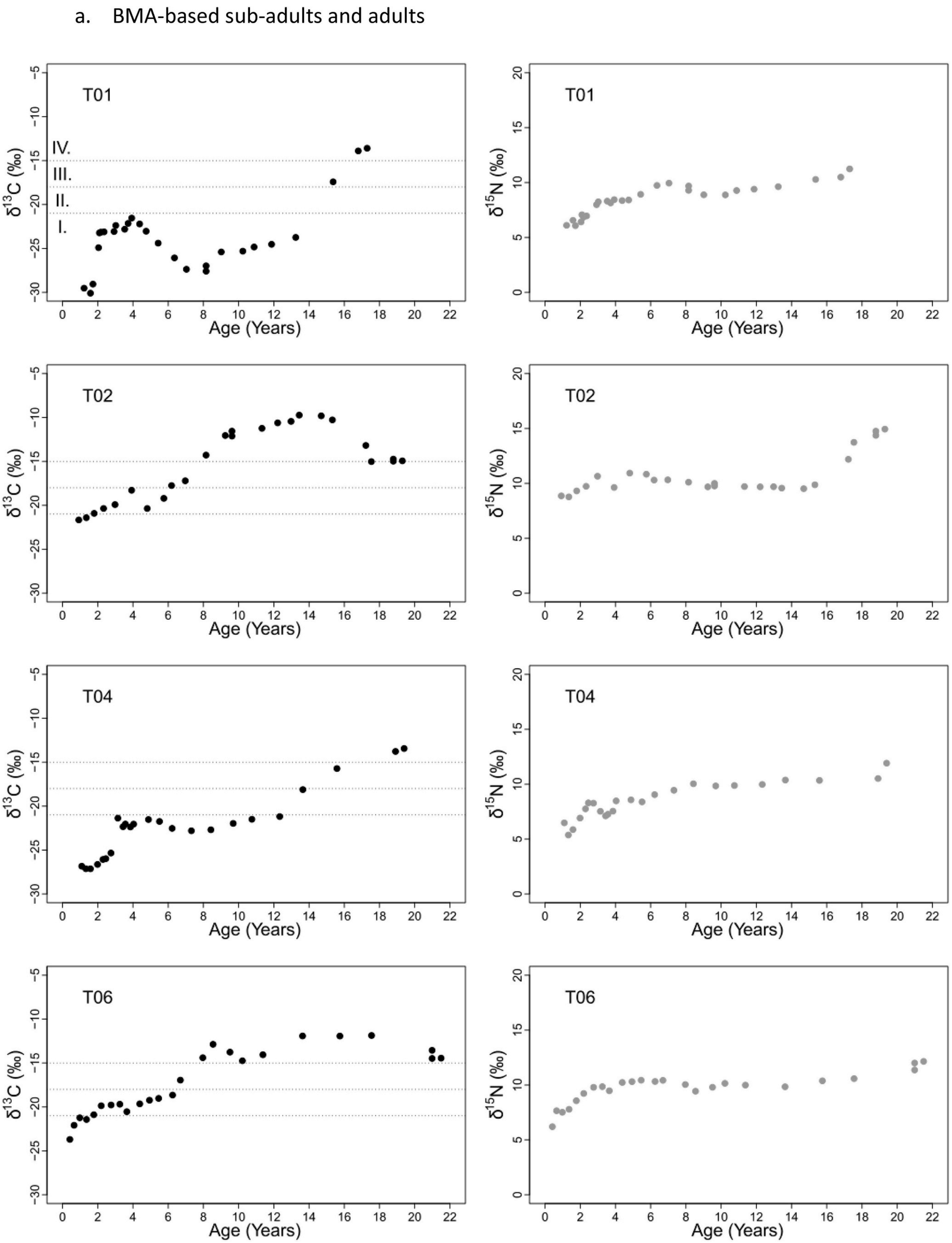
### 2.6. *Data analysis*

Isotope profiles (re-created lifetime records) were generated for $\delta^{13}$C and $\delta^{15}$N values vs. both age and TL for each specimen and were interpreted using the rules of interpretation presented in Table 2 and discussed in section 4.1. The profiles were separated into three distinct time periods based on $\delta^{13}$C values; these are referred to as 1) the upper estuarine phase, characterized by very light and variable $\delta^{13}$C less than −21‰, 2) a transitional period, or ontogenetic shift, represented by an elevation of $\delta^{13}$C values, and 3) the coastal phase, in waters with $\delta^{13}$C values greater than −21‰. Coastal-phase Atlantic Tarpon were then subdivided according to dominant basal resource; BMA-based, PP-based, or mixed PP-BMA. We quantified the variation in $\delta^{13}$C and $\delta^{15}$N values during the coastal phase by calculating coefficients of variation of $\delta^{13}$C and $\delta^{15}$N for each individual and then calculating the mean of all individuals. The mean age at ontogenetic shift was calculated, as were the mean $\delta^{13}$C and $\delta^{15}$N values of the and coastal phases, the final outside layer of the eye lens, and muscle-tissue samples. These mean values were compared between states (FL and LA) using parametric (*t*-test) and non-parametric tests (Wilcoxon) based on whether the data met parametric assumptions.

**Table 2**

Rules of interpretation for stable isotope data. Discussion of these rules is presented in section 4.1

| Isotope | Data Pattern | Interpretation | Reference |
|---|---|---|---|
| **$\delta^{13}$C** | < -21‰ | Upper-estuarine habitat use | Frazer et al., (2001), Hollander and Peebles (2004), Malkin, 2010 |
| **$\delta^{13}$C** | −21‰ to −18‰ | Coastal phytoplankton-based food-web | Peterson and Fry (1987), McMahon et al. (2013), Radabaugh el al. 2013 |
| **$\delta^{13}$C** | > =-15‰ | Benthic-microalgae-based food web | France (1995), Doi et al., (2010), Radabaugh et al., (2014) |
| **$\delta^{13}$C and $\delta^{15}$N** | Coordinated change | Change in trophic position | McCutchan et al., (2003), Hussey et al., (2014) |



a. BMA-based sub-adults and adults

**Fig. 1.** Individual $\delta^{13}C$ and $\delta^{15}N$ stable isotope profiles. The $\delta^{13}C$ profiles were separated into four regions with each indicating different basal-resource dependence: I, Upper estuarine-based; II, phytoplankton-based; III, mixed dependence; IV, benthic-microalgae-based. Individuals were grouped into subsets based on basal resource use after transition to coastal habitats.

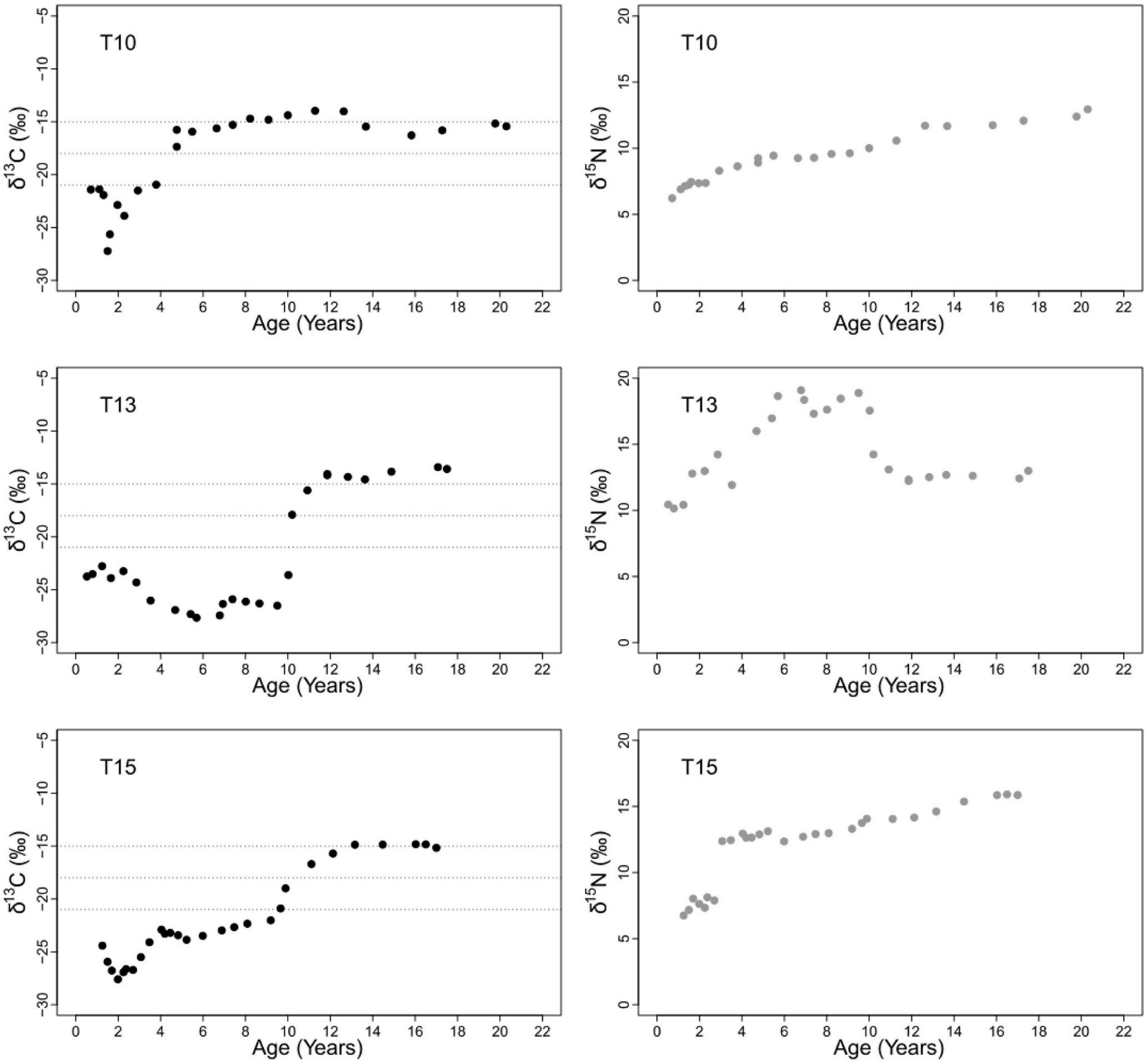


**Fig. 1.** (*continued*)

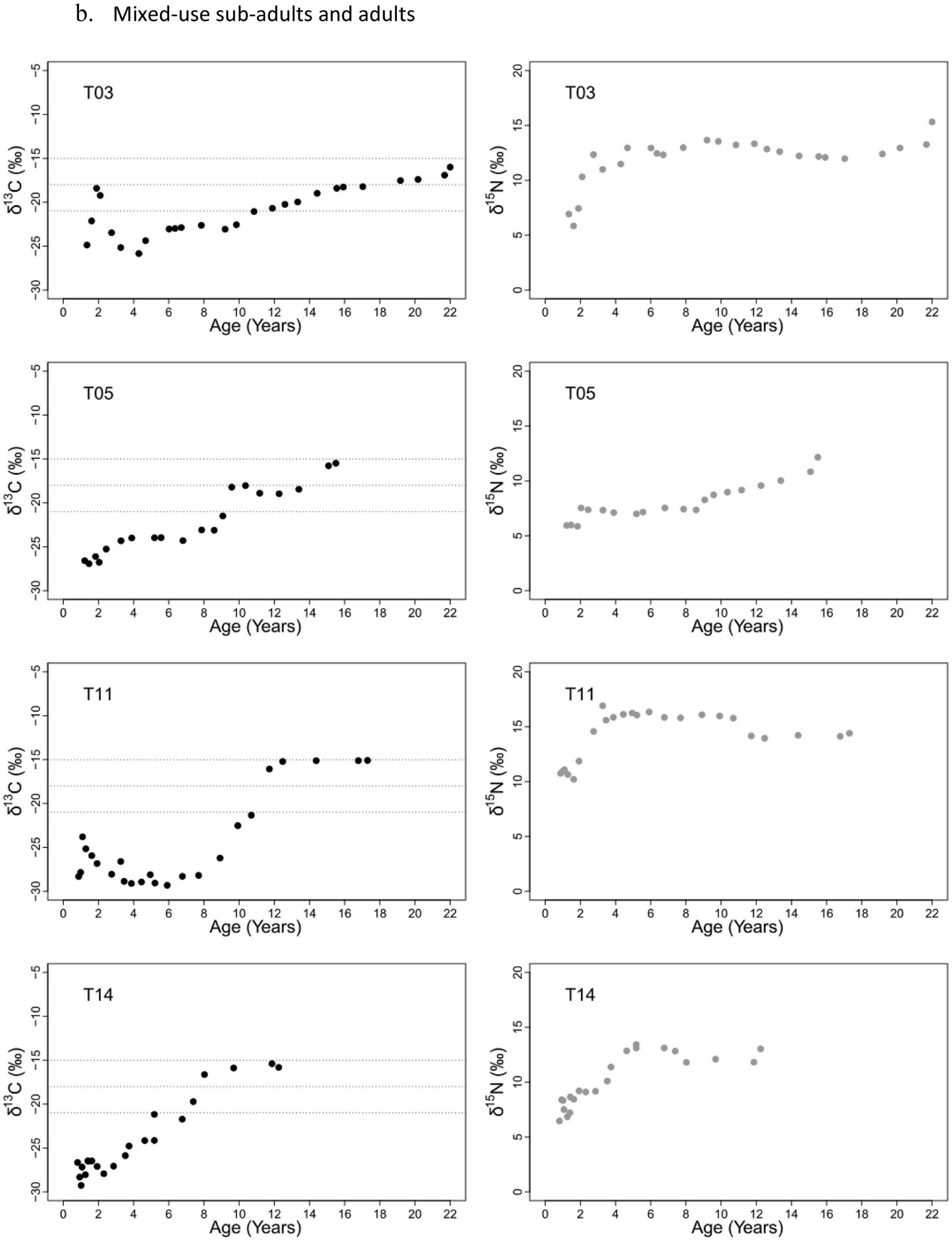
## 3. Results

All Atlantic Tarpon profiles (Fig. 1) strongly suggested recruitment to and use of upper estuarine habitats during early life. The mean ± standard error (SE) $\delta^{13}$C value during this phase was −24.83 ( ± 0.19) ‰, which is well within the range that characterizes upper estuarine habitats. On average, Atlantic Tarpon used upper estuarine habitats for 9.8 ( ± 0.91) years, corresponding with 1390.56 ( ± 76.76) mm TL, before migrating into coastal waters, as indicated by $\delta^{13}$C values greater than −21‰. Two of the 16 individuals had an isotopic shift to values just greater than −21‰ at a mean age of 1.78 ( ± 0.01) years, before displaying another shift to coastal waters at approximately the same age as the other specimens. After the ontogenetic shift, $\delta^{13}$C values were indicative of coastal habitat use, averaging −16.03‰ ( ± 0.17). Atlantic Tarpon from Florida had lower coastal phase $\delta^{15}$N values, averaging 11.48‰ ( ± 0.15), while Louisiana averaged 15.19‰ ( ± 0.19) (Wilcoxon: W = 48, $p < 0.001$). Once in the coastal phase, Atlantic Tarpon appeared to depend on a variety of prey types and basal resources.

During the coastal phase, seven of the 16 (44%) $\delta^{13}$C profiles for sub-adults and adults were indicative of primarily feeding within a BMA-based food web, and six (38%) profiles were indicative of dependence on a mixture of PP- and BMA-based food webs. One profile indicated dependence on a PP-based food web, one individual had not been mature long enough to develop a complete post-shift profile, and another individual displayed a mixed-use diet during the beginning of the coastal phase before gradually shifting to a completely PP-based diet (Table 3). Atlantic Tarpon isotope values were consistent throughout the coastal phase, indicating reliance on the same food web and basal resources. Individual coefficients of variation during the coastal phase ranged from −0.03 to −0.14‰, with a mean of −0.10‰ ± 0.009 for $\delta^{13}$C and a range of 0.01–0.14‰ with a mean of 0.06‰ ± 0.009 for $\delta^{15}$N.

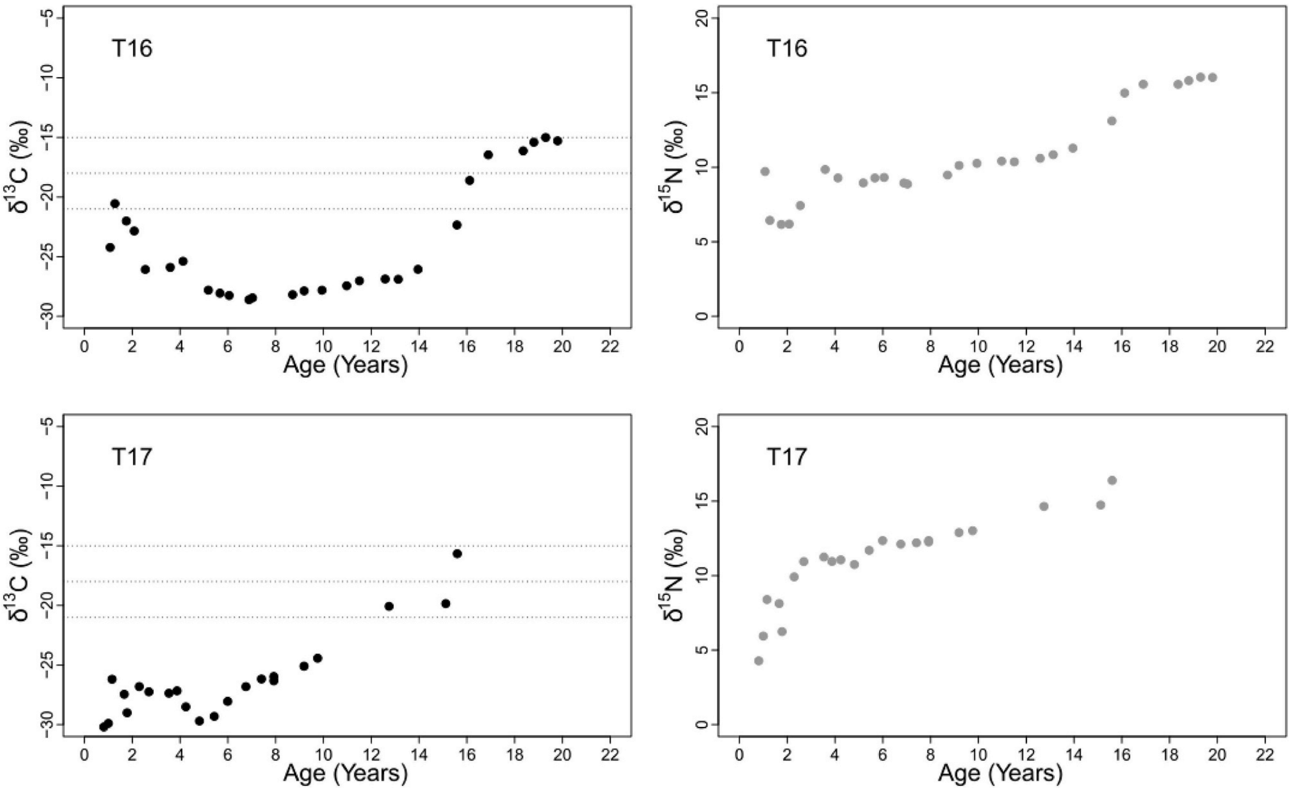
## 4. Discussion

The research presented here provides the trophic history of the Atlantic Tarpon at the highest temporal resolution to date, which was

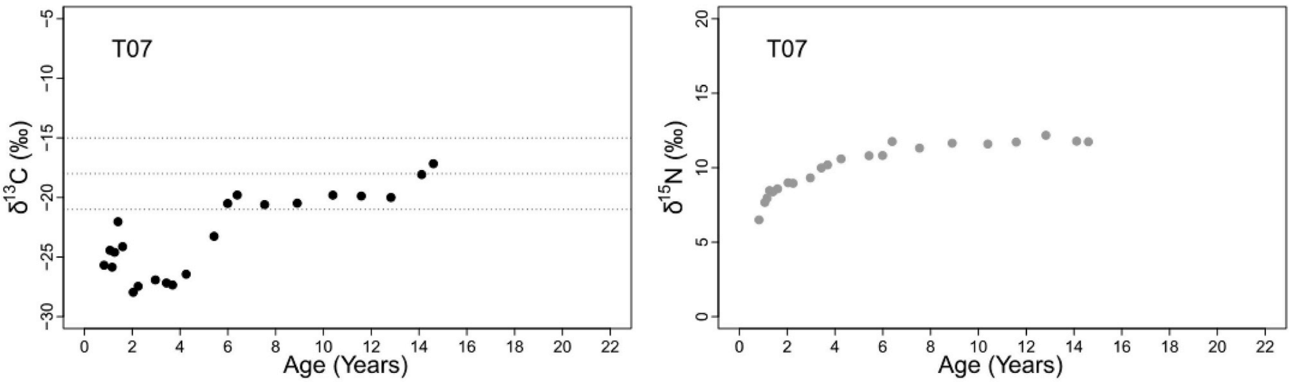


b. Mixed-use sub-adults and adults

Fig. 1. (*continued*)



c. PP-based



d. No coastal phase detected (young fish)

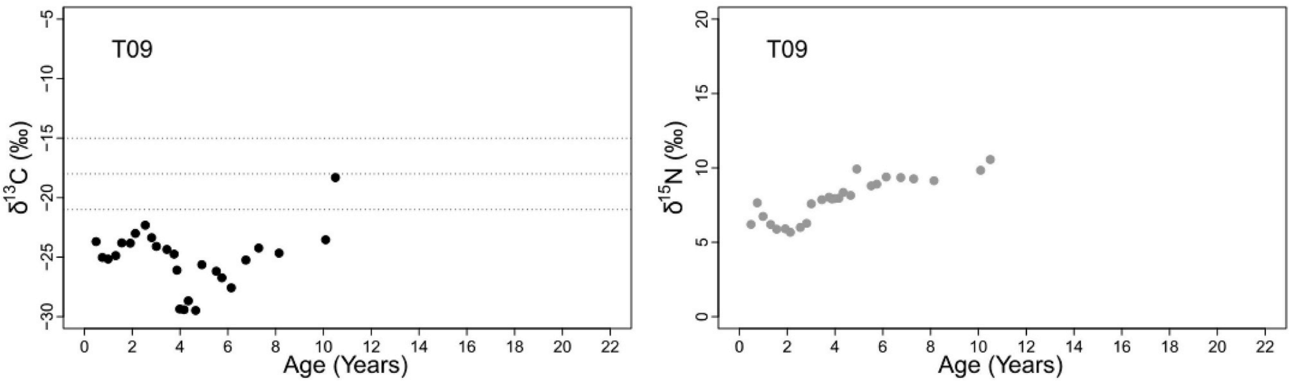


**Fig. 1.** (*continued*)

e. Mixed-use transitioning to PP-based

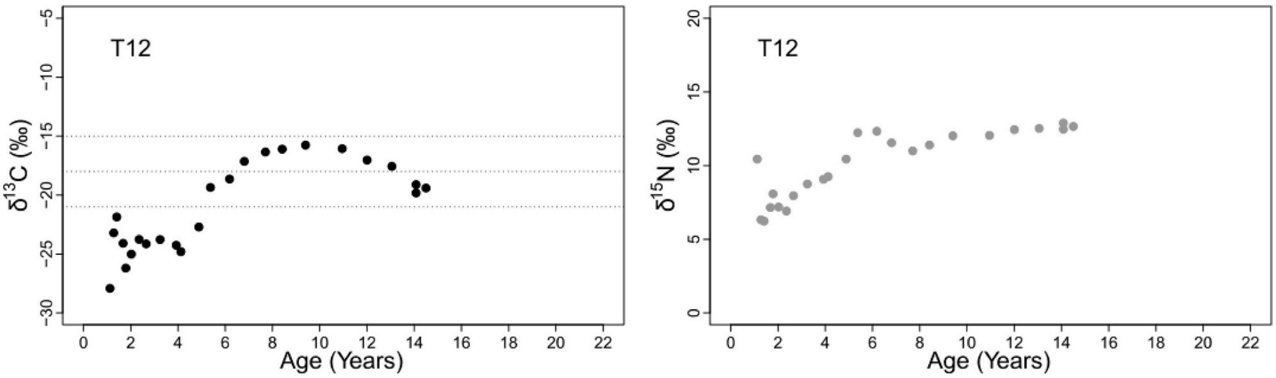


**Fig. 1.** (*continued*)

**Table 3**

Percentage of habitat usage at different life stages based on basal-resource dependence. Note that basal-resource dependence in the upper estuary could involve either phytoplankton or vascular plants (e.g., mangroves, marsh grasses, allochthonous riparian vegetation).

| | Upper Estuarine | PP-Based | Mixed-Use | BMA-Based | Other |
|---|---|---|---|---|---|
| **Juvenile** | 100% | 0% | 0% | 0% | 0% |
| **Adult** | 0% | 6% | 38% | 44% | 12% |

accomplished with the newly described use of eye lens SIA. Our work is the first to describe the lifelong trophic- and habitat-use history of Atlantic Tarpon in the eastern Gulf of Mexico. This work builds upon previous snapshot observations of habitat use for this species at different life stages. The results support previous suggestions concerning the importance of upper estuarine habitat and the timing of ontogenetic habitat shifts, while revealing new insights about the feeding ecology and trophodynamics that relate to seasonal migrations.

### *4.1. Isotopic interpretations*

Three persistent tendencies in environmental $\delta^{13}C$ were used to characterize habitats occupied by tarpon. The first of these is the tendency for coastal phytoplankton (as POM) to have $\delta^{13}C$ values near −22‰. Radabaugh et al. (2013) reported POM $\delta^{13}C$ within the northeastern Gulf of Mexico as having a range of −25 to −20‰, except in areas that are under freshwater influence (i.e., areas near the Florida Everglades or near river discharges in the north-central Gulf of Mexico), where the values tend to be more negative. This range corresponds with the range reported by McMahon et al. (2013) for the entire, open Gulf of Mexico, and also with the value of −22‰ that is often cited as being representative of ocean POM (e.g., Peterson and Fry, 1987). Thus, in the northeastern Gulf of Mexico, large, well-mixed bodies of water that have open connections to the Gulf of Mexico tend to have POM $\delta^{13}C$ values that are within one of two per mil of −22‰.

A second tendency is the tendency for POM $\delta^{13}C$ from the interiors of semi-confined waters, including the tidal portions of rivers, to be (1) more negative than open coastal waters, ranging to −30‰ or lower, and (2) more temporally variable (Frazer et al., 2001; Hollander and Peebles, 2004, Malkin, 2010). The process behind these reduced, variable POM $\delta^{13}C$ values is thought to be the enhanced likelihood of carbon recycling within quiescent, organic-rich waters such as swamps, marshes and other habitats where the $CO_2$ evolving from respiring, microbial, detritus decomposers is more likely to taken up for new photosynthesis, thereby repeating negative photosynthetic fractionation and making the overall pool of POM $\delta^{13}C$ more negative (Keough et al., 1998). Dissolved gases are more likely to be reincorporated into new photosynthesis in habitats where the gases are not advected or outgassed via enhanced turbulence and flux at the water-atmosphere interface. Notably, freshwater-inflow hydrographs are often highly unstable, particularly within small watersheds, and this can create a temporally variable effect on the POM $\delta^{13}C$ pool in upper estuarine areas (Frazer et al., 2001). Compared with open coastal waters, the small water volumes of shallow, semi-confined habitats are thus more prone to the periodic, mass-balanced effects of dilution and turbulence, creating instabilities that change the likelihood of DIC recycling.

The third tendency is for the $\delta^{13}C$ of benthic algae to be about 5‰, on average, higher than that of the local phytoplankton (France, 1995; Doi et al., 2010). This phenomenon was investigated by Radabaugh et al. (2014), who suggested light limitation at depth results in less photosynthetic fractionation, yielding more positive $\delta^{13}C$ values for benthic algae. Benthic algae tend to be most abundant in clear, shallow, uncolored (low CDOM) waters, which occur in the lower estuary and shallow Gulf of Mexico. In areas that receive runoff from surface drainage, CDOM inhibits benthic algal growth through light absorption, and thus elevated $\delta^{13}C$ usually is not indicative of the upper estuary. It should be noted that literal interpretation of each of these numerical guidelines can be confounded by variation in isotopic baselines and various ecosystem processes that affect isotopic fractionation.

Whereas $\delta^{15}N$ isoscapes for the continental-shelf waters of the eastern Gulf of Mexico waters are known to have generalized spatial trends (Radabaugh et al., 2013; Radabaugh and Peebles, 2014), $\delta^{15}N$ isoscapes within the shallow estuarine waters of the region are known to be spatiotemporally complex. For rainy times of year, Malkin (2010) was able to accurately and precisely model the $\delta^{15}N$ of fish muscle in 29 different estuarine areas by weighting land-use-specific $\delta^{15}N$ by the proportional spatial coverage of different land-use classes within estuarine watersheds. During dry times of year, this isotopic connectivity with land use in the watershed became diminished, as did the accuracy and precision of Malkin's regression-based models. Because the Atlantic Tarpon used in the present study occupied such highly variable habitats, no attempt was made to interpret habitat use based on $\delta^{15}N$. These trends are, however, presented here graphically along with lifetime trends in $\delta^{13}C$ (Fig. 1, Supplemental Fig. 1).

For $\delta^{13}C$, the principal process used in data interpretation was the contrast between the highly variable and often more negative $\delta^{13}C$ of the semi-enclosed waters of the upper estuary (Deegan and Garritt, 1997; Keough et al., 1998; Fry, 2002) and the more stable $\delta^{13}C$ values of the coastal ocean, where POM $\delta^{13}C$ tends to center on −22‰ with much less variability (Peterson and Fry, 1987; Deegan and Garritt, 1997; Chanton and Lewis, 2002).

Complexities associated with trophic fractionation of $\delta^{13}C$ during life are also made uncertain by variability in the rates of trophic fractionation among species and tissue types (McCutchan et al., 2003), and these fractionations are possibly dependent on trophic position (Hussey et al., 2014), wherein individuals at higher trophic positions have lower $\delta^{15}N$ fractionations than those at lower trophic positions. Another potentially confounding relationship is fish species that have fast rates of increase in mouth size during life (such as Atlantic Tarpon) also tend to increase their trophic position during life (Ríos et al., 2019); because trophic fractionations among vertebrates are often positive (particularly for $\delta^{15}N$, McCutchan et al., 2003), an increase in both $\delta^{15}N$ and $\delta^{13}C$ is expected during life in such species. Thus, coordinated changes in $\delta^{15}N$ and $\delta^{13}C$ values (i.e., where both values change together either positively or negatively) are likely to occur as trophic position increases or decreases.

The environmental processes that affect $\delta^{15}N$ and $\delta^{13}$ Cisoscapes are largely independent (Radabaugh et al., 2013; Radabaugh and Peebles, 2014). Change in trophic position is the only process that the authors are aware of that would result in simultaneous positive or negative changes in $\delta^{13}C$ and $\delta^{15}N$ (Peterson and Fry, 1987). In Atlantic Tarpon, there appeared to be considerable lifetime coordination between $\delta^{13}C$ and $\delta^{15}N$ (Supplemental Fig. 1) that we thus interpret as lifetime changes in trophic position. In general, there was more variability in this relationship during early life, when $\delta^{13}C$ values were $< -21‰$ (Supplemental Fig. 1), presumably due to greater influence of dynamic environmental processes in the upper estuary.

### 4.2. Juvenile upper estuarine habitat use

Atlantic Tarpon are considered to have facultative habitat dependence that may vary geographically (Brown and Severin, 2007; Shen et al., 2009; Rohtla and Vetemaa, 2016). In Florida, stable isotope profiles suggested Atlantic Tarpon were consistently dependent upon upper estuarine habitat during the juvenile life stage; every adult Atlantic Tarpon sampled in this study used the upper estuary during early life. Previous speculation on the importance of upper estuarine habitats to Atlantic Tarpon in the eastern Gulf of Mexico suggested the habitat's fitness advantage takes the form of decreased predation and decreased competition (Harrington, 1958; Wade, 1962; Rickards, 1968; Zerbi et al., 2001; Jud et al., 2011; Adams and Cooke, 2015). Atlantic Tarpon have a vascularized swim bladder that allows them to inhabit low-oxygen habitats where negative interspecific interactions may be reduced due to the metabolic and aerobic constraints on their predators and competitors (Shlaifer and Breder, 1940; Geiger et al., 2000; Seymour et al., 2008). For instance, hypoxic conditions would preclude the Atlantic Tarpon's most likely competitor, Common Snook *Centropomus undecimalis*, as well as limit predation by aquatic species, most likely sharks and large fishes.

The Atlantic Tarpon's dependence on upper estuarine habitat was also supported by recent otolith microchemistry work. Brown and Severin (2007) found 33% of Atlantic Tarpon sampled in the western Gulf of Mexico had recruited to fresh or brackish habitats, and 67% recruited to marine waters. Rohtla and Vetemaa (2016) found 92% of Atlantic Tarpon sampled in French Guiana had recruited to fresh or brackish water habitats, and 8% had recruited to marine or hypersaline waters. Thus, unlike our study, which found 100% use of upper estuarine habitats, neither of these microchemistry-based efforts found consistent recruitment to, or dependence on, upper estuarine habitats during early life even with similar sample sizes. Regional differences in Atlantic Tarpon life history have been suggested (Crabtree et al., 1997; Brown and Severin, 2007), possibly explaining this variability across the species' geographic range. These differences may occur for a variety of reasons, including variation in habitat availability and quality, variation in species assemblages and competition, and variation in population connectivity within ecological landscapes.

### 4.3. Ontogenetic habitat shift to coastal waters

After the upper estuarine phase, the isotope profiles displayed a distinct shift in $\delta^{13}C$ values that was indicative of an ontogenetic migration to coastal waters (i.e., $\delta^{13}C >= -21‰$). The conclusion of the shift occurred, on average, at approximately 10 years of age and 140 cm in total length, corresponding closely with the findings of Crabtree et al. (1997), who reported Atlantic Tarpon in Florida reach sexual maturity at approximately 10.5 years and 125 cm fork length (~140 cm total length based on FL:TL relationship reported by Ault et al., 2008). Thus, the ontogenetic shift from the upper estuary to coastal waters may occur as individuals approached or reached maturation. Other studies have also surmised that Atlantic Tarpon begin to move to estuarine and coastal waters at the end of the juvenile and sub-adult stage in response to increasing food requirements and efforts to join spawning populations (Wade, 1962; Rickards, 1968; Cyr, 1991; Crabtree et al., 1992; Crabtree et al., 1995; Zerbi et al., 2001; Stein III et al., 2012; Adams and Cooke, 2015; Seeley et al., 2017; Seeley and Walther, 2018). In addition, Woodcock and Walther (2014) observed similar shifts in stable isotope values in subsamples of Atlantic Tarpon scales (i.e., core, middle, edge) that corresponded with increased foraging on higher-trophic-level prey (indicated by $\delta^{15}N$) and movements from inshore to marine and coastal habitats (indicated by $\delta^{13}C$). Although Woodcock and Walther (2014) interpreted $\delta^{13}C$ as a proxy for salinity and not directly to basal-resource dependence, the conclusions of both studies support similar ontogenetic habitat shifts.

The transitional period of the ontogenetic shift had $\delta^{13}C$ values that increased until they reached intermediate levels indicative of coastal habitat. These intermediate values may have reflected a mixture of upper estuarine and coastal food webs, with fish moving back and forth between the two, or the use of estuarine habitats with intermediate isotope values. The present study was unable to distinguish between these two possibilities because each eye-lens layer conserves the average stable isotope history over the corresponding period of growth, and therefore it was not possible to interpret finer resolutions in the feeding or movement patterns within individual laminae. Three individuals (T03, T06, and T10) appeared to have undergone the ontogenetic shift out of upper estuarine habitats earlier than the other fish. It is possible—and perhaps more likely—that changing conditions in the upper estuary, rather than fish movement, caused this pattern. Upper estuarine locations are often subjected to variation in circulation patterns due to variation in freshwater runoff, and there are times when DIC recycling (low $\delta^{13}C$) is more likely to occur than at other times; the higher $\delta^{13}C$ in the upper estuary can resemble the higher $\delta^{13}C$ at more seaward locations (Keough et al., 1998; Radabaugh et al., 2014). This explanation is consistent with the highly variable $\delta^{13}C$ that was evident during the early life of most of the tarpon examined. The $-21‰$ threshold between upper estuarine and coastal waters is thus not always a definitive one.

### 4.4. Patterns in basal-resource dependence and habitat use

We observed *among*-individual variation in basal-resource dependence during the coastal phase (i.e., PP, BMA, mixed PP-BMA), while *within*-individual basal-resource dependence remained consistent. Many specimens were sampled from the same coastal ecosystems, at the same time of year, and neither age nor size were important factors in basal-resource dependence. Because Atlantic Tarpon is considered a generalist predator, this variation in foraging behavior was not expected; it was thought that individual diets would integrate across spatiotemporal differences in basal-resource availability. However, it is possible that individual feeding specialization (e.g., learning to forage for different prey types such as crustaceans vs. fishes) resulted in the observed consistency in basal-resource dependence within individuals (Bryan and Larkin, 1972; Bolnick et al., 2003; Toscano et al., 2016). While the mechanism behind the individual variability in forage selection remains unclear, within-individual consistency in basal resource dependence was clear.

### 4.5. Foraging system fidelity and Florida-Louisiana comparisons

Despite well-described $\delta^{13}C$ and $\delta^{15}N$ isoscapes in the eastern Gulf of Mexico (Radabaugh et al., 2013), and the fact that Atlantic Tarpon is known to migrate across these isoscapes (Ault et al., 2008; Luo et al., 2008), we observed extremely steady values of both $\delta^{13}C$ and $\delta^{15}N$ during the coastal phase. The within-individual consistency indicated that Atlantic Tarpon were feeding at similar trophic levels and were dependent on basal resources with similar baseline values throughout the entire coastal phase. Importantly, eye lenses only grow and add laminae during periods of somatic growth (Nicol and Somiya, 1989; Horwitz, 2003). In fishes, most energy is used for somatic growth during the juvenile phase (Sogard, 1992; Stallings et al., 2010), and can be diverted to gonadal growth during spawning periods and increased metabolism during migration in adults (Perga and Gerdeaux, 2005). Therefore, the consistency observed in the isotope profiles were only representative of periods of somatic growth. One explanation for the consistency in basal-resource dependence is that Atlantic Tarpon do not migrate. However, we can exclude this explanation since multiple tagging studies have shown that Atlantic Tarpon undergo long-distance migrations (FWC Unpublished Data, Ault et al., 2008; Luo et al., 2008; Hammerschlag et al., 2012). Instead, we suggest Atlantic Tarpon return to the same coastal system each year to feed and grow. Although Atlantic Tarpon may feed during the migratory and spawning periods, the energy from feeding is likely diverted away from growth and therefore would not be reflected in the eye lens. It has been suggested that Atlantic Tarpon feed from late summer through the early fall to recover from migration and spawning in the spring and summer (Crabtree et al., 1997; Ault et al., 2008). Based on the lack of variability in the isotope profiles, the current study suggests that Atlantic Tarpon returned to the same coastal system after spawning to recover and feed in the same food webs. This conclusion is supported by tagging data that indicate adult Atlantic Tarpon returned to the same coastal systems year after year (FWC personal communication). In addition, despite there being no statistical difference in $\delta^{13}C$ values between Louisiana and Florida, we observed significant elevations (~3‰) of $\delta^{15}N$ values in Atlantic Tarpon from Louisiana, which is likely an isoscape effect, rather than a trophic effect (Radabaugh et al., 2013; Radabaugh and Peebles, 2014); the Louisiana fish also had consistent isotope values during the coastal phase. While we note that the sample size from Louisiana was low and should be expanded in the future, these results suggest that these fish may have had fidelity to coastal Louisiana for foraging and growth. Atlantic Tarpon from both Florida and Louisiana reflected this pattern of repeatedly returning to locations with similar isotope values and basal-resource availabilities.

Port Aransas, Texas was known as the “Tarpon Capital of the World” from the 1920s through the 1940s (Holt et al., 2005; Ault, 2008). By the 1950s, Atlantic Tarpon in the region were nearly extirpated. The downfall of the Texas fishery has never been fully explained. However, it has been proposed that recruitment failure, due to the loss of juvenile habitat and altered freshwater flows, was a likely contributor (Holt et al., 2005). In addition, Winemiller and Dailey (2002) modeled populations of Atlantic Tarpon and found that a small, 1% increase in juvenile survival resulted in a tenfold increase in adult cohort abundance. Prior to our research, there had been a lack of strong evidence to link upper estuarine habitats as a major source of juveniles to the adult population. Upper estuarine habitats can be extremely susceptible to development, alteration, and destruction, especially in Florida (Bortone, 2005). In addition, recent work has shown that habitat alteration may be especially deleterious to juvenile Atlantic Tarpon survival, and the amount of habitat alteration may pose a significant threat to the Atlantic Tarpon population (Wilson et al., 2019). The findings of our work re-emphasize the importance of juvenile habitat. Further research is warranted on how Atlantic Tarpon use upper estuarine habitats as nursery habitat (*sensu* Beck et al., 2001; Dahlgren et al., 2006).

## Contributors

Conceived and designed the research: BNK, EBP & CDS. Performed the research: BNK. Analyzed the data: BNK, EBP & CDS. Wrote the paper: BNK, EBP & CDS.

All authors have approved the final manuscript for submission.

## Declaration of interest

All authors indicate that no conflict of interest exists.

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## Appendix A. Supplementary data

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