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Trace elements and stable isotopes in Atlantic tarpon scales reveal movements across estuarine gradients

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ABSTRACT

Atlantic tarpon, *Megalops atlanticus*, are large migratory fish that make use of a wide array of habitats during the course of their lifetime, including oceanic, coastal and upper estuaries. Many aspects of the migratory ecology of this species are poorly described, including the scope of individual variability in movements across estuarine gradients. Population abundances have declined precipitously in recent decades leading to its classification as "Vulnerable" under the IUCN, lethal methods of identifying migration patterns such as otolith analyses are not feasible. We therefore examined the non-lethal alternative method of combined stable isotope and trace element analysis in subsamples of scales removed from living fish collected in subtropical areas of the western Gulf of Mexico and Puerto Rico. We found significant differences in chemical signatures from edges of scales collected from separate geographic regions. Within scales, we observed consistent enrichments in $\delta^{15}N$ values indicating ontogenetic trophic shifts and individual variation in the remaining proxies (Sr:Ca, Ba:Ca, and $\delta^{13}C$) that suggested differential patterns of movement between marine and fresh waters. Notably, values of $\delta^{13}C$ were positively related to Sr:Ca in all geographic regions, suggesting that scale $\delta^{13}C$ values primarily reflected movement across salinity gradients rather than fractionation associated with trophic increases. Multi-proxy chemical analysis of Atlantic tarpon scales therefore provides a non-lethal alternative to otolith geochemistry for identifying individual movement and trophic patterns of this highly mobile species.

1. Introduction

Highly migratory fish species make use of a range of coastal (inshore) and oceanic (offshore) habitats over the course of their lifetime, often at specific life history stages (Able, 2005; Gillanders, 2005). Key habitats include those that serve as juvenile nurseries and function as adult spawning grounds, migratory routes and feeding areas. These habitats are often widely separated geographically, and both are vital for the health and sustainability of these species. A growing field in migratory fish ecology is the use of chemical signatures in biogenic hard parts as proxies for movement and habitat residence (Elsdon et al., 2008; McMahon et al., 2013). The chemical composition of otoliths, in particular, has been used extensively to estimate natal origin, connectivity patterns and lifetime habitat movements (Almany et al., 2007; Elsdon et al., 2008; Walther and Limburg, 2012). Otoliths have many useful features that make them particularly well suited for this approach, including the fact that they are metabolically inert and grow over the entire lifetime of a fish (Campana, 1999; Campana and Thorrold, 2001). This method is particularly successful in retrospectively identifying movements between chemically distinct bodies of water, such as between low salinity reaches of upper estuaries and oceanic regions, which are recorded in specific growth increments of the structures. However, the unavoidable downside of otoliths is that fish must be sacrificed in order to obtain them.

A non-lethal alternative for chemical analyses of biogenic hard parts is the use of fish scales (Ennevor and Beames, 1993; Muhlfeld et al., 2005; Trueman and Moore, 2007), and elemental compositions of scales have been found to be highly correlated with otolith chemistry for elements such as Sr and Ba in some species (Muhlfeld et al., 2005; Wells et al., 2000a; Wells et al., 2003). Scale sampling does not decrease the market values of fish, in comparison to otolith sampling, as the fish do not need to be dissected and allows for the examination of life histories of rare and endangered species without reducing already limited stocks (Clarke et al., 2007; Gillanders, 2001). Similar to otoliths, scales grow and mineralize continuously throughout the life of teleost fishes (Schonborner et al., 1979), however, growth can cease under conditions of food deprivation, and in cases of severe stress, resorption may occur (Campana and Neilson,

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1985). Fish scales consist of both organic (e.g. proteins, such as collagen and keratin) and inorganic (e.g. carbonate and apatite) fractions (Perga and Gerdeaux, 2003; Sinnatamby et al., 2007). Most previous work on scale chemistry has focused on either elemental or stable isotope proxies, and rarely have both proxy types been explored simultaneously (Ramsay et al., 2012).

Before scales can be reliably used to infer dietary or migratory histories, the influence of their architecture and composition on proxy reliability must be considered. First, because the inorganic fraction may include varying amounts of dissolved inorganic carbon (Sinnatamby et al., 2007), decalcification to remove this inorganic fraction may be required prior to analysis for $\delta^{13}C$ values (Perga and Gerdeaux, 2003). Second, sampling discrete growth increments from a particular region of a scale for the organic matrix is made challenging by the arrangement of their growth structures whereby new growth increments extend outward from the older material but also lie on top of prior increments (Hutchinson and Trueman, 2006). This means that for stable isotope analyses of scales will contain some mixture of latter-accreted material and thus may not provide a pure signature of juvenile chemistry. This phenomenon of "overplating" applies primarily to the organic portion of scales, whereas the inorganic surface layer grows via the addition of concentric rings with minimal overlap (Trueman and Moore, 2007). As a result, while overplating may influence signatures of organic proxies such as $\delta^{13}C$ from interior scale samples, inorganic proxies such as Sr:Ca should be minimally affected by overplating. Comparisons between these inorganic and organic proxies will therefore be informative to assess the magnitude of potential overplating effects on stable isotope ratios. This is ideally investigated in migratory fishes that cross significant chemical gradients in their lifetime and that possess large scales suitable for subsampling across increments.

Atlantic tarpon, *Megalops atlanticus*, are large migratory elopomorphs that make frequent movements between oceanic, coastal and estuarine waters of the tropical and subtropical Atlantic Ocean. A key feature of Atlantic tarpon is their very large scales, which begin to develop after metamorphosis at fish body lengths of approximately 30–40 mm SL (standard length) and provided scales are not shed, they continue to grow throughout life until reaching diameters of 6 cm or more as adults for scales near the lateral line (Harrington, 1958; Wade, 1962). Although historically abundant in the Atlantic and the Gulf of Mexico, populations of Atlantic tarpon crashed from the 1950's onward leading to its current listed status as "Vulnerable" with the IUCN and regional restrictions on harvest in the United States (Adams et al., 2012). The causes of population declines remain in question, although certain local populations such as those in southern Texas waters appear to be rebuilding in recent years (Holt et al., 2005). Atlantic tarpon is still one of the most highly sought-after inshore sports fish in the Western Atlantic, supporting economically important recreational fisheries (Crabtree et al., 1992; Seyoum et al., 2008). This fishery is primarily catch-and-release, with fishers removing scales from released individuals as trophies. Yet, despite the intensity of management and the economic and ecological importance of tarpon, many aspects of its biology are poorly described.

Juvenile tarpon typically recruit to coastal habitats where they mature after a leptocephalus pelagic larval stage. Juvenile and even adult Atlantic tarpon are often found in a variety of upper estuarine habitats including brackish lagoons, mangroves and freshwater tidal creeks and streams (Crabtree et al., 1992; Luo and Ault, 2012; Seyoum et al., 2008). These habitats are frequently of poor quality, and Atlantic tarpon are tolerant of low pH and low dissolved oxygen content. After a juvenile period of several years, adults are thought to embark on seasonal spawning and feeding migrations offshore. However, adults may reside in inshore or even freshwater, estuarine, habitats for significant periods of time, and not all individuals may make regular movements to oceanic marine habitats. Because of the large-sized scales in this species, there is thus significant opportunity to validate the use of these structures as non-lethal alternatives to otoliths for tracking movement across estuarine gradients over their lifetime.

We drew on collections of Atlantic tarpon scales, collected opportunistically, from a variety of locations in tropical and subtropical regions of the Gulf of Mexico and Caribbean to determine if combined elemental and isotopic proxies can be used to obtain a multifaceted snapshot of trophic and migratory dynamic from scales. Our study had several aims in order to investigate the utility of geochemical signatures in scales as migratory proxies. First, we compared calcified to decalcified subsamples to determine the influence of inorganic material on stable isotope ratios. Second, we compared trace element and stable isotope ratios from subsamples of scale edges between fish captured in a variety of locations to determine geographical signature separation. Third, we compared stable isotope and trace element proxies from paired subsamples within scales to determine concordance among proxies. Fourth, we compared changes in elemental and stable isotope proxies between subsamples taken from across scales to evaluate variation in putative migratory patterns at the population and individual level.

2. Methods

2.1. Scale collection and preparation

Atlantic tarpon scales were collected opportunistically in late summer and early fall of 2011 and 2012. Scales were obtained from local anglers and participants in regional fishing tournaments, with anglers supplying capture location, date of capture and estimated size measurements (length or weight) of fish. In total, scales were collected from 47 individual tarpon (2011 $n = 19$, 2012 $n = 28$) from four general locations. Scales from Texas were obtained from either Port Aransas ($n = 18$, with 16 collected in 2011 and two in 2012), Matagorda Bay ($n = 21$, with two collected in 2011 and 19 in 2012) or Galveston Bay ($n = 1$, collected in 2011) and scales from Puerto Rico ($n = 7$, collected in 2012) were collected from the northwest side of the island (Fig. 1). Reported fish size measurements ranged from 0.53–2.13 m in length with a weight range from 2.27–81.6 kg.

Once collected and air-dried, scales were alternatively sonicated for 5 min in ultrapure water and scrubbed clean under a class-100 laminar flow hood until all adhering tissue was removed using a soft bristle brush. Scales were then dried in the laminar flow hood between two panels of glass to flatten scales for analysis. Subsamples were taken from the core and edge of all 2011 scales, with an additional intermediate sample at a position in the middle between the core and edge was taken from each of the 2012 scales, as well as three larger scales collected 2011, two from Port Aransas and the Galveston Bay scale. Subsampled sections, approximately 5 mg, of the cleaned scales were taken along the central growth axis and cut into small pieces (1–2 mm^2). Portions of these 5 mg subsamples were then used to run both stable isotope (2011 & 2012) and trace element (2012 only) analysis. Care was taken to insure paired subsamples were taken from comparable increments so analyses yielded information from identical time periods at each sampling location.

2.2. De-calcification

To determine if scales required de-calcification for stable isotope analysis, prior to analysis, scales from 2011 were cut in half and one half was soaked in 1.2 M HCl for 6 min and then rinsed in ultrapure water for 2 min (Perga and Gerdeaux, 2003; Sinnatamby et al., 2007; Ventura and Jeppesen, 2010). The other half was soaked in