

Otolith chemistry chimes in: migratory environmental histories of Atlantic tarpon (*Megalops atlanticus*) caught from offshore waters of French Guiana

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Abstract The migratory life histories of 37 Atlantic tarpon (*Megalops atlanticus*) caught from offshore waters of French Guiana were quantified using otolith Sr:Ca and Ba:Ca ratios. In general Sr:Ca ratio was more informative marker for inferring movements along salinity gradients, but Ba:Ca ratio was used to infer movements to estuarine mixing zones with high Ba availability. All sampled individuals had made use of marine and brackish water but only 8 % had experienced fresh water and 24 % hypersaline water. The newly-hatched post-metamorphic larvae recruited to brackish (49 %), sea (43 %), fresh (5 %) and hypersaline (3 %) water nursery areas. Following the settlement to nursery areas Atlantic tarpon likely displayed facultative habitat selection and complex set of inter-habitat shifting among waters of various salinity. The combined use of both markers allowed us to conclude that brackish (estuarine) areas are likely the main habitat for Atlantic tarpon in French Guiana, and fresh water use is surprisingly rare. As no general migratory life-history emerged, and because Atlantic tarpon seemed rather facultative in its habitat use, it should be regarded as ‘euryhaline marine migrant’.

Keywords Atlantic tarpon · Otolith microchemistry · French Guiana · Migration

Introduction

Tarpons are euryhaline migratory fish of the Megalopidae with Atlantic tarpon *Megalops atlanticus* and Pacific tarpon *Megalops cyprinoides* being the only two species of the family. They are the most ancestral among teleost fish and also share a common oceanic offshore spawning trait and leptocephalus larval stage (Forey et al. 1996; Adams et al. 2014). Atlantic tarpon are large predatory fish that mainly inhabit the tropical and subtropical regions of the Atlantic Ocean and can tolerate wide range of environmental conditions including oxygen-poor and hypersaline water (Adams et al. 2014). In these regions Atlantic tarpon can be found anywhere between offshore marine areas and sea-connected freshwater lakes, however, they usually inhabit coastal areas and estuaries (Crabtree et al. 1995; Brown and Severin 2008; Adams et al. 2014). Atlantic tarpon have a long life span of up to 50 or even 80 years, and relatively late maturity (i.e. 7–12 years depending on sex and region) (Crabtree et al. 1995; Andrews et al. 2001; Adams et al. 2012). Although world-renowned as a sport fish, the economic importance of Atlantic tarpon varies among regions with catch-and-release angling being more widespread in Gulf of Mexico and Caribbean Sea, and commercial-artisanal fishing in equatorial South America (de Menezes and Paiva 1966; Adams et al. 2012; Mateos-Molina et al. 2013). Atlantic tarpon is currently listed as “Vulnerable” in the IUCN Red List as the population abundances are still declining since the 1950 s mainly due to consumptive fisheries, habitat degradation, and bycatch mortality (Adams et al. 2012).

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Considerable ambiguity exists in the literature concerning the life-history of Atlantic tarpon. While researchers *seem to agree* that Atlantic tarpon spawn in unknown offshore areas and larvae recruit to various coastal and inland waters ranging from 0 to 45 PSU (Crabtree et al. 1992; Adams et al. 2014), there is still considerable uncertainty around the migratory ecology. According to Myers (1949) and Riede (2004) Atlantic tarpon is amphidromous. Brown and Severin (2009) state that Atlantic tarpon is catadromous, but then go on and note that it is not obligated to migrate into fresh water. Finally, McDowall (1988) suggests that Atlantic tarpon are not strictly diadromous at all. Although it has been suggested that individuals inhabiting Lake Nicaragua may complete their life cycles in fresh water (see reference in Jones et al. 1977), this conclusion was most likely incorrect because Brown and Severin (2008) recently demonstrated that the individuals sampled from Lake Nicaragua actually originated from the ocean. In fact all Atlantic tarpon ($n = 12$) studied by Brown and Severin (2008) clearly made use of freshwater habitats (some large specimens for extended time periods), therefore rendering the possibility of freshwater or at least estuarine spawning. Hence, further studies on individual variability in life-time migration patterns and the importance of freshwater habitats are warranted to elucidate the migratory ecology of Atlantic tarpon.

The chemical composition of otoliths can be used to retrospectively determine the environmental life-history of Teleostei. Otoliths offer a continuous and permanent growth history of fish, but additionally incorporate minor and trace elements from the water (Campana 1999). These chemical markers, if incorporated in proportion with ambient concentrations, can be then used to infer fish migration patterns among habitats with different water chemistries (Elsdon et al. 2008; Walther and Limburg 2012). Strontium-to-calcium ratio (Sr:Ca) is one of such markers that generally displays a positive relationship with salinity (Secor and Rooker 2000; Walther and Limburg 2012), and has been successfully used in various environmental settings (e.g., Rohitla et al. 2014; Payne Wynne et al. 2015). Barium-to-calcium ratio (Ba:Ca), however, generally displays a negative relationship with salinity (Walther and Limburg 2012), but the usefulness of this marker seems to vary among locations (e.g., Crook et al. 2006; Rohitla et al. 2015). Although the relationships between otolith Sr:Ca or Ba:Ca and salinity have not been validated for Atlantic tarpon, a validated relationship between otolith

Sr:Ca and salinity exists for Pacific tarpon (Chen et al. 2008). The aims of the present study were to: (i) investigate the variability of individual migration patterns of Atlantic tarpon using otolith Sr:Ca and Ba:Ca profiles, and (ii) if possible look into detailed movements patterns between habitats with different salinity.

Materials and methods

Atlantic tarpon samples ($n = 37$) were purchased from a local fish market at Cayenne (French Guiana) in October of 2013. These fish were caught with drift gillnets (“Guyana seine”) by commercial fishers from various offshore sites near Cayenne. Although Atlantic tarpon are not specifically targeted by fishers, they are landed selectively and marketed if they weigh <15 kg. Otoliths were extracted from the heads, cleaned and stored dry in micro-tubes. Biological parameters of the fish were also recorded when feasible (Table 1). In most of the individuals an additional length measurement (termed JOL in Table 1) was taken from the tip of the closed lower jaw to the tip of the opercle to help to estimate the size of the individuals in which only heads were available. No Atlantic tarpon with a total weight (TW) of >20 kg was sampled due to the reasons mentioned above. Sex could not be determined in most of the sampled fish as only gutted individuals were available at the fish market. Two individuals were purchased unprocessed (including the largest one in the sample), but only small juvenile gonads were found. In Brazil, the *smallest* mature male and female Atlantic tarpon were 95 and 125 cm (FL) respectively (de Menezes and Paiva 1966), and therefore it can be assumed that the majority of Atlantic tarpon sampled in the present study were immature.

In the laboratory, otoliths were embedded into epoxy resin and transverse thin-sections were subsequently obtained with a low-speed saw. These thin-sections were ground and then polished with abrasive paper (grit size P1200 to P4000) until the core area was visible. Finally they were glued onto standard glass slides and stored in clean plastic bags for later analysis. Otolith ^{43}Ca , ^{86}Sr and ^{137}Ba were quantified with laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) in WM Keck Collaboratory of Plasma Spectrometry (Oregon, USA). A VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser was used. Before analysis, all otoliths were ultrasonically

Table 1 Recorded biological parameters of sampled Atlantic tarpon from the offshore waters of French Guiana. Asterisk denotes the individuals in which only the heads were obtained. All measured lengths are in cm and masses in kg. JOL denotes the additional length measurement that was taken from the tip of the closed lower jaw to the tip of the opercule to help to estimate the size of the individuals in which only the heads were available

ID	TL	FL	SL	JOL	SW	TW
1	130	112	108	-	14.3	-
2	111	94	92	-	8.9	-
3	91	81	76	-	4.9	-
4	98	85	81	21	6.5	-
5	102	96	86	22	7.6	-
6	121	108	105	-	12.1	-
7	120	106	102	23	11.5	-
8	84	76	73	-	4.5	-
9*	-	-	-	17	-	-
10	-	-	109	-	14.1	-
11*	-	-	-	29	-	-
12	94	83	79	21	5.6	-
13	60	54	52	-	1.7	-
14*	-	-	-	16	-	-
15	96	86	82	18.5	6.2	6.7
16	137	121	117	27.5	17.2	19.2
17	100	87	83	-	6.9	-
18	103	91	88	-	7.4	-
19	98	94	81	-	5.6	-
20	109	97	91	-	10.4	-
21	112	100	95	-	9.7	-
22	100	89	85	-	6.8	-
23	103	91	87	21	8.0	-
24	110	95	91	23	8.6	-
25	110	94	90	21	9.0	-
26	87	76	73	-	5.0	-
27	95	83	80	20	6.1	-
28	97	86	82	19.5	6.8	-
29*	-	-	-	28	-	-
30	77	67	64	14.5	3.5	-
31	96	85	81	20.5	6.7	-
32	88	80	76	18	5.4	-
33*	-	-	-	16	-	-
34	108	93	90	21	7.5	-
35	119	106	102	25	11.8	-
36	129	115	110	27	14.5	-
37	100	89	85	22	9.0	-

cleaned for 15 min in NANOPure water and dried in a laminar flow hood. The laser was set at 7 Hz with a 40 μm ablation spot size and a scan speed of 10 μm s⁻¹. A continuous line scan was traced from the core area to the ventral edge (Fig. 1), although not all transects actually reached the edge of the otolith because some edges were still embedded into epoxy resin. Helium was used as a carrier gas. A glass reference material (NIST612) was analysed before and after every 6–10 otoliths. Data reduction was achieved by following the methods of Miller (2007) as described in Rohrla et al. (2014). A nine-point running mean followed by nine-point running median was used to reduce the noise and smooth the Sr:Ca and Ba:Ca data.

In order to infer detailed fish migration patterns using otolith Sr:Ca and Ba:Ca profiles threshold values of the relevant biomes or habitats must be established. With Atlantic tarpon biomes that are potentially identifiable with otolith chemistry are fresh, brackish, sea, and hypersaline water. Unfortunately, only limited amount of background data are available for our study region. We know that Sr:Ca and Ba:Ca ratios in the estuarine waters of Oyapock and Approuague rivers are ≈ 10.4 and 6.1 mmol·mol⁻¹, respectively; the same values for the upper reaches of Kaw River are ≈ 5.8 and 1.8 mmol·mol⁻¹ (Kalle Kirsimäe, personal communication). We also drew on otolith threshold values provided elsewhere, but also on current biological knowledge on Atlantic tarpon and our results to determine the threshold values for our case. Conceptual life-history models have been used before to aid the estimation of threshold values for a studied species (e.g., Morales-Nin et al. 2012). Brown and Severin (2008) reported, based on a limited sample size, that the otolith Sr:Ca threshold values for Atlantic tarpon inhabiting the Gulf of

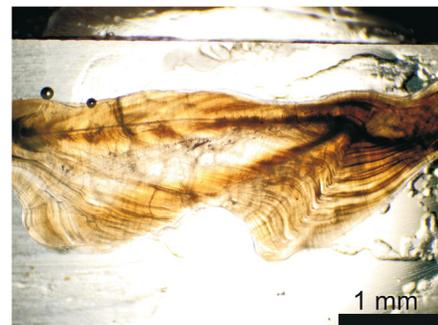


Fig. 1 Image of Atlantic tarpon otolith sectioned and polished in a transverse plane. Note the laser transect starting from the core and running towards the ventral edge

Mexico and the Caribbean Sea are $<2.1 \text{ mmol}\cdot\text{mol}^{-1}$ for fresh water, $2.1\text{--}4.1 \text{ mmol}\cdot\text{mol}^{-1}$ for sea water, and $>4.1 \text{ mmol}\cdot\text{mol}^{-1}$ for hypersaline water. They did not record a brackish water threshold and suggested it to be somewhere in between the two first modes. In the present study, however, we recorded considerably higher variation in otolith Sr:Ca ratios throughout the profiles (i.e. up to $11 \text{ mmol}\cdot\text{mol}^{-1}$ for presumed hypersaline experiences). Most importantly, lower Sr:Ca values (i.e. fresh to brackish water) were mostly present in the first parts of the profiles, which were usually followed by a significant increase to higher Sr:Ca values (i.e. sea water) in the later parts of the profiles. This is consistent with current knowledge that Atlantic tarpon spawn in offshore waters, recruit to coastal areas (e.g., lagoons, estuaries-rivers), and sometime later in life embark on longer marine migrations (Crabtree et al. 1995; Adams et al. 2014). Therefore, based on available literature and our results we considered the otolith Sr:Ca thresholds to be: $< 2.0 \text{ mmol}\cdot\text{mol}^{-1}$ for fresh water, > 2.0 and $<4.0 \text{ mmol}\cdot\text{mol}^{-1}$ for estuarine/brackish water, > 4.0 and $<6.0 \text{ mmol}\cdot\text{mol}^{-1}$ for sea water, and $>6.0 \text{ mmol}\cdot\text{mol}^{-1}$ for hypersaline water. Similar values, although presented in wt%, are also reported by Shen et al. (2009) who investigated Pacific tarpon in Taiwan.

To our best knowledge, otolith Ba:Ca thresholds have been rarely reported in the literature. For example, a otolith Ba:Ca estuarine threshold of $>0.001 \text{ mmol}\cdot\text{mol}^{-1}$ was reported for the Gulf of Cádiz (Spain), but this was actually based on hatchery-reared individuals from the Mediterranean Sea (Morales-Nin et al. 2012). In the present study, eight individuals had relatively stable and low Ba:Ca values throughout their profiles with a mean of 0.003 ± 0.002 (SD) $\text{mmol}\cdot\text{mol}^{-1}$ (e.g., Figs. 2a, c). Furthermore, nearly all of the sampled individuals had similarly low Ba:Ca values (at least) in the end of their profiles (e.g., Figs. 2d, j), which should represent the latest ambient conditions experienced by the fish before capture. As all of the sampled individuals were landed in full strength sea water (i.e. low Ba:Ca), marine experience was considered to occur at Ba:Ca values of $<0.005 \text{ mmol}\cdot\text{mol}^{-1}$ (mean + 1 SD) and *estuarine experience* at $>0.005 \text{ mmol}\cdot\text{mol}^{-1}$. Estuarine experience is here somewhat distinguished from brackish water experience and defined as individual fish being exposed to an area in the estuary (i.e. within the mixing zone) or ocean (i.e. within the estuarine plume) where releases of Ba from riverine particulate matter occur in a manner that result in elevated concentrations of available Ba (Coffey

et al. 1997; Stecher and Kogut 1999) while Sr:Ca concentrations also remain high (i.e. brackish to sea water). Dissolved Ba maxima in estuaries can occur at salinities between 2.5 and 30 PSU (typically <20) depending on river hydrology and Ba desorption dynamics from intertidal sediments (Coffey et al. 1997; Colbert and McManus 2005). Therefore, due to the complicated nature of estuarine mixing dynamics, the absence of estuarine experience in otolith profiles (estimated from Ba:Ca) does not exclude the possibility of brackish water experience (estimated from Sr:Ca) and vice versa. Hypersaline and freshwater experiences were estimated from Sr:Ca values only.

Results

Sr:Ca values in the smoothed profiles varied between 0.6 and $11.5 \text{ mmol}\cdot\text{mol}^{-1}$ with a mean of 4.4 ± 0.8 (SD) $\text{mmol}\cdot\text{mol}^{-1}$. Ba:Ca values in the smoothed profiles varied between 0.0004 and $0.18 \text{ mmol}\cdot\text{mol}^{-1}$ with a mean of 0.009 ± 0.008 (SD) $\text{mmol}\cdot\text{mol}^{-1}$. Extremely high Sr:Ca ratios were often accompanied by high or extremely high Ba:Ca ratios that together strongly indicate hypersaline experiences (e.g., Figs. 2g, h). However, high or extremely high Ba:Ca ratios were also present in some individuals that did not possess extremely high Sr:Ca ratios, which was interpreted as estuarine experience (e.g., Figs. 2b, j). This is also supported by water chemistry analyses from the estuaries of Oyapock and Approuague, where high Ba:Ca and Sr:Ca ratios were recorded simultaneously (Kalle Kirsimäe, personal communication). In some individual profiles, clear oscillatory Ba:Ca patterns were evident with or without coinciding Sr:Ca patterns (e.g., Figs. 2b, f). In general, Sr:Ca profiles were deemed more reliable for estimating movement patterns, but Ba:Ca profiles were used complementary to infer estuarine use in cases where fish had experienced high ambient Ba conditions (i.e. the estuarine mixing zone).

All sampled individuals made use of marine and brackish water (although in varying extent), but only some of them had experienced hypersaline (24 %) or fresh water (8 %). After the offshore spawning/hatching event the following facultative habitat use patterns were identified based on Sr:Ca profiles: Type I ($n = 18$): recruitment to brackish water (e.g., Figs. 2a-d) followed by a complex set of inter-habitat shifting with marine-brackish (100 %; i.e. all individuals) and/or fresh water

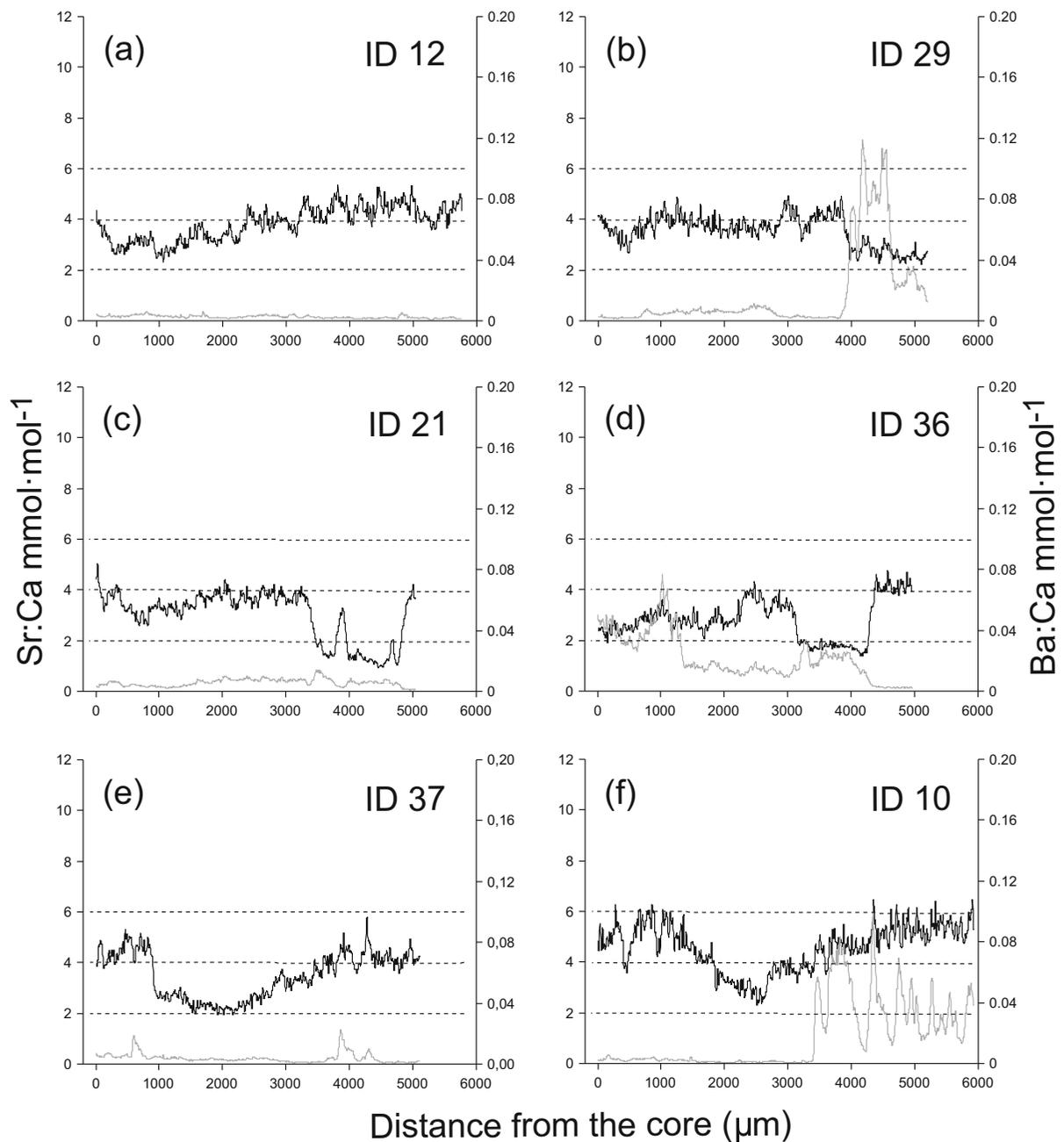


Fig. 2 Representative otolith Sr:Ca (—) and Ba:Ca (—) profiles of Atlantic tarpon collected from offshore areas of French Guiana: **a-d** brackish water recruits (Type I); **e-i** marine recruits (Type II); **j-k** freshwater recruits (Type III); **l** hypersaline water recruit (Type IV). Dashed lines indicate Sr:Ca thresholds between

fresh (< 2.0 mmol·mol⁻¹), brackish (> 2.0 and <4.0 mmol·mol⁻¹), marine (> 4.0 and <6.0 mmol·mol⁻¹) and hypersaline (> 6.0 mmol·mol⁻¹) waters. ID numbers correspond to the numbers given in Table 1

(11 %) experiences; Type II (*n* = 16): recruitment to marine water (e.g., Figs. 2e-i) followed by a complex set of inter-habitat shifting with marine-brackish (100 %), hypersaline (50 %) and/or fresh water (6 %)

experiences; Type III (*n* = 2): recruitment to freshwater (e.g., Figs. 2j, k) followed by a complex set of inter-habitat shifting with marine-brackish, hypersaline and/or freshwater experiences; Type IV (*n* = 1): recruitment

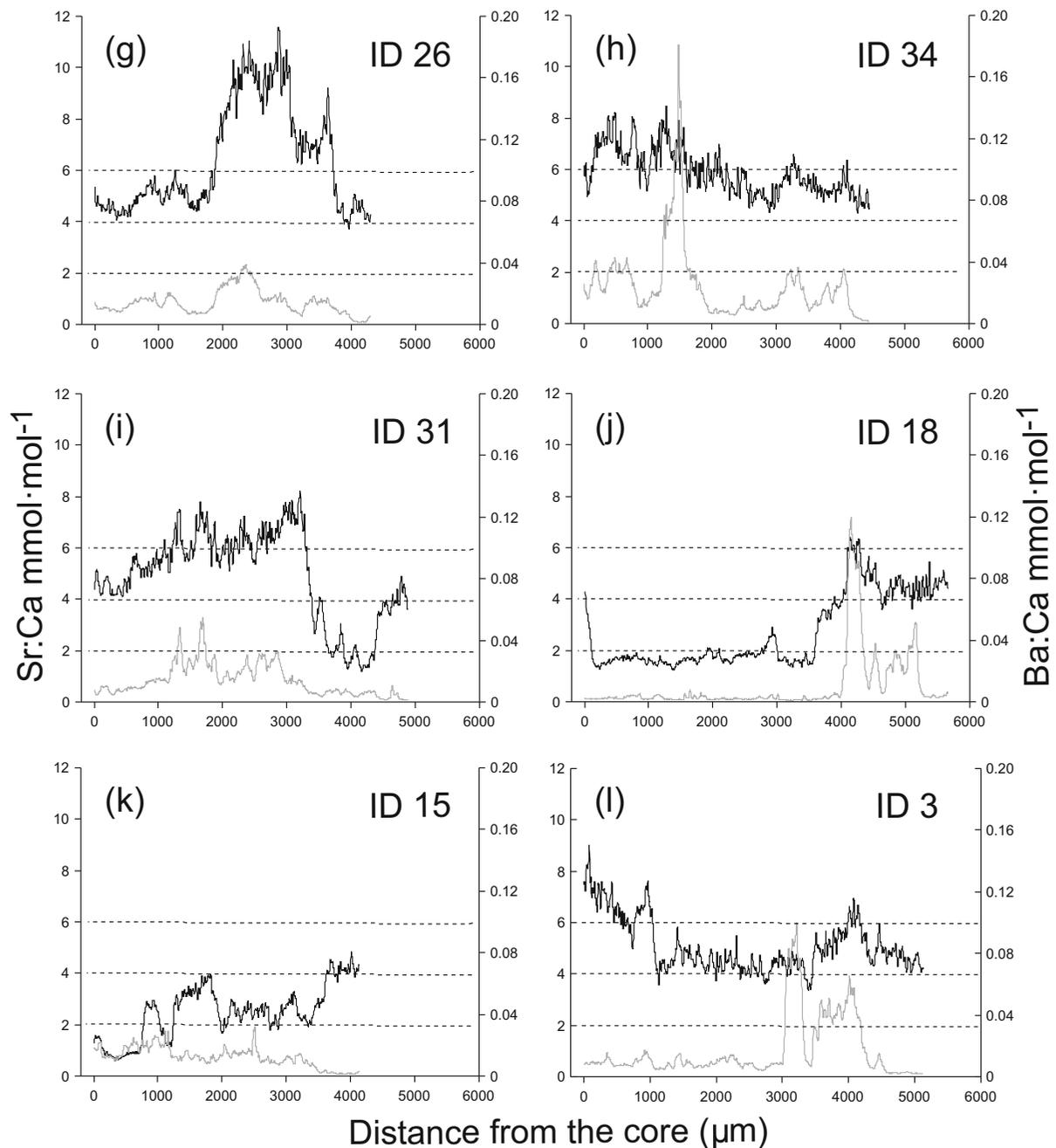


Fig. 2 (continued)

to hypersaline water (e.g., Fig. 2l) followed by inter-habitat shifting between marine-brackish and hypersaline water.

The prevailing habitat use pattern of Type I recruitment was inter-habitat shifting between marine and brackish water with 44.5 % of individuals having no or only occasional estuarine experience (i.e. Ba:Ca

values mostly stable and $<0.005 \text{ mmol}\cdot\text{mol}^{-1}$; e.g., Figs. 2a, c) and 44.5 % having frequent estuarine experience (i.e. strong and prevalent peaks in Ba:Ca values; e.g., Figs. 2b, d). Only 11 % of Type I individuals had ventured into freshwater and stayed there for a considerable time (Figs. 2c, d). The prevailing habitat use pattern of Type II recruitment was inter-habitat shifting

between marine and brackish water with 25 % of individuals using estuarine waters occasionally (e.g., Fig. 2e) and 69 % frequently (e.g., Figs. 2f, h). Only 6 % of Type II individuals had ventured into freshwater (Fig. 2i). Fifty percent of Type II individuals had also experienced hypersaline conditions (e.g., Figs. 2g-i).

Discussion

There is no general migratory life-history utilized by Atlantic tarpon inhabiting the offshore waters of French Guiana. Instead, a myriad of recruitment and movement patterns across a wide salinity range seem to exist. We feel confident in the established thresholds because similar thresholds have also been reported by Shen et al. (2009) for Pacific tarpon in Taiwan (albeit presented as wt%) and by Brown and Severin (2008) for Atlantic tarpon in Central America. The use of otolith Sr:Ca as a marker for investigating migratory behaviour and habitat selection of Atlantic tarpon is indirectly supported by experimental work conducted by Chen et al. (2008) who demonstrated that the average otolith Sr:Ca range of Pacific tarpon reared in salinities of 0, 10 and 35 were 0.9 to 1.8 mmol·mol⁻¹, 2.7 to 3.7 mmol·mol⁻¹ and 3.2 to 5.0 mmol·mol⁻¹, respectively. This means that it is possible to differentiate even between brackish and marine waters, although some overlap is expected to occur. However, a lot is still unclear, including the temperature effects on otolith elemental incorporation which is totally unknown for the tarpons (Chen et al. 2008). All this implies that the relationships between Atlantic tarpon otolith chemistry and ambient factors such as salinity and temperature need to be investigated more thoroughly in the future. As a consequence, the results of present study should be taken with some precaution.

Four distinct types of recruitment were identified in the present study. It was estimated that 49 % of the sampled individuals recruited to brackish water and 43 % to sea water. Only 5 % recruited to fresh water and 3 % to hypersaline water. Although it was previously known that post-metamorphic larvae of Atlantic tarpon can recruit to various coastal and inland nurseries with varying levels of salinity (Zale and Merrifield 1989; Crabtree et al. 1995; Adams et al. 2014), the proportional importance of such habitats has not been previously quantified in detail. From a preliminary study ($n = 12$) by Brown and Severin (2008) it can be judged that 67 % of the sampled individuals recruited to *marine*

water and 33 % to fresh water. The authors were unable to distinguish between marine and brackish water, so it is likely that these are combined in their study. It is also noteworthy that the present study recorded considerably higher Sr:Ca values than reported by Brown and Severin (2008), and it almost seems that a whole set of higher (i.e. marine) values are missing in their dataset. This could be plausible because Brown and Severin (2008) collected their samples from inshore or nearshore sites (no offshore collections), while the individuals in the present study originated from offshore sites. Notwithstanding the aforementioned disparities in discriminating between marine and brackish water, it seems that recruitment to freshwater nursery areas is more widespread in the Caribbean Sea and especially the Gulf of Mexico region than in the coast of French Guiana. This could imply that different life-history strategies are at work or differences in the quality of freshwater habitats exist.

Presumed movement patterns across salinity gradients after the recruitment to nursery areas varied among individuals. While some individuals seemingly resided in a relatively constant ambient Sr:Ca regime, others displayed large variations in otolith Sr:Ca that represent shifts in ambient salinity, and therefore movements. Although we cannot totally rule out the possibility of alternating ambient chemistry around a sedentary individual, this is unlikely because major shifts in elemental profiles were always prolonged in duration, and therefore cannot account for temporary changes in ambient chemistry. Most of the presumed movements recorded in the present study occurred between brackish and marine water. This result is in agreement with previous knowledge that Atlantic tarpon subadults and adults mainly inhabit coastal areas and estuaries, but also fresh water (Crabtree et al. 1995; Adams et al. 2014). However, only 8 % of the individuals sampled in the offshore waters of French Guiana had made use of fresh water. This contrasts to the results of Brown and Severin (2008) who demonstrated that all Atlantic tarpon sampled from the Gulf of Mexico and the Caribbean Sea ($n = 8$) clearly made use of freshwater habitats. Whether this disparity in reported results is due to distinct life-history strategies, differences in available freshwater habitats or simply due to the fact that the Atlantic tarpon included in Brown and Severin (2008) study were collected from inshore and nearshore habitats, is unknown. The hypothesis of distinct regional life-history patterns was put forward also by Brown and Severin (2008).

Then again, the low share of post-settlement freshwater usage among French Guiana Atlantic tarpon further suggest that freshwaters of French Guiana may be unsuitable for most Atlantic tarpon, at least for longer terms. However, there is some evidence that small sized Atlantic tarpon penetrate the upper reaches of Kaw River during monsoon periods in relatively large numbers (Sergei Pölme, personal communication).

At least 27 % of the sampled individuals were interpreted as having had hypersaline water experience. This result is somewhat to be expected as Atlantic tarpon are known for wide salinity tolerance (Crabtree et al. 1992; Adams et al. 2014). However, the proportional importance of hypersaline habitats has not been previously quantified. As many estuaries throughout the world are becoming hypersaline due to droughts induced by climate change (Diouf et al. 2006; Gillanders and Munro 2012), such habitats may become increasingly widespread. This will undoubtedly affect spatial structuring of species or their populations (e.g., Simier et al. 2004), but will also add an extra dimension to otolith chemistry based migratory history reconstructions in fish. These challenges were recently addressed by Gillanders and Munro (2012) who stressed that a combined set of elemental and isotopic ratios will be necessary to determine whether fish have been exposed to hypersaline water. Although the present study did not look into isotopic ratios, there is some evidence that Mg:Ca and Mn:Ca are of no use in identifying hypersaline experiences in Atlantic tarpon (M.R., unpublished data). It may also be that some individuals down-regulate their Sr incorporation to otoliths irrespective of the ambient salinity (i.e. including hypersaline) (Panfili et al. 2015), in which case, hypersaline experiences may be underestimated in the present study.

Atlantic tarpon cannot be regarded as catadromous or amphidromous. The results presented in this study support the notion of McDowall (1988) that Atlantic tarpon are not strictly diadromous. Instead we propose the term ‘euryhaline marine migrant’ (modified from McDowall 1988; Whitfield 1999) as Atlantic tarpon can inhabit fresh to hypersaline water and are clearly facultative in habitat selection after hatching in offshore areas. We decided not use the term ‘marine migrant’ (sensu Elliott et al. 2007) because Atlantic tarpon are known to use fresh water rather extensively. Otolith element-to-calcium profiles obtained in the present study enable us to quantify the entire environmental life-history of each individual and can be regarded as one of the best methods out there for answering such questions. Although otolith

chemistry is generally the method of choice in inferring the environmental history of fish, scale chemistry is often the only method to work with if a species or population under study is facing serious conservation issues (Gillanders 2001; Campbell et al. 2015). Recent studies on Atlantic tarpon scale chemistry show promising results in obtaining continuous element-to-calcium line-scans (Seeley et al. 2015), but the inherent questions about elemental incorporation mechanisms into scales warrant further study. Although otolith sampling in Atlantic tarpon is termed “not feasible” in countries where catch-and-release angling is the only fishing practice (e.g., USA; Woodcock and Walther 2014), it can still be utilized in countries where commercial and subsistence fisheries target Atlantic tarpon.

In summary, this is the first study to provide some insights into the migratory ecology of Atlantic tarpon living in equatorial South-America, and only the second in the whole distribution area that reports movements from early ontogeny to subadult and adult stage. After hatching in offshore areas most sampled individuals recruited to brackish and marine nursery areas, only a small proportion recruited to fresh and hypersaline water. After settlement to nursery areas, individual Atlantic tarpon likely made use of various salinities in varying extent. As Atlantic tarpon seemingly displayed facultative habitat selection after metamorphosis and no general migratory life-history emerged, it should be regarded as ‘euryhaline marine migrant’. Further study is needed to look into potential regional correlations between the share of Atlantic tarpon fresh water usage and the quality of freshwater habitats as this may indicate habitat suitability and preference. Also, relationships between ambient and otolith chemistry should be studied in detail, especially in hypersaline conditions.

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References

- Adams A, Guindon K, Horodysky A, MacDonald T, McBride R, Shenker J, Ward R (2012) *Megalops atlanticus*. The IUCN Red List Threatened Species 2012: e.T191823 A2006676

- Adams AJ, Horodysky AZ, McBride RS, Guindon K, Shenker J, MacDonald TC, Harwell HD, Ward R, Carpenter K (2014) Global conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae). *Fish Fish* 15:280–311
- Andrews AH, Burton EJ, Coale KH, Cailliet GM, Crabtree RE (2001) Radiometric age validation of Atlantic tarpon, *Megalops atlanticus*. *Fish B-NOAA* 99:389–398
- Brown RJ, Severin KP (2008) A preliminary otolith microchemical examination of the diadromous migrations of Atlantic tarpon *Megalops atlanticus*. In: Ault JS (ed) *Biology and Management of the World Tarpon and Bonefish Fisheries*, pp 259–274
- Brown RJ, Severin KP (2009) Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish. *Can J Fish Aquat Sci* 66:1790–1808
- Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms, and applications. *Mar Ecol-Prog Ser* 188:263–297
- Campbell LA, Bottom DL, Volk EC, Fleming IA (2015) Correspondence between Scale Morphometrics and Scale and Otolith Chemistry for Interpreting Juvenile Salmon Life Histories. *T Am Fish Soc* 144:55–67
- Chen HL, Shen KN, Chang CW, Iizuka Y, Tzeng WN (2008) Effects of water temperature, salinity and feeding regimes on metamorphosis, growth and otolith Sr:Ca ratios of *Megalops cyprinoides* leptocephali. *Aquat Biol* 3:41–50
- Coffey M, Dehairs F, Collette O, Luther G, Church T, Jickells T (1997) The behaviour of dissolved barium in estuaries. *Estuar Coast Shelf S* 45:113–121
- Colbert D, McManus J (2005) Importance of seasonal variability and coastal processes on estuarine manganese and barium cycling in a Pacific Northwest estuary. *Cont Shelf Res* 25:1395–1414
- Crabtree RE, Cyr EC, Bishop RE, Falkenstein LM, Dean JM (1992) Age and growth of tarpon, *Megalops atlanticus*, larvae in the eastern Gulf of Mexico, with notes on relative abundance and probable spawning areas. *Environ Biol Fish* 35:361–370
- Crabtree RE, Cyr EC, Dean JM (1995) Age and growth of tarpon, *Megalops atlanticus*, from south Florida waters. *Fish B-NOAA* 93:619–628
- Crook DA, Macdonald JI, O'Connor JP, Barry B (2006) Use of otolith chemistry to examine patterns of diadromy in the threatened Australian grayling *Prototroctes maraena*. *J Fish Biol* 69:1330–1344
- de Menezes MF, Paiva MP (1966) Notes on the biology of tarpon, *Tarpon atlanticus* (Cuvier and Valenciennes), from coastal waters of Ceara State, Brazil. *Arquivos da Estação de Biologia Marinha da Universidade Federal do Ceará* 6:83–98
- Diouf K, Panfili J, Labonne M, Aliaume C, Tomás J, Do Chi T (2006) Effects of salinity on strontium:calcium ratios in the otoliths of the West African black-chinned tilapia *Sarotherodon melanotheron* in a hypersaline estuary. *Environ Biol Fish* 77:9–20
- Elliott M, Whitfield AK, Potter IC, Blaber SJM, Cyrus DP, Nordlie FG, Harrison TD (2007) The guild approach to categorizing estuarine fish assemblages: a global review. *Fish Fish* 8:241–268
- Elsdon TS, Wells BK, Campana SE, Gillanders BM, Jones CM, Limburg KE, Secor DH, Thorrold SR, Walther BD (2008) Otolith chemistry to describe movements and life-history measurements of fishes: hypotheses, assumptions, limitations, and inferences using five methods. *Oceanography and Marine Biology: An Annual Review* 46:297–330
- Forey PL, Littlewood DTJ, Ritchie P, Meyer A (1996) Interrelationships of elopomorph fishes. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) *Interrelationships of fishes*. Academic Press, San Diego, pp 175–191
- Gillanders BM (2001) Trace metals in four structures of fish and their use for estimates of stock structure. *Fish B-NOAA* 99:410–419
- Gillanders BM, Munro AR (2012) Hypersaline waters pose new challenges for reconstructing environmental histories of fish based on otolith chemistry. *Limnol Oceanogr* 57:1136–1148
- Jones PW, Martin FD, Hardy JD (1977) Development of fishes of the Mid-Atlantic Bight: an atlas of egg, larval and juvenile stages. Vol. 1: Acipenseridae through Ictaluridae. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-78/12. 366 pp
- Mateos-Molina D, Schärer-Umpierre M, Nemeth M, Ruiz H, Ruiz-Valentín I, Vargas-Santiago, J. (2013) Ecology and Distribution of Tarpons (*Megalops atlanticus*) at the Boquerón Wildlife Refuge, Puerto Rico. *Proceedings of the 65th Gulf and Caribbean Fisheries Institute*, pp 262–265
- McDowall RM (1988) *Diadromy in fishes: Migrations between freshwater and marine environments*. Timber Press, Portland, 250 pp
- Miller JA (2007) Scales of variation in otolith elemental chemistry of juvenile staghorn sculpin (*Leptocottus armatus*) in three Pacific northwest estuaries. *Mar Biol* 151:483–494
- Morales-Nin B, Geffen AJ, Pérez-Mayol S, Palmer M, González-Quirós R, Grau A (2012) Seasonal and ontogenic migrations of meagre (*Argyrosomus regius*) determined by otolith geochemical signatures. *Fish Res* 127–128:154–165
- Myers GS (1949) Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia* 1949:89–97
- Panfili J, Darnaude AM, Vigliola L, Jacquart A, Labonne M, Gilles S (2015) Experimental evidence of complex relationships between the ambient salinity and the strontium signature of fish otoliths. *J Exp Mar Biol Ecol* 467:65–70
- Payne Wynne ML, Wilson KA, Limburg KE (2015) Retrospective examination of habitat use by blueback herring (*Alosa aestivalis*) using otolith microchemical methods. *Can J Fish Aquat Sci* 72:1073–1086
- Riede K. (2004) Global register of migratory species - from global to regional scales. Final Report of the R&D-Projekt 808 05 081. Federal Agency for Nature Conservation, Bonn, Germany, 329 p
- Rohtla M, Vetemaa M, Taal I, Svirgsden R, Urtson K, Saks L, Verliin A, Kesler M, Saat T (2014) Life history of anadromous burbot (*Lota lota*, Linnaeus) in the brackish Baltic Sea inferred from otolith microchemistry. *Ecol Freshw Fish* 23: 141–148
- Rohtla M, Svirgsden R, Taal I, Saks L, Eschbaum R, Vetemaa M (2015) Life-history characteristics of ide *Leuciscus idus* in the eastern Baltic Sea. *Fisheries Manag. Ecol* 22:239–248
- Secor DH, Rooker JR (2000) Is otolith strontium a useful scalar of life cycles in estuarine fishes? *Fish Res* 46:359–371
- Seeley M, Miller N, Walther B (2015) High resolution profiles of elements in Atlantic tarpon (*Megalops atlanticus*) scales obtained via cross-sectioning and laser ablation ICP-MS: a

- literature survey and novel approach for scale analyses. *Environ Biol Fish* 98:2223–2238
- Shen KN, Chang CW, Iizuka Y, Tzeng WN (2009) Facultative habitat selection in Pacific tarpon *Megalops cyprinoides* as revealed by otolith Sr:Ca ratios. *Mar Ecol-Prog. Ser* 387:255–263
- Simier M, Blanc L, Aliaume C, Diouf PS, Albaret JJ (2004) Spatial and temporal structure of fish assemblages in an “inverse estuary”, the Sine Saloum system (Senegal). *Est Coast Shelf Sci* 59:69–86
- Stecher HA, Kogut MB (1999) Rapid barium removal in the Delaware estuary. *Geochim Cosmochim Acta* 63:1003–1012
- Walther BD, Limburg KE (2012) The use of otolith chemistry to characterize diadromous migrations. *J Fish Biol* 81:796–825
- Whitfield A (1999) Ichthyofaunal assemblages in estuaries: A South African case study. *Rev Fish Biol and Fisher* 9:151–186
- Woodcock SH, Walther BD (2014) Trace elements and stable isotopes in *Atlantic tarpon* scales reveal movements across estuarine gradients. *Fish Res* 153:9–17
- Zale AV, Merrifield SG (1989) Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida) – Ladyfish and Tarpon. U.S. Fish and Wildlife Service Biological Report 82(11.104). 17 pp