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Contribution to the Theme Section 'Marine functional connectivity'

Importance of estuaries for the horse-eye jack *Caranx latus* in northeastern Brazil: a case study of underestimated connectivity at the land–sea interface

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ABSTRACT: This study aimed to evaluate the importance of inshore estuarine habitats for the maintenance of offshore exploited stocks of the horse-eye jack *Caranx latus*, a marine tropical species of high economic value. Otoliths of 143 yearlings were used to develop a data set of multi-elemental fingerprints for different juvenile habitats of *C. latus* in northeastern Brazil, including 7 estuaries and the coastal zone. This data set was then compared to the signatures in the juvenile part of the otolith of 40 sub-adult and adult fish caught at sea to identify their origin. Although otolith multi-elemental concentrations overlapped for some of the estuaries investigated, the maximum overall discrimination accuracy between them was only 58%. However, grouping several estuaries according to their similarity in elemental signatures increased accuracy to 80%. In both cases, correct re-assignment rates for the coastal zone were above 94%, and strontium (Sr) was the most significant element in juvenile habitat discrimination. The remaining elements (B, Ba, Co, P, Rb, and Zn) allowed us to distinguish between 3 distinct groups of estuaries, for which correct re-assignment rates were 70–88%. Juvenile fingerprints in sub-adult and adult otoliths revealed that most of the fish in the local, exploited stock (75%) originate from an inshore estuarine habitat, particularly from larger estuaries under constant marine influence (32.5%). This biological connectivity between continental and coastal waters should be considered for the conservation of tropical marine coastal stocks in general, as it is likely to apply to other exploited marine species, in Brazil and elsewhere.

KEY WORDS: Marine fish · Transitional waters · Otolith chemistry · Elemental fingerprints · Juvenile habitat

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1. INTRODUCTION

Juvenile fish often use different habitats than the adults of their population in search of higher food availability and lower predation risk (Beck et al.

2001). Transitional coastal environments such as estuaries and lagoons are used as juvenile habitats by a diverse number of marine coastal species, including some exploited by fisheries (Nagelkerken et al. 2008, Sheaves et al. 2015). The biological and

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environmental constraints to which fish are subjected during juvenile life can lead to critical survival bottlenecks that largely shape recruitment success to adult stock (Andersen et al. 2017, van Poorten et al. 2018). Therefore, elucidating the role of transitional ecosystems in sustaining coastal fish populations is critical to defining effective strategies for fisheries management (Nagelkerken et al. 2015, Sheaves et al. 2015). It is also essential to understand connectivity at the land–sea interface since the biomass of juvenile fish derived from estuarine production and riverine inputs ultimately contributes to the productivity of the adjacent coastal areas, where most adult fish will eventually reside (e.g. Toledo et al. 2019).

Over the last few decades, there has been an emerging consensus that juvenile habitats can contribute disproportionately to the maintenance of fish populations (Beck et al. 2001, Vasconcelos et al. 2011, Schloesser & Fabrizio 2019). Of the diverse number of habitats that juvenile fish may inhabit, only some are referred to as ‘nursery grounds’ based on their contribution to the adult population (Beck et al. 2001). These nursery grounds allow juveniles to occur at higher densities and/or to benefit from processes that enhance their survival (Isnard et al. 2015, Schloesser & Fabrizio 2019), thereby maximizing recruitment to the adult stock (Beck et al. 2001). Identifying fish nursery grounds in coastal estuaries is crucial because most of these transitional ecosystems are under high and growing levels of human pressure, ranging from eutrophication and habitat alteration to overfishing (Kennish 2002). These threats not only endanger the health and food security of local human communities but also alter the quality of estuarine habitats for juvenile fish (Nagelkerken et al. 2008, Crook et al. 2015), impairing the size of the exploited adult stocks (Vasconcelos et al. 2011, Schloesser & Fabrizio 2019). This is particularly relevant in the tropics, where rapid coastal urbanization and growing demand for seafood are expected to affect both the quality of inshore habitats and the status of coastal fish stocks in the near future (Barlow et al. 2018, FAO 2018). In this part of the world, identifying and sustainably managing inshore areas that are key for coastal fisheries productivity in the coastal zone is a particularly pressing issue.

The horse-eye jack *Caranx latus* is a tropical marine fish that represents a substantial source of food and income in the southwestern Atlantic (Lessa et al. 2009, Pinheiro et al. 2010). Although it is commonly referred to as a reef-associated marine species, *C.*

latus can colonize a mosaic of coastal and marine environments during its life. Like other jack species (Smith & Parrish 2002), it may use inshore estuaries as nursery grounds, at least in northeastern Brazil. To date, the movements and migratory patterns of the species have only been assessed at the adult stage (Novak et al. 2020), and most studies regarding its lifetime habitats solely investigated its abundance in particular habitats or at specific locations (Campos et al. 2010, Paiva & Araújo 2010, Felizola-Freire et al. 2018). In Brazil, large *C. latus* specimens are generally associated with deeper waters (>40 m) and offshore reefs near the shelf break (Lessa et al. 2009, Felizola-Freire et al. 2018). Reproduction can occur over several months, with peaks in April and August (Figueroa-Fernández et al. 2008, Heyman & Kjerfve 2008). As a result, *C. latus* larvae are mainly found offshore, along the continental shelf (Campos et al. 2010). The juveniles of the species are also reported at sea (Figueiredo & Menezes 1980, Medeiros et al. 2017). However, *C. latus* juveniles are commonly found within local estuaries (Figueiredo & Menezes 1980, Paiva & Araújo 2010, Medeiros et al. 2017, Silva-Júnior et al. 2017), where they feed on a wide diversity of fish and crustaceans (Figueiredo et al. 2006, Gonzalez et al. 2021), playing a key role in estuarine food webs (Lira et al. 2018, 2022).

To evaluate whether these inshore habitats currently serve as nursery grounds for this marine species, we investigated the lifetime otolith chemical fingerprints of *C. latus* in northeastern Brazil. Otoliths are calcified structures present in the inner ear of most bony fishes. They grow throughout the life of fish by the daily accretion of concentric layers, which explains their ubiquitous use for age estimation (Panfili et al. 2002). Otolith chemistry takes advantage of this constant growth and the inert nature of the otoliths. The incorporation of chemical elements in the otolith is largely influenced by their availability in the environment (Izzo et al. 2015, 2018, Sturrock et al. 2015). Because elements are rarely reabsorbed after being incorporated into the otoliths (Walther 2019), fine-scale analysis of otolith composition allows for the identification of elements that were deposited in each period of the individual's life (Campana 1999, Sturrock et al. 2012, Reis-Santos et al. 2023). Thus, if the varied habitats occupied by the fish present well-established and contrasting elemental compositions, it is possible to reconstruct their lifetime movements between them (Gillanders 2005, Toledo et al. 2019, Reis-Santos et al. 2023). This technique has been successfully ap-

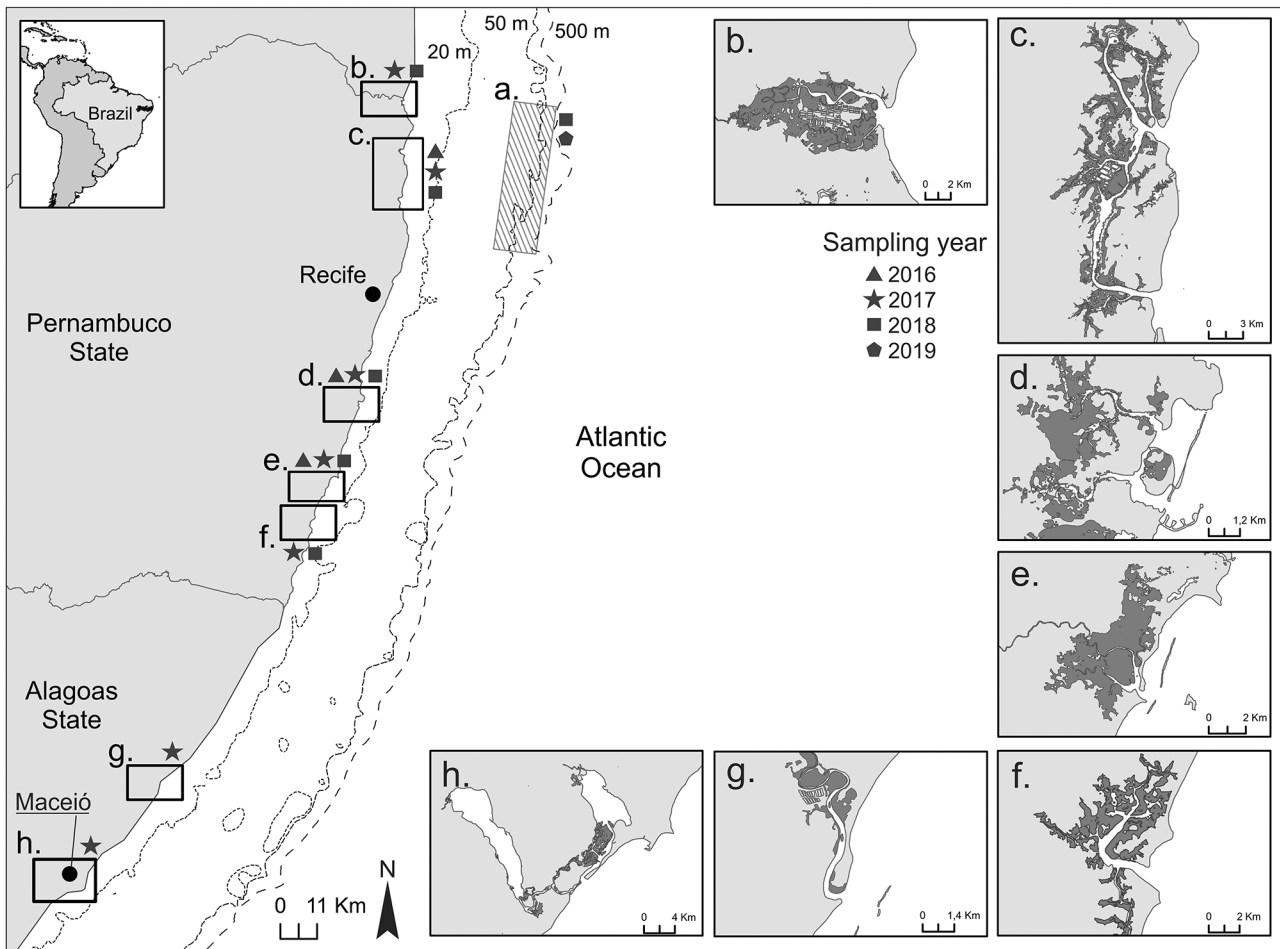


Fig. 1. Sampling locations for this study. (a) The offshore fishing area for *Caranx latus* (hatched rectangle) and inshore estuaries (open rectangles) of (b) Goiana, (c) Santa Cruz, (d) Suape, (e) Sirinhaém, (f) Rio Formoso, (g) Santo Antônio, and (h) Mundaú-Manguaba. Years when fish were captured in each location are represented by the different symbols. Mangrove vegetation cover is shown in dark grey on the detailed view for each estuary

plied to estimate the relative contribution of distinct nursery grounds to adult stocks (Tournois et al. 2017, Reis-Santos et al. 2023).

In this study, we assessed the juvenile otolith multi-elemental fingerprints from the marine coastal zone and several estuaries along the northeastern Brazilian coast and used them to identify the main juvenile habitat(s) for sub-adult and adult *C. latus* captured offshore. Assessing the contribution of estuarine habitats to marine adult stocks of *C. latus* is particularly relevant because, at least in Brazil, the species is targeted by both inshore and nearshore fisheries, and most catches occur before the individuals reach sexual maturity (Pelage 2020). Therefore, knowledge of the species' lifetime habitats and the connectivity among them may improve fishery and ecosystem management strategies, at least in this part of the world.

2. MATERIALS AND METHODS

2.1. Study area

The study area was located in the southwestern Atlantic Ocean, along the coasts of the Pernambuco and Alagoas states in northeastern Brazil (Fig. 1). The local climate is subtropical, with temperatures ranging from 18 to 32°C throughout the year (CPRH 2003a,b, Domingues et al. 2017). In this region, the continental shelf is approximately 35 km wide and has a maximum depth of 60 m near its break (Domingues et al. 2017). The coastal zone is characterized by a mosaic of habitats, including several estuaries along the coastline and coral reef patches spread across the continental shelf (Paiva & Araújo 2010, Silva et al. 2011). Coral reef patches in the outer area of the shelf represent key habitats for

Table 1. Morphological characteristics and environmental conditions of the 7 estuaries investigated along the northeastern Brazilian coast. Water transparency was determined using a Secchi disk in the middle and lower estuarine zones of each location. Salinity and temperature ranges were obtained during the local dry season along the middle and lower estuary

Characteristics	Pernambuco State					Alagoas State	
	Goiana	Santa Cruz	Suape	Sirinhaém	Rio Formoso	Santo Antônio	Mandaú-Manguaba
Water surface area (km ²)	8.11	25.5	6.6	1.7	7.83	1.88	79.93
Mean depth (m)	4.4	3.0	3.1	2.6	4.0	–	2.0
No. of marine entrances	1	2	2	1	1	1	1
Width of marine entrances (km; mean and range)	1.41	0.90 (0.5–1.3)	0.27 (0.1–0.3)	0.60	1.07	0.26	0.92
Water transparency (m; mean)	0.97	1.30	2.05	0.87	2.20	–	0.87
Salinity range	4.2–36.4	24.0–37.0	32.0–37.0	1.0–36.6	29.3–36.3	15.0–30.0	6.0–24.0
Temperature range (°C)	27.0–30.8	28.8–30.9	28.1–29.0	27.0–33.4	27.0–29.5	28.0–31.0	25.0–31.0

References:
Oliveira & Kjerfve (1993), Medeiros et al. (2001), Honorato da Silva et al. (2004), Nogueira et al. (2005), Silva et al. (2009, 2019), Borges (2011), Costa et al. (2011), Otsuka et al. (2014), Lima et al. (2015), Ferreira et al. (2016), Lins et al. (2018), Conti et al. (2020)

many exploited fish species as well as several other endemic and reef-associated species (Vila-Nova et al. 2014, Aschenbrenner et al. 2016b, Eduardo et al. 2018).

The 7 estuarine systems investigated in the present study (Goiana [GOI], Santa Cruz [STC], Suape [SUA], Sirinhaém [SIR], Rio Formoso [RIO], Santo Antônio [STA], and Mandaú-Manguaba [MM]) were selected based on their size, the presence of *C. latus* juveniles in their fish assemblages (Paiva & Araújo 2010, Ramos et al. 2011, Silva-Júnior et al. 2017, da Silva et al. 2018) and their relevance for local marine management. They exhibit distinct morphological features and are subject to different freshwater inputs, making them representative of the variety of local inshore environmental settings (Table 1).

Located in the northern part of Pernambuco state, the estuaries of GOI and STC have neighboring watersheds and are both of great socio-economic and ecological importance (Medeiros et al. 2001, Barletta et al. 2009). However, they differ drastically in terms of riverine inputs. Freshwater influence is strong in the GOI estuary, which consists of a small river channel (17 km long) and its floodplain (Barletta et al. 2009). In contrast, the STC estuary is the largest in the state. It forms a shallow, U-shaped channel connected to the sea by 2 large inlets (Silva et al. 2011). As local seawater inflows at both entrances are high, it is under strong marine influence (Medeiros et al. 2001, Figueiredo et al. 2006), and hypersaline conditions can occur in some of its areas during the driest months of the year (Medeiros et al. 2001).

The estuaries of SUA, SIR, and RIO are all located in the southern part of Pernambuco state but differ in their environmental settings (Fig. 1). The SUA estuary is formed by 2 rivers that flow into a shallow brackish lagoon with limited connection to the sea. As a result, it is largely euryhaline (Silva et al. 2019). The other 2 estuaries have similar hydrologic basins but differ in geomorphological and environmental characteristics. The SIR estuary is located within 2 marine protected areas (CPRH 2003b) and gathers a variety of interconnected lagoons and channels in the shallow floodplain around the main bed of the SIR river, which constitutes their sole connection to the sea (CPRH 2003b). Thus, it is subject to a greater freshwater influence than the RIO estuary, which is formed by larger tributaries, all under marked marine influence (Silva et al. 2009). Lastly, the estuaries of STA and MM are both located to the south, in Alagoas state. However, while the former is brackish and includes only one small river, the latter is formed by 2 inland lagoons connected to the sea through a single small channel and is, therefore, largely oligohaline (Oliveira & Kjerfve 1993). Additionally, the MM estuary is subject to particularly high levels of domestic and industrial contamination, as the capital of Alagoas state (Maceió) is located on its banks (Oliveira & Kjerfve 1993, Costa et al. 2011).

2.2. Fish sampling

The sampling design for the present study involved capturing both early juveniles and sub-adult

and adult individuals of *C. latus* from different cohorts. A total of 143 young-of-the-year (YOY), ranging from 56 to 165 mm in size (standard length [SL]), were collected across the 7 estuaries studied (Fig. 1b–h) between 2016 and 2019, using both beach seines (20 × 1.9 m; 20 mm mesh) trawled along the river banks and block nets (350 × 2.9 m; 70 mm mesh) set close to mangrove creeks. All fish were sampled during the local dry season, which spans from September to February (CPRH 2003a) and when the densities of *C. latus* juveniles in estuaries are highest (da Silva et al. 2018). Monthly surveys targeting the juveniles of the species were conducted each year in all estuaries during the whole dry season, with the exception of the STA and MM estuaries. In these 2 estuaries, located in Alagoas state, YOY were captured only during the 2017 dry season (STA, $n = 9$; MM, $n = 5$). For the other 5 estuaries along the coast of Pernambuco (GOI, STC, SUA, SIR, and RIO), YOY were captured in the dry seasons of 2017 and 2018; for 3 of these sites (STC, SUA, and SIR; Fig. 1), YOY were also captured during the 2016 dry season. For simplification, YOY were assigned to the year in which their dry season of capture started. For instance, the fish sampled between September 2016 and February 2017 were attributed to the same cohort (2016). Then, amongst the largest individuals collected, up to 10 fish of similar sizes (approximately 100 mm SL and of ages of ca. 5 mo; Gonzalez et al. 2021) were randomly sub-sampled for each estuary and year to provide consistent otolith fingerprints for all inshore habitats (Fig. 1). In addition, 40 sub-adult and adult individuals of the species, ranging from 2–11 yr old and 317–750 mm SL (Gonzalez et al. 2022), were captured on the continental shelf of Pernambuco state between 2018 and 2019. These specimens were caught by handline by the local artisanal fleet at offshore reef fishing spots, located approximately 30 km from the coastline (Fig. 1a). Upon collection, all fish were identified following specific literature (Figueiredo & Menezes 1980, Smith-Vaniz 2002), measured (SL, in mm), and stored frozen until further analysis.

2.3. Otolith preparation and elemental analysis

Following standard protocols for otolith chemistry (Panfili et al. 2002), all equipment used for otolith extraction and handling was acid-washed in a 4% ultrapure nitric solution bath, rinsed in ultrapure water, and dried in a Class-100 laminar flow hood before use. The left sagittal otoliths were extracted

using plastic tweezers, manually cleaned with a plastic brush, sonicated for 5 min in separate clean vials filled with ultrapure water, and dried under a Class-100 laminar flow hood. The otoliths were then individually embedded in epoxy resin (Araldite 2020 epoxy adhesive) and cut transversally to produce thin sections containing the core (500 μm width) using a low-speed precision saw (Buehler; Isomet 1000). Otolith sections were subsequently polished using sandpapers (800, 1200, and 2400 grit) and diamond-coated polishing paper (4000 grit) until the core was exposed on the surface, resulting in thin sections of 250–350 μm width. Finally, each otolith section was glued to a glass slide, sonicated for 5 min in ultrapure water to decontaminate its surface, and dried under the laminar flow hood before being stored in a separate plastic bag.

All sections were photographed before and after analysis using a camera (Olympus ProgRes C5) linked to a microscope (Olympus BX41; magnification 100× and 200×; software ProgRes). Otolith elemental composition was determined by laser-ablation inductively coupled plasma mass spectrometry (LA-ICPMS) at the University of Montpellier (UMR 5243 Geosciences) using a 193 nm Excimer Laser System (CompEx 102; Lambda-Physik) coupled to an Element XR sector field ICPMS (ThermoFisher). To reduce potential bias linked to variations in machine accuracy between analysis sessions, otoliths from different sampling sites and years were mixed on each of the analysis plates run on the LA-ICPMS system. For each otolith, the analysis was performed in raster mode along a transect following the maximum growth axis of the otolith, from the otolith core to its dorsal edge, allowing the variation in otolith elemental composition throughout the fish's lifetime to be measured (Fig. 2a,b). The transect of each otolith was pre-ablated before the analysis to avoid external contamination. The laser beam diameter for the analysis was set at 51 μm , and the laser was operated at an energy of 6 J cm^{-2} , a repetition rate of 7 Hz, and a speed of 21 $\mu\text{m s}^{-1}$. The total time to complete each cycle was 700 ms and comprised the time spent to measure the elements' concentration and the settling time. Machine calibration and instrumental drift control were performed by analyzing standard reference glass material (NIST 612) every 5 samples. Moreover, analysis of a certified otolith reference material (MACS 3) at the beginning and end of each analysis session was used for inter-session measurement quality control. Calculations of final otolith concentrations and the machine limits of detection (LOD) were made using the 'ElementR' package (Sirot et al. 2017) in R v.4.1.2 (R Core Team

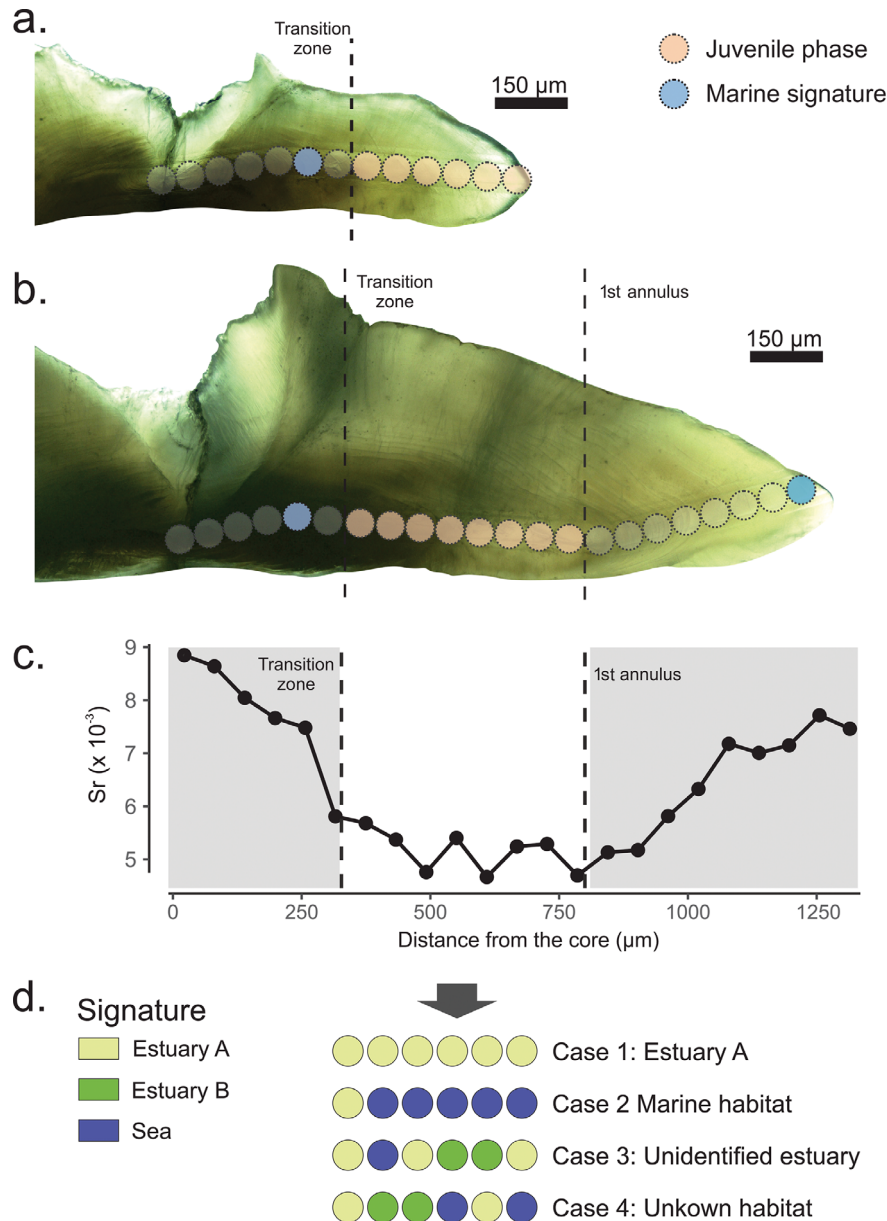


Fig. 2. Otolith sections (dorsal side, transmitted light) of (a) young-of-the-year and (b) sub-adult of *Caranx latus*, captured in an estuary and at sea, respectively. In each case, the position of the raster analyzed is indicated, together with that of the otolith structures (transition zone and first annulus) used to delineate the portions of the otolith reflecting the elemental signatures recorded during the juvenile phase and larval or adult life at sea. (c) Typical pattern of life span variations in Sr concentrations for the *C. latus* sub-adults, indicating the portion of the otolith selected to represent the (estuarine) juvenile phase (in white). (d) Procedure for identifying past juvenile habitat in sub-adult and adult *C. latus*, based on the results of spot assignment using the random forest algorithm

2021). Apart from ⁴³Ca, which was used as a proxy of the ablated otolith material, a total of 22 chemical elements were originally analyzed. However, only 10 (¹¹B, ¹³⁸Ba, ⁵⁹Co, ⁵²Cr, ⁶⁵Cu, ³¹P, ⁸⁵Rb, ⁸⁶Sr, ⁶⁶Zn, and ⁸⁹Y) had at least 25% of their measures above the LOD in at least one of the habitats sampled and were therefore retained for subsequent analysis. All element concentrations were normalized to the respective concentrations of ⁴³Ca and are expressed in mg g⁻¹

for Sr; μg g⁻¹ for B, Ba, Co, Cr, P, and Zn; and pg g⁻¹ for Cu, Rb, and Y.

2.4. Signal treatment

To avoid bias caused by autocorrelation in elemental signatures, the continuous record of otolith elemental concentrations obtained by each raster analy-

sis was first filtered to retain only non-overlapping sequential signatures, corresponding to adjacent 51 μm diameter spots along the analyzed transect, referred to as 'spots'. Based on the analytic settings of the LA-ICPMS, this was achieved by retaining only one signature out of 2 along the transect, starting from the edge to the core. The respective positions of the otolith zones corresponding to the larval, YOY, and sub-adult or adult life phases (if any) were identified for each fish, and the corresponding adjacent spots were regrouped accordingly. Different structural marks in the otoliths were used to identify these zones based on previous studies that validated the annual deposition of annuli for *C. latus* in northeastern Brazil (Gonzalez et al. 2022). The central opaque zone in the otolith of *C. latus* in this area extends up to 300–350 μm away from the core and ends with an inflection of the otolith growth axis, called the transition zone (Fig. 2a,b), which is observed for all the YOY caught in estuaries and is presumed to reflect the change in physiology associated with the arrival in inshore systems (Gonzalez et al. 2022). Variations in otolith concentrations of Sr for all fish allowed for the verification of this assumption (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m14359_supp.pdf), given that *C. latus* is an offshore spawner (Heyman & Kjerfve 2008). As expected for this element, which is commonly assumed to reflect changes in salinity (Reis-Santos et al. 2023), Sr values decreased near the end of the transition zone in most of the otoliths analyzed (Fig. S1). They subsequently remained low until the edge of the otolith was reached, except for the adult fish collected offshore, where a subsequent increase in Sr was observed after the first annulus (Fig. 2c). Therefore, for all the *C. latus* specimens studied, the position of the end of the transition zone and the first annulus along the transect analyzed were used to delimit the portions of the otolith laid down during the larval life at sea (before the transition zone) and the juvenile stage (after the transition zone and before the first annulus) during the first year of life. In the sub-adult and adult specimens investigated, this latter portion of the transect comprised between 5 and 10 spots, depending on the fish.

In order to create a database of juvenile otolith fingerprints capturing most of the spatiotemporal variability in otolith chemical record for each estuary, all spots between the transition zone and the otolith edge (3–8, depending on the fish) were kept for each YOY analyzed. The number of spots obtained for each fish varied due to a few factors, including the size and age of the fish captured from

different estuaries, their date of entry into the estuary, the respective location of the transition zone structure in each individual, and differences in the otolith radius. Each spot is expected to comprise approximately a few weeks to a month, considering an average width of 2.2 μm for each daily increment in otoliths (Gonzalez et al. 2022). However, there is a trend of otolith increment width decreasing with age and size, ranging from ~ 4.2 μm at 80 mm SL to ~ 2.4 μm at 150 mm SL (J. G. Gonzalez pers. obs). Therefore, a 51 μm wide spot should represent a period between 10 d (for the first spots near the transition zone) and 1 mo; while 8 spots are expected to provide a coverage of up to 4–5 mo. Within a 51 μm spot and within the coverage time of the analysis, we cannot guarantee that fish remained in the same location, as they could move between neighboring habitats (e.g. sandy beaches) and the estuary (Fig. S1a). However, this issue was minimized by targeting small individuals for our analysis (~ 100 mm SL), which are less likely to actively move across habitats.

To obtain otolith elemental signatures reflecting juvenile *C. latus* life at sea, a single spot corresponding to the last part of the larval life at sea (~ 200 μm away from the core) was selected in all the otoliths of the YOY analyzed (Fig. 2a). This data set for marine fingerprints was complemented with the otolith edge signatures (a single spot per fish) of all sub-adult and adult fish below 400 mm SL ($n = 13$, age: 2–4 yr), which were assumed to reflect the elemental composition of the water masses they inhabited offshore just before their capture (Fig. 2b). Considering that the size-at-maturity of *C. latus* (L_{100}) is 420 mm fork length (Figueroa-Fernández et al. 2008), all these fish were still immature, which allowed limiting the potential bias associated with otolith composition change due to age or physiological processes such as gonad development and maturation (Sturrock et al. 2015, Reis-Santos et al. 2023).

2.5. Identifying otolith fingerprints for local habitats

A total of 770 multi-elemental signatures from 156 fish were used to investigate differences in otolith fingerprints among locations. These included the juvenile life of all YOY and the larval and sub-adult signatures selected as proxies for the sea (Table 2). As most of the elements analyzed did not meet the assumptions of normality and homoscedasticity, only non-parametric tests were applied. Spatial differ-

Table 2. Mean (\pm SD) standard lengths (SL) of the 156 *Caranx latus* specimens used to build the data set of estuarine and marine otolith elemental fingerprints in northeastern Brazil. For each sampling site, the total number of otolith signatures gathered and the years of otolith records are indicated

Region	Location	No. of fish	SL (mm)	No. of signatures	Year
Pernambuco state	Goiana (GOI)	20	104 \pm 24	71	2017, 2018
	Santa Cruz (STC)	30	105 \pm 9	137	2016, 2017, 2018
	Suape (SUA)	30	108 \pm 11	140	2016, 2017, 2018
	Sirinhaém (SIR)	29	105 \pm 20	122	2016, 2017, 2018
	Rio Formoso (RIO)	20	113 \pm 6	100	2017, 2018
Alagoas state	Santo Antônio (STA)	9	69 \pm 3	29	2017
	Mundaú-Manguaba (MM)	5	68 \pm 11	15	2017
Sea	Larval life (Sea _L)	143	103 \pm 18	143	2016, 2017, 2018
	Sub-adult (Sea _A)	13	353 \pm 30	13	2018

ences in elemental signatures were assessed using separate Kruskal-Wallis tests for each element, followed by pairwise comparisons between locations (Dunn's tests) to determine which locations were responsible for the observed differences. In addition, a principal component analysis (PCA) was performed on otolith multi-elemental signatures to illustrate the variability of fingerprints at each site. Temporal stability in the multi-elemental signatures between sampling years within each site was investigated using non-parametric permutational multivariate analyses of variance (PERMANOVAs) based on the Euclidian distance of the $\log(x + 1)$ -transformed multi-elemental data set. Moreover, PERMANOVA tests were applied for all locations where fish were captured in more than one year (i.e. at sea and in the GOI, STC, SUA, SIR, and RIO estuaries). Whenever a site exhibited a significant inter-annual difference in otolith fingerprints, Mann-Whitney and Kruskal-Wallis tests were applied, followed by post hoc comparisons (Dunn's tests), when applicable, to elucidate which elements contributed to the observed temporal differences.

To discriminate among sampling sites based on the elemental fingerprints they leave on *C. latus* otoliths, the random forest (RF) algorithm was applied as a machine-learning method. The RF approach has several advantages, such as not requiring any assumptions about data distribution or normality, and has been effective in discriminating fish habitats using otolith multi-elemental fingerprints (Mercier et al. 2011, Tournois et al. 2017, Delerue-Ricard et al. 2019). Following Mercier et al. (2011), all possible combinations of the 10 chemical elements (B, Ba, Co, Cr, Cu, P, Rb, Sr, Zn, and Y) retained after data pretreatment were tested to identify the combinations that provided the best discrimination accuracy among the studied sites. For each potential RF train-

ing data set, 500 classification trees and 1000 iterations were used to assess the average overall discrimination accuracy. A cross-validation procedure was used for each potential RF training data set, which consisted of randomly selecting 75% of the multi-elemental signatures to train the RF and then using the remaining signatures (25%) to assess the accuracy in re-assigning each sample to its known origin. After identifying the optimal RF training data set, which consisted of the number and list of elements providing the best discrimination between locations, the contribution of each individual element to the overall spatial discrimination was assessed by calculating the mean decrease in Gini Index following its removal from the training data set (Breiman 2001). A higher decrease for an element indicates it is more essential for discrimination. To specify the re-assignment errors between juvenile habitats using the optimal training data set, specific accuracies and true skill statistics (TSS; Allouche et al. 2006) were calculated for each location. The accuracy represents the average percentage of spots correctly re-assigned to the fish's actual sampling location, while TSS represents a balance between correct predictions and errors in re-assignments. The TSS ranges from -1 to 1, where 1 (-1) indicates 100% correct (incorrect) predictions of presence or absence in re-assignment, while 0 indicates totally random predictions. The TSS is calculated as $(ab - cd) / [(a + d) \times (b + c)]$, where a is the correct prediction of presence at re-assignment, b is the correct prediction of absence, c is the incorrect prediction of presence, and d is the incorrect predictions of absence (Allouche et al. 2006).

The procedure described above was applied considering all potential juvenile habitats (i.e. the 7 estuaries and the sea) separately, but also after regrouping estuaries based on the similarities in their elemental signatures revealed by the PCA. The

results obtained from both approaches were compared to identify the list of chemical elements and grouping of habitats (optimal RF training data set), allowing the most accurate discrimination of local *C. latus* juvenile habitats from otolith fingerprints.

All analyses were performed in R v.4.1.2 (R Core Team 2021), using the 'randomForest' (Liaw & Wiener 2002) and 'vegan' (Oksanen et al. 2017) packages, and considering a threshold of 5% for statistical significance ($p < 0.05$).

2.6. Juvenile habitat assignment for sub-adult and adult fish

The optimal RF training data set was used to identify the origin of the 40 sub-adult and adult fish captured offshore based on the 307 multi-elemental signatures obtained from the juvenile portion of their otoliths (RF test data set). To minimize errors in habitat assignment due to spatiotemporal variation in environmental conditions during the juvenile life of individual fish and evaluate the reliability of juvenile habitat prediction for each fish, the most probable habitat of origin was predicted for each of the successive signatures acquired from the juvenile part of the otoliths (Fig. 2d). A threshold of 70% consistent assignment was set as an *a priori* limit for allocating each fish to a specific habitat. Therefore, fish were assigned to a past juvenile origin (site or habitat type) only if more than 70% of the signatures from their juvenile life were specifically attributed to it (Fig. 2d, Cases 1 and 2). If at least 70% of the signatures for their juvenile phase were attributed to a mix of estuary types, they were assigned to an unidentified estuary (Fig. 2d, Case 3). If their juvenile signatures were randomly assigned to any of the possible habitat types, they were assigned to an unknown habitat (Fig. 2d, Case 4).

3. RESULTS

The multi-elemental chemical fingerprints gathered from 183 *Caranx latus* specimens analyzed in this study allowed for the specification of the optimal list of chemical elements in the otoliths to analyze in order to distinguish between estuarine and marine juvenile habitats of this species in northeastern Brazil. In addition, our analysis revealed the main origin of the offshore biomass of *C. latus* exploited in this area, with significant implications for local land–sea connectivity and coastal ecosystem functioning.

3.1. Spatial differences in elemental fingerprints

When considering all potential juvenile habitats separately, the overall discrimination accuracy was highest when using 7 out of the 10 elements analyzed (B, Ba, Cr, P, Rb, Sr, and Zn; Fig. 3). However, due to frequent re-assignment errors among most of the studied estuaries (Table 3), the accuracy did not exceed 58%. Indeed, discrimination accuracy and TSS were high only for the marine habitat (>94% and 0.94, respectively). While 82% of the signatures for MM were correctly re-assigned, the average accuracy for the other estuaries did not exceed 60%. Similarly, although the TSS was positive in all estuaries, it was low for most of them (Table 3).

The high variability in otolith multi-elemental signatures for *C. latus* across all habitats, except for the sea and the MM estuary, resulted in frequent re-assignment errors (Fig. 4a). Sr was the element contributing most to overall discrimination, with a mean decrease in the Gini Index of 177.2 (Fig. 4b,c), and significantly higher values ($p < 0.001$) recorded at sea (Fig. 5). Sr values also varied among estuarine habitats but were higher ($p < 0.012$) in SIR (mean \pm SD; $5.63 \pm 0.43 \text{ mg g}^{-1}$) and GOI ($5.42 \pm 0.46 \text{ mg g}^{-1}$) than in other sites (Fig. 5). Ba was the second-most important element for spatial discrimination, with a mean decrease in Gini Index of 94.9 (Fig. 4b,c), mainly due to significantly higher Ba values ($p < 0.031$; Fig. 5) in the estuaries of SIR ($1.19 \pm 0.94 \text{ } \mu\text{g g}^{-1}$) and GOI ($1.05 \pm 0.70 \text{ } \mu\text{g g}^{-1}$) and at sea ($0.88 \pm 0.24 \text{ } \mu\text{g g}^{-1}$). The 5 remaining chemical elements also contributed to spatial discrimination (Fig. 5). The absence of signal above the LOD for B in the MM estuary and its significantly higher ($p < 0.014$; Fig. 5) concentrations of Rb ($342.92 \pm 104.37 \text{ pg g}^{-1}$) both contributed to the discrimination of this estuary (Fig. 4) and supported its high re-assignment accuracy, despite the low number of fish sampled at this site ($n = 5$). Significant spatial differences in Cr, P, and Zn signatures were also observed ($p < 0.012$; Fig. 5) and contributed to the discrimination of the other estuarine systems.

As shown on the first plan of the PCA (Fig. 4a), the overlap in otolith multi-elemental signatures was high between some of the estuaries investigated, suggesting similar environmental conditions between them. Based on the distance between the centroids of each site (Fig. 4a), the estuaries investigated were assigned to 3 groups of distinct chemical fingerprints: the MM estuary; a group comprising the estuaries of GOI, SIR, and STA, referred to as 'type-1' estuaries; and another group comprising the estuaries of STC, SUA, and RIO, referred to as 'type-2'

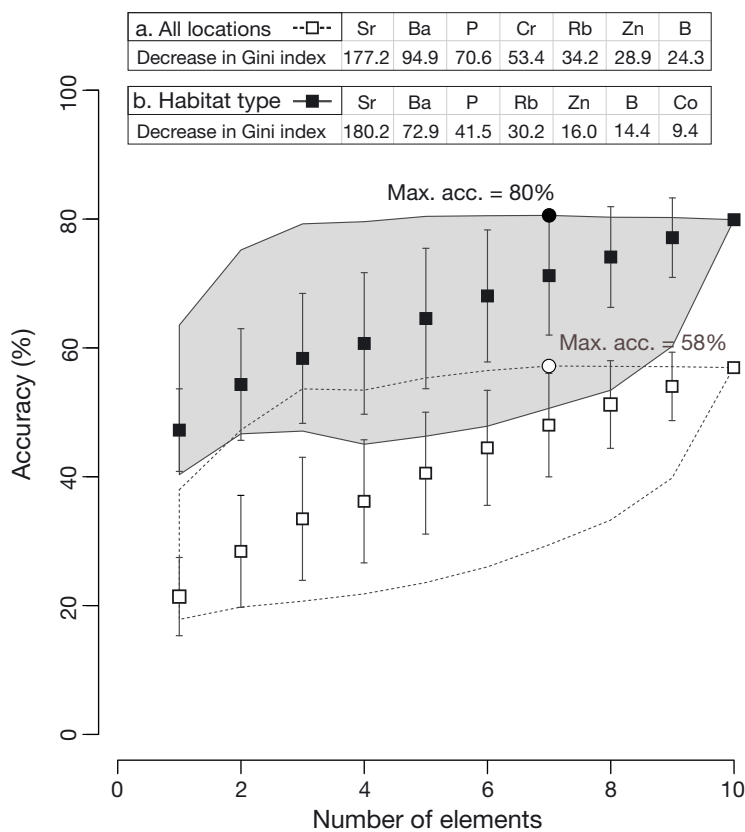


Fig. 3. Effect of the number of elements included in the random forest (RF) procedure on the overall spatial discrimination accuracy between the local lagoons studied and the sea, when considering either (a) all the 7 estuaries separately or (b) the Mundaú-Manguaba estuary alone and all the other estuaries grouped according to the principal component analysis. The maximum accuracy obtained for the optimal RF training data set in each case is indicated (dashed lines). For each size combination and RF training data set, the minimum and maximum accuracy obtained is indicated by the grey area, while the mean (\pm SD) is presented by squares. The list of selected elements for each optimal RF training data set is presented in the tables and according to their mean decrease in Gini Index

estuaries. The second plan of the PCA supported this grouping, further illustrating the differences in multi-elemental signatures between all 3 estuary types and the sea (Fig. 4c).

The new grouping slightly altered the composition of the RF training data set (by replacing Cr with Co in the list of retained elements) but improved the overall discrimination accuracy among potential juvenile habitats of *C. latus* to 80% (Fig. 3, Table 4). Sr and Ba remained the most important elements for habitat discrimination, with respective mean decreases in the Gini Index of 180.2 and 72.9 (Fig. 3). Therefore, the re-assignment accuracies for the sea (95%) and the MM estuary (88%) remained roughly the same. However, Sr and Ba signatures significantly differed

between the 2 remaining habitat types ($p < 0.001$), with higher values (Sr: $5.51 \pm 0.45 \text{ mg g}^{-1}$; Ba: $1.13 \pm 0.86 \text{ } \mu\text{g g}^{-1}$) in type-1 estuaries than in type-2 (Sr: $5.11 \pm 0.48 \text{ mg g}^{-1}$; Ba: $0.68 \pm 0.27 \text{ } \mu\text{g g}^{-1}$). Consequently, the discrimination accuracy was above 70% for both these estuary types (Table 4). However, the corresponding TSS did not exceed 0.64, as more than 19% of their signatures were incorrectly re-assigned: 25.30% for type-1 estuaries and 19.47% for type-2. These errors were due to high overlap in multi-elemental concentrations between the estuaries of GOI, STA, SIR, STC, SUA, and RIO, caused by the high variability of the signatures recorded at each site. In type-1 estuaries, the high variability observed for all elements prevented inter-annual differences in otolith signatures from being significant ($p = 0.372$). However, these differences were marked in type-2 estuaries ($p = 0.001$), with significantly higher Sr values ($p < 0.005$) in 2017 ($5.35 \pm 0.44 \text{ } \mu\text{g g}^{-1}$, $p < 0.001$) than in 2016 ($5.08 \pm 0.47 \text{ } \mu\text{g g}^{-1}$) and 2018 ($4.95 \pm 0.44 \text{ } \mu\text{g g}^{-1}$) overall and significant inter-annual differences at these sites in P ($p < 0.001$), Rb ($p = 0.001$), Co ($p < 0.001$), and B ($p = 0.018$) values. Significant inter-annual variation in otolith fingerprints was also found at sea ($p < 0.001$), with higher Sr ($p < 0.001$), Cr ($p < 0.001$), and Ba ($p = 0.048$) signatures in 2018 than in the 2 other years sampled, while otolith signatures in Zn ($p < 0.001$) and P ($p = 0.002$) showed the opposite trend.

3.2. Juvenile habitat origin in the marine exploited stock

Assignment of the 307 juvenile multi-elemental signatures recorded in the otoliths of sub-adult and adult fish to the 4 discriminable juvenile habitat types in the area (i.e. the MM estuary, type-1 and type-2 estuaries, and the sea) revealed significant variability in the juvenile habitat origin of *C. latus* specimens caught offshore in the Pernambuco state (Fig. 6). The majority of the fish analyzed (75%) were found to have spent their first year of life in an estuary; typically, a 'type-2' one (32.5%). None of the fish investigated was assigned to the MM estuary, and only 12.5% of the fish spent their first year in type-1

Table 3. List of elements retained, cross-validation contingency table, and true skill statistics (TSS) per juvenile habitat in the random forest training data set allowing to reach maximum discrimination accuracy (58%) among all sampling locations. Correct assignments in the contingency table are shown in **bold**. GOI: Goiana; STC: Santa Cruz; SUA: Suape; SIR: Sirinhaém; RIO: Rio Formoso; STA: Santo Antônio; MM: Mundaú-Manguaba

Assignment (%)	Location (B, Ba, Cr, P, Rb, Sr, Zn)							
	Origin							
	GOI	STC	SUA	SIR	RIO	STA	MM	Sea
GOI	36.93	6.56	6.90	13.12	8.74	8.04	0.06	2.04
STC	10.02	53.33	21.71	6.05	10.07	1.88	6.82	0
SUA	14.42	22.33	40.82	11.70	10.86	4.74	2.23	0.68
SIR	21.49	5.30	10.64	48.49	13.48	23.37	5.62	1.66
RIO	8.61	10.26	14.58	7.35	52.02	4.70	1.05	0.95
STA	6.48	1.24	3.19	8.74	2.94	55.73	2.93	0.01
MM	1.65	0.69	1.19	1.81	0.04	2.41	82.00	0.01
Sea	0.30	0.18	0.86	2.64	1.72	0.02	0.02	94.51
TSS	0.22	0.44	0.35	0.44	0.38	0.16	0.59	0.94

estuaries (Fig. 6). In total, 20.2% of the 307 multi-elemental fingerprints recorded in the juvenile part of the otoliths of sub-adult and adult fish were assigned to the sea. However, very few fish (5%) were assigned purely to the marine habitat during their first year of life (Fig. 6). Most of the marine assignments were observed at the end of the juvenile transect in fish attributed to an estuary, for the last or the last 2 spot(s) measured before the annulus, depending on the fish. Therefore, they were assumed to reflect fish returning to the sea at the end of their first year of life. In 30% of the sub-adults and adults analyzed, a mixture of fingerprints from type-1 and type-2 estuaries was ob-

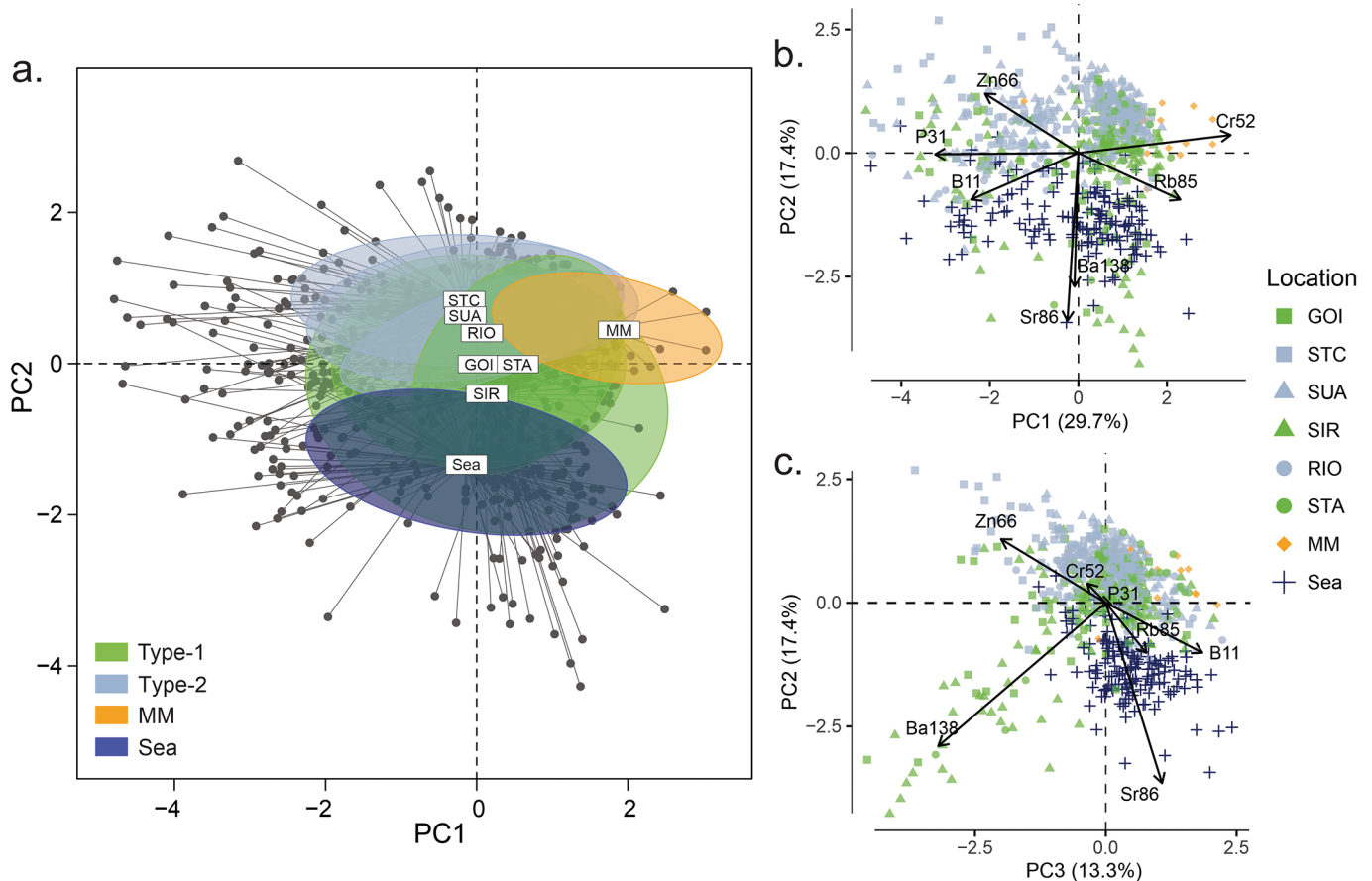


Fig. 4. Score plots for the first three principal components (PC1, PC2, and PC3) of the PCA based on the 770 otolith multi-elemental signatures (from 156 individual *Caranx latus*) gathered for the 8 juvenile habitats (7 estuaries and sea) of *C. latus* investigated in northeastern Brazil. (a) Projection of the position of juvenile elemental signatures for all habitats in the plane PC1 \times PC2. For each habitat, the position of the centroid is indicated in the white box. Correlation projections for all variables (elements) driving the distribution of multi-elemental signatures in the planes (b) PC1 \times PC2 and (c) PC2 \times PC3. Black arrows: the correlation of each variable (element) with the 2 respective principal components. Colors represent the 3 groups of estuaries ('type-1', 'type-2', and the Mundaú-Manguaba lagoon system) and the sea. See Table 2 for location definitions

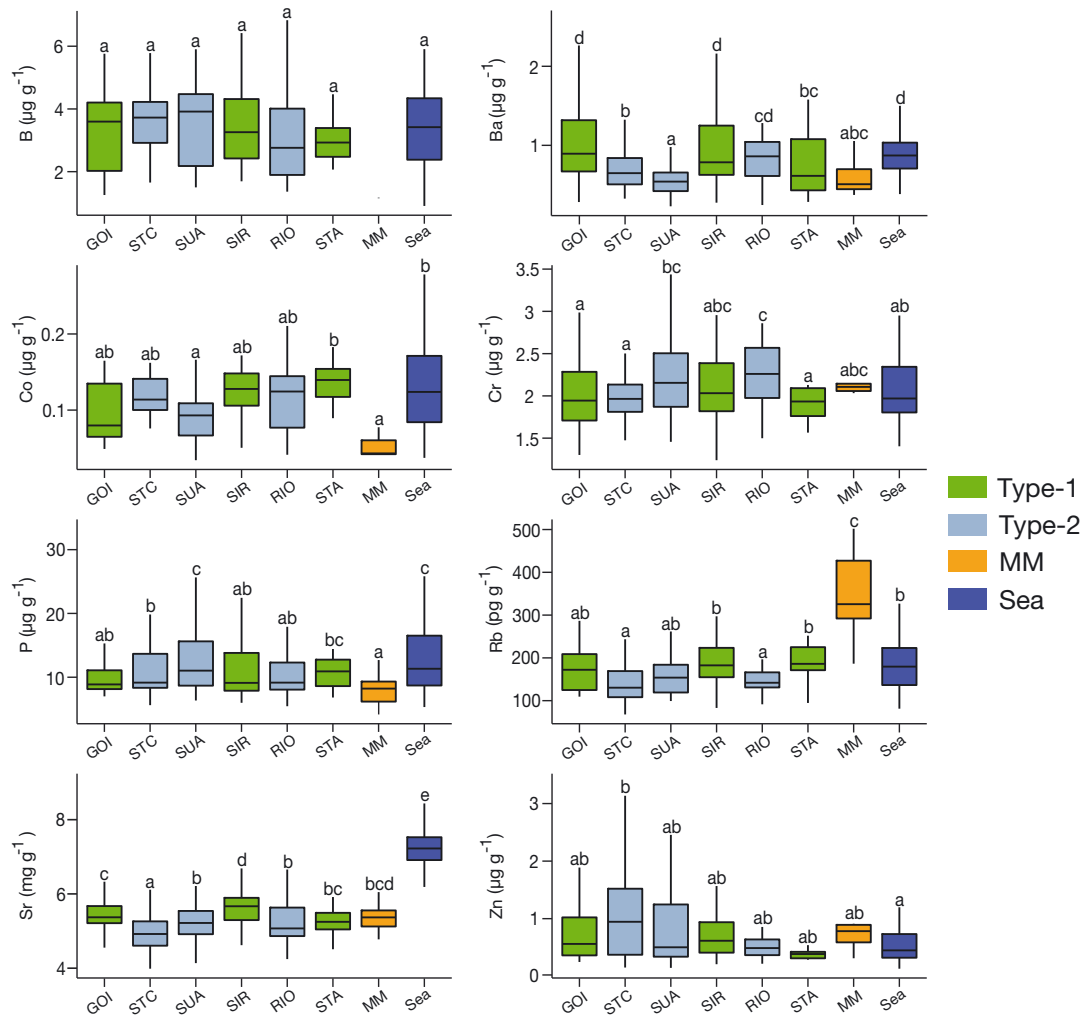


Fig. 5. Elemental fingerprints recorded on otoliths of *Caranx latus* during their life in the 7 estuaries studied and at sea (see Table 2). Elemental signatures for the sea include those recorded during the larval life and the otolith edge signature of sub-adult specimens captured at sea. Element concentrations were normalized to ^{43}Ca and are expressed as ratios to Ca. In each case, the horizontal line and the box correspond to the median and the interquartile range. Letters indicate significant differences in elements based on post hoc Dunn's tests ($p < 0.05$). Colors represent the 3 groups of estuaries ('type-1', 'type-2', and the Mundaú-Manguaba lagoon system) and the sea. See Table 2 for location definitions

served. These fish were, therefore, assigned to an unidentified type of local estuary. Lastly, 20% of the fish exhibited a complex mixture of marine and varied estuarine elemental signatures during their juvenile life. Therefore, they were assigned to an 'unknown' juvenile habitat.

4. DISCUSSION

Assessing the connectivity between fish coastal habitats and their importance in supporting exploited adult stocks is crucial for developing appropriate strategies for fishery management and conservation (Nagelkerken 2009, Sheaves et al. 2015). This

study provides valuable insights into this matter by elucidating the use of inshore habitats by an exploited yet poorly studied marine fish in northeastern Brazil. Otolith elemental compositions revealed that a significant proportion of the *Caranx latus* adults that were fished off the Pernambuco state inhabit local estuaries during their first year of life, demonstrating that these inshore habitats play a crucial role in sustaining the productivity of the local coastal marine stock.

4.1. Variation in otolith elemental fingerprints

The accuracy of re-assignment was highest (94–95%) for the marine coastal zone, regardless of the RF

Table 4. List of elements retained, cross-validation contingency table, and true skill statistics (TSS) per juvenile habitat type in the random forest training data set allowing to reach maximum overall discrimination accuracy (80%) among the 3 retained estuarine habitat types (type-1, type-2 and the Mundaú-Manguaba lagoon system [MM]) and the sea. Correct assignments in the contingency table are shown in **bold**

		Origin			
		Type-1	Type-2	MM	Sea
Assignment (%)	Type-1	70.10	19.47	5.26	2.43
	Type-2	25.30	78.90	7.35	0.01
	MM	2.40	0.66	88.30	1.41
	Sea	2.06	0.80	0.01	95.98
	TSS	0.52	0.64	0.55	0.94

training data set used and despite the strong marine influence in studied estuaries (Table 1). This discrimination efficiency was mainly due to the contrasting Sr values recorded in *C. latus* otoliths during life at sea. Sr values were significantly higher both in the larval portion of all otoliths and on the otolith edge for specimens captured at sea, probably due to the higher salinities at sea (Reis-Santos et al. 2023). This supports the use of otolith Sr concentrations to assess *C. latus* lifetime migrations between marine and inshore coastal habitats in northeastern Brazil, as previously suggested for other migratory species (Aschenbrenner et al. 2016a, Santana et al. 2018, Menezes et al. 2021). Otolith fingerprints in Ba were also useful but were not consistent among life stages at sea. While Ba values in the portion of the otolith representing the larval life at sea (mean \pm SD; $0.91 \pm 0.22 \mu\text{g g}^{-1}$ in all fish) were globally similar to those

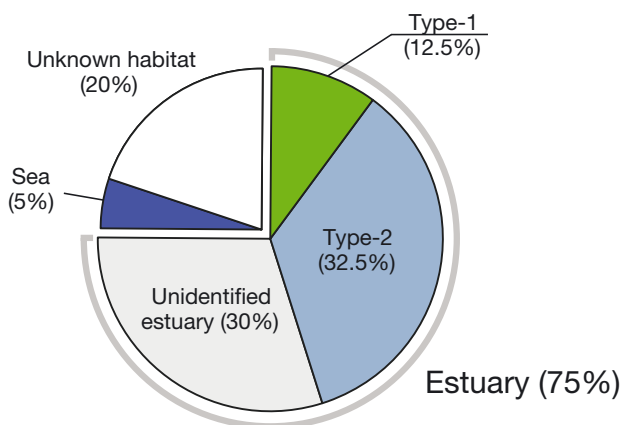


Fig. 6. Relative contribution of juvenile habitats to the exploited population of *Caranx latus* in northeastern Brazil

recorded in the estuaries, they were significantly lower on the edge of the otoliths of the sub-adults and adults captured offshore ($0.57 \pm 0.16 \mu\text{g g}^{-1}$). Otolith Ba concentration is commonly associated with increased freshwater influence (Elsdon & Gillanders 2005, Gillanders 2005, Sturrock et al. 2012), as Ba is carried downstream by terrestrial runoff (Coffey et al. 1997). This could indicate that *C. latus* post-larvae reside on nearshore reefs under the estuarine influence before actually entering the estuaries, as observed in several coral reef species (Hamilton & Warner 2009). However, changes in fish diet (Buckel et al. 2004, Walther et al. 2010) and physiological processes during ontogeny are likely to modulate Ba incorporation into the otolith (Hicks et al. 2010, Walther et al. 2010, Miller 2011). In particular, a negative effect of fish somatic growth on Ba uptake has been reported in some species (Miller 2011, Hüsey et al. 2021), which may also happen in *C. latus*, as Ba concentrations decreased continuously from the larval to the juvenile portion of the otoliths, whereas the opposite trend would be expected during fish colonization of estuaries if Ba was a marker of freshwater influence.

Otolith elemental compositions of *C. latus* juveniles largely overlapped among several of the studied estuaries. While otolith Sr signatures in the studied estuaries were notably lower on average than those recorded at sea, they were variable irrespective of the site, and differences between estuarine sites were low. Most type-2 estuaries (STC, SUA, and RIO) are larger than those in the type-1 group (GOI, SIR, and STA). They are also subject to stronger tidal exchange and can therefore be considered to be under a stronger marine influence (Table 1). However, mean otolith Sr concentrations were significantly lower in type-2 estuaries than those observed for type-1, which contrasts with the usual trend observed in estuarine environments (Miller 2011, Sturrock et al. 2012, Izzo et al. 2015). A possible explanation for this observation is that the micro-habitats used by *C. latus* juveniles within type-2 estuaries are those under the strongest freshwater influence. Alternatively, in these large estuaries, the juveniles might inhabit deep and well-mixed areas where salinity conditions are more stable over the dry season. In the smaller and shallower type-1 estuaries, the micro-habitats that they live in may be subject to more marked and frequent changes in water salinity, depending on the daily tidal range and on the weather conditions (punctual rainfalls, droughts, and heatwaves) during the dry season. Such an alternation of short oligohaline and longer hypersaline

conditions would explain the more variable but slightly higher otolith Sr concentrations in type-1 estuaries. Nonetheless, the absence of information on local water chemistry in the studied estuaries hinders our ability to identify the factors driving the variation in otolith Sr concentrations between them.

Ba fingerprints in the otoliths of *C. latus* juveniles improved the discrimination between the 3 types of estuaries. Even in environments with low variations in salinity and Sr concentrations, Ba concentrations in otoliths prove to be a reliable tracer of terrestrial inputs, often reflecting the turbidity load of an environment (Condini et al. 2016, Menezes et al. 2021). This might be the case in the studied locations, where higher Ba concentrations in the otoliths of juvenile *C. latus* were observed in several type-1 estuaries, such as GOI and SIR. During the dry season, both GOI and SIR exhibit more turbid waters (24–60 nephelometric turbidity units [NTU]) than type-2 estuaries, i.e. STC, SUA, and RIO (<8 NTU; Table 1) (Borges 2011, CPRH 2019, Silva et al. 2019). Therefore, it is likely that the turbidity load in the studied locations has a greater influence on otolith Ba concentrations of juvenile *C. latus* in the smaller estuaries.

The MM estuary exhibited intermediate otolith Ba signatures despite being the only oligohaline environment investigated in this work (Table 1). The intermediate values observed at this site might indicate a bias in our otolith fingerprint due to the low number of fish collected locally. However, *C. latus* juveniles might remain close to the estuary mouth in this oligohaline system to avoid low-salinity habitats. This apparent contradiction with the low otolith Ba concentrations may suggest that other processes influence the local availability of dissolved Ba in the water and its incorporation in *C. latus* otoliths. Among all the estuaries studied, MM is the only one to experience eutrophic conditions during the dry season (Oliveira & Kjerfve 1993). As seasonal algal blooms in estuaries can result in rapid and nearly complete removal of dissolved Ba from the water (Stecher & Kogut 1999), the low Ba concentrations observed in *C. latus* otoliths in this lagoon could be somehow associated with its eutrophic status, similar to what has been suggested for some bivalve shells (Thébault et al. 2009). Nonetheless, this estuary was found to have markedly distinct otolith elemental fingerprints, particularly in terms of Rb. Although the main causes for Rb uptake in fish otoliths are not yet fully understood (Sturrock et al. 2012), high levels of Rb in the otoliths have been associated with freshwater inputs (Hicks et al. 2010). As all the estuaries under the significant freshwater influence in this

work tended to show higher Rb concentrations, the particularly high Rb values observed for the MM estuary might reflect life in freshwater bodies for local *C. latus* juveniles. High Rb concentration in otoliths could also reflect the strong urbanization around this lagoon, which is surrounded by one of the largest cities in the region. Accordingly, the dissolved Rb:Sr ratio in the water has shown to be a conservative tracer of wastewater and diffuse pollution (Nirel & Lazzarotto 2005, Smith et al. 2021). However, further information on water chemistry is needed to elucidate the link between the Rb incorporation in otoliths and anthropogenic pressures in MM.

Reliable reconstruction of fish life history using otolith chemistry requires that differences in elemental fingerprints between inhabited locations are stable through time (Gillanders 2002, 2005, Sturrock et al. 2012). This is less likely to be the case for estuaries and other transitional areas, as the constant variations in hydrologic regimes and environmental conditions in these environments generally result in fluctuations in chemical fingerprints within otoliths (Elsdon & Gillanders 2006, Walther & Thorrold 2009). In this study, although YOY fish sampling only occurred during the dry season (i.e. when the marine influence is the strongest in all estuaries), juvenile jacks arrive in these environments earlier in the year, beginning in the late rainy season (Gonzalez et al. 2021). Therefore, the juvenile portions of the otoliths analyzed also included some elemental signatures that were deposited during periods of high freshwater inputs. This might explain the high variability in otolith elemental signatures observed for some estuaries. The use of sequential otolith signatures increases the inter-annual stability of the elemental fingerprints database by covering most of the spatiotemporal variability of elements recorded within the estuarine life of the juvenile specimens (Tournois et al. 2017). As a result of this intra-annual variability, otolith signatures in estuaries were relatively stable across years. Only 2 of the sites investigated (SUA and RIO) presented significant inter-annual changes in their otolith signatures. Yet spatial differences exceeded temporal ones for all investigated sites. This supports the reliability of the otolith elemental fingerprints data set obtained in this study to assess juvenile origin for *C. latus* adults in northeastern Brazil.

4.2. Reliability in local habitat assignment

Estimating the relative importance of different nursery grounds for stock recruitment implies that all

potential juvenile habitats are considered and adequately characterized (Campana 1999). In this study, as local marine habitats occupied by *C. latus* juveniles such as sandy beaches and shallow nearshore reefs (Mazzei et al. 2011, Medeiros et al. 2017) could not be sampled, otolith fingerprints from the marine larval life and from the otolith edge of the youngest sub-adults caught offshore were used as proxies for the signatures recorded by the species during its juvenile life at sea. Therefore, the signatures for the marine habitat in this work might not fully reflect the individual's life in these specific areas, and some specific elemental fingerprints may be missing, such as the unique concentrations in Ba or in other elements observed in some coral reefs (Hamilton & Warner 2009). Nevertheless, some signatures in the juvenile part of the otoliths of our sub-adult and adult samples were assigned to the sea, suggesting that at least part of the local juvenile marine habitats have been correctly characterized in our analysis. Moreover, a particular subset of these fish (20%) was attributed to an unknown habitat because they exhibited a balanced mixture of elemental signatures assigned to several estuaries and the sea. This subset of fish might encompass *C. latus* individuals that perform migrations across varied coastal areas in northeastern Brazil and inhabit multiple estuaries for short periods of time during their juvenile life (e.g. Schilling et al. 2018), but also fish that have spent most of their first year of life in a habitat not described in our juvenile fingerprints data set, either offshore the coastline sampled or in other areas along the Brazilian coast.

The RF algorithm has been shown to be valuable and versatile in identifying fish past habitats using otolith elemental fingerprints from different life stages (Tournois et al. 2013, Delerue-Ricard et al. 2019) in both temperate (Mercier et al. 2011, Tournois et al. 2017, Prichard et al. 2018) and tropical regions (Paillon et al. 2014, Teichert et al. 2018). In this study, the overall accuracy of the RF algorithm with the optimal training data set (80%) confirms its value for discriminating juvenile habitats for tropical coastal fishes. However, the RF algorithm had a limited capacity to discriminate each site separately due to the high overlap in multi-elemental fingerprints between some estuaries. The use of sequential elemental signatures of a given fish considered the temporal and spatial variability in elemental composition during the estuarine life, but it may also have artificially increased the precision of our local fingerprints of each estuary. Nonetheless, the use of several signatures for habitat description and juvenile origin assignment offers the advantage of identifying habi-

tats outside of those described in the juvenile fingerprint training data set and reduces the likelihood of generating false positives for a given location (Tournois et al. 2017). This is illustrated here by the considerable part of sub-adult and adult specimens attributed to an unidentified estuary (30%). Given the numerous small estuaries spread along the northeastern Brazilian coast—up to 15 in the state of Pernambuco alone (Paiva & Araújo 2010, Silva et al. 2011)—it is reasonable to expect that some of them may also contribute to the local offshore exploited population.

4.3. Juvenile habitat contributions to coastal fisheries

Overall, estuaries contributed the most to the offshore exploited population of *C. latus*, with 75% of sub-adult and adult specimens analyzed originating from one of them. This suggests that *C. latus* displays partial-migration behavior in Brazil (Chapman et al. 2012), similar to other tropical species in this area (Franco et al. 2019, Menezes et al. 2021). While most *C. latus* individuals can be classified as marine migrants, migrating between estuaries and the sea at least once in their life (Elliott et al. 2007), only a few strictly inhabit the marine environment (marine residents, 5%). As a top-predator fish, *C. latus* significantly contributes to the export of organic matter produced in local inshore habitats, acting as a biological vector linking distinct littoral and coastal environments across the shelf (e.g. Pelage et al. 2021). Although the estuarine lifespan of *C. latus* is relatively short (usually limited to a few months during the first year of life), it corresponds to the period when individual growth is the highest and most variable (Gonzalez et al. 2022). Thus, estuarine use by *C. latus* juveniles may have important consequences in terms of organic matter transfer from the continent to the sea. These results complement existing knowledge on the local ecology of the species (Lessa et al. 2009, Gonzalez et al. 2021, 2022), highlighting the fact that the quality of inshore environments plays a key role in maintaining offshore stocks, thereby affecting the productivity of the adjacent coastal zone.

Among the estuaries studied, the larger ones with a more constant marine influence contributed the most to the exploited stock (32.5%), consistent with the species' ecology as a marine migrant (Elliott et al. 2007). The remaining estuaries and juvenile habitats at sea had notably lower contributions, even considering that some of the fish attributed to an 'unidenti-

fied estuary' (30%) or an 'unknown habitat' (20%) originate from these environments. This suggests that estuaries in northeastern Brazil should be considered as local nursery grounds for the species (Dahlgren et al. 2006). This idea is supported by the higher occurrence of *C. latus* juveniles in at least some of them (Silva-Júnior et al. 2017), which may provide better environmental conditions for juvenile growth in the species (Gonzalez et al. 2022). However, since Beck et al. (2001) formalized the concept of fish nursery ground, the general understanding of the role of coastal habitats in stock maintenance has evolved, and there are increasing calls to improve knowledge of nursery functions and their drivers (Nagelkerken et al. 2015, Litvin et al. 2018, Lefcheck et al. 2019). Obtaining precise estimates of the respective contribution of each site to the adult population is key to the conservation of the stock and ecosystem protection or management. This will require further studies using complementary water chemistry analysis to understand the drivers of otolith elemental composition in the studied locations. The use of other biogeochemical markers, such as stable isotope ratios of otoliths (Reis-Santos et al. 2023), might prove to be particularly useful to discriminate among all potential estuarine juvenile habitats in the area. Moreover, precise information on the location and features of specific juvenile habitats of *C. latus* at sea is needed to reliably evaluate the value of each site (or group of estuaries) as a nursery ground, as this allows comparing the contribution of each habitat according to its surface area (e.g. Beck et al. 2001, Tournois et al. 2017). Complementary studies are also needed before conclusions can be drawn about the actual factors underpinning the importance of different estuarine settings for *C. latus* in this area, as they may comprise both biological and environmental constraints affecting the juvenile fish condition of this species (Vasconcelos et al. 2009, Isnard et al. 2015, Litvin et al. 2018).

5. CONCLUSIONS

This study provides valuable insights into the land–sea connectivity and local life strategies of an exploited yet poorly studied tropical fish species. Our results indicate that as with other coastal and reef species, estuarine systems play a key role in maintaining populations of the horse-eye jack in northeastern Brazil, with up to 75% of *Caranx latus* adult specimens that are caught offshore originating from these inshore environments. These findings are key

to improving local fisheries and ecosystem management, especially given the recurrent anthropogenic pressures to which estuarine habitats are subjected. These pressures threaten the quality of estuaries for juvenile fish growth and survival, with potential implications for stock recruitment success. Furthermore, the unexpected responses to local environmental settings found for some chemical elements in this study (e.g. Sr and Ba) reinforce previous calls for a more comprehensive investigation of the factors influencing element uptake and composition in fish otoliths, particularly in the tropics.

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