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ESTUARIES AS NURSERY HABITATS FOR THE HORSE-EYE JACK (*Caranx latus*) IN NORTH-EASTERN BRAZIL

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Le 29 septembre 2021

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Estuaries as nursery habitats for the horse-eye jack (*Caranx latus*) in North-Eastern Brazil

Júlio Guazzelli Gonzalez

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At the end, the important is to have
a nice story to tell.

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ABSTRACT

Evaluating the importance of inshore coastal habitats for the maintenance of exploited coastal fish populations is key to delineate sustainable strategies for both fishery and ecosystem management. Jacks are highly prized tropical marine fishes. Most of them complete their whole life cycle at sea, but some use estuaries at the juvenile stage before moving back to coastal waters and joining offshore adult exploited stocks. This is the case of the horse-eye jack (*Caranx latus*), an exploited yet poorly studied species frequently found in estuaries in North-Eastern Brazil, at least at the juvenile stage. However, little was known on the species' ecology in these inshore habitats, nor on their importance for the maintenance of its local exploited stock. To start filling this knowledge gap, this thesis combined three complementary research axes. The first one investigated the local size-at-age and growth of *C. latus* using size data and otolith readings from 282 specimens captured both at Sea and in varied inshore habitats. This allowed to specify fish ages in all the environments colonised by the species in the area and to infer the growth parameters for its local exploited stock. The second axis investigated local variations in the diet and food resources of *C. latus* juveniles in estuaries and their causes, by a combined analysis of the stomach contents and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) signatures of 439 juveniles of both *C. latus* and another sympatric jack species (*C. hippos*), in three neighboring estuaries with contrasted morphological and biological features. It highlighted a plasticity in local resources use by juvenile jacks according to the estuarine environmental settings, allowing them to limit the trophic competition among them, with potential consequences on their respective sizes and abundances. Finally, the third research axis aimed to quantify the importance of local estuaries for sustaining the adult stock of *C. latus* exploited offshore, by analysing different chemical elements incorporated in the juvenile part of 183 otoliths of juveniles and adults captured in varied estuarine and marine habitats in this area. This revealed that 75% of the sub-adults and adults exploited by the fisheries off the coast of the Pernambuco state have spent their first year of life growing in local estuaries, particularly those under strong marine influence. These findings significantly advance previous knowledge on *C. latus* ecology and demonstrate that estuaries play a key role in the maintenance of the *C. latus* population in North-Eastern Brazil. Yet, local differences in the abiotic and biotic environmental conditions experienced by juvenile jacks during their estuarine stay strongly modulate the respective value of these inshore habitats for the renewal of the stock fished at Sea, with strong implications in terms of local fishery and ecosystem management.

Keywords: Coastal fisheries, Marine fish, Connectivity, Growth, Trophic ecology, Juvenile habitat

RÉSUMÉ

Comprendre le rôle des habitats côtiers dans le maintien des populations de poissons marins exploités est essentiel pour définir des stratégies durables pour la gestion des pêches et des écosystèmes. Les carangues sont des poissons marins tropicaux très prisés. La plupart d'entre elles effectuent tout leur cycle de vie en mer, mais certaines utilisent les estuaires au stade juvénile, avant de regagner les eaux côtières pour rejoindre les stocks adultes exploités. C'est le cas de la carangue mayole (*Caranx latus*), une espèce exploitée mais peu étudiée, que l'on trouve souvent en estuaires au nord-est du Brésil, au moins au stade juvénile. Afin de préciser l'importance de ces habitats côtiers pour le maintien du stock de *C. latus* exploité dans la région, cette thèse a été construite sur trois axes de recherche complémentaires. Le premier avait pour but de décrire la croissance locale de *C. latus*, sur la base de données de taille et de lectures d'otolithes pour 282 individus de l'espèce, capturés en mer et dans divers estuaires de la région. Il a permis de préciser l'âge des poissons dans tous les environnements colonisés à chaque stade de vie et d'inférer les caractéristiques de croissance du stock local. Le deuxième axe visait à décrire la variabilité du régime alimentaire et des sources de nourriture des juvéniles de *C. latus* en estuaire et leurs causes, par une approche combinant l'analyse des contenus stomacaux et des signatures isotopiques (δ^{13}C and δ^{15}N) de 439 juvéniles, de *C. latus* et d'une autre espèce sympatrique (*C. hippos*), dans trois estuaires voisins aux caractéristiques biotiques et abiotiques contrastées. Il a montré une plasticité dans l'utilisation des ressources par les juvéniles des deux espèces suivant les caractéristiques estuariennes locales, qui leur permet de réduire la compétition trophique entre eux, avec des conséquences potentielles sur leurs tailles et leurs abondances respectives. Enfin, le troisième axe s'est attaché à quantifier l'importance des estuaires pour le maintien du stock de *C. latus* exploité en mer, par l'analyse des teneurs en différents éléments chimiques dans la portion juvénile de 183 otolithes de juvéniles et d'adultes capturés dans divers habitats estuariens et hauturiers de l'espèce. Ceci a révélé que 75 % des spécimens pêchés au large ont passé leur première année de vie en estuaire, surtout dans ceux sous forte influence marine. Ces résultats avancent de façon significative les connaissances sur l'écologie de *C. latus* et indiquent que les estuaires jouent un rôle clé dans le maintien de ses populations dans le nord-est du Brésil. Cependant, les différences locales de conditions environnementales que les juvéniles de carangue connaissent pendant leur séjour estuarien modulent fortement la valeur respective de ces habitats côtiers pour le renouvellement du stock pêché en mer, avec des implications fortes pour la gestion des pêcheries et des estuaires dans cette région du Globe.

Mot-clés : Pêcheries côtières, Poissons marins, Connectivité, Croissance, Écologie trophique, Habitat juvénile

RESUMO

Compreender a importância dos habitats costeiros para a manutenção das populações de peixes explotados é fundamental para delinear estratégias sustentáveis para a pesca e o manejo do ecossistema. Os xaréus são peixes marinhos tropicais muito apreciados. A maioria deles completa todo o seu ciclo de vida no mar, porém alguns utilizam os estuários na fase juvenil antes de retornarem ao mar e adentrarem ao estoque adulto explotado pela pesca. Este é o caso do aracimbora (*Caranx latus*), uma espécie explotada mas pouco estudada e que pode ser encontrada com frequência em estuários no Nordeste do Brasil, pelo menos no estágio juvenil. Entretanto, pouco se sabia sobre a ecologia da espécie nestes habitats costeiros, assim como a importância destes locais para a manutenção do estoque exlpotado localmente. Esta tese combina três eixos de pesquisa complementares para começar a preencher esta lacuna de conhecimento. O primeiro deles investigou o comprimento por idade e o crescimento de *C. latus* na região com base nos dados de tamanho e na leitura dos otólitos de 282 espécimes capturados no mar e em diversos habitats costeiros. Isto permitiu especificar a idade dos peixes nos habitats colonizados pela espécie e inferir os parâmetros de crescimento para o estoque explotado. O segundo eixo investigou as variações locais na dieta e nos recursos alimentares dos indivíduos juvenis nos estuários através de uma análise conjunta do conteúdo estomacal e razão isotópica ($\delta^{13}C$ e $\delta^{15}N$) de 439 indivíduos juvenis de *C.latus* e uma outra espécie simpátrica de xaréu (*C. hippos*), em três estuários vizinhos e com características morfológicas e biológicas contrastantes. Isso demonstrou a plasticidade no uso de recursos das espécies de acordo com as configurações ambientais de cada estuário, permitindo-lhes limitar a competição trófica entre elas, com potenciais consequências em seus respectivos tamanhos e abundâncias. Por fim, o terceiro eixo de pesquisa visou quantificar a importância dos estuários da região para a manutenção do estoque adulto de *C. latus* explotado pela pesca ao analisar os elementos químicos incorporados na porção do otólito referente ao estágio juvenil de 183 otólitos de indivíduos juvenis e adultos capturados em diversos ambientes estuarinos e marinhos da região. Isso revelou que 75% dos indivíduos sub-adultos e adultos explotados pela pesca ao largo da costa do estado de Pernambuco passaram seu primeiro ano de vida crescendo em estuários próximos da região, particularmente naqueles sob forte influência marinha. Esses resultados avançam significativamente os conhecimentos pretéritos sobre a ecologia de *C. latus* e demonstram que os estuários desempenham um papel fundamental na manutenção da população de *C. latus* no nordeste do Brasil. No entanto, as diferenças locais nas condições ambientais as quais os juvenis da espécie estão sujeitos durante sua estadia nos estuários modulam fortemente o respectivo valor desses habitats para a renovação do estoque, com fortes implicações no manejo pesqueiro e do ecossistema.

Palavras-chave: Pesca costeira, Peixe marinho, Conectividade, Crescimento, Ecologia trófica, Habitat juvenil

SYNTHÈSE DES TRAVAUX EN FRANÇAIS

INTRODUCTION GENERALE

Le succès du recrutement dans les populations adultes est essentiel pour le maintien des stocks de poissons exploités (Beverton & Holt 1993). Bien qu'il soit également en partie influencé par l'état de la population adulte qui se reproduit ainsi que par les taux de survie au stade larvaire, ce recrutement dépend largement de la croissance et de la survie pendant la phase juvénile (Chamber & Trippel 1997). En effet, les contraintes biologiques et environnementales constituent des obstacles majeurs pour les juvéniles et déterminent souvent la taille et la condition des populations recrutées (Walters & Korman 1999, Andersen et al. 2017). Les juvéniles occupent souvent des habitats différents des adultes, généralement à la recherche d'une plus grande disponibilité de nourriture et d'un risque de prédation plus faible (Dahlgren & Eggleston 2000). Parmi la diversité d'habitats fréquentés par les poissons au stade juvénile, certains sont qualifiés de "nurseries" car ils leurs permettent d'être présents en nombre plus élevé ou de bénéficier de processus (biologiques) qui améliorent leur survie et maximisent leur recrutement dans le stock adulte (Beck et al. 2001).

Les environnements côtiers de transition, comme les estuaires et les lagunes, sont utilisés comme zones de nurserie par diverses espèces marines, dont certaines sont exploitées par la pêche (Nagelkerken et al. 2008, Sheaves et al. 2015). Cependant, ils sont soumis à des niveaux constants et élevés de pressions humaines, allant de l'eutrophisation à la surpêche (Kennish 2002, Mitra & Zaman 2016). Ces dernières menacent la santé et la sécurité alimentaire des communautés humaines locales, mais aussi la qualité des habitats côtiers pour les poissons juvéniles (Nagelkerken et al. 2008, Crook et al. 2014). Il est aussi de plus en plus évident que même des habitats côtiers du même type peuvent ne pas offrir des conditions de vie équivalentes pour les juvéniles de poissons (Isnard et al. 2015, Schloesser & Fabrizio 2019). Par conséquent, comprendre comment les zones côtières de transition peuvent contribuer au maintien des populations de poissons exploités en mer est essentiel pour définir des stratégies efficaces pour la conservation des espèces et la gestion des pêches (Nagelkerken et al. 2015, Sheaves et al. 2015). Cela est particulièrement vrai sous les tropiques, où le développement rapide des villes côtières et la demande croissante pour les produits de la mer menacent les ressources halieutiques locales à court et moyen terme (Barlow et al. 2018, FAO 2018), et où la sensibilisation à l'environnement ne fait qu'émerger (Prandle & Lane 2015, Mitra & Zaman 2016).

Cette étude a pour objectif d’évaluer l'importance des estuaires pour le renouvellement des stocks d’un poisson marin tropical exploité, la carangue mayole (*Caranx latus*). Cette espèce pélagique est largement répandue dans l’Atlantique occidental et constitue une importante source de nourriture et de revenus pour les populations du Sud-Ouest de l'Atlantique (Lessa et al. 2009, Pinheiro et al. 2010). Au Brésil, plus de 3400 tonnes de *C. latus* ont été capturées chaque année par la pêche artisanale entre 2009 et 2011, représentant 45% du total des débarquements nationaux de carangues (MPA 2011). Cependant, la biologie et la dynamique des populations de *C. latus* sont encore largement méconnues, au Brésil et ailleurs.

Jusqu'à présent la plupart des études menées au Brésil se sont concentrées sur un stade de vie particulier ou se sont limitées à certains endroits, ne fournissant qu'une information de base, sur la présence ou non de *C. latus* dans différents habitats côtiers (Paiva & Araújo 2010, Felizola-Freire et al. 2018). Les connaissances ainsi récoltées sur l'écologie de *C. latus* montrent que son cycle de vie comprend l'utilisation d'une mosaïque d'environnements côtiers et marins. Les grands spécimens de l'espèce sont généralement associés aux eaux profondes (> 40 m) et aux récifs près du bord du plateau continental (Lessa et al. 2009, Felizola-Freire et al. 2018), où ils se reproduisent principalement pendant les mois d’Avril et Août (Figuerola-Fernández et al. 2008, Heyman & Kjerfve 2008). Par conséquent, les larves de *C. latus* se s'observent essentiellement au large, sur la partie externe du plateau continental (Berry 1959, Campos et al. 2010). Ses juvéniles, cependant, sont le plus souvent pêchés dans les zones estuariennes ou le long des plages (Figueiredo & Menezes 1980, Mazzei et al. 2011, Silva et al. 2011), où ils se nourrissent d'une grande diversité de poissons et de crustacés (Vasconcelos Filho et al. 2010, Figueiredo & Pessanha 2015).

Dans le nord-est du Brésil, la présence fréquente de juvéniles de *C. latus* dans les estuaires pose la question de son utilisation de ces environnements côtiers comme zones de nurserie, comme observé pour d'autres espèces de carangues (Smith & Parrish 2002). En effet, les informations disponibles jusqu'à présent limitent notre compréhension des stratégies locales de vie de l'espèce. Estimer l'importance des estuaires pour la population locale de *C. latus* et la connectivité entre ses habitats juvéniles et ses habitats adultes est particulièrement pertinent étant donné que l'espèce est essentiellement ciblée par la pêche côtière avant d'atteindre sa taille de maturité sexuelle (Pelage 2020). Par ailleurs, un certain nombre d'informations de base sur la dynamique de populations de l'espèce sont nécessaires pour le développement durable de sa pêche (Lessa et al. 2009, Novak et al. 2020), au Brésil mais aussi dans d'autres parties du monde où *C. latus* représente une source de revenus non négligeable pour les communautés locales. Par conséquent, l’identification des habitats clés de l'espèce peut non seulement contribuer à une meilleure la gestion des pêcheries locales, mais aussi contribuer à estimer la valeur générale des estuaires en tant que nurseries pour les poissons marins migrateurs de cette région du Globe.

L'objectif principal de cette thèse est d'étudier l'importance des environnements littoraux de transition (estuaires) pour le maintien de la population de *C. latus* exploitée au large de la côte nord-est du Brésil. Pour cela, une étude approfondie de la biologie et de l'écologie de *C. latus* a été effectuée, dans divers habitats côtiers et au large, et pour la plupart des stades de vie. Les sites considérés englobent sept estuaires distribués le long de la côte du nord-est du Brésil (Goiana, Santa Cruz, Suape, Sirinhaém, Rio Formoso, Santo Antônio et Mundaú-Manguaba) et sa zone hauturière. À chaque fois, l'accent a été mis sur la phase juvénile du cycle de vie pour permettre de répondre à trois grandes questions :

(1) Combien de temps les individus de *C. latus* passent-ils dans les estuaires et quelles sont les conséquences sur leur croissance ?

(2) Le régime alimentaire des juvéniles de *C. latus* varie-t-il en fonction des paramètres environnementaux dans les estuaires ?

(3) Les estuaires sont-ils des habitats clés pour le maintien de la population locale exploitée au large ?

Le présent manuscrit est organisé autour de ces trois questions, chacune d'entre elles apportant une perspective complémentaire sur la valeur des estuaires pour le maintien de la population adulte de *C. latus* dans cette région.

AGE ET CROISSANCE DE *Caranx latus*

Les carangues (Caranx spp.) sont des poissons marins très prisés, exploités par la pêche sportive et artisanale dans de nombreuses régions tropicales et subtropicales (Smith-Vaniz 2002, FAO 2003, Arra et al. 2020). Par conséquent, des efforts considérables ont été déployés pour étudier leur biologie dans le monde entier (Berry 1959, Smith-Vaniz 2002, Heyman & Kjerfve 2008). Cependant, les connaissances de base faisaient encore défaut pour plusieurs des 18 espèces de ce genre. C'était le cas pour *C. latus*, pour laquelle on ne disposait pas d'informations fiables en termes de croissance somatique, les études précédentes sur le sujet se limitant à définir la relation taille-poids des individus (*e.g.* Figuerola-Fernández et al. (2008) et Viana et al. (2016)). Afin de combler cette lacune, les paramètres d'âge et de croissance de *C. latus* au Nord-Est du Brésil ont été étudiés à l'aide de données de taille et de lectures d'otolithes provenant de spécimens capturés à la plupart des stades de vie et dans les différents habitats côtiers et hauturiers, y compris dans plusieurs estuaires où se trouvent les juvéniles de l'année (Paiva & Araújo 2010, Silva-Júnior et al. 2017).

Un total de 282 individus de *C. latus*, dont les tailles (longueur standard - SL) étaient comprises entre 36 et 760 mm et les poids entre 1 et 7090 g, a été utilisé. Ces individus avaient été capturés dans la zone d'étude entre août/2017 et août/2019, tout au long de l'année afin de valider la période de dépôt des stries de croissance sur leurs otolithes. En effet, l'estimation de l'âge par lecture des otolithes doit être validée avant d'être appliquée à toute nouvelle espèce. Ainsi, le moment de la formation saisonnière des anneaux de croissance sur les otolithes de *C. latus* a été précisé avant d'utiliser leur décompte pour estimer l'âges des individus dans tous les environnements colonisés à chaque stade de vie et d'en déduire les caractéristiques de croissance globale de l'espèce dans la zone. La nature du bord de l'otolithe et les largeurs des incréments marginaux suggèrent la présence d'un seul annulus par an pour *C. latus*, les bandes opaques de l'otolithes étant formées de mai et août. De plus, les âges estimés par comptage des stries journalières pour un sous-échantillon de 40 juvéniles sans marque saisonnière visible variaient entre 77 (pour un spécimen de 36 mm de long) et 272 jours (pour un poisson de 170 mm de long). Ceci a permis de valider que les annuli sont déposés annuellement sur les otolithes de *C. latus* dans le nord-est du Brésil. Les âges estimés (en années) pour l'ensemble des spécimens étudiés variaient entre 0,21 et 13 ans, même si la plupart des spécimens de notre échantillon (67,4%) avaient moins de 1 an. La structure d'âge des sous-populations était également distincte entre les habitats estuariens et la mer. En effet, bien que toutes les classes d'âge (0-13 ans) aient été observées en mer, pour des tailles (SL) variant de 155 à 760 mm, la plupart des spécimens capturés dans les estuaires étaient des jeunes de l'année (36 à 223 mm SL). Les tailles des poissons d'âge 0 capturés en mer variaient de 155 à 195 mm SL et étaient donc proches de la valeur maximale observée à cet âge dans les estuaires (177 mm SL). Ceci indique que les estuaires du Nord-Est du Brésil sont essentiellement utilisés comme habitats juvéniles par l'espèce, au cours de sa première année de vie.

Comme chez la plupart des espèces de poissons, la croissance de *C. latus* est maximale pendant la première année de vie, avec un gain de taille estimé à 177 mm en moyenne, ce qui représente 22,75 % de la taille maximale prédite pour l'espèce dans notre zone d'étude. Les valeurs des paramètres de croissance estimées par le meilleur modèle ajusté aux données de taille-à-l'âge de *C. latus* (von Bertalanffy) étaient de 782,37 mm pour L_{inf}, de 0,179 pour k et de -0,436 années pour t_0. Elles se situent dans la gamme des valeurs rapportées pour d'autres espèces de *Caranx* autour du monde et sont comparables à celles trouvées pour d'autres espèces de carangues de grande taille au Brésil, qui atteignent toutes entre 60 et 75% de leur taille maximale au cours de leur 7ème année de vie. D'après les résultats antérieurs sur la reproduction de l'espèce dans la région, rapportant une L_{50} de 305 mm et 325 mm SL pour les mâles et les femelles, respectivement (Figuerola-Fernández et al. 2008), l'âge de première maturité sexuelle devrait se situer entre 2 et 3 ans suivant les individus.

Au cours de leur vie juvénile, les poissons rencontrent des conditions biologiques et environnementales variables qui peuvent influencer leur croissance et leur condition (Fodrie et al. 2009, Schloesser & Fabrizio 2019), avec des implications potentielles sur leur fitness et le succès du recrutement des populations. À cet égard, les estimations d'âge des poissons sélectionnés pour l'analyse des stries journalières suggèrent que les juvéniles colonisent les estuaires de la côte nord-est du Brésil à l'âge de 3-4 mois. Ils peuvent y rester jusqu'à neuf mois de leur première année et avant de retourner en mer. Pendant cette période, leur croissance est la plus rapide mais aussi plus variable suivant l'individu, avec comme résultat une forte diversité des tailles à la fin de la première année de vie. Cette variabilité semble être liée aux conditions environnementales rencontrées par les juvéniles dans les estuaires étudiés et suggère que les différents habitats occupés par *C. latus* génèrent différents taux de croissance chez ses juvéniles. En effet, la largeur des micro-incréments, un indicateur de la croissance somatique des poissons, était significativement plus forte dans les estuaires de Suape (4.7 ± 0.9 µm.jour^{-1}) et de Santa Cruz (4.5 ± 0.5 µm.jour^{-1}) qu'à Sirinhaém (3.7 ± 0.5 µm.jour^{-1}). Bien que non définitifs en raison du faible nombre de poissons utilisés pour l'analyse des stries journalières, ces différences entre sites mettent en lumière un effet potentiellement fort de la variabilité des conditions environnementales rencontrées localement sur la croissance de *C. latus*, au moins au stade juvénile. Cependant, de nombreux facteurs peuvent moduler la croissance des juvéniles de poissons, comme la température (Morrongiello et al. 2014, Doubleday et al. 2015), la salinité (Cardona 2000, Diouf et al. 2009), la qualité de l'habitat et la disponibilité de la nourriture (Vasconcelos et al. 2009, Isnard et al. 2015, Escalas et al. 2015). Ces éléments doivent être étudiés plus en détail afin d'expliquer et de préciser les différences constatées dans notre étude.

ÉCOLOGIE TROPHIQUE DES JUVENILES DANS LES ESTUAIRES

Comme démontré plus haut, au Nord-Est du Brésil, les individus de *C. latus* colonisent les estuaires surtout pendant leur première année de vie, période pendant laquelle leur croissance est plus rapide mais aussi plus variable entre individus. Les tailles différentes observées d'un estuaire à l'autre au moment du retour de ces juvéniles en mer pourraient refléter des variations spatiales de leur alimentation et de la qualité des sources de nourriture ingérées pendant la phase estuarienne. En effet, les différences d'utilisation des ressources entre habitats juvéniles peuvent affecter la croissance précoce et la condition corporelle des poissons (*e.g.* Isnard et al. 2015) et donc moduler le succès du recrutement des populations exploitées (Gillanders et al. 2015). Pour tester cette hypothèse, l'analyse des contenus stomacaux des poissons et le traçage isotopique ($\delta^{13}C$ et $\delta^{15}N$) de la matière organique ont été combinés pour préciser le régime alimentaire et la niche trophique des juvéniles de *C. latus* dans les estuaires de notre zone d’étude, en présence d'une autre espèce de carangue (*C. hippos*), dont les juvéniles présentent une écologie similaire.

Au total, 439 carangues juvéniles, dont les tailles variaient de 35 à 157 mm SL, ont été recueillies sur cinq années d'échantillonnage (2015 - 2019) dans trois estuaires contrastés en termes d'environnement (Santa Cruz, Suape et Sirinhaém). Le nombre et les tailles des juvéniles variaient également entre espèces et suivant l'estuaires. Alors que les abondances totales étaient comparables sur tous les sites pour *C. latus*, les juvéniles de *C. hippos* étaient 2 à 3 fois moins abondants à Sirinhaém et à Suape. Par conséquent, le nombre total de juvéniles collectés était plus élevé pour *C. latus* (n = 266) que pour *C. hippos* (n= 173). De plus, les juvéniles de *C. latus* (105 ± 25 mm SL) étaient systématiquement plus grands que ceux de *C. hippos* (88 ± 26 mm SL). Parmi l'ensemble des individus récoltés, 338 (207 *C. latus* et 131 *C. hippos*) des 394 poissons sélectionnés pour l'analyse du régime alimentaire avaient des proies dans leurs estomacs. Leurs effectifs leurs distributions de tailles étaient similaires à ceux observés dans les captures totales. Au total, 112 échantillons de muscles de poissons (60 *C. latus* et 52 *C. hippos*) et 136 échantillons d'algues, de matière organique en suspension et de sédiment ont également été analysés pour déterminer la niche isotopique en carbone ($\delta^{13}C$) et en azote ($\delta^{15}N$) des deux espèces et ses causes de variation pour chaque site.

Les résultats obtenus montrent que bien que les juvéniles de *C. latus* aient un régime plus piscivore que ceux de *C. hippos*, les deux espèces mangent principalement des poissons (Ni = 20.1-46.2%, Wi = 60.1-75.1%, essentiellement Gobiidae et Clupeidae) et des crustacés (Ni = 26.0-65.9%, Wi = 23.3-38.2%, principalement des crevettes Penaeidae) en estuaires. Toutefois, la composition du régime alimentaire des deux espèces varie selon les sites, indiquant que leurs juvéniles adaptent en partie leurs préférences alimentaires à la disponibilité locale des proies. Ceci était particulièrement clair pour *C. hippos* dont le régime alimentaire ne comprenait que des poissons dans l'estuaire de Suape. De plus, les différences de composition du régime alimentaire entre les deux espèces n'étaient significatives qu'à Santa Cruz, indépendamment du niveau d'identification des proies appliqué. Dans cet estuaire, les poissons de la famille Gobiidae prédominaient dans le régime de *C. latus* et les crevettes décapodes dans celui de *C. hippos*.

Les juvéniles des deux espèces occupent également une niche trophique globale très similaire en estuaire, avec des valeurs moyennes de $\delta^{13}C$ et $\delta^{15}N$ de -19.35 ± 2.10‰ et 11.03 ± 1.11‰ et de -19.10 ± 1.82‰ et 10.21 ± 1.21‰, pour *C. hippos* et *C. latus* respectivement et un recouvrement des niches isotopiques globales de plus de 68%. Les différences entre les deux espèces dans l'ensemble sont principalement dues aux valeurs de $\delta^{15}N$ plus élevées chez *C. hippos*. Cependant, la taille des niches isotopiques et leur degré de superposition variaient en fonction de l'estuaire. En effet, des différences combinées du régime alimentaire des juvéniles et de la structure des réseaux trophiques à chaque endroit permettent une forte réduction du chevauchement des niches isotopique entre les deux espèces à l'échelle locale (de 27% à Suape à 57% à Santa Cruz). Ceci soutient l'idée que les juvéniles de carangues adaptent leurs stratégies alimentaires à la disponibilité des ressources alimentaires locales afin de réduire la compétition trophique entre elles. Cela semble toutefois se produire de différentes manières, en fonction des conditions environnementales et biologiques locales. Notamment, les préférences de proies ne diffèrent significativement entre les deux espèces que dans l'estuaire de Santa Cruz, où les valeurs de $\delta^{15}N$ étaient les plus élevées pour les deux espèces. Inversement, les différences interspécifiques dans les rapports $\delta^{13}C$ étaient plus importantes dans les estuaires de Suape et de Sirinhaém, reflétant probablement une plus grande diversité des sources de carbone à la base des réseaux trophiques locaux. Ces résultats plaident pour une comparaison entre sites systématique lors de l'étude comparative de l'écologie trophique d'espèces de poissons sympatriques, en particulier dans les estuaires tropicaux qui présentent une grande diversité de sources alimentaires (Layman 2007). Etant donné que les variations spatiales de la position trophique des prédateurs comme *C. latus* et *C. hippos* peuvent non seulement influencer la croissance et la survie de leurs juvéniles, mais aussi leurs rôles respectifs dans le fonctionnement des réseaux trophiques estuariens, de telles études multisites pourraient être essentielles pour évaluer l'implication de différents scénarios de coexistence entre elles, non seulement pour le maintien des stocks de poissons, mais aussi pour la composition et le fonctionnement des systèmes estuariens.

IMPORTANCE DES ESTUAIRES POUR LA POPULATION EXPLOITÉE

Estimer la connectivité entre les habitats côtiers et leurs importances respectives pour le maintien des populations de poissons exploitées est essentiel pour la gestion des pêches et les stratégies de conservation (Nagelkerken 2009, Sheaves et al. 2015). De plus, les chapitres précédents ont démontré que, pendant leur phase estuarienne, les juvéniles de *C. latus* sont localement confrontés à des conditions de vie variables, notamment en termes de ressources alimentaires, avec des conséquences sur leur croissance. Dans ce contexte, le troisième axe de cette thèse visait à préciser la contribution de différents type d'estuaires au maintien de la population de *C. latus* exploitée dans le nord-est du Brésil. Pour cela, nous avons d'abord analysé la composition multi-élémentaire des otolithes de 143 juvéniles de *C. latus* récoltés dans plusieurs estuaires sur la côte nord-est du Brésil et de 40 (sub)adultes de l'espèce capturés par les pêcheurs au large des côtes de l'état du Pernambuco. Ceci a permis de développer une base pluriannuelle d'empreintes chimiques d'otolithes pour les principaux habitats juvéniles utilisés par l'espèce dans cette zone. Nous avons ensuite confronté ces données aux signatures multi-élémentaires enregistrées dans la partie juvénile des otolithes des (sub)adultes capturés en mer, afin d'identifier leur habitat de résidence au cours de leur première année de vie et évaluer la proportion d'utilisateurs des estuaires parmi eux, en utilisant un algorithme Random Forest.

Dix éléments (B, Ba, Co, Cr, Cu, P, Rb, Sr, Zn et Y) avaient plus de 25% de leurs mesures au-dessus de la limite de détection dans au moins un des sites échantillonnés et ont été retenus pour l'analyse. Cependant, seuls huit d'entre eux (B, Ba, Co, Cr, P, Rb, Sr et Zn) contribuaient au final à distinguer les sept estuaires étudiés et l'environnement marin. Le Sr est l'élément qui a le plus contribué à la discrimination des sites échantillonnés, la mer présentant des valeurs significativement plus élevées que celles observées pour les estuaires. En effet, la précision du taux de ré-assignement pour l'habitat marin était le plus élevé (95%). De plus, des valeurs significativement plus élevées de Sr ont été observées à la fois dans la partie de l'otolithe représentant la vie larvaire et sur le bord de l'otolithe pour les poissons (sub)adultes en mer, probablement en lien avec les salinités plus élevées en mer (Sturrock et al. 2012, Izzo et al. 2015). Cela confirme la fiabilité de Sr pour évaluer les migrations à vie de *C. latus* entre les habitats marins et côtiers du nord-est du Brésil, comme l'ont déjà suggéré des études antérieures sur d'autres espèces de poissons migrateurs. Le Ba est le deuxième élément qui a le plus contribué à discriminer les lieux. Cependant, il était plus utile pour distinguer les estuaires étudiés plutôt que les estuaires et la mer. En particulier, les systèmes estuariens sous forte influence d'eau douce qui présentaient des concentrations de Ba les plus élevées.

Les signatures élémentaires des estuaires se sont largement superposées, entraînant une faible précision de discrimination maximale globale (58 %). Il est intéressant de noter que même les endroits relativement distants présentaient une plus grande ressemblance que les estuaires voisins. Les caractéristiques de régions ou de bassins hydrologiques spécifiques produisent souvent des empreintes uniques, car les charges d'éléments sont susceptibles de varier d'un endroit à l'autre (Moore & Simpfendorfer 2014). Toutefois, dans notre cas, les conditions environnementales locales (c'est-à-dire les régimes hydrologiques), semblent avoir une plus grande influence dans la discrimination des empreintes élémentaires des estuaires que leur localisation. Cela semble particulièrement vrai étant donné que Sr et Ba, deux éléments communs utilisés pour discriminer les environnements sous différents régimes de salinité (Sturrock et al. 2012), étaient les principaux facteurs de distinction des lieux étudiés. Le regroupement des estuaires en fonction de leur niveau d'influence de l'eau douce (c'est-à-dire les estuaires salins et les estuaires saumâtres) a permis d'augmenter la précision de discrimination maximale globale jusqu'à 80 %. Seul un estuaire étudié (Mundaú-Manguaba) a présenté des empreintes élémentaires distinctes avec des valeurs élevées de Rb mesurées sur ce site.

Les empreintes élémentaires des otolithes des poissons (sub)adultes analysés ont révélé que la plupart des spécimens de *C. latus* capturés par la pêche (75%) ont passé leur première année de vie dans un estuaire. Pourtant, la variation observée dans la contribution des estuaires en fonction de leurs conditions environnementales confirme que la valeur des estuaires pour les poissons juvéniles n'est pas homogène et que les paramètres estuariens locaux sont susceptibles de moduler leur qualité en tant que nurserie. Parmi les estuaires étudiés, ceux sous forte influence marine (salins) ont montré une contribution relative plus importante (32.5 %), ce qui est conforme à la stratégie attendue de migration marine de l'espèce. Les estuaires saumâtres et les habitats juvéniles en mer avaient des contributions nettement plus faibles, de 12.5% et 5% respectivement. Même si l'on considère qu'une partie des poissons a été attribuée à un estuaire non identifié (30%) ou à un "habitat inconnu" (20%), les estuaires salins dépassent toujours les autres habitats de juvéniles. En effet, des résultats préliminaires suggèrent que les juvéniles de *C. latus* pourraient également présenter des taux de croissance plus rapides à ces endroits (*i.e.* Santa Cruz et Suape), car ils offrent probablement de meilleures conditions de vie aux juvéniles. Ces derniers peuvent avoir un impact significatif sur la croissance et la forme physique de la population globale (*e.g.* Fodrie et al. (2009)). Cependant, des études supplémentaires seront nécessaires avant de pouvoir déterminer avec certitude les facteurs importants pour les juvéniles de *C. latus* dans cette zone. Ces résultats soulignent l'intérêt de la microchimie des otolithes pour identifier les habitats juvéniles des poissons côtiers dans les tropiques et indiquent que les estuaires jouent un rôle clé dans le maintien des populations de *C. latus* dans le nord-est du Brésil.

CONCLUSION

Dans cette étude, la combinaison de marqueurs naturels (isotopes stables et microchimie des otolithes) et de techniques empiriques (*e.g.* l'otolithométrie) a permis (i) de mieux comprendre le cycle de vie d'une espèce de carangue peu étudiée et (ii) de souligner l'importance des estuaires dans le maintien de la population exploitée par la pêche dans le nord-est du Brésil. Les résultats obtenus par cette étude indiquent que *C. latuss* peut vivre plus de 13 ans et que les estuaires pourraient jouer un rôle important dans les stratégies d'histoire de vie de la population. Cette information souligne les connaissances précédentes selon lesquelles *C. latus* utilise occasionnellement les estuaires en tant que juvéniles (Figueiredo & Menezes 1980, Smith-Vaniz 2002) et permet de mieux comprendre les stratégies d'histoire de vie employées par l'espèce. En outre, cette étude apporte des informations importantes pour la compréhension de la dynamique de la population de l'espèce dans le nord-est du Brésil en fournissant la première évaluation de la croissance basée sur des données détaillées de taille et d'âge pour la plupart des stades de vie.

Les informations disponibles jusqu'à présent sur les traits d'histoire de vie de *C. latus* suggèrent qu'ils utilisent une mosaïque d'habitats côtiers tout au long de leur vie (Smith-Vaniz 2002). Les résultats obtenus ici soutiennent et améliorent encore cette hypothèse dans le nord-est du Brésil. Les jeunes de l'année semblent coloniser les estuaires et, dans une moindre mesure, d'autres habitats littoraux comme les récifs peu profonds sur le littoral lorsqu'ils ont 3-4 mois. Pendant la phase estuarienne, *C. latus* se nourrit principalement de poissons et de crustacés. Cependant, les résultats rassemblés ici ont souligné que les différences locales dans les conditions environnementales et biologiques variables auxquelles les carangues sont soumises au stade juvénile semblent moduler la valeur respective de ces habitats côtiers pour le renouvellement du stock de (sub)adultes pêchés en mer.

Dans l'ensemble, les estuaires ont une contribution majeure à la population exploitée de *C. latus* dans le nord-est du Brésil, comprenant 75% des spécimens capturés par la pêche marine de Pernambuco. Cela indique que les estuaires peuvent caractériser des zones de nurserie pour le *C. latus*, au moins dans le nord-est du Brésil. Néanmoins, les estuaires soumis à une plus forte influence marine semblent contribuer davantage à la population adulte, représentant jusqu'à 32,5% des spécimens capturés par les pêcheries offshore. Il est intéressant de noter que ce sont les mêmes estuaires où les poissons semblent avoir des taux de croissance plus rapides. Par conséquent, les conditions de vie rencontrées par les poissons au cours de leur première année peuvent être liées au succès du recrutement de la population adulte, en améliorant la survie ou la forme physique des *C. latus* juvéniles. Ces résultats confirment que la valeur des estuaires pour les poissons juvéniles n'est pas homogène et que les variations des conditions estuariennes sont susceptibles d'affecter leur qualité en tant que zones de nurserie. Bien que les facteurs exacts de la croissance juvénile et du succès de la survie de *C. latus* ne soient pas encore connus, ils semblent être liés à des habitats plus salins, soit parce que ceux-ci présentent une plus grande disponibilité de proies (préférentielles), soit parce que les contraintes physiologiques de l'espèce sont plus faibles. Dans ce dernier cas, le régime hydrologique des estuaires pourrait agir comme un facteur de forçage physiologique limitant la distribution et la croissance des juvéniles de *C. latus* dans ces habitats.

Bien que les stocks de *C. latus* ne soient pas menacés de surexploitation dans l'Atlantique, des menaces spécifiques peuvent néanmoins survenir à l'échelle locale (Smith-Vaniz et al. 2019). Il est probable que les menaces les plus importantes pour la population globale se produisent dans les zones côtières. En effet, l'altération de l'habitat due à l'utilisation des terres et à la pollution dans les sites étudiés est causée par une urbanisation intense, l'aquaculture et le développement industriel. Ces derniers pourraient menacer la qualité des environnements côtiers pour les poissons juvéniles. Précisément, altérations dans l'habitat qui affectent le régime hydrologique des estuaires peuvent avoir des effets significatifs sur la distribution et la croissance des *C. latus* juvéniles, avec des implications potentielles sur leur valeur de nurserie respective. Donc, stratégies de conservation soutenant la préservation des caractéristiques estuariennes qui soutiennent la connectivité avec la zone marine adjacente sont cruciales pour maintenir les processus de colonisation (et d'émigration) et donc la valeur de ces zones pour les *C. latus* juvéniles.

Cette étude constitue un pas en avant vers la compréhension de l'importance des habitats côtiers pour le maintien des stocks de poissons exploités par la pêche au Brésil. Cependant, des travaux supplémentaires sont nécessaires pour valider les facteurs de croissance et de survie des juvéniles de *C. latus* au cours de leur première année de vie, ainsi comme déduire les mouvements potentiels des juvéniles de l'espèce entre les sites estuariens jusqu'à ce qu'ils atteignent le stade adulte (Moulton et al. 2017, Rooker et al. 2018). Cela permettrait de compléter les résultats obtenus ici et de faire correspondre les contributions au stock adulte avec d'autres critères tenant compte de la superficie des estuaires, afin d'estimer réellement leur valeur en tant que nurseries ou habitats essentiels pour les juvéniles (Beck et al. 2001). Dans l'ensemble, ces connaissances peuvent aider à répondre aux besoins des modèles basés sur les écosystèmes qui améliorent la gestion locale en considérant la connectivité entre les habitats côtiers (Sheaves et al. 2015).

CHAPTER 1. General introduction

Fish have historically been an important source of food and income worldwide, but their consumption increased at a higher rate than the growth of human population in the last decades (FAO 2020). In 2017, fish food supply reached its highest so far, accounting for 20.3 kg per year and capita on average and outpacing most sources of animal protein. Following the decline of most of the main fisheries in the 90's, managers and decision-makers around the globe have engaged in the implementation of sustainable development strategies based on fisheries socio-economic frameworks and respecting ecosystem health and functioning (FAO 1999). However, 34.2% of marine fish stocks are still under unsustainable levels of exploitation (FAO 2020). Indeed, despite the continuous improvement of methods for assessing the status of fish stock (Hilborn 2003, Cardin & Dickey-Collas 2015, Punt 2019), particularly in data-poor scenarios (Hodryk et al.2015, Prince et al. 2015), knowledge on the population dynamics of many exploited fish species is not yet robust enough to allow defining effective strategies for sustainable fisheries development (Walters & Martell 2004). This understanding requires comprehensive information on the size-at-age and reproduction strategy of populations, as well as on their interaction with the environment and other living organisms (Cochrane & Garcia 2009). In this regard, identifying key habitats for exploited fish populations is a primary concern. Indeed, when fish stocks are spatially structured, treating them as a spatially heterogeneous entity might not only improve their assessment (Punt 2019, Godefroid et al. 2019), but also help decision-makers to apply distinct management policies, focused on specific areas or life stages (Baker & Harris 2020). This is particularly true for coastal fish species undergoing ontogenetic habitat shifts or using a mosaic of habitats throughout their life, as anthropogenic pressures, such as fishing and habitat degradation, are likely to affect more than one life stage.

In recent years, increasing attention has been given to marine resources in tropical regions and their management. First, because the tropics hosts a considerable part of world's marine biodiversity (Worm & Branch 2012). Second, because people living in the tropics already account for 47% of the total human population, and their numbers are expected to surpass those of people living in other regions of the globe in a few decades (State of the Tropics 2020). Lastly, while marine fish captures in the rest of the world seem to decrease, those in the tropics are relatively steady as a result of varying trends among the different tropical oceanic provinces (State of the Tropics 2020). In tropical regions, small-scale fisheries are responsible for more than half of fish captures and employ more than 90% of the fishermen, representing a crucial source of food and income for local communities (FAO 2020). However, most of these fisheries are unreported, preventing an adequate assessment of their status and adequate management (FAO 2020). Therefore, gathering biological and ecological information on tropical marine resources is key for their sustainable development. This is particularly true when considering that, in the tropics, the rapid development of coastal cities particularly threatens local coastal fish resources, as the demand for seafood is growing (Barlow et al. 2018, FAO 2018) and environmental awareness is only just emerging (Prandle & Lane 2015, Mitra & Zaman 2016, Barlow et al. 2018).

Brazil is a good example of this problem (Abdallah & Sumaila 2007). With an exclusive marine economic zone of 3.5 million km², the Brazilian coast presents a myriad of habitats exploited by several types of fisheries, which vary according to local environment settings (Isaac et al. 2006). These latter are mainly composed of small-scale and artisanal fisheries targeting multiple species (MMA 2006, Isaac et al. 2006, Lessa et al. 2009), for which a better understanding of population dynamics is urgently needed. Besides, the few existing management and conservation measures in the country, like fishing closure periods and the delimitation of marine protected areas, often result in conflicts between the multiple stakeholders involved in the exploitation of local marine resources, which weakens their efficiency (Reis & Incao 2000, Jablonski & Filet 2008). Therefore, identifying key fish habitats along the Brazilian coast and assessing their connection with neighboring environments across the seascape will help improving both national and local marine conservation strategies and fishery and ecosystem management.

1.1. What are the juvenile habitats of marine fish?

The success of the recruitment to the adult population, *i.e.* the number of young adults being able to reproduce for the first time in their life, is key for the renewal of exploited fish stocks (Beverton & Holt 1993), and its variations have implications for both stock assessment and management strategies (Poorten et al. 2018, Haltuch et al. 2019, Plagányi et al. 2019). Recruitment success in fish is partly influenced by the condition of the adult spawning population and survival during the larval stage, but important bottlenecks also occur during the juvenile stage (Chamber & Trippel 1997). As result, biological and environmental constrains during juvenile life often shape the size and condition of recruiting fish populations (Walters & Korman 1999, Andersen et al. 2017, Poorten et al. 2018).

Juvenile fish tend to occupy different habitats than the adults of their population, often in search of high food availability and lower predation risk to increase survival (Dahlgren & Eggleston 2000). In practice, juvenile habitats comprehend all the habitats used by fish throughout their juvenile life. Among them, those with high juvenile abundances and maximizing juvenile growth have been called 'nurseries' for long and were largely studied worldwide (*e.g.*, Van Engel & Joseph (1968), Lenanton (1982) and Deegan (1993)). However, it was only two decades ago that Beck et al. (2001) formalized the concept of nursery ground and provided a comprehensive description of when a habitat should be considered as such. Following this definition, habitats may be considered as nursery grounds if they allow the juveniles of a given species to occur at higher densities or to benefit from (biological) processes that enhance their survival (Beck et al. 2001). Further studies since complemented this initial definition by incorporating connectivity requirements, species' behavioral processes (*e.g.* ontogenetic shifts in habitat use), resource dynamics among the organisms of the food webs and environmental factors and provided a robust and comparable approach to evaluate the nursery function of habitats (Dahlgren et al. 2006, Nagelkerken et al. 2015, Sheaves et al. 2015).

Habitat selection and use by juvenile fish is strongly dependent on the species' life history strategies and the environmental settings of each habitat (Bakun 2006, Litvin et al. 2018, Reynolds et al. 2018). Coastal environments worldwide are key habitats for juvenile fish, often recognized as nursery grounds for many estuarine, nearshore and marine species (McDevitt-Irwin et al. 2016, Litvin et al. 2018, Lefcheck et al. 2019). They are highly diverse (e.g. estuaries, lagoons, fjords, bays, etc.) and mostly comprehend physically structured habitats, like rocky, sandy or muddy shores, mangrove beds, marshes, coral and biogenic reefs and macroalgae or seagrass patches (Igulu et al. 2014, Litvin et al. 2018, Lefcheck et al. 2019). Conversely, in pelagic and oceanic environments, essential habitats for fish juveniles are related to oceanographic processes like fronts, eddies and surface slicks (Bakun 2006, Shulzitski et al. 2015, Whitney et al. 2021). These processes, occurring at local and meso- scales, help retaining small planktonic organisms and organic particles, enhancing food availability for the fishes (Bakun 2006, Shulzitski et al. 2015).

1.2. The value of inshore habitats for juvenile fish

One classical example of the nursery grounds of coastal marine fish, and perhaps the most studied so far, is that of inshore transitional waters habitats like estuaries and lagoons (Potter et al. 2015, Lefcheck et al. 2019). Several studies demonstrated the importance of these ecosystems in supporting the adult population of different species (Gillanders et al. 2003, Vasconcelos et al. 2008, Tournois et al. 2017). Further research focused on disentangling the main factors underling their value as nursery grounds, investigating their capacity to enhance the abundance (Dolinsek et al. 2007), or the growth and fitness of the juveniles (Fodrie et al. 2009, Vasconcelos et al. 2009, Isnard et al. 2015), assessing their respective quality and suitability for juvenile fish (Giannoulaki et al. 2011, Yeung & Yang 2017) or measuring their connectivity with adult populations (Fodrie & Levin 2008). It is now clear that even similar environments (*e.g.* estuaries) may not provide equivalent life conditions for juvenile fish (Isnard et al. 2015, Schloesser & Fabrizio 2019). Indeed, both biotic and abiotic factors affect the importance of the nursery role of a given habitat. A systematic and comparative perspective on the implications of nursery grounds on the recruitment process is therefore still needed (Lefcheck et al. 2019).

Identifying nursery habitats for a given population can be particularly challenging. Indeed, habitat use is species-specific so detailed *a priori* information on the biology of the species is needed to determine whether a given juvenile habitat can be a nursery ground (*e.g.* Vasconcelos et al. (2008)). While identifying nursery habitats can be a straightforward process for fish species that present well established lifetime migrations (*e.g.* snappers (Aburto-Oropeza et al. 2009, Dance & Rooker 2019)), highly mobile amphidromous species or species that present facultative catadromy challenge the evaluation of the nursery paradigm (Barbour et al. 2014, Schilling et al. 2018). Moreover, fish often exhibit opportunistic behaviours and are capable to partially adapt to local biological and environmental settings, which in turn are modulated by the spatiotemporal dynamics of the sites studied (Harrison & Whitfield 2012, Baker et al. 2015, Vasconcelos et al. 2015). As this inter-site variability is likely to differently affect juvenile fish (Vasconcelos et al. 2009, Isnard et al. 2015), a comprehensive cross-site comparison is required to determine the actual nursery value of a given location. This has to be done considering that both environmental and geographic settings may shape the biological processes underpinning the value of specific nursery grounds (McDevitt-Irwin et al. 2016, Bradley et al. 2019, Lefcheck et al. 2019). Lastly, the nursery value of habitats is usually scale-dependent and most studies consider each putative habitat as a homogenous entity (Sheaves et al. 2015). Despite being less laborious, this approach does not recognize the potential existence of varied micro-habitats within a nursery ground, all of which can play distinct roles in its global functioning (Nagelkerken et al. 2015, Sheaves et al. 2015). Consequently, an emerging concept to describe fish nurseries was proposed in recent years, with emphasis on the connectivity among micro-habitat patches and the respective contributions of these latter to the global functioning of nursery grounds (Nagelkerken et al. 2015).

The rapid growth of human populations and the resulting development of urbanized areas along the coastline have many impacts on inshore ecosystems, through varied and increasing pressures that range from eutrophication and habitat alteration to overfishing (Kennish 2002, Mitra & Zaman 2016). These latter not only threaten the health and food security of local human communities, but also the quality of inshore environments for fish, especially at the juvenile stage (Nagelkerken et al. 2008, Crook et al. 2014, Ogden et al. 2014). Therefore, understanding how fish species might be affected by the multiple human uses of coastal habitats is key to forecast the evolution of the ecosystem services they provided in future scenarios. In particular, identifying the inshore habitats that sustain costal exploited fish populations, along with those that present optimal conditions for fish early growth, can help delineating adequate conservation strategies for attenuating the impact of the growing human presence in the coastal zone.

1.3. A case of study in North-Eastern Brazil

The coastline investigated in this work mainly spreads along the coast of the Pernambuco state, although it also extends along that of the Alagoas state (Fig.1). The local climate is sub-tropical, with temperatures fluctuating between 18 and 32 °C each year (CPRH 2003, 2003a, Domingues et al. 2017). Due to the northward displacement of the Intertropical Convergence Zone (ICTZ) in the Atlantic and to strong winds blowing from the southeast (CPRH 2003, 2003a, Hounsou-gbo et al. 2015), precipitations in the area are at their highest in the austral late autumn and winter (May to August), while the driest period lasts from late spring to early summer (October to December). The local marine region is mainly influenced by the North Brazilian Current (NBC), which is responsible for carrying warm oligotrophic waters from the South Equatorial Atlantic towards the north hemisphere (Ekau & Knoppers 1999).

The local coastal area has a relatively narrow continental shelf (~35 km wide, Fig. 1), reaching maximum depths of 60 m near its break (Vital et al. 2010). It hosts a great diversity of habitats, including estuaries, seagrass meadows and coral reefs, all connected through local fluvial discharges, marine currents and the movements of migratory species (Schwamborn et al. 1999, Claudino et al. 2015, Pelage et al. 2021). Although fluvial discharge provides an important source of nutrients into local littoral areas, its influence does not extend far offshore (Ekau and Koppers 1999, Schwamborn et al. 1999). As a result, the pelagic environment beyond the local shelf edge is largely oligotrophic and constitutes one of the less productive marine areas in Brazil (Ekau & Knoppers 1999). Low productivity levels may even extend to nearshore waters locally (Ekau & Knoppers 1999). Nonetheless, the presence of fringing reefs in the outer region and upper slope of the shelf has led to its recognition as an Ecologically or Biologically Significant Marine Area (CDB 2014). Indeed, this particular configuration provides favourable habitats for many resident and migratory fish species, including some exploited ones (CDB 2014). In particular, the coastline is characterized by the presence of numerous estuaries across the shore and coral reefs patches on the inner and outer parts of the continental shelf (Paiva & Araújo 2010, Leão et al. 2016). These habitats are key for many local exploited species, and several of them are considered biodiversity hotspots as they host some endemic reef-associated fish species (Vila-Nova et al. 2014, Eduardo et al. 2018).

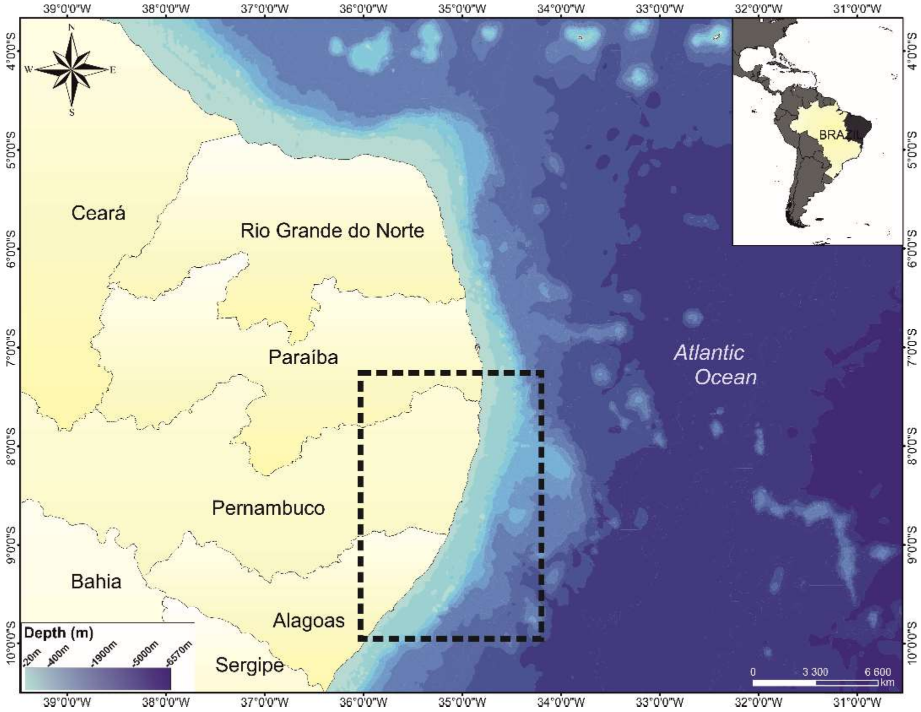

Figure 1 – Location of the area investigated in this study (dashed rectangle), along the North-Eastern coast of Brazil (image provided by A. S. Lira).

Despite this ecological importance, the North-Eastern Brazilian coast is amongst the most populated in Brazil, where the state of Pernambuco in particular is a noticeable hub of national development and urbanization. Human activities affect the whole range of marine and inshore habitats along the coat of Pernambuco and neighbouring states. Habitat alteration on the littoral is mainly due to land use, driven by intense urbanization, aquaculture and industrial development (Muniz et al. 2005, Guimarães et al. 2010, Pelage et al. 2019). Multi-species fisheries take place in most inshore habitats and throughout the shelf (Lessa et al. 2009, Frédou et al. 2009, Pelage 2020), while tourism prevail in nearshore reef environments (Ferreira & Maida 2006). Domestic and industrial discharges are also reported for most inshore sites (CPRH 2003, 2003a), with few of them also presenting heavy levels of contamination by metals, including mercury

(Medeiros et al. 2001, Macedo et al. 2007, Albuquerque et al. 2019). Lastly, important changes in their local physico-chemical conditions have been observed in the last decades, like that which followed the building of an industrial harbour on the southern shore of the Suape estuary (Muniz et al. 2005). These recurrent pressures are likely to alter the quality of inshore environments for fish and call for a better understanding on their effects on local marine fauna.

Due to all these characteristics, the North-Eastern coast of Brazil is particularly suited for evaluating the importance of inshore environments for coastal marine fish stocks. Indeed, the multiple and increasing human activities found along its mosaic of marine and inshore habitats, combined with the importance of fisheries as a local source of income and food security, urgently calls for increasing scientific knowledge on this matter to support sustainable management strategies in the area. Moreover, the numerous and interconnected inshore and coastal habitats in the coastal region of Pernambuco may act as ecological corridors and favour the movement of migratory fish across the shelf (Aschenbrenner et al. 2016).

1.4. A model species: the horse-eye jack (*Caranx latus*)

The horse-eye jack (*Caranx latus*, Fig. 2) is a fish species widely spread along the Western Atlantic coasts, with catches spanning from the New Jersey state in the US to Rio Grande do Sul in southern Brazil (Figueiredo & Menezes 1980, Smith-Vaniz 2002). Populations of *C. latus* are also found around oceanic islands in the Western (St. Peter and St. Paul archipelago, Vaske Jr et al., (2005)) and Eastern (Ascension Island, Smith-Vaniz (2002)) Atlantic. This pelagic fish can reach up to 100 cm in length and constitutes an important source of food and income in the South-Western Atlantic (Lessa et al. 2009, Pinheiro et al. 2010, Rombenso et al. 2016). In Brazil, more than 3400 tons of *C. latus* were caught by artisanal fisheries each year between 2009 and 2011 (last national fisheries' statistics available), representing 45% of the total national landings of jacks (MPA 2011). In North-Eastern Brazil, the species is usually sold for R$ 15/kg (~US$ 2.7/kg), which is comparable to the local prices applied for highly exploited fish species (*e.g.* snappers: R$ 15 to 20/kg) and slightly higher to those observed for other local jack species (*e.g. C. hippos*: R$ 10/kg). Individuals of *C. latus* achieve their highest marketable price around 300 mm of SL and 0.5 kg of weight (up to R$ 20/kg), when the quality of their flesh is considered best. Consequently, the species is mostly targeted by local inshore and nearshore fisheries before it reaches its sexual maturity (Pelage 2020), as values for its L_{50} are of 325 and 345 mm FL for males and females, respectively, and its L_{100} is of 420 mm FL for both sexes (Figuerola-Fernández et al. 2008).

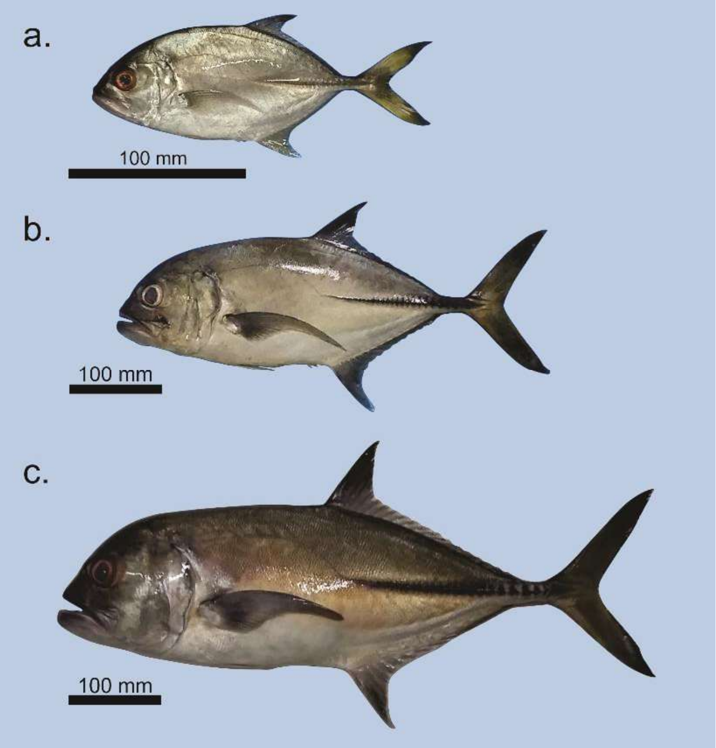

Figure 2 – Pictures of juvenile (a, 157 mm SL), sub-adult (b, 389 mm SL) and adult (c. 524 mm SL) specimens of *Caranx latus* captured in the study area.

Despite its commercial importance, the migratory ecology and population dynamics of *C. latus* are still largely unknown, in Brazil and elsewhere. So far, previous studies investigated the species' length-weight relationship (Forta et al. 2004, Mazzei et al. 2011, Viana et al. 2016), its reproduction (Graham & Castellanos 2005, Figuerola-Fernández et al. 2008, Heyman & Kjerfve 2008), its spatiotemporal movements (Novak et al. 2020), its feeding ecology (Silvano 2001, Figueiredo & Pessanha 2015, Medeiros et al. 2017), and its role in local food webs (Rosado-Solórzano & Guzmán del Próo 1998, Lira et al. 2018). This has shown that *C. latus* life cycle involves the use of a mosaic of coastal and marine environments (Fig. 3). However, most of the studies so far focused only on one given life stage or were limited to pinpoint locations, so they only provided primary information on *C. latus* occurrence in different coastal habitats (Campos et al. 2010, Paiva & Araújo 2010, Felizola-Freire et al. 2018). Large specimens of *C. latus* were thus associated to deep waters (> 40 m) and offshore reefs near the shelf break (Lessa et al. 2009, Felizola-Freire et al. 2018, Novak et al. 2020), where they are thought to breed each year, mainly in April and in August (Figuerola-Fernández et al. 2008, Heyman & Kjerfve 2008). As a result, *C. latus* larvae have been observed offshore, along the continental shelf (Berry 1959, Campos et al. 2010). The juveniles of the species are commonly found along coastal sandy beaches, but also within local estuaries, where they can occur in high abundances (Figueiredo & Menezes 1980, Mazzei et al. 2011, da Silva et al 2018). They apparently occupy these inshore habitats for at least several months before joining the offshore adult population (Figueiredo & Menezes 1980, Smith-Vaniz 2002).

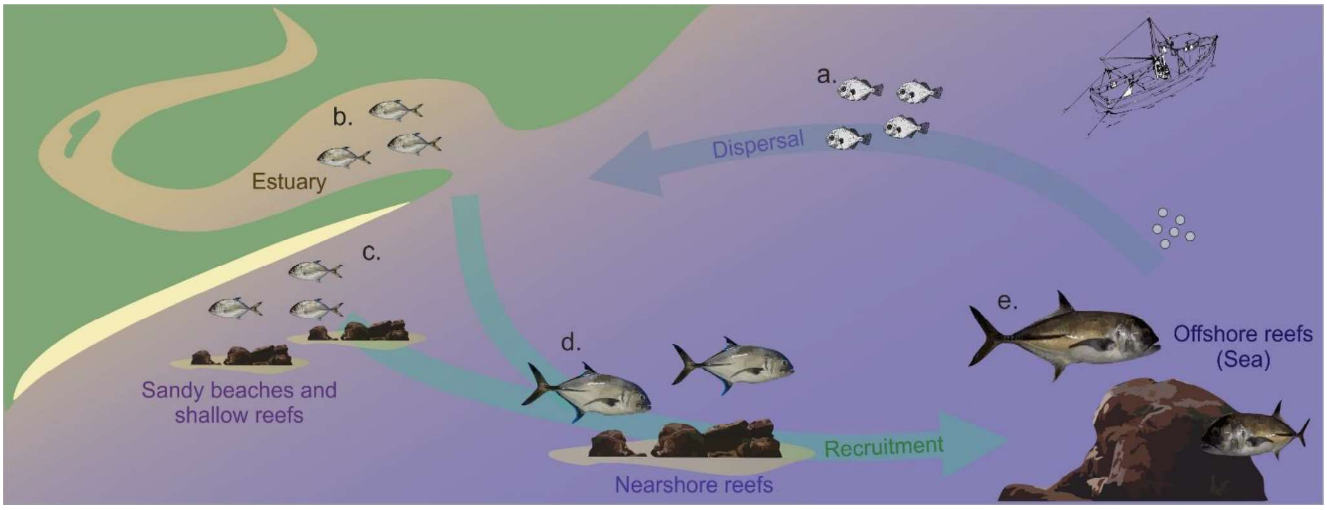

Figure 3 Conceptual model of the life cycle of *Caranx latus* in Brazil, with arrows illustrating the ontogenetic habitat shifts performed by the population between the larval (a), the juvenile (b-d) and the (d-e) adult stages.

The horse-eye jack is commonly referred as a reef-associated marine species. In North-East Brazil, while this assumption can be true for the adult of the species, the frequent occurrence of its juveniles in estuarine environments raises the question whether these inshore environments can act as nursery grounds for the local population, as observed in other jack species (Smith & Parrish 2002). Understanding the role of estuaries for the maintenance of the local *C. latus* population and the connectivity between its juvenile and adult habitats is particularly relevant given that the species is targeted by both inshore and nearshore fisheries at sizes below that of sexual maturity (Pelage 2020). Likewise, basic information on *C. latus* population dynamics is needed for sustainable fishery management (Lessa et al. 2009, Novak et al. 2020), in Brazil but also in other parts of the world where the species represents a non-negligible source of income for local communities. Finally, *C. latus* may also act as biological vector connecting coastal habitats along the North-Eastern Brazilian coastline, enhancing the cross-shelf linkage between local inshore and oceanic domains by exporting organic matter from nutrient-rich inshore areas to the oligotrophic outer regions of the shelf. Therefore, identifying key habitats for this exploited population and evaluating their connectivity may not only help improve local fishery management but also support the evaluation of the nursery value of local estuaries for marine migratory fish and their importance in the global seascape.

1.5. Objectives

The goal of this thesis was to investigate the importance of inshore environments (estuaries) in sustaining the population of *Caranx latus* exploited offshore the Pernambuco state, in North-Eastern Brazil. To this aim, comprehensive knowledge was gathered on the local biology and ecology of *C. latus* specimens, across a variety of coastal and offshore habitats. To evaluate the potential nursery role of local estuaries, special emphasis was put on the juvenile part of the species' life-cycle. However, information was gathered for all life stages, to answer the following three main questions:

(1) How long do *C. latus* specimens stay in estuaries for and what are the consequences on their growth?
(2) Do the diet and food sources of juvenile *C. latus* vary according to environmental settings in estuaries?
(3) Are estuaries key habitats for the maintenance of the local exploited population?

The present manuscript is organised around these three main questions, as each one provides a complementary perspective on the value of the estuaries for the maintenance of the local adult population. After the general introduction (CHAPTER 1), CHAPTER 2 focusses on the population's life-history traits, investigating the size-at-age and the growth of *C. latus* in varied inshore (estuaries) and offshore areas. CHAPTER 3 describes how the juveniles of *C. latus* make use of estuarine food resources in North-Eastern Brazil, under contrasting environmental settings and in the presence of the juveniles of another sympatric species of jack with close ecological and biological features. Lastly, CHAPTER 4 investigates the connectivity between the juvenile and adult habitats of the species, particularly the importance of estuaries in sustaining the offshore stock of *C. latus*. A final section (CHAPTER 5) gathers all these results to provide a comprehensive understanding of the value of estuaries for the maintenance of *C. latus* stocks in North-Eastern Brazil and discuss its potential implications for local management strategies.

CHAPTER 2: Age and growth of *Caranx latus*

Despite its commercial importance, the biology and population dynamics of *C. latus* are still largely unknown worldwide (Lessa et al. 2009, Novak et al. 2020). The species' size-at-age has not been described before, and previous studies on its growth are limited to length-weight relationship of individuals (Figuerola-Fernández et al. 2008, Mazzei et al. 2011, Viana et al. 2016). To start filling this gap of knowledge, the first research axis of this study investigated the age structure and the growth of the *C. latus* population fished in North-Eastern Brazil, using size data and otolith readings from 282 juvenile and adult specimens captured across a variety of inshore (estuaries) and offshore habitats (**Article I**). This allowed to specify fish sizes and ages in all the environments colonised at each life stage and to infer the species' global growth features in this area. In particular, it clarified the period during which *C. latus* individuals inhabit local estuaries and shed light on the impact of the variation in biotic and abiotic and environmental conditions among sites on the growth of the species' yearlings. To our knowledge, this constiitutes the first comprehensive assessment of *C. latus* growth in the tropical Atlantic, based on detailed size-at-age data from most life-stages and lifetime habitats.

Article I

This section has been submitted for publication in the journal *Fisheries Research*.

Age validation and growth in an exploited, yet poorly studied, tropical fish species: the horse-eye jack (*Caranx latus*)

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2.1. Abstract

The horse-eye jack (*Caranx latus*) is a highly prized and neritic species whose information on its population dynamics calls for a more comprehensive description of the parameters controlling growth in this highly mobile fish. In this study, the growth of *C. latus* was investigated using 282 otoliths from specimens of both sexes captured across a range of inshore (estuaries) and offshore habitats in North-Eastern Brazil between August/2017 and August/2019. The nature of the otolith's edge and the widths of their marginal increments both suggest that annuli are only deposited once a year for *C. latus*, with the opaque bands being formed between May and August. Most of the individuals captured in the estuaries (36 to 223 mm of standard length - SL) were age-0 fish (91.8%) and only a few individuals were on their second year of life. Conversely, all age classes (0 to 13 years old) were found in the offshore area at the sea, where sizes ranged from 155 to 760 mm SL. A subsample of 40 estuarine age-0 fish selected for micro-increment analysis suggests that juveniles can colonize the estuaries spread along the North-Eastern Brazilian coast early as 3 to 4 months old, and may remain there from few months to 9 months during their first year of life before moving back to marine habitats. During this period, their growth is the fastest, comprising 22.75% of the maximum size expected for the species. However, inter-individual variation in specimens' body size within the first year of life was also the greatest, probably in link with the variability in the environmental conditions encountered. The corresponding growth parameters estimated by the best model fitted to size-at-age data of *C. latus* (von Bertalanffy) were 782.37 mm for L_{inf}, 0.179 for *k* and -0.436 years for t_0. The present study provides the first assessment of *C. latus* growth based on detailed size-at-age data for most life-stages and lifetime habitats in the Southwestern Atlantic.

Keywords: Marine fish; Coastal habitats; Otolithometry; von Bertalanffy.

2.2. Introduction

Jacks (*Caranx* spp.) are highly prized marine fish, exploited by sport and artisanal fisheries in many tropical and subtropical regions (Smith-Vaniz 2002, FAO 2003, Arra et al. 2020). Accordingly, considerable effort has been made to study their biology around the globe (Berry 1959, Smith-Vaniz 2002, Heyman & Kjerfve 2008). The knowledge gathered thus far on the age structure and mortality rate (*e.g.* Goodwin & Johnson (1986) and Arra et al. (2020)), growth (*e.g.* Gallardo-Cabello et al. (2007) and Espino-Barr et al. (2008)) and size at maturity (*e.g.* Brewer et al. (1994) and Figuerola-Fernández et al. (2008)) of varied populations of Jacks worldwide is key for effective management of their stocks (Rochet & Trenkel 2003). However, this basic knowledge is still lacking for several of the 18 species found within this wide genus (Froese & Pauly 2021). It is the case of the horse-eye jack (*Caranx latus*), a species widely spread along the West Atlantic coast of America, with catches spanning from the New Jersey state in the US to Rio Grande do Sul in southern Brazil (Figueiredo & Menezes 1980). This pelagic fish can reach up to 100 cm in length and constitutes an important source of food and income in the Southwestern Atlantic (Lessa et al. 2009, Rombenso et al. 2016, Arra et al. 2020). In Brazil, for example, more than 3400 tons of *C. latus* were caught by artisanal fisheries each year between 2009 and 2011, representing 45% of the local total landings of jacks (MPA 2011).

Despite its commercial importance, the biology and population dynamics of *C. latus* is still largely unknown, in Brazil and elsewhere. There is no knowledge on size-at-age information so far and previous studies with regard its growth are limited to length weight relationship of individuals (*e.g.* Figuerola-Fernández et al. (2008) and Viana et al. (2016)). However, available information on the species' life cycle indicates that it uses a mosaic of coastal and marine environments (Smith-Vaniz 2002), among which its growth rates are likely to vary. Indeed, large specimens of *C. latus* are usually associated to deep waters (> 40 m) and offshore reefs near the shelf break (Lessa et al. 2009, Novak et al. 2020), where they are expected to breed, mainly in April and August (Figuerola-Fernández et al. 2008, Heyman & Kjerfve 2008). As a result, *C. latus* larvae are mainly found offshore, along the continental shelf (Berry 1959, Campos et al. 2010). Its juveniles however are commonly found within estuaries or along sand beaches (Figueiredo & Menezes 1980, Mazzei et al. 2011,da Silva et al 2018), which they apparently occupy for a few months or years before joining the offshore adult population (Figueiredo & Menezes 1980, Smith-Vaniz 2002). Namely, L_{50} of 325 and 345 mm FL for males and females, respectively, and L_{100} of 420 mm FL for both sexes (Figuerola-Fernández et al. 2008). This calls for a more comprehensive description of the growth of

C. latus, encompassing the diversity of habitats used through their life (Lessa et al. 2009, Novak et al. 2020). Thus, age and growth parameters of the North-east Brazil were investigated using size data and otolith readings from specimens captured at most life stages across different coastal and offshore habitats, including several estuaries where yearlings of *C. latus* are found (Paiva & Araújo 2010, Silva-Júnior et al. 2017). Otolith age reading is routinely applied for describing growth in bony fish, and the method has been shown to provide reliable estimates of individual ages both at the annual and daily scales (Panfili et al. 2002, 2009). However, the method needs to be validated before its application to any new species (Campana 2001). Here, the timing for local seasonal otolith ring deposition in *C. latus* was investigated before using otolith growth patterns to specify the ages in all the environments colonized at each life stage and infer the species' global growth features in the area. This basic information is urgently needed for sustainable fishery development in Brazil, but also in other areas of the world where *C. latus* represents a non-negligible source of food and income for local communities.

2.3. Material and Methods

2.3.1. Study area and fish sampling

The study was carried out along the coast of the Pernambuco state in North-east Brazil (Fig.1). The local climate is sub-tropical, with temperatures ranging from 18 to 32 °C throughout the year (CPRH 2003, 2003a, Domingues et al. 2017). As a result of the northward displacement of the Intertropical Convergence Zone (ICTZ) in the Atlantic and of the presence of strong winds blowing from the south-east in the area (CPRH 2003, 2003a, Hounsou-gbo et al. 2015), precipitations along the coast are at their highest in the late autumn and winter (May to August), and the driest period lasts from late spring to early summer (October to December).

The coastline of Pernambuco state is 187 km long. Its continental shelf is ~35 km wide and has a maximum depth of 60 m near its break (Vital et al. 2010, Domingues et al. 2017). The presence of fringing reefs in the outer region and upper slope of the shelf led to its recognition as an Ecologically or Biologically Significant Marine Area (CDB 2014). This particular configuration provides favourable habitats for many resident and migratory fish species (CDB 2014), including *C. latus*. In the present work, *C. latus* specimens from the continental shelf were obtained from artisanal fisheries landings. All were captured by hand line fishing on the offshore reefs used as fishing spots by the artisanal fleet, at ~30 km from the coastline.

Based on previous exploratory surveys on *C. latus* distribution in the area (Paiva & Araújo 2010, Ramos et al. 2011, Silva-Júnior et al. 2017), five local coastal estuaries (Goiana, Santa Cruz, Suape, Sirinhaém and Rio Formoso) were selected to represent the variety in the inshore environments colonized by the species. Besides their geographical proximity, they exhibit distinct morphological features and are subject to different freshwater inputs, resulting in varying environmental settings (Supplementary Table S1). Located in the north of the Pernambuco state, the estuaries of Goiana and Santa Cruz have neighbouring hydrological basins and present high socio-economic and ecological importance (Medeiros et al. 2001, Barletta et al. 2009). While the estuary of Goaiana comprehends a main river channel of 17 km long and its respective flooding area (Barletta et al. 2009), Santa Cruz is the largest estuary of Pernambuco's state and consists in a shallow U-shape channel that connects to the sea by two large entrances (Silva et al. 2011). Because the seawater inflow in the latter is high, the estuary is under a strong marine influence (Flores Montes et al. 1998, Figueiredo et al. 2006), and hypersaline conditions may occur during the driest months of the year (Medeiros & Kjerfve 1993)

In the south coast of Pernambuco there are the estuaries of Suape, Sirinhaém, and Rio Formoso (Fig. 1). The Suape's estuary is formed by two rivers, which flow into a shallow brackish lagoon with limited connection to the sea, resulting in an euryhaline system (Silva et al. 2019). The estuaries of Srinhaém and Rio Formoso have neighbouring hydrologic basins, yet, they differ in geomorphological and environmental characteristics. The former is located within two marine protected areas (CPRH 2003a), it gathers a variety of interconnected lagoons and channels that spread on the shallow flood plain around the main bed of the Sirinhaém river, which constitutes its sole connection to the sea (CPRH 2003a). Conversely, Rio Formoso presents larger tributaries and suffers greater influence from marine environment (Silva et al. 2009). At all these sites, *C. latus* specimens were mainly caught using beach seines trawled along the river banks and block nets set close to mangrove creeks.

Caranx latus specimens were collected monthly between August 2017 and August 2019 in both inshore and offshore areas. All individuals were identified according to the specialized literature (Figueiredo & Menezes 1980, Smith-Vaniz 2002)**,** measured (standard length, SL, in mm) and weighted (eviscerated weight, EW, in g). As most of the fish obtained from offshore fisheries were eviscerated onboard and those collected in the estuary were all immature, the effect of sex could not be included in our analyses.

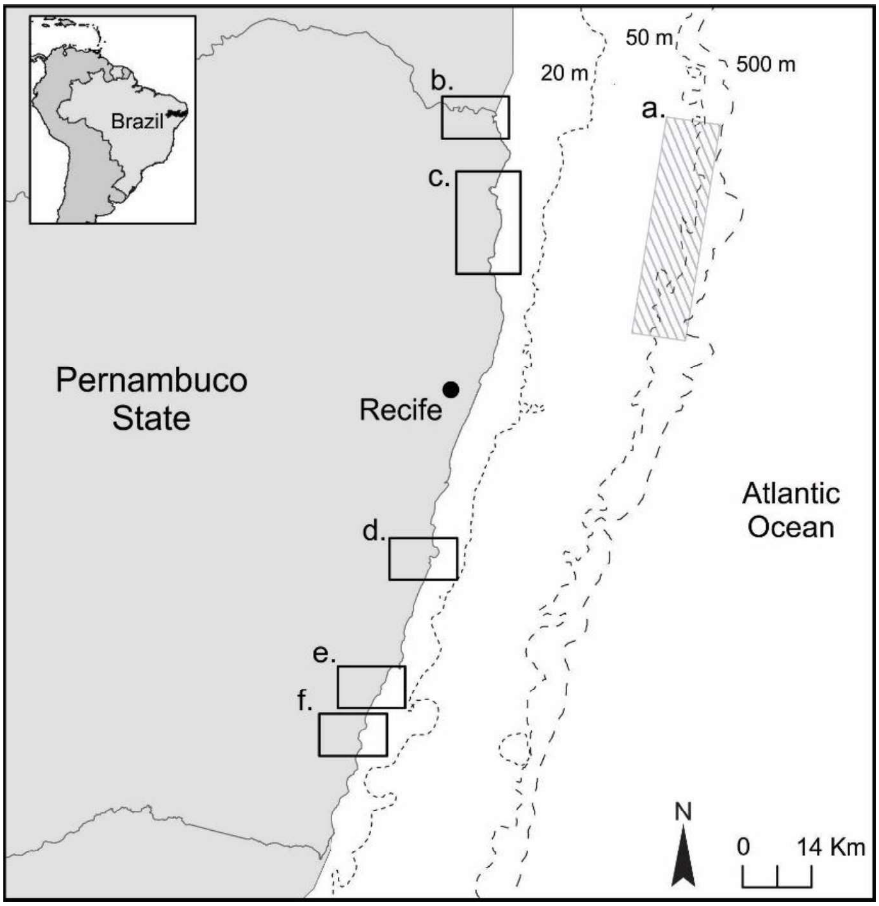


Figure 1 Sampling locations along the coast of the Pernambuco state (North-Eastern Brazil) for this study. The offshore fishing area for *C. latus* (a) is indicated by the dashed rectangle. Inshore ones*, i.e*. the estuaries of Goiana (b), Santa Cruz (c), Suape (d), Sirinhaém (e) and Rio Formoso (f), are indicated by plain rectangles.

2.3.2. Otolith preparation and annuli reading

For each month of the year, a maximum of 25 fish in total, with mixed sizes, was selected from those collected, *i.e.,* all fish sampled on the offshore region was selected and then they were complemented with those collected in the estuaries until reaching the desired sample size to provide a more balanced design between size classes. Both left and right sagittal otoliths of each individual were extracted but only the left one was used for age estimation, unless damaged during the laboratorial procedures (4.2%). All otoliths were embedded in epoxy resin (Araldite 2020) and cut transversally to produce thin sections containing the core (500 µm width) using a precision saw (Buehler, Isomet 1000). Sections were then polished on the anterior side using sandpapers (800, 1200 and 2400 grit) and diluted alumina powder (particle size 1 to 0.3 µm) until the core was exposed on the surface, resulting in thin sections of 200 to 300 µm width. All sections were then cleaned with water, dried and kept in individual clean vials until further processing.

The otolith sections were each etched with EDTA 5% for 1 minute and then stained with Toluidine Blue 1% during 1 min 30 s to enhance growth marks' visibility following Panfili et al. (2002) protocol. All sections were photographed before and after the staining process, under both transmitted and reflected lights, using a stereomicroscope (Olympus SZX12, ×12.5 to ×40 magnification, depending on the size of the otolith) equipped with a computer-linked camera (Jenoptik Prog Res C5, software Progress capture). Fish ages were estimated separately by two distinct readers. Stained sections were observed under the stereomicroscope, to assess the status (translucent or opaque) of the edge of the otolith for each fish. The seasonal growth marks on the otolith (annuli), comprising one translucent and one opaque zone, were then identified and counted by each reader from the core to the outer edge. When the two readings differed, the otolith was reanalysed until a consensus was reached, otherwise the sample was removed from further analysis. Differences in age estimations between the two readers were evaluated using the coefficient of variation index (CV):

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{\left(X_{ij} - X_j\right)^2}{R - 1}}}{X_j}$$

where R is the number of times that each fish was aged, X_{ij} is the ith age estimation for the jth fish and X_j is the mean age obtained for the jth fish (Chang 1982). Although there’s no *a priori* value for CV estimates (Campana 2001, McBride et al. 2006), a mean CV < 7.6% is considered acceptable in ageing studies (Campana 2001).

Otolith growth was measured from the pictures of the stained sections taken under reflected light, using the software ImageJ (https://imagej.nih.gov/ij). Two different types of otolith radius measures were investigated along both the ventral and dorsal axes of each otolith: the actual radius of the otolith consisting in a straight line from the core to the edge (Z_1 and Z_2), and the sum of each increment’s maximum width plus that of the last band on the outer edge (Z_{S1} and Z_{S2}; Fig. 2). Linear regressions on the *log* transformed values of these measures and corresponding fish standard lengths allowed to determine which axis (ventral or dorsal) and radius type better reflected fish body growth.

The timing for annulus formation in *C. latus* was investigated by two complementary approaches: the status of the otolith edge (opaque or translucent), evaluated for all fish, and the relative marginal increment width (I_{MR}), estimated only for specimens with more than one identified annulus:

$$I_{MR} = 100 \times \left(M \times D_{(n,n-1)}^{-1}\right)$$

where M is the distance from the last annulus to the edge of the otolith and D is the distance between the last two annuli. For fish with only one annulus, D comprised the average distance between the first two annuli of every fish with two or more annuli, aiming to keep the proportionality of the I_{MR} values of group 1 individuals in comparison with other ages. The group-1 fish were included in the analysis due the low number of group 2+ specimens in particular months of the period studied.

The periodicity in annulus formation was investigated through circular-linear regression models with random effects, using the I_{MR} of individuals and their capture dates (Okamura et al. 2013) to fit three distinct models, each one with a different assumption on the periodicity of annulus formation: (1) annuli are formed anytime along the year (no cycle); (2) they are formed on an annual basis (one cycle) or (3) they are formed twice per year (two cycles). The three models were applied separately using every fish with at least one annulus (group 1+) and using only those exhibiting two or more annuli (group 2+) allowing us to evaluate whether the inclusion of group 1 fish, and thereby the particular I_{MR} estimation approach used for them, improved the identification the time of annulus deposition. In each case, the model fitting best the data for *C. latus* was selected based on the Akaike Information Criteria (AIC (Akaike, 1974).

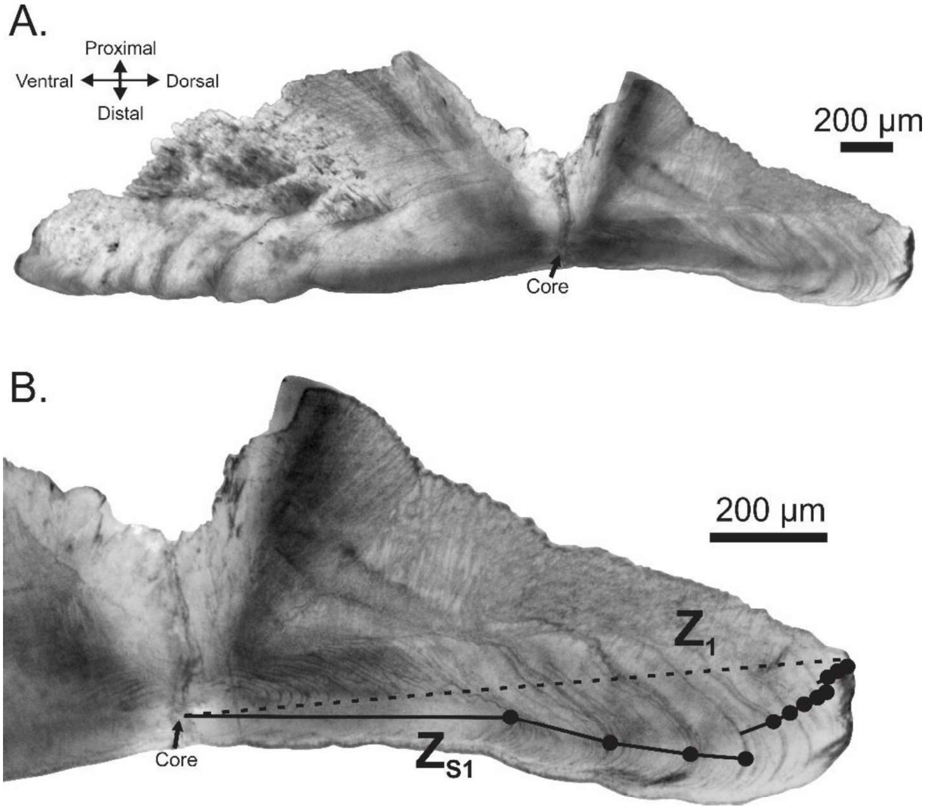


Figure 2 A. Transverse section of the left otolith of a 12 year-old individual of *Caranx latus* photographed under transmitted light (**A.**) and detail of its dorsal half, photographed under a combination of transmitted and reflected light after otolith staining (**B.**). On both pictures, the otolith core is indicated by the black arrow. On (B) the two types of otolith radius measures investigated in the present work (Z_1, dashed line and Z_{S1}, solid line) are illustrated for the dorsal growth axis.

2.3.3. Micro-increment analysis

Based on previous work in another *Caranx* species (*C. melampygus* (Sudekum et al. 1991)), it is reasonable to assume that otolith micro-increments are formed daily in *C. latus*. To clarify this however, and estimate growth during the first year of life in the species, 40 individuals without any visible annulus (group 0 fish), with sizes ranging from 36 to 170 mm (SL), were selected among the *C. latus* specimens collected. All of them were collected at three of the five estuaries studied (Santa Cruz, Suape and Sirinhaém). Their right otoliths were prepared for micro-increments analysis following the same protocol used for annuli reading. However, in this case, each transverse section was polished until the otolith core was ~5 µm below the surface. All sections were then glued to glass slides with the core facing down. The opposite side was polished down until the final width of the section was 10-30 µm. The thin sections obtained were photographed using a camera (Olympus ProgRes C5) linked to a microscope (Olympus

BX41, magnification × 100 and × 400; software Image Pro Plus). Fish ages (in days) were estimated separately by two distinct readers. For this, each thin section was analysed under a microscope and the micro-increments were counted along the dorsal axis of the otolith, from the core to the outer edge. When the ages estimates from the two readers differed, the otolith was reanalysed until a consensus was reached, otherwise the sample was removed from further analysis. As for the annuli counts, differences in age estimations between the two readers were evaluated using the coefficient of variation index (CV, see above). The average width of the daily increments (in $\mu m.day^{-1}$) was obtained for each individual using the respective number of increments and otolith radius. Differences in the average increments width between locations was evaluated through a Kruskall-Walis test, followed by a post-hoc comparison (Dunn's test), once the data did not met the assumptions of normality and homoscedasticity.

2.3.4. Growth modelling

The general growth features for *C. latus* in North-Eastern Brazil were assessed by combining the detailed size-at-age data (in days) from the group 0 specimens used for otolith daily increments analysis and the broader estimates (in years) obtained for all the fish with more than one annulus (group 1+). As a common spawning date could not be defined for these latter, they were all assigned the same fixed age (*e.g.* 1.0 year, 2.0 years, 3.0 years, etc.) irrespective of their month of capture.

Three candidate models were fitted to the data: the growth function of von Bertalanffy (VB), the Gompertz (GM) and the Logistic (LM) models (Supplementary Table S2). Their respective accuracies in describing the growth of the species were evaluated using their differences (Δ_i) in the Akaike information criterion corrected for small samples (AIC_c) as indicated by Burnham & Anderson (2002):

$$AIC_c = AIC + \frac{2k \times (k+1)}{n-k-1}$$

$$\Delta_i = AIC_{C,i} - AIC_{C,min}$$

where n is the sample size and k is the total number of parameters (plus one for the estimated variance), and $AIC_{C,i}$ and $AIC_{C,min}$ comprehend the AIC of model i and the model with lowest AIC respectively. Although these information-criteria approaches do not allow classical hypothesis testing (Anderson & Burnham 2002), differences higher than 2 in Δ_i were considered significant in distinguishing the performance of two or more models (Burnham & Anderson 2002).

All analyses were carried out in R (R Core Team 2021), using the packages *ggplot2* (Wickham 2016), *fishmethods* (Nelson 2019) and *AICcmodavg* (Mazerolle 2020).

2.4. Results

A total of 282 *C. latus* individuals, with sizes (SL) ranging from 36 to 760 mm and weights (EW) between 1 to 7090 g, were used for this study. They had been caught all year round in the study area, yet in very variable proportions. Notably, during both of the years sampled, *C. latus* turned out to be nearly absent in the local catches from April to July: only a few individuals were caught in the estuaries surveyed over this period and none was captured at sea between June and July. This explains the very low numbers of otoliths analysed for these four months.

2.4.1. Timing of annulus deposition

Seasonal growth increments were visible in both the ventral and dorsal regions of the otoliths of *C. latus*, under both transmitted and reflected light. By enhancing the contrast of the denser growth marks, otolith staining substantially helped identifying annuli and measuring their width, although the presence of thin coloured rings within each translucent zone complicated growth mark interpretation, especially the identification of the first annulus. The four types of otolith radius measures investigated presented a good linear relationship with fish body length ($p < 0.001$, $r^2 = 0.895$ to 0.965). However, that following the maximum growth axis (Fig. 2) consistently presented the best fit, both on the dorsal (Z_{S1}, $r^2 = 0.950$) and ventral (Z_{S2}, $r^2 = 0.965$) side (Supplementary Fig S1). Although its fit with body size was slightly lower than that of Z_{S2}, Z_{S1} was chosen for otolith radius measurement because growth marks (particularly the first one) proved to be easier to locate on the dorsal side of *C. latus* otoliths.

The status of the otolith edge was identifiable in 90% of the specimens analysed. Opaque and translucent margins were observed irrespective of the month, but their proportions varied along the year (Fig. 3). Translucent margins were predominant (in ≥75% of the fish analysed) from November to February, *i.e.* during the austral summer. Conversely, a greater proportion of opaque margins were found between May and August (i.e. in the late autumn and early winter), with a peak in August (for 76.9% of the fish analysed). These results suggest that annuli in *C. latus* otoliths are only deposited once during the year in this area of the Globe and were corroborated by the results from the marginal increment analysis.

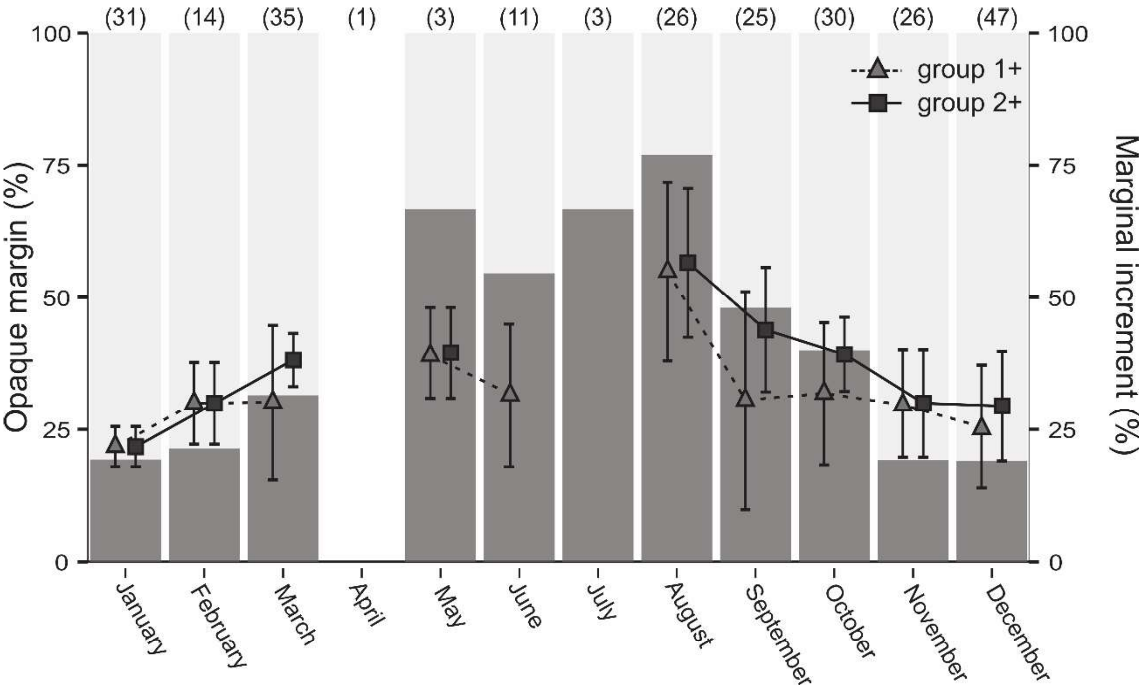


Figure 3 Monthly proportions of opaque edges in the otoliths of 252 specimens of *Caranx latus* (56 -760 mm) captured in North-Eastern Brazil between 2017 and 2019, and corresponding marginal increment widths (I_{MR}, mean ± standard deviation) in the otoliths of the group 1+ and group 2+ specimens among them. For each month, the number of individuals analysed for otolith edge status is indicated between brackets, and results are shown only if more than 3 fish were available for each variable.

As expected, I_{MR} was more variable in group 1+ fish, probably because of the decrease in otolith increment width with age, which results in the greatest inter-individual variability for this parameter being observed in the first year of life. Nonetheless, the inclusion of group 1 fish in the I_{MR} analysis allowed to fill the gaps in our sampling design, especially for the few months with low number of group 2+ specimens (*e.g.* June), and the results were similar for the two groups of fish. Indeed, the model best fitting to I_{MR} data was that, assuming the ring formation occurs on an annual basis, either when including all group 1+ specimens ($n = 92$, $\text{AIC}_{\text{no cycle}} = -50.46$; $\text{AIC}_{1\text{ cycle}} = -56.53$; $\text{AIC}_{2\text{ cycles}} = -51.22$) or when considering group 2+ fish only ($n = 70$, $\text{AIC}_{\text{no cycle}} = -42.41$; $\text{AIC}_{1\text{ cycle}} = -45.01$; $\text{AIC}_{2\text{ cycles}} = -39.97$). Moreover, for both groups, monthly I_{MR} means were the highest in August (of 55.0 ± 16.8% for group 1+ fish, and 56.6 ± 14.0% for group 2+ fish) and the lowest in January (21.9 ± 3.8% for both group1+ and group2+ fish, Fig. 3). All these results suggest that the opaque and translucent bands in the otoliths of *C. latus* are mainly deposited between May and August and between November and January, respectively, in the study area. Accordingly, the denser (chromophilic) mark corresponding to the annulus and the start of the translucent band each year should essentially be deposited between September and November and therefore validating the use of one annulus as a representative of one year for *C. latus* age estimation.

2.4.2. Variation in sizes and ages

The average coefficient of variation (CV) between readers for individual annuli counts was of 2.92%, lower than the criteria provided by the meta-analysis of Campana (2001). The presence of thin coloured rings within each translucent zone complicated growth mark interpretation, especially the identification of the first annulus. However, ages were confidently estimated for 282 specimens of *C. latus*, with sizes (SL) ranging from 36 to 760 mm and weights (EW) between 1 to 7090 g. Estimated ages (in years) for these fish varied between 0.21 and 13, although most specimens in our sample (67.4%) were age-0 fish (Fig. 4). Indeed, in the estuaries, where observed sizes ranged from 36 to 223 mm SL (for weights between 1 and 282 g), almost all individuals (91.8 %), individuals were less than 1 year old. Conversely, all age classes (0-13 years) were found at sea, where sizes (SL) ranged from 155 to 760 mm, and weights from 105 to 7090g. The sizes of the age-0 fish captured at sea varied from 155 to 195 mm SL and were, thus, close to the maximum value observed at this age in the estuaries (177 mm SL).

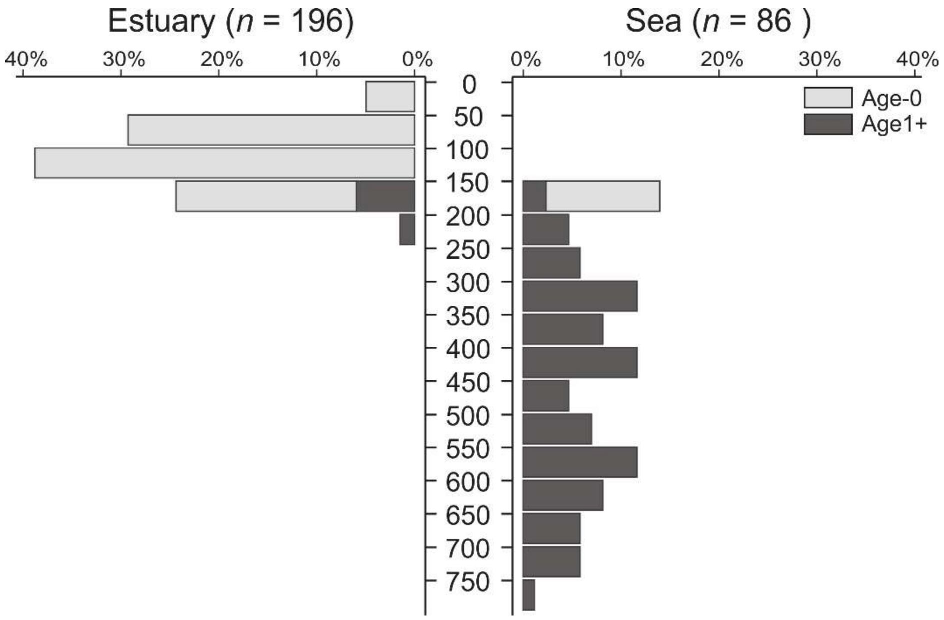


Figure 4 Length frequency distribution (SL, in mm) of the *Caranx latus* specimens collected for this work in estuaries spread along the shore and at the sea in North-Eastern Brazilian coast.

Otolith micro-increments analysis allowed to deepen our understanding of the early growth and size-at-age in *C. latus*. Indeed, marks assumed to be daily rings were clearly visible on the right otolith of the 40 age-0 individuals analysed for this, especially on the dorsal side of the sections (Fig. 5). Although they were slightly more difficult to count nearby the otolith core, the average CV between readers for daily ring count was low (3.33%). Estimated ages for these group-0 fish ranged between 77 (for a specimens of 36 mm SL) and 272 days (in a fish of 170 mm SL). This further supports that annuli are likely to be deposited on an annual basis in the otoliths of *C. latus* in North-Eastern Brazil. Furthermore, two distinct growth zones were noticeable in the otoliths of these fish: a central opaque zone starting at the core, with a progressive inflexion of the otolith growth axis, and an external translucent zone, with no change in the otolith growth axis (Fig. 5). The transition between these two zones was progressive in 90% of the fish analysed, occurring in an area located 290-380 µm away from the core, corresponding to ages ranging between 72 and 132 days.

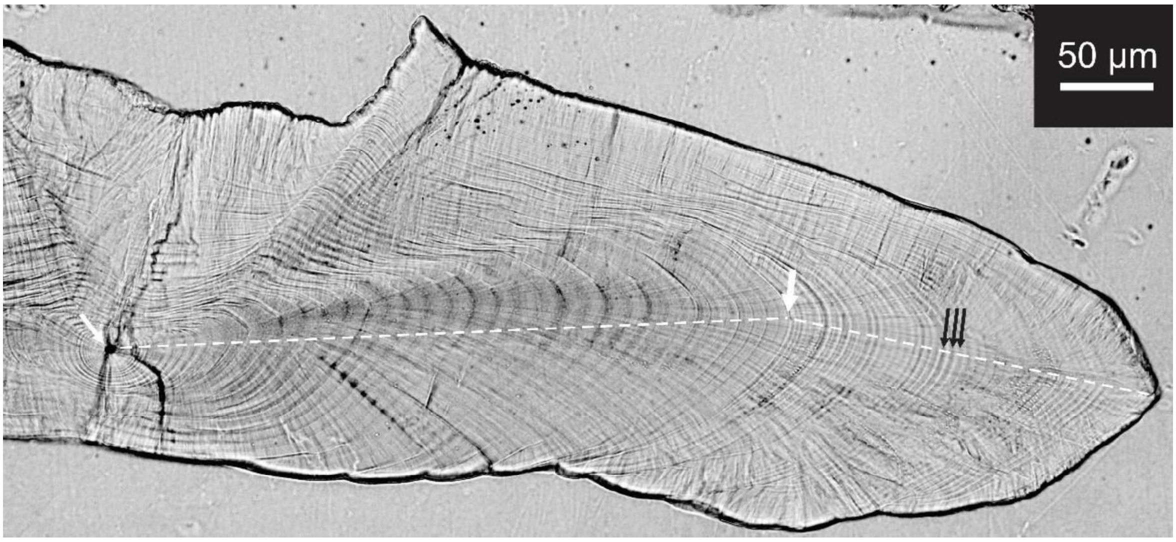


Figure 5 Transverse section (dorsal side) of the otolith of a juvenile of *Caranx latus* (SL = 85 mm, age = 154 days) prepared for micro-increment (black arrows) analysis. The position of the otolith core and that of the transition between central opaque and external translucent zones along the growth axis (dashed line) are indicated by white arrows.

2.4.3. Growth

The von Bertalanffy growth model presented the best fit to the size-at-age data for *C. latus*, showing the lowest AIC_C (1347.9). Its corresponding estimates for local growth parameters were 782.37

mm for L_{inf}, 0.179 for k and -0.436 years for t_0 (Fig. 6). The Gompertz ($AIC_C = 1379.0$) and Logistic ($AIC_C = 1403.8$) models had significantly poorer performances ($\Delta AIC_C > 2$). Their estimates for local growth parameter were: Gompertz, 701.11 mm for L_{inf}, 0.346 for G (effect on slope of the curve) and 1.998 years for t_I (age at inflexion of the curve); and Logistic, 670.10 mm for L_{inf}, 0.529 for the scaling of the curve and 3.039 years for its age at inflexion. Both models predicted lower L_{inf} than the maximum size observed in this study (760 mm SL), supporting that the von Bertalanffy was the most suitable model for predicting *C. latus* size-at-age in our study area.

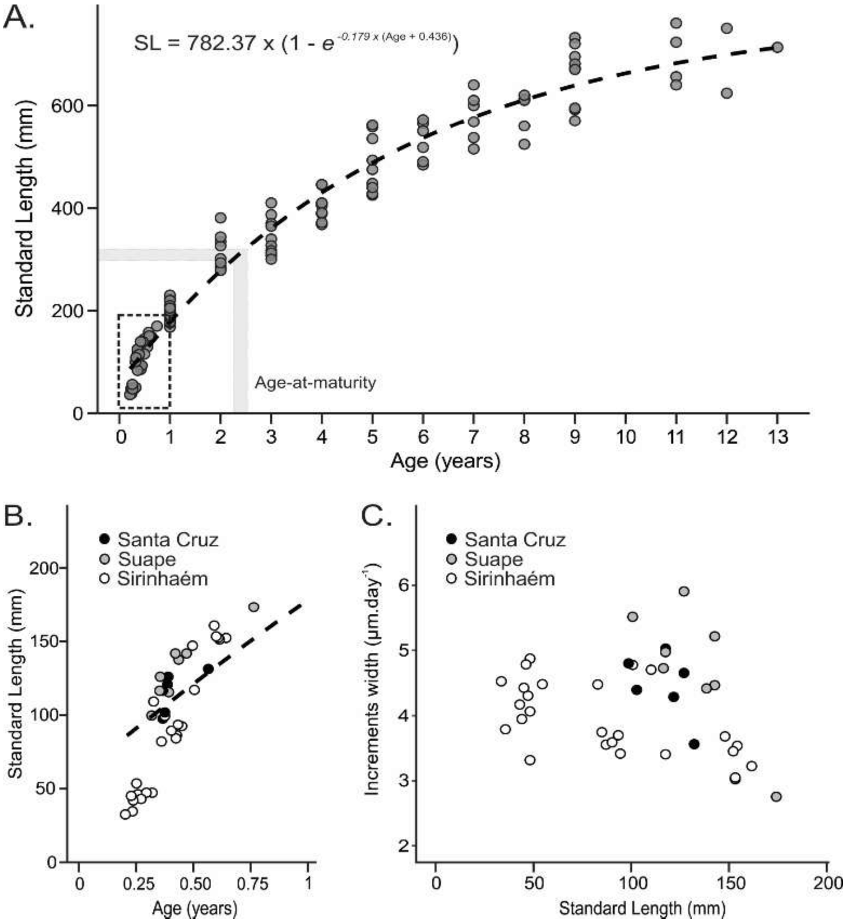


Figure 6 Growth pattern of *Caranx latus* in North-Eastern Brazil. (**A.**) General growth of *C. latus*, where each age-class and the respective observed lengths are represented by grey points and the von Bertalanffy equation is shown, with the light grey bars representing the expected age-at-maturity estimated by this equation. (**B.**) A detailed view of the size-at-age of age-0 specimens used for micro-increment analysis from three of the five estuaries studied **(**dashed rectangle from **A.**). (**C.**) The corresponding average widths of their daily increments. The growth curve obtained with the von Bertalanffy model is represented by the dashed line in panels **A** and **B**.

The von Bertalanffy equation predicted an average size of 178 mm at age 1, 277 mm at age 2, 360 mm at age 3, 488 mm at age 5 and 662 mm at age 10. Based on previous findings by Figuerola-Fernández et al. (2008), age at first maturity is expected takes place after the second year of life (L_{50} of 305 mm and 325 mm SL for males and females, respectively). However, the use of the relationship between Z_{S1} and fish body size ($log(\mathrm{SL}) = -7.340 + 1.894 \times log(Z_{S1})$, $r^2 = 0.950$) allowed gathering precious additional information regarding *C. latus* growth and biology in the area. Using this type of measure, the first annulus on the otolith was found to be deposited at an average distance of 754 ± 85 µm from the core. Increments widths for the subsequent annuli were drastically lower, ranging from 163 ± 41 µm (for the 2nd annulus) to 19 ± 2 µm (for the twelfth). This suggested that the most part of *C. latus* growth in North-Eastern Brazil occurs during the first year of life, comprehending 22.75% of its local L_{inf} and around 56% of their size-at-maturity. In addition, the inter-individual variation in the width of the first annulus (620 to 900 µm) suggested a difference of up to 130 mm in fish body size at the end of this first year of life, probably in link with the variability in the environmental conditions encountered and the direction of otolith growth axis. Variations in Z_{S1} at the end of year 2 were notably lower, comprehending a difference of up to 80 mm in size, and meaningless at the end of the twelfth year (difference in size < 15 mm). This suggests that most of the inter-individual variation in specimens' body size results from their first years of life.

The average width of the daily increments varied along the otolith radius and among the age-0 specimens studied, ranging from 2.8 to 5.8 µm per day, suggesting that growth during the first year of life was not constant. For instance, the maximum size at 100 days was 56 mm SL, while the minimum one at 200 days was more than twice higher (130 mm SL, Fig. 6B). Moreover, whereas average daily increment widths in smaller specimens, *i.e.* those that were likely to recently colonize the estuary (36 – 56 mm SL), varied between 3.3 and 4.8 $\mu\mathrm{m.day}^{-1}$, increment widths of the remaining ones covered the whole range of values found among individuals (2.8 to 5.8 $\mu\mathrm{m.day}^{-1}$, Fig 6C). These latter had significant differences between locations ($p = 0.010$), reflecting the varying fish body sizes found among individuals (Fig 6B, C). They were larger in Suape (4.7 ± 0.9 $\mu\mathrm{m.day}^{-1}$, $n = 8$) and Santa Cruz estuaries (4.5 ± 0.5 $\mu\mathrm{m.day}^{-1}$, $n = 6$) than in Sirinhaém (3.7 ± 0.5 $\mu\mathrm{m.day}^{-1}$, $n = 15$, $p < 0.030$).

2.5. Discussion

Previous studies on the growth of the horse-eye jack *C. latus* were limited to only length weight relationship of individuals (*e.g*. Mazzei et al. (2011) and Viana et al. (2016)), which hampered a proper understanding of the population dynamics of this highly mobile species (Lessa et al. 2009, Novak et al. 2020). The present work brings novel insights on this matter as, to our knowledge, it is the first assessment of *C. latus* growth based on detailed size-at-age data for most life-stages (juveniles and adults) and lifetime habitats (estuarine and marine) in North-Eastern Brazil. As such, it brings valuable information on the growth, structural patterns of the otoliths and life history strategies deployed by the species.

2.5.1. Otolith structure

Cyclical variations in the physiology and somatic growth of species have been associated to the deposition of growth bands in fish, where opaque and translucent bands are expect to reflect periods of slow and fast growth rates, respectively (Panfili et al. 2002). However, the exact driver of these variations are not fully understood since it is dependent of the life strategy history of species studied and local environmental settings (Panfili et al. 2002, Høie et al. 2009, Albuquerque et al. 2019a). Disentangling these factors may be challenging as they are sometimes correlated and have a significant impact on their development (*e.g.* reproduction (Val et al. 2005)). While the temperature can be a primary driver of fish growth in temperate regions (Høie et al. 2009), fish growth in the tropics has been associated to life history strategies, habitat diversity and food availability (Val et al. 2005, Espino-Barr et al. 2008).

In this study, the deposition of annuli occurred only once a year for *C. latus*, supporting the reliability of otolith methods in estimating the age of marine fish in North-Eastern Brazil. Both edge status and otolith marginal increments width suggest that translucent bands are deposited yearly from November to February, *i.e*., during the local dry period (austral spring and summer), while opaque bands seem to be formed between May and August, *i.e.,* during the local rainy period (austral autumn and winter). This indicates that the formation of translucent bands, representing faster growth rates, prevail during the local dry period, probably related to warmer and more saline waters at both estuarine and marine areas. Conversely, the opaque band formation is likely to be associated with local period of increased rainfall along the coast. This is particularly true in the estuarine and inshore areas, where seasonal changes in temperatures (Morrongiello et al. 2014, Doubleday et al. 2015) and in freshwater inputs controlling salinity and prey availability may influence the growth of juvenile fish (Cardona 2000, Diouf et al. 2009, Isnard et al. 2015). Moreover, although juvenile *C. latus* inhabit inshore areas with varying salinities (Paiva & Araújo 2010, Medeiros et al. 2017), their occurrences are rather low in periods of high freshwater inputs (da Silva et al. 2018), suggesting that they might be subject to physiological limitations. Similarly, temperature reaches the lowest values during this specific period (~25 ° C) and could equally influence their growth within estuaries.

In the offshore area, both the water temperature (26 – 29.5 º C) and salinity (36.5 – 37.0) are quite stable over the year (Domingues et al. 2017), suggesting that other (biological) processes may drive seasonal changes in metabolism and otolith growth band formation in large *C. latus*. Indeed, the band formation in other jack species (*C. caninus* and *C. caballus*) in the Pacific have been attributed to variations in local food availability and consumption. Accordingly, the translucent band formation, representing faster growth rates, was associated to periods of higher rainfall and food availability (Gallardo-Cabello et al. 2007, Espino-Barr et al. 2008). These results contrast in part with the growth band formation found for *C. latus* in North-Eastern Brazil. In our case, the primary productivity along the shelf increases from May to July following the continental nutrient input from at the rainy period (Eskinazi-Leça et al. 1997), the expected period of opaque band deposition. Secondary production however increases after September and reaches its maximum during summer (Hazin, 2009). Bearing in mind the potential lagged effect between increasing nutrient input and rapidly available prey for *C. latus*, it is likely that the formation of translucent band, and thereby their fastest growth rates, is associated to enhanced food availability. Although the low number of individuals caught between April and July in this study hinders a comprehensive understanding of the factors underpinning the seasonal growth in *C. latus,* the cyclical variation in the deposition of opaque and translucent bands of *C. latus* at the sea is probably primarily associated to food availability.

2.5.2. Size-at-age and growth modelling

Like in most fish species, growth in *C. latus* is the highest during the first year of life, with an estimated gain in size of 177 mm on average in our study area, which represents 22.75% of the local L_{inf} for the species. The growth parameters obtained here for the species ($L_{\mathrm{inf}} = 782.37$ mm, $k = 0.179$) are were within the range reported for other *Caranx* species around the Globe and present comparable values to those found in other large sized species of jacks (Table 1), which all reach between 60 and 75% of their maximum sizes during their 7th year of life (Sudekum et al. 1991, Kishore & Solomon 2005, Espino-Barr et al. 2008, Andrews 2020). However, among them, *C. latus* is one of the species with the lowest L_{inf}. Interestingly, growth parameters for *C. latus* are very close to those reported for *C. hippos* (Table 1). Since both species have similar life cycles and coexists in inshore and offshore areas across the Brazilian coast (Paiva & Araújo 2010, Silva-Júnior et al. 2017), variations in growth rates among large size jacks might be largely caused by small differences in lifetime strategies and local environmental conditions. Conversely, small sized jacks (*e.g. C. crysos, C. caballus* and *C. ronchus*) with higher growth rates may achieve >75% of their maximum size on their 5th year of life (FAO 1979, Goodwin & Johnson 1986, Gallardo-Cabello et al. 2007).

Table 1 Von Bertalanffy growth parameters (L_{inf}; k and t_0) in *Caranx* species from distinct localities (adapted from Gallardo-Cabello et al. (2007)). In each case the type of length (standard – SL, furcal – FL or total length – TL) used to estimate *L*inf is shown between brackets.

Species	Location	Method†	Growth parameters		
			L_{inf} (mm)	k	t_0
Caranx ignoblilis (Andrews 2020)	USA (Hawaii)	Otolithometry	1500.0 (FL)	0.180	0.100
Caranx hippos (Kishore & Solomon 2005)	Trinidad and Tobago	Otolithometry	908.4 (FL)	0.121	-1.625
Caranx melampygus (Sudekum et al. 1991)	USA (Hawaii)	Otolithometry	897.0 (SL)	0.233	-0.044
Caranx caninus (Espino-Barr et al. 2008)	Mexico (Collima)	Otolithometry	832.6 (SL)	0.202	-0.283
Caranx latus (This study)	Brazil, (North-east coast)	Otolithometry	782.3 (SL)	0.179	-0.436
Caranx sexfasciatus (Cruz-Romero et al. 1993)	México (Colima)	Length frequency	755.8 (*)	0.339	-0.063
Caranx ruber (García-Artega & Reshetnikov 1985)	Cuba	*	560.0 (*)	0.100	-1.728
Caranx bucculentus (Brewer et al. 1994)	Australia (Gulf of Carpentina)	Length frequency	538.8 (SL)	0.305	*
Caranx caballus (Gallardo-Cabello et al. 2007)	Mexico (Collima)	Otolithometry	520.2 (SL)	0.362	-0.085
Caranx senegallus (Arra et al. 2020)	Guinea (Côte d'Ivoire)	Length frequency	514.5 (FL)	0.460	-0.310
Caranx ronchus (FAO 1979)	Senegal	Otolithometry	453.0 (TL)	0.303	-0.515
Caranx crysos (Goodwin & Johnson 1986)	Mexico (Norte del Golfo)	Otolithometry	412.0 (FL)	0.350	-1.170

† Methodology applied to estimate the von Bertalanffy growth parameters. For each species, preference was given for studies using hard parts. * Information not available

Because of its versatility in estimating key growth parameters and comparison with indirect growth assessment methods (*e.g.* length frequency analysis) the von Bertalanffy model has been applied for a diverse number of fish species, including some of the *Caranx* genus (Kishore & Solomon 2005, Gallardo-Cabello et al. 2007). However, an increasing number of studies have suggested that it may not provide realistic size-at-age estimates for some species or life stages (Charnov 2008, Mercier et al. 2011, Sirot et al. 2015). In our case, the von Bertallanfy was the best model fitting the size-at-age data of *C. latus*. The growth parameters obtained here for *C. latus* are within the range found for other *Caranx* species and the L_{inf} suggested by the model is close to the maximum size (858 mm FL and ~812 mm SL) reported for the species in Brazilian coastal waters (Lessa et al. 2009). Nonetheless, considering that jack species may live up to 20 years old and above (Goodwin & Johnson 1986, Andrews 2020), the low number of old specimens (age 12+) in our sample could have biased the performance of the von Bertalanffy model and led to an under-estimation of the actual local values of L_{inf}.

A precise age determination is a key information for a consistent assessment of species growth. When evaluating fish age by annulus counts, specific ages can be interpreted as years or months depending on the complementary information available on life history processes, namely the expected date of birth (Panfili et al. 2002). Indeed, fish age in number of months or subdivisions within a year (1.5, 2.5, etc.) can provide more detailed information on the growth of species though their life and has been successfully applied in tropical (*e.g.* Sirot et al. (2015) and Soeth et al. (2019)) and temperate regions (*e.g.* Moore et al. (2007) and Mercier et al. (2011)). However, in our case, age was determined in years due the inconclusive knowledge on the date of birth of *C. latus*. Accordingly, reproduction for this species takes place mainly in April and August, but spawning may extends from February to October and even occurs year-round at different locations in the Atlantic (Figuerola-Fernández et al. 2008, Heyman & Kjerfve 2008). Although the decision to estimate *C. latus* age in years rather than months was oriented by precaution, it can influence the slope of the growth curve and thereby the parameter obtained for the species. Therefore, further studies addressing older fish and at different aging scales (*e.g.* months) are needed to improve the assessment of *C. latus* growth parameters in North-Eastern Brazil and also elsewhere in the Atlantic where it is exploited by fisheries.

2.5.3. Implications to the life history ecology

Unlike other jack species in the area (*e.g. Caranx hippos*), large specimens of *C. latus* are rarely fished inside the estuaries of North-Eastern Brazil. Most of the fish collected in these inshore environments for the present study were age-0 specimens. Because of sampling surveys were carried out in distinct estuarine areas spread along the coast, it is reasonable to assume that this reflects the natural occurrence of *C. latus* in estuarine environments. It suggests that estuaries in North-Eastern Brazil are essentially used as juvenile habitats by the species, at least during its first year of life (Nagelkerken et al. 2000, Beck et al. 2001). Apparently, *C. latus* juveniles colonize them earlier as their third month of life (from ages starting at 77 days) and may remain there for up to one year, before moving to the offshore areas occupied by the adult population. The colonization of estuarine environments by early juveniles (around 80 to 250 days) has already been observed in jacks, *e.g.* for *C. melampygus* and *C. ignobilis* in Hawaii (Smith & Parrish 2002). It is worth noting, though, that the low number of age-0 fish collected in the marine region in this study does not necessarily reflect their actual abundance in this area due to the gear selectivity. Indeed, the fishing gear used at sea was targeting bigger fish, and nearshore marine habitats like sandy beaches and shallow reefs, that also serve as juvenile habitats for *C. latus* (Mazzei et al. 2011, Medeiros et al. 2017), were not included in our surveys.

Most of fish analysed for micro-increment count showed a progressive transition from the central opaque to the external translucent zone found between 290 and 380 µm away from the core, suggesting that *C. latus* juveniles experiment a unique change in their physiology during their first few months of life, before entering the estuaries. Such changes in otolith structure are expected to occur in species undergoing physiological stress or major environment disturbances (Lessa et al. 2008, Panfili et al. 2009, Sponaugle 2010). They are found in many tropical reef fish and seem to be related to the settlement of species at a given habitat (Wilson & McCormick 1999). Based on the assumption that *C. latus* is an offshore spawner (Berry 1959, Heyman & Kjerfve 2008), this change could either reflect the migration of juvenile *C. latus* to inshore regions or significant biological processes at the post-larval stage (Panfili et al. 2009). Nonetheless, specific studies on otolith larval development in *C. latus* are needed before one can conclude on the actual life-history event underpinning this change in the otolith structure.

During the juvenile life, fish species are subject to varying biological and environmental conditions that may influence their growth and fitness (Fonseca & Cabral 2007, Fodrie et al. 2009, Schloesser & Fabrizio 2019), with potential implications on their recruitment (Chamber & Trippel 1997). In this regard, the first year of life in *C. latus* comprehended the period where its growth is the highest but also more variable among individuals. This variability appears to be reflected by the yearlings within estuaries studied and suggests that the habitats occupied by *C. latus* could play a role in driving the growth of their juveniles. Nonetheless, there are numerous factors that can modulate juvenile fish growth, like temperature (Morrongiello et al. 2014, Doubleday et al. 2015), salinity (Cardona 2000, Diouf et al. 2009) and habitat quality and food availability (Vasconcelos et al. 2009, Isnard et al. 2015), and which need further investigation before ascertaining the differences found in this study. Therefore, although inconclusive due to the low number of fish analysed for micro-increment count, the variation in growth of *C. latus* yearlings across locations sheds light on the potential effects of local biological and environmental conditions at the juvenile stage.

2.6. Conclusion

This study provided novel information about the life history and the growth of an economically important yet poorly studied species in the Southwestern Atlantic. It showed that the juveniles of this marine species largely colonize the estuaries spread along the North-Eastern Brazilian coast when 3-4 months old and remain there for up to 9 months during their first year of life before moving back to marine habitats. During this period, growth is particularly fast, so *C. latus* juveniles may reach 22.75% of its maximum size on their second year of life. Likewise, differences in size-at-age were also greatest within the first year. They were reflected in part by the distinct growth rates found in estuaries studied, indicating that their growth could be affected by local biological and environmental conditions of habitats used at the juvenile stage. The von Bertalanffy model was the best fitted to size-at-age data of *C. latus*. Corresponding estimates for local growth parameters were 782.37 mm for L_{inf}, 0.179 for k and -0.436 years for t_0. Although the population stock of *C. latus* is not under any threat of exploitation in the Atlantic, specific threats may still arise at the local scale (Smith-Vaniz et al. 2019), particularly those associated to habitat degradation in estuarine and nearshore environments used by juvenile *C. latus*. To overcome this issue, further studies are needed on the efficiency of these habitats in maintaining the adult population in the North-Eastern Brazilian coast.

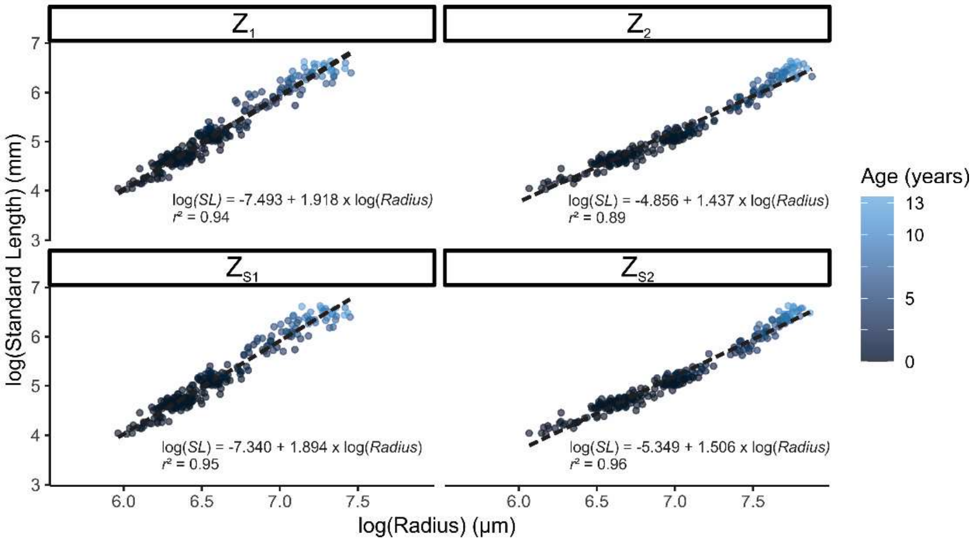
2.7. Supplementary Material

Supplementary Table S1 Summary of morphological characteristics and environmental settings of the estuaries studied along the North-Eastern Brazilian coast.

Charactheristics	Estuary				
	Goiana	Santa Cruz	Suape	Sirinhaém	Rio Formoso
Vegeted area (km²)	28.43	48	23.1	17	19.96
Water surface area (km²)	8.11	25.5	6.6	1.7	7.83
Mean depth (m)	4.4.	3	3.1	2.6	4
N of marine entrances	1	2	2	1	1
Width of marine entrances (km, mean and range)	1.41	0.90 (0.5 - 1.3)	0.27 (0.18 – 0.35)	0.6	1.07
Salinity range	0.3 – 36.4	4.7 – 37.0	4.2 – 37.7	0.2 – 36.6	10.0 – 36.3
Temperature range (°C)	26.1 – 30.8	25.0 – 30.9	27.2 – 31.7	25.0 – 33.4	24.5 – 29.5
Reference	(Medeiros & Kjerfve 1993, Medeiros et al. 2001, Honorato da Silva et al. 2004, Silva et al. 2009, Otsuka et al. 2014, Lima et al. 2015, Gonzalez et al. 2019, Conti et al. 2020)				

Supplementary Table S2 Growth models fitted to the size-at-age data of *Caranx latus* in North-Eastern Brazilian coast: the formula and parameters (*p1*, *p2* and *p3*) in each case are specified. L_{inf} is the asymptotic length. *k* and *G* are the growth coefficients of the von Bertalanffy and Gompertz models, respectively. The parameter *a* in the Losgistic model is the scaling parameter of which influences the slope of the curve. t_0 is the estimated age at which the length is 0. t_i (Gompertz) and *b* (Logistic) are the age at inflexion of the curve.

Model	Parameters		
	p1	*p2*	*p3*
von Bertalanffy $f(x) \sim p1 \times (1\text{-exp}(\ -p2\ (x - p3))$	L_{inf}	k	t_0
Gompertz $f(x) \sim p1 \times \text{exp}(\text{-exp}(\ -p2(x - p3))$	L_{inf}	G	t_{i}
Logistic $f(x) \sim p1\ /[1 + \text{exp}(-p2 \times (\text{x} - p3))]$	L_{inf}	a	b



Supplementary Figure S1 Linear regression of fish size and the four radii measures investigated on the otoliths of *Caranx latus* in North-eatern Brazil.

2.8. IN A NUTSHELL

- *Caranx latus* specimens in North-Eastern Brazil may live up to 13 years old for a maximum expected size of 782 mm of standard length.
- Sexual maturity is expected to be reached only between the third and forth year of life, when have been targeted by local fisheries for at least one entire year.
- Size and age structures differ between estuarine and offshore habitats: while all age classes can be found at sea, the vast majority of the specimens caught in estuaries are yearlings.
- Most fish colonize the estuaries when 3-4 months old and occupy them for up to 9 months during their first year of life.
- *C. latus* growth in North-Eastern Brazil is particularly fast during the first year of life (accounting for up to 22.75% of the maximum size).
- However, inter-individual variation in growth is also the highest during this period, with differences across estuaries suggesting that it could be largely site dependent.
- Further research is needed to evaluate the implications of the biotic and abiotic environmental conditions encountered in the habitats colonized at the juvenile stage on fish lifetime size-at-age and fitness.

This first research axis contributes to answering the general research question of the thesis by quantifying the duration of the estuarine life for *C. latus* in North-Eastern Brazil, thereby clarifying the period of life the other chapters should focus on. It also highlights that, during their first year of life, *C. latus* juveniles may experience drastically different life conditions, which are likely to affect not only their juvenile growth, but also their future fitness.

CHAPTER 3: Estuarine trophic ecology of juvenile *Caranx latus*

Little is known about jacks' trophic ecology in estuaries, although the ability of fish juveniles to successfully exploit available resources in these productive environments may strongly affect stock recruitment success in the populations concerned (Cardona 2000, Fodrie et al. 2009, Isnard et al. 2015). The differences in early growth observed among estuarine habitats in CHAPTER 2 could be driven by spatial differences in resources availability and use. Therefore, the second research axis of this study focussed on describing how juveniles of *C. latus* use available food resources in the estuarine areas of North-Eastern Brazil. Juvenile diets and isotopic niches were assessed for both *C. latus* (*n* = 266) and another sympatric jack species, the crevalle jack (*Caranx hippos, n* = 173, in three neighbouring estuaries with contrasted morphological and biological features (**Article II**). It allowed understanding the plasticity in the use of estuarine resources by juvenile jacks and how it varies according to local estuarine characteristics. Moreover, it provided an estimation of the degree of trophic competition between the juveniles of *C. latus* and those of other sympatric species under varying scenarios of co-occurence. Our results highlight the importance of cross-sites comparisons when investigating the trophic ecology of fish species, particularly in tropical estuaries that can exhibit a high diversity of environmental settings, biocenoses and food sources.

Article II

This section was presented at the 9th European Coastal Lagoons Symposium in January of 2020, where it was granted an award for its contribution to elucidating the processes in transitional environments. It has been published in the journal *Estuarine, Coastal and Shelf Science* in 2021.

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Trophic ecology of the juveniles of two jack species (*Caranx latus* and *C. hippos*) in contrasted tropical estuaries

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3.1. Abstract

Jacks are highly prized tropical marine fish. Most of them complete their whole life cycle at sea but some use estuaries at the juvenile stage before moving back to coastal waters and joining the adult exploited stocks. Little is known about jacks' trophic ecology in estuaries, although their juveniles' ability to successfully exploit available resources in these productive environments may strongly affect stock recruitment success in the species concerned. In this study, stomach content and stable isotope analyses were combined to investigate diet and food niche overlap of juveniles from two sympatric species of jacks (*Caranx latus* and *C. hippos*) in three contrasted estuaries (Suape, Sirinhaém and Santa Cruz) spread along the North-Eastern Brazilian coast. Overall, although the juveniles of *C. latus* exhibited a more piscivorous diet than those of *C. hippos*, the two species had very similar isotopic niches, with mean $\delta^{13}C$ and $\delta^{15}N$ values of -19.35 ± 2.10‰ and 11.03 ± 1.11‰ and of -19.10 ± 1.82‰ and 10.21 ± 1.21‰, for *C. hippos* and *C. latus* respectively. In all the estuaries sampled, both species mostly ate fish (N_i = 20.1 - 46.2%, W_i = 60.1 - 75.1%, essentially Gobiidae and Clupeidae) and crustaceans (N_i = 26.0 - 65.9%, W_i = 23.3 - 38.2%, mainly Penaeidae shrimps). As a result, the overlap between their global estuarine isotopic niches was >68%. However, diet composition for the two species varied among estuaries, indicating that their juveniles partly adapt their food preferences to local prey availability. Notably, prey preferences differed significantly between the two species only in the Santa Cruz estuary, where $\delta^{15}N$ values were the highest for both species. Conversely, interspecific differences in $\delta^{13}C$ ratios were greater in the Suape and the Sirinhaém estuaries, likely reflecting a wider diversity in the carbon sources sustaining local food webs. Thus, combined differences in juvenile diet and food web structure at each location resulted in much-reduced local isotopic niche overlaps between the two species (from 27% in Suape to 57% in Santa Cruz). These results have important implications for resource and ecosystem management in North-Eastern Brazil and call for systematic cross-site comparisons when evaluating fish ecology and resource partitioning within estuarine systems.

Keywords: Marine fish, Trophic relationships, Stomach content, Stable isotope analysis, Carbon, Nitrogen.

3.2. Introduction

Estuaries are highly exploited ecosystems a host a high number of fish species (Blaber 1997, Vasconcelos et al. 2015), many of which colonize them during the juvenile stage seeking for protection and favorable growth conditions (Nagelkerken et al. 2000, Beck et al. 2001, Dahlgren et al. 2006). Although knowledge on the use of estuaries by tropical fishes has significantly grown in recent years (Blaber 2013), the information available concerns only a few estuarine systems so further research is needed to assess the actual value of tropical estuaries as fish juvenile habitats (Blaber & Barletta 2016). Indeed, a variety of biological and physical factors might affect the physiology of fish and their resource use in estuaries (Blaber 2007). For instance, estuaries' morphology and spatiotemporal dynamics modulate not only fish diversity (França et al. 2012, Vasconcelos et al. 2015), but also food web structure and composition (Harrison & Whitfield 2006, 2012, Silva-Júnior et al. 2017), resource availability (Doi et al. 2009, Hoeinghaus et al. 2011, Boucek & Rehage 2013) and seascape connectivity (Sheaves 2009, Ogden et al. 2014). The degree to which each species benefits from available food resources in these complex environments may also influence the survival and fitness of fish juveniles (Le Pape & Bonhommeau 2015, Yeung & Yang 2017, Hiraoka et al. 2019). Therefore, investigating species' resource use in contrasted estuarine juvenile habitats can not only improve the knowledge and understanding of their ecology (*e.g.* Stevens et al. 2018) but also help defining local management strategies (Sheaves et al. 2015). This is particularly true in tropical regions where the socio-economic demand for coastal fish resources is growing (Barlow et al. 2018, FAO 2018) and where environmental awareness is only just emerging (Mitra & Zaman 2016).

Species ecological niches play a central role in defining available resource use and interspecific interactions at the community level (Van Valen 1965, Ross 1986). Among the many facets of the ecological niche, the trophic niche is perhaps the easiest to evaluate (Ross 1986). It can be studied using empirical methods like stomach content analysis (SCA), which provides a snapshot of the items ingested by the individuals (Hyslop 1980, Pinnegar & Polunin 2000), or through the use of natural tags such as stable isotope analysis (SIA). This latter approach, usually combines nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic ratios (Fry 2006) to provide an integrated image of the food resources assimilated by the individuals over periods of time ranging from a few weeks to a few months (Herzka 2005). The method relies on the assumption that the isotope ratios of an organism reflect, in a predictive way, those of its food sources (Fry 2006). In general, the $\delta^{15}N$ is used as a proxy for organisms' trophic position in the food chain (Post 2002, Martínez Del Rio et al. 2009), while the $\delta^{13}C$ allows identifying the main organic matter source(s) supporting their growth (Fry 2006, Layman 2007). Combining SIA and SCA enables better resolution of dietary patterns and accurate identification of the food sources sustaining animal growth (Silveira et al. 2020). In this study, we applied these complementary methods to describe variations in diet and compare strategies of estuary resource use in the juveniles of two sympatric species of jacks along the North-Eastern coast of Brazil.

Jacks (*Caranx* spp.) are marine fish found both in inshore and offshore coastal environments (Figueiredo & Menezes 1980, Smith-Vaniz 2002). Although these large predators are neritic and reef associated when adult, some of them may use a mosaic of habitats along their life cycle and colonize inshore estuaries as juveniles (Smith-Vaniz 2002). This is the case for both the horse-eye jack (*Caranx latus*, Agassiz 1831) and the crevalle jack (*Caranx hippos*, Linnaeus 1766), two highly prized species with a widespread distribution in the Atlantic Ocean (Figueiredo & Menezes 1980). In Brazil, *C. latus* and *C. hippos* represent almost 75% of the national landings for jacks, with more than 6.000 tons fished annually between 2009 and 2011 (MPA 2011). Yet, little is known about their life cycle and their ecology at the juvenile stage. The yearlings of the two species are found in a broad range of inshore and coastal habitats along the Brazilian coast (Figueiredo & Menezes 1980, Paiva & Araújo 2010), and information regarding their trophic ecology in estuaries is particularly scarce (*e.g.* Vasconcelos Filho et al. 2010, Medeiros et al. 2017).

Differences in resource use among juvenile habitats may affect fish early growth and body condition (*e.g*. Isnard et al. 2015) and modulate recruitment success in exploited species (Gillanders et al. 2015). To avoid competition for food and optimize energy acquisition, sympatric species usually tend to partition resources at multiple scales (Schoener 1974, Losos 2000). However, *C. latus* and *C. hippos* not only have similar body shapes and lengths, but they are also both reported to feed mainly on fish and crustaceans (Hofling et al. 1998, Smith-Vaniz 2002, Vasconcelos Filho et al. 2010). Therefore, they might have similar uses of estuarine resources and their co-occurrence in certain estuaries might result in an interspecific competition for food, with potentially high consequences in terms of local fisheries production. To investigate this, we assessed variations in the diets and isotopic niches of their juveniles among three neighboring Brazilian estuaries with contrasted morphological and biological features, and where the relative densities for the juveniles of the two species differ markedly (Paiva & Araújo 2010, Silva-Júnior et al. 2017), which allowed exploring whether their feeding strategies change under different degrees of potential competition.

3.3. Material and Methods

3.3.1. Study area

The three tropical estuarine systems selected for this work (Santa Cruz, Suape and Sirinhaém, Fig. 1) are located in the western South Atlantic Ocean, along the coast of the Pernambuco state, on the North-Eastern coast of Brazil. In this area, the climate is sub-tropical, with annual temperatures ranging from 18 to 32ºC, around an annual mean of 24ºC (CPRH 2003, 2003a). Rainfalls occur all year round along the shore but they are more intense in the late autumn and winter (May to August). The driest period of the year is late spring and early summer (from October to December) due to the northward displacement of the Intertropical Convergence Zone (ICTZ) in the Atlantic and the occurrence of stronger southeast trade winds (CPRH 2003, 2003a, Hounsou-gbo et al. 2015). The local climate is influenced both by seasonal (displacement of the ICTZ) and by inter-annual (*e.g.* El Niño Southern Oscillation – ENSO) meteorological phenomena, which results in a highly variable weather and precipitation patterns among years (Hastenrath 2012).

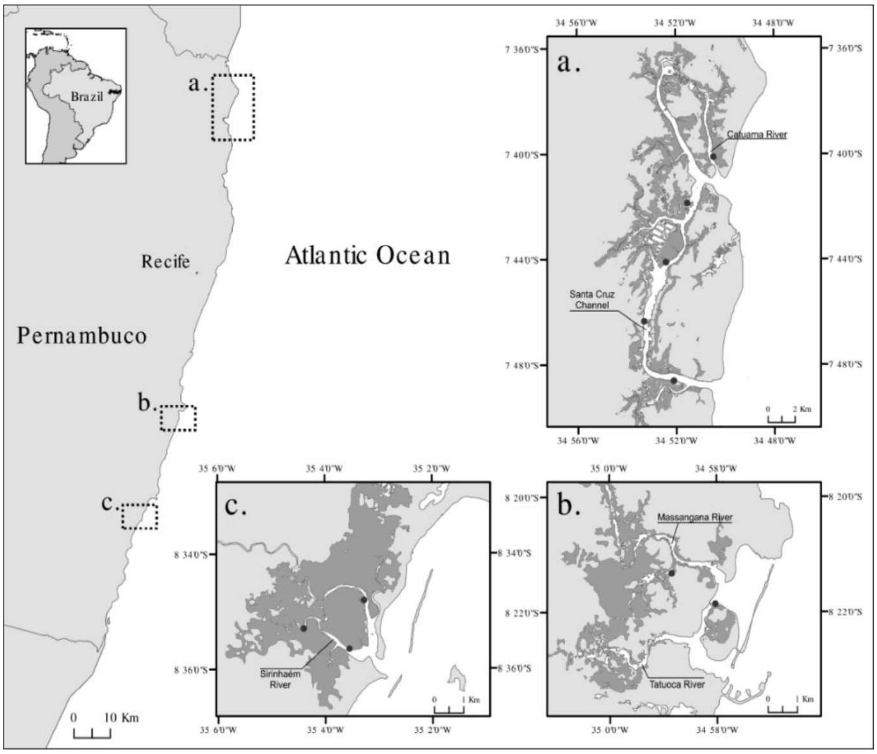


Figure 1 Study area in northeastern Brazil, showing sampling locations within the Santa Cruz (a.), Suape (b.) and Sirinhaém (c.) estuaries (black dots). For each estuary, mangrove cover is indicated in dark grey.

Although relatively close to each other, the Santa Cruz, Suape and Sirinhaém estuaries exhibit distinct morphological and biological features and are subject to different freshwater inputs and degrees of anthropogenic pressures (Table 1). Located in the north of the Pernambuco state, the estuarine complex of Santa Cruz is the largest estuary of the three, and one of the most important fishery ground of the state (Medeiros et al. 2001). It consists in a shallow U-shape channel that receives continental inputs from six rivers (draining three hydrological basins) and is connected to the sea by two large entrances (Silva et al. 2011). Because the seawater inflow is high, the estuary is under a strong marine influence (Flores Montes et al. 1998, Figueiredo et al. 2006). Furthermore, the reduced current velocity in the inner part of the main channel results in a predominance of muddy substrates along the estuary (CPRH, 2003), where hypersaline conditions may occur during the driest months of the year (Medeiros & Kjerfve 1993). The local fauna comprises a large number of marine and estuarine invertebrates and fish that use this estuary at different stages of their life (Vasconcelos-Filho & Oliveira 1999). The fish assemblage is diverse, with numerous species with distinct morphologies, as illustrated by the presence of bottom-associated species like gobies (Silva-Júnior et al. 2017, Ferreira et al. 2019).

Table 1 Summary of morphological characteristics, environmental settings and anthropogenic activities of the three estuaries (Santa Cruz, Suape and Sirinhaém) along the coast of Pernambuco, North-Eastern Brazil

Characteristics	Estuary		
	Santa Cruz	Suape	Sirinhaém
Type	Ria	Coastal lagoon	Coastal plain
Human pressures	Aquaculture, agricultural, industrial and domestic waste	Industrial harbour, industrial and agriculture waste	Industrial and domestic waste
Vegetated area (km^2)	48.0	23.1	17.0
Water surface area (km^2)	25.5	6.6	1.7
Mean depth (m)	3.0	3.1	2.6
Max. depth (m)	20	5	5
N of marine entrances	2	1	1
Width of marine entrances (km, mean and range)	0.9 (0.5 - 1.3)	0.3	0.4
Pelagic productivity (mgCm^{-3}h^{-1})	14.7	2.0	34.2
Temperature (°C, mean± SD)	28.5 ± 1.1	27.1 ± 1.1	27.2 ± 2.4
Salinity (mean± SD)	31.1 ± 2.9	17.7 ± 2.4	9.5 ± 3.6
Pluviometry (mm, mean± SD)	1517 ± 122	1869 ± 367	2053 ± 699
References	Medeiros & Kjerfve 1993, Medeiros et al., 2001, Neuman-Leitão et al. 2001, CPRH 2003, 2003a, Borges 2011, Silva 2009, Guimarães et al. 2010, Silva et al. 2011, APAC 2019, Gonzalez et al. 2019, Silva et al. 2019		

Type, geomorphological classification on the type of estuary according to Pritchard's classification. Human pressure, existent anthropogenic activity with potential impact on the estuary. Vegetated area, area of mangrove cover vegetation. Max. depth, maximum depth during the high tide, usually near the estuary's entrance. N of marine entrances, number of connections to the sea. Pelagic productivity, mean annual phytoplankton productivity. Temperature, water surface temperature. Pluviometry, annual rainfall between 2014 and 2018.

The estuaries of Suape and Sirinhaém, both situated in the south of the Pernambuco state, are smaller (Table 1). Because the annual rainfall in the state increases southwards (CPRH 2003a), they receive higher freshwater inputs, especially Sirinhaém (Table 1). The Suape estuary is formed by two rivers, which flow into a shallow brackish lagoon with limited connection to the sea. It can be classified as euryhaline and exhibits the lowest primary productivity of the three estuaries studied (Silva et al. 2019, Table 1). The estuary of Sirinhaém is the smallest estuary studied, but that with the highest percentage of mangrove cover (Table 1). Located within two marine protected areas (CPRH 2003a), it gathers a variety of interconnected lagoons and channels that spread on the shallow flood plain around the main bed of the Sirinhaém river, which constitutes its sole connection to the sea (CPRH 2003a). This particular configuration intensifies the effects of the watershed dynamics, with salinities ranging from nearly 0 at low tide to up to 30 at high tide (Silva et al. 2009). The fish assemblages of the Sirinhaém and Suape estuaries are similar, with a common dominance of pelagic species (Bezerra Junior et al. 2011). Moreover, both estuaries exhibit much lower densities of *C. hippos* than those observed in Santa-Cruz (Silva-Júnior et al. 2017).

3.3.2. Fish sampling and diet composition

The *Caranx latus* and *C. hippos* juveniles used for this work were captured over five successive years (2015-2019), using both beach seines (20 x 1.9 m, mesh 20 mm), trawled along the river banks, and block nets (350 x 2.9 m, mesh 70 mm) set close to mangrove creeks. Although sampling design was not even among years and estuaries, sampling surveys in each estuary were carried out for all months and always included the same locations (Fig. 1). To account for potential changes in feeding habitat preferences according to the season or increasing fish size, juvenile jacks were systematically sampled in all the main types of habitat they occupy in each estuary. These habitat types were determined according to local fishermen's knowledge on *Caranx* sp. occurrence in the estuaries and confirmed by prior exploratory surveys. They comprise main foraging grounds for the two species, within and outside the shore-fringed mangroves that predominate in the three estuaries. In all three estuaries, both the mudbanks below fringing mangrove and the adjacent river banks, of maximum 1.5 m depth, were sampled at low tide. However, in the larger and deeper Santa Cruz estuary, juvenile jacks were also systematically collected within the central channel of the estuary, where water depth remains above 5 m at low tide. On the river banks and in the Santa Cruz central channel, sediments are composed of a mix of thin sand and silt, and mangrove litter and macroalgae occasionally found on the bottom. Depending on the size and geomorphology of the estuary, fish juveniles were collected at 2 to 5 sites per habitat type for each sampling date. This allowed covering most of the spatiotemporal variability in juvenile distribution, and associated diet variation, between and within estuaries for the two species.

Upon collection, all juveniles were identified following specific literature (Figueiredo & Menezes 1980, Smith-Vaniz 2002), measured (standard length – SL in mm) and stored frozen until further analysis. Their stomach contents were assessed under a stereomicroscope until 70 non-empty stomachs per species and estuary could be gathered. As densities for the two jack species are rather low in estuaries during the wetter months of the year (Vilar et al. 2011, Silva-Júnior et al. 2017, da Silva et al. 2018), fish from different years had to be pooled to reach a minimum number of 10 non-empty stomachs for both the dry (September to March) and the rainy (April to August) seasons in the area (CPRH 2003, 2003a), and a maximum of 30 individuals per year for each estuary. Prey items in all stomachs were identified to the lowest taxonomic level possible, depending on their degree of digestion. All identified prey items were counted and weighed (g) and well-preserved ones, *i.e.* those only slightly digested, were measured (total length, in mm).

For both species, global diet composition was characterized using the frequency of occurrence (F_i) and the relative percentage in number (N_i) and in weight (W_i) of each prey item. F_i corresponds to the number of individual stomachs containing the prey item i divided by the total number of stomachs containing food. N_i and W_i represent the relative number or weight of the prey item i divided by the total number or total weight of prey in the stomachs, respectively. In order to account for the uncertainty associated to these indexes and provide a confidence interval (95%) for each prey item, a bootstrap procedure based on 5000 re-sampling trials was used (Tirasin & Jorgensen 1999). The importance of each prey item in the diet was estimated using the alimentary coefficient (Q) proposed by Hureau (1970):

$$Q = N_i \text{ x } W_i.$$

According to Hureau (1970), prey items should be considered preferential when $Q \geq 200$, secondary when $20 \leq Q < 200$, and occasional ($Q < 20$). All dietary indexes were calculated both using major taxonomic groups (*e.g.* Teleostei) and applying the lowest possible identification levels, down to family.

3.3.3. Stable isotope analyses (SIA)

For each species, 10 to 30 juveniles from each estuary were selected for SIA. As the minimum size for both species in our samples was 35 mm SL, these fish were chosen to measure at least 60 mm in size (SL) to ensure that the isotopic compositions from their local prey were incorporated within the tissue at the time of capture (Herzka 2005). Fish were collected in 2015, 2018 and 2019 during both the dry and the rainy seasons (APAC 2019), so their isotopic ratios should accurately reflect the temporal (inter and intra-annual) variabilities in fish diet and food web composition at each estuary. Basal estuarine organic matter sources, *i.e.* the main benthic algae (*Sargassum* spp., *Ulva* spp., *Gracilaria cervicornis*), the microphytobenthos, the mangrove trees (rotten leaves from *Rhizophorae mangle*), and the organic matter present in the surface sediment (SOM) and in the water column (POM), were collected in each estuary in 2015, both during the dry (January to March) and the rainy (July to September) seasons (APAC 2019). Mangrove tree leaves and algae were collected manually at low tide. POM was obtained by filtering water (0.5 – 1 L) on precombusted fiberglass filters (0.75 µm), whereas SOM was sampled from the 2 mm surface layer of the sediment. Benthic microphytobenthos was collected from the sediment surface at low tide and extracted in the laboratory following Riera & Richard (1996). Other potential organic matter sources for the three estuaries studied, such as marine POM and SOM from the adjacent coastal zone were also collected, at two locations: one near the entrance of the Santa Cruz estuary and one further south, near the mouths of the Sirinhaém and Suape estuaries.

For fish specimens, white muscle was extracted and rinsed with distilled water while, for organic matter sources, samples were analyzed whole. Samples were dried in an oven at 60°C for 48 hours and ground into a fine powder with a mortar and pestle. For all POM and SOM samples, a subsample was acidified to remove the inorganic carbon prior $\delta^{13}C$ analysis, while the remaining material was used directly for $\delta^{15}N$ analyses (Pinnegar & Polunin 1999). Carbon and nitrogen isotope ratios were analyzed with a mass spectrometer (Thermo Delta V+) coupled to an element analyzer (Thermo Flash 2000, interface Thermo ConFio IV) at the Pôle de Spectrométrie Océan (PSO - IUEM, Plouzané, France). Carbon and nitrogen isotopic ratios are reported as $\delta^{13}C$ and $\delta^{15}N$ values (in ‰), respectively, derived from the formula:

$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) -1] \times 10^3$$

where δX corresponds to $\delta^{13}C$ or $\delta^{15}N$ and R to the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and a known standard, for carbon or nitrogen, respectively. The standards used for $\delta^{13}C$ and $\delta^{15}N$ were the Pee Dee Belemnite (PDB) limestone and atmospheric nitrogen, respectively. The analytical precisions of the analyses, monitored through the repeated analysis (every six samples) of an internal standard (Thermo – Acétanilide), was of 0.10‰ and 0.07‰ for carbon and nitrogen isotopes, respectively.

3.3.4. Data analysis

All statistical analyses were made with the R software (R Core Team 2019), using the packages *vegan* (Oksanen *et al.* 2017), *boot* (Canty & Ripley 2020) and *SIBER* ("Stable Isotope Bayesian Ellipses in R" (Jackson & Parnell 2016)). Only the prey items observed more than once within the stomachs analyzed were kept for SCA data analyses.

Because body size modulates the type and size of the prey consumed by an organism (Shelton et al. 1977), potential differences in the size (SL in mm) of the fish used for SCA were investigated, among estuaries and between species. Kruskal-Wallis tests were used for this, as the assumptions of data normality and homoscedasticity were not met. Then, the relationship between fish size and prey length was assessed for each species using covariance analyses (ANCOVA). Differences in prey length according to the species and the sampling location were also tested, using Kruskal-Wallis tests as data did not meet the assumptions of normality and homoscedasticity. Lastly, differences in diet composition according to fish size were evaluated for both *C. latus* and *C. hippos*, using two non-parametric permutational multivariate analyses of variance (PERMANOVA), one per species. The PERMANOVA procedure performs a sequential test of terms based on distance matrices and allows for hypotheses testing between predictor variables (Anderson, 2001).

PERMANOVA tests were also applied to investigate differences in diet composition between species (*C. latus*/ *C. hippos*), among estuaries (Santa Cruz/ Suape/ Sirinhaém) and between the two species in each estuary. *Post-hoc* comparisons were applied only for variables with a significant effect on the diet ($p < 0.05$). The distance matrices were based on Bray-Curtis dissimilarity computed from $log(x+1)$ transformed data of prey relative weight for each individual fish. In addition, two dietary matrixes were used separately to assess the effect of prey identification on the analyses: one including all prey items and the other with only the prey items identified at least to the order level.

Potential differences in the size (SL in mm) of the juveniles used for SIA and in their isotopic ratios (both for carbon and for nitrogen, separately) were tested between locations and fish species using separate ANOVA models. *Post-hoc* Tukey's tests were applied on variables with significant effects in the isotopic composition of jacks ($p < 0.05$). The trophic positions of the juveniles of the two jack species were compared by evaluating the areas occupied by their isotopic niches, computed using the corrected standard ellipses area (SEA_C) method, which measures the space occupied by a species in a bi-dimensional plane, here $\delta^{13}C$ *vs*. $\delta^{15}N$ (Jackson et al. 2011). This approach is less sensitive to variations in sample size than other conventional metrics (Jackson et al. 2011, Syväranta et al. 2013), and provides insightful information on predators' resource use by incorporating both the variance in the isotopic ratios of local basal food sources and the difference in the energy pathways that their prey rely on (Bearhop et al. 2004). Indeed, although a considerable part of the variation in predator isotopic niches can be attributed to diet, it may also reflect differences in prey isotope ratios and in the organic matter sources sustaining food webs (Newsome et al. 2007, Flaherty & Ben-David 2010). Therefore, the percentage of overlap between the isotopic niches (SEA_C) of the two species was used to measure the degree to which they may rely on similar food resources. In order to account for the uncertainty associated to SEA_C overlaps, a Bayesian approach was applied to assess the mean and 95% credible intervals ($CI_{95\%}$) of isotopic niche overlaps between the two species (Jackson et al. 2011).

3.4. Results

Although the total sample of juvenile jacks gathered over the five years of survey was more than satisfactory (n = 439 of SL = 35 - 157 mm), the numbers and the sizes of the juveniles varied between species and estuaries. For example, while total abundances were comparable at all locations for *C. latus*, *C. hippos* juveniles were 2- to 3-fold less common in Sirinhaém and Suape (Fig. 2). As a result, the total number of juveniles collected was higher for *C. latus* (*n* = 266) than for *C. hippos* (*n*= 173). In turn, although the juveniles of *C. latus* (SL = 105 ± 25 mm) were consistently bigger ($p < 0.001$) than those of *C. hippos* (SL = 88 ± 26 mm), patterns of size variation between estuaries were similar for the two species, with consistently bigger juveniles ($p < 0.001$) in Suape and smaller ones ($p < 0.001$) in Sirinhaém (Fig. 2). These differences were considered during fish sub-sampling for both stomach content analysis and SIA, in order to reduce bias in our conclusions and provide a realistic overview of the global trophic ecology of the two species.

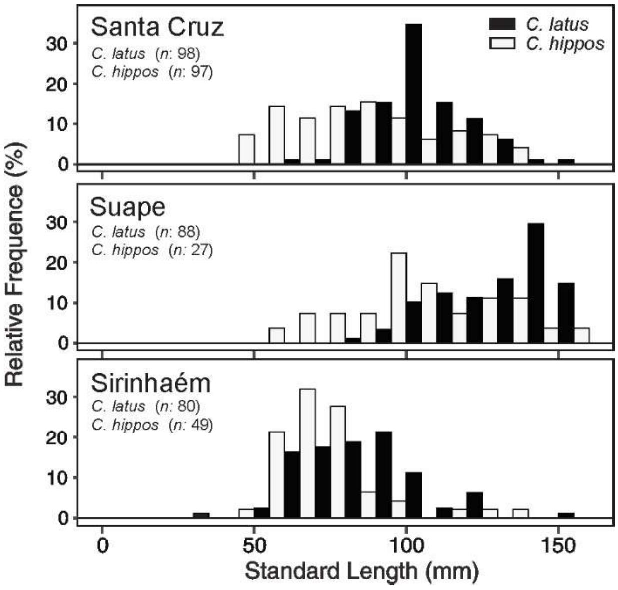


Figure 2 Number of individuals (*n*) and length frequency distributions of the *Caranx latus* and *C. hippos* juveniles sampled in the estuaries of Santa Cruz, Suape and Sirinhaém.

Among the 394 fish selected for stomach content analysis, few had empty stomachs (33% for *C. latus* and 6% for *C. hippos*). Relative numbers and size distributions in the 338 remaining ones (207 *C. latus* and 131 *C. hippos*) were similar to those observed in the total catches, with slightly higher mean SL values for *C. latus* than for *C. hippos* in every estuary, and larger juvenile sizes in Suape for both species

(Table 2). Muscle samples from 112 juvenile fish (60 *C. latus* and 52 *C. hippos*) were analyzed in SIA (Table 2). To allow for muscle signature to reflect the diet in the estuaries, the minimum size of the fish selected for the SIA was 65 mm (SL). Altogether, the distribution of SIA juvenile sizes was similar for the two species ($p = 0.905$), however it varied between estuaries ($p < 0.001$), reflecting the differences in sizes observed in the field. As for SCA, this sub-sample contained a larger number of individuals from Santa Cruz in order to reflect the higher abundance of juvenile jacks at this estuary.

Table 2 Number of individuals (n), their mean standard length (SL ± S.D.) and isotopic ratio mean values (± S.D.) for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of *Caranx latus* and *C. hippos* analysed for stomach content and stable isotopes compositions, in the three estuaries (Santa Cruz, Suape and Sirinhaém). Minimum and maximum values of each variable are between brackets.

Estuary	Species	Stomach content analysis†		Stable isotopes analysis			
		n	SL (mm)	n	SL (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Santa Cruz	*C. latus*	70	98 ± 17 [50 – 135]	30	109 ± 18 [80 – 138]	-18.85 ± 1.59 [-23.4 – -16.5]	10.89 ± 1.09 [8.6 – 13.0]
	C. hippos	70	82 ± 24 [36 – 131]	30	111 ± 17 [82 – 142]	-18.94 ± 1.66 [-22.3 – -16.3]	11.61 ± 0.87 [10.4 – 13.7]
Suape	*C. latus*	67	129 ± 18 [82 – 157]	15	113 ± 16 [86 – 141]	-18.65 ± 1.45 [-21.9 – -16.6]	9.38 ± 0.73 [8.0 – 10.2]
	C. hippos	20	112 ± 29 [49 – 156]	10	114 ± 29 [65 – 145]	-20.25 ± 2.77 [-23.6 – -15.7]	10.28 ± 1.00 [8.8 – 12.0]
Sirinhaém	*C. latus*	70	79 ± 16 [35 – 116]	15	90 ± 20 [70 – 124]	-20.07 ± 1.08 [-24.4 – -15.9]	9.34 ± 1.16 [8.2 – 11.6]
	C. hippos	39	73 ± 12 [47 – 98]	12	87 ± 27 [65 – 138]	-19.64 ± 2.39 [-23.6 – -16.1]	10.22 ± 0.86 [8.7 – 11.7]

† Fish with non-empty stomachs only.

3.4.1. Diet composition

Overall, diet composition was not significantly different between the two jack species ($p = 0.089$) which both mainly ate fish and crustaceans ($Q > 1205$, Table 3). All other prey items were found to be occasional ($Q < 20$), irrespective of the species (Table 3). However, when considering only the prey items identified to at least the order level, the two species did show significant differences in diet composition ($p = 0.010$). Although fish remains in the stomachs were often too digested to be identified, fish prey belonged to at least nine different families for *C. latus*; six for *C. hippos* (Table 3). Fish (Teleostei) were the main prey of the juveniles of *C. latus* ($Q = 3252$), whereas *C. hippos* fed on fish ($Q = 1205$) and crustaceans (Q

= 2537) in similar proportions (Table 3). Fish dominated the diet of both species in terms of occurrence and weight, but crustaceans prevailed in number in the diet of *C. hippos* (Table 3). For both species, most of the fish prey identified were Gobiidae (F_i = 19.0 to 23.6; N_i = 4.3 to 7.5; W_i = 33.2 to 39.9%), but their consumption was higher in *C. latus* (F_i = 23.6; N_i = 7.5; W_i = 39.9%). Decapods, in particular Penaeidae shrimps, were the main crustacean prey found in the stomachs of the juveniles of the two species (Table 3). However, mysids also contributed significantly to their diet, especially for *C. hippos*, in which they were the most abundant crustacean prey (N_i = 36.6%).

Overall diet composition was found to be similar across the full size-range of the juveniles studied irrespective of the species (*C. latus*: $p = 0.089$; *C. hippos*: $p = 0.193$) and, when considering only the prey items identified to at least the order level, significant differences in diet according to fish size were found solely for *C. latus* ($p = 0.034$). Even then, only a slightly higher contribution in weight of fish prey was observed in *C. latus* juveniles larger than 60 mm (SL). The standard length of the juveniles did not have any significant effect on the sizes of their two main prey, namely fish (adjusted $r^2 = 0.01$, $p = 0.591$) and shrimps (adjusted $r^2 < 0.01$, $p = 0.376$). The size of these latter were similar in all estuaries (Fish, $p = 0.292$; Shrimps, $p = 0.839$) and for both jack species (Fish, $p = 0.184$; Shrimps, $p = 0.515$) (Supplementary Fig. S1).

Table 3 Frequency of occurrence (F_i), relative abundance (N_i) and weight (W_i) and alimentary coefficient (Q) of prey items of *Caranx latus* and *Caranx hippos* in North-Eastern Brazil estuaries. Dietary indexes estimate for major taxonomic groups are shown in bold. Confidence interval estimates (95%) for dietary indexes are displayed between square brackets. The number of fish specimens (n) and their mean standard length (SL, ±SD) are presented for each species.

Item	Species							
	Caranx latus (n = 207; 102±27 mm)				*Caranx hippos* (n = 131; 84±25 mm)			
	F_i (%)	N_i (%)	W_i (%)	Q	F_i (%)	N_i (%)	W_i (%)	Q
ALGAE	**12.08** **[7.7 – 16.9]**	**4.19** **[2.4 – 6.6]**	**0.29** **[0.1 – 0.7]**	**0.82**	**2.90** **[0.8 – 6.1]**	**0.86** **[0.1 – 2.2]**	**0.18** **[0 – 0.6]**	**0.14**
Chlorophyta (Unidentified)	0.97 [0 – 2.4]	0.40 [0 – 1.1]	0.01 [0 – 0.1]	0.01	-	-	-	-
Unidentified Algae	11.11 [7.2 – 15.5]	4.87 [2.6 – 7.9]	0.28 [0.1 – 0.7]	1.36	3.05 [0.8 – 6.1]	1.00 [0.1 – 2.6]	0.18 [0 – 0.6]	0.18
FORAMINIFERA (Unidentified)	**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**-**	**-**	**-**	**-**
	0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01	-	-	-	-
NEMATODA (Unidentified)	**5.31** **[2.4 – 8.7]**	**1.11** **[0.5 – 1.8]**	**<0.01**	**0.01**	**2.90** **[0.8 – 61]**	**0.48** **[0.1 – 1.1]**	**<0.01**	**0.01**
	5.31 [2.4 – 8.7]	1.39 [0.6 – 2.3]	<0.01	0.01	3.05 [0.8 – 6.1]	0.56 [0.1 – 1.3]	<0.01	0.01
BIVALVIA (Unidentified)	**0.48** **[0 – 1.4]**	**0.32** **[0 – 1.0]**	**<0.01**	**0.01**	**0.72** **[0 – 2.3]**	**0.10** **[0 – 0.4]**	**<0.01**	**0.01**
	0.48 [0 – 1.4]	0.40 [0 – 1.3]	<0.01	0.01	0.76 [0 – 2.3]	0.11 [0 – 0.4]	<0.01]	0.01
GASTROPODA (Unidentified)	**2.90** **[1.0 – 5.3]**	**1.26** **[0.3 – 2.6]**	**0.01** **[0 – 0.1]**	**0.01**	**-**	**-**	**-**	**-**
	2.90 [1.0 – 5.3]	1.59 [0.3 – 3.3]	0.01 [0 – 0.1]	0.01	-	-	-	-

Table 3 Continued.

POLYCHAETA (Unidentified)				**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**1.45** **[0 – 3.8]**	**0.57** **[0 – 1.7]**	**0.01** **[0 – 0.1]**	**0.01**
				0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01	1.53 [0 – 3.8]	0.67 [0 – 1.9]	0.01 [0 – 0.1]	0.01
OLIGOCHAETA (Unidentified)				**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**2.17** **[0 – 17.1]**	**0.29** **[0 – 0.7]**	**<0.01**	**0.01**
				0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01	2.29 [0 – 5.3]	0.33 [0 – 0.9]	<0.01	0.01
CRUSTACEA				**49.28** **[42.5 – 56.0]**	**26.07** **[19.7 – 33.3]**	**23.30** **[14.2 – 34.6]**	**705.34**	**60.87** **[51.9 – 68.7]**	**65.97** **[51.7 – 75.4]**	**38.22** **[22.8 – 60.3]**	**2537.20**
Cirripedia (Unidentified)				0.48 [0 – 1.4]	0.60 [0 – 2.0]	<0.01	0.01	0.76 [0 – 2.3]	0.78 [0 – 2.9]	<0.01	0.01
Copepoda (Unidentified)				1.45 [0 – 3.4]	1.79 [0 – 4.6]	<0.01	0.01	7.63 [3.1 – 12.2]	2.12 [0.8 – 2.1]	<0.01	0.01
Malacostraca	Decapoda	Brachyura	Portunidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.10 [0 – 0.4]	0.01	1.53 [0 – 3.8]	0.22 [0 – 0.6]	0.05 [0 – 0.2]	0.01
			Sesarmidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.05 [0 – 0.2]	0.01	-	-	-	-
			Unidentified Brachyura	0.97 [0 – 2.4]	0.70 [0 – 2.1]	0.14 [0 – 0.5]	0.09	1.53 [0 – 3.8]	0.33 [0 – 1.0]	0.32 [0 – 1.2]	0.10
		Caridea	Alpheidae	4.83 [1.9 – 8.2]	1.99 [0.7 – 3.9]	1.56 [0.1 – 4.7]	3.10	1.53 [0 – 3.8]	0.22 [0 – 0.6]	1.22 [0 – 4.8]	0.26
			Unidentified Caridea	2.90 [1.0 – 5.3]	0.99 [0.7 – 2.0]	1.38 [0.3 – 2.9]	1.36	-	-	-	-
		Dendrobranchiata	Aristeidae	0.48 [0 – 1.4]	0.20 [0 – 0.7]	0.06 [0 – 0.2]	0.01	-	-	-	-
			Penaeidae	11.59 [7.2 – 15.9]	4.87 [2.6 – 7.7]	14.60 [7.8 – 23.5]	71.10	20.61 [13.7 – 27.5]	8.37 [3.8 – 15.4]	19.26 [9.9 – 33.3]	161.20
		Unidentified Decapoda		15.46 [10.6 – 20.3]	8.84 [4.6 – 15.0]	4.86 [2.2 – 8.6]	42.96	23.66 [16.8 – 31.3]	15.07 [7.9 – 15.4]	10.56 [4.0 – 22.2]	159.13
	Isopoda (Unidentified)			2.90 [1.0 – 5.3]	0.79 [0.2 – 1.6]	0.01 [0 – 0.1]	0.01	3.82 [0.8 – 7.6]	0.56 [0.1 – 1.2]	0.06 [0 – 0.2]	0.03

Table 3 Continued.

	Mysida (Unidentified)		1.93 [0.5 – 3.9]	0.79 [0.1 – 1.7]	0.01 [0 – 0.1]	0.01	7.63 [3.1 – 12.2]	36.61 [12.7 – 53.9]	4.67 [0.9 – 11.1]	170.96
	Stomatopoda (Unidentified)		-	-	-	-	0.76 [0 – 2.3]	0.11 [0 – 0.4]	0.03 [0 – 0.1]	0.01
Ostracoda (Unidentified)			4.35 [1.9 – 7.2]	2.78 [0.8 – 5.6]	<0.01	0.01	1.53 [0 – 3.8]	0.56 [0 – 1.5]	<0.01	0.1
Unidentified Crustacea			14.98 [10.1 – 19.8]	8.34 [4.5 – 13.2]	0.90 [0.4 – 1.7]	7.50	9.92 [5.3 – 15.3]	9.49 [2.9 – 17.9]	2.61 [0.2 – 6.9]	24.76
HEXAPODA			**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**-**	**-**	**-**	**-**
Unidentified Insecta			0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01	-	-	-	-
VERTEBRATA			**84.06** **[78.8 – 88.9]**	**46.29** **[37.7 – 54.9]**	**75.10** **[63.5 – 84.4]**	**3252.60**	**71.74** **[64.1 – 79.4]**	**20.17** **[13.8 – 29.1]**	**60.13** **[37.9 – 76.0]**	**1205.15**
Thaliacea	Salpida	Salpidae	0.97 [0 – 2.4]	0.20 [0 – 0.5]	0.09 [0 – 0.3]	0.01	-	-	-	-
Teleostei	Clupeiformes	Clupeidae	1.93 [0.5 – 3.9]	0.70 [0.1 – 1.6]	2.61 [0 – 6.8]	1.82	2.29 [0 – 5.3]	0.89 [0 – 2.5]	7.18 [0 – 19.5]	6.39
		Engraulidae	4.35 [1.9 – 7.2]	1.59 [0.5 – 3.1]	2.46 [0.4 – 5.7]	3.91	3.05 [0.8 – 6.1]	0.45 [0.1 – 1.0]	4.43 [0.6 – 9.9]	1.99
	Gobiiformes	Eleotridae	1.45 [0 – 3.4]	0.30 [0 – 0.7]	0.44 [0 – 1.1]	0.13	0.76 [0 – 2.3]	0.11 [0 – 0.4]	0.90 [0 – 3.4]	0.09
		Gobiidae	23.67 [17.9 – 29.9]	7.55 [5.3 – 10.4]	39.99 [19.7 – 57.6]	301.92	19.08 [12.2 – 26.0]	4.35 [2.4 – 7.3]	33.28 [7.4 – 57.7]	144.76
	Perciformes	Carangidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.16 [0 – 0.6]	0.01	2.29 [0 – 5.3]	2.01 [0 – 5.9]	0.74 [0 – 2.6]	1.48
		Gerreidae	9.66 [5.8 – 14.0]	4.37 [2.0 – 7.8]	2.73 [0.6 – 6.0]	11.93	0.76 [0 – 2.3]	0.11 [0 – 0.4]	0.08 [0 – 0.3]	0.01
		Scianidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.24 [0 – 0.9]	0.02	-	-	-	-

Table 3 Continued.

Pleuronectiformes	Cynoglossidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.14 [0 – 0.5]	0.01	-	-	-	-
	Paralichthyidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.04 [0 – 0.2]	0.01	-	-	-	-
Unidentified teleostei		60.39 [53.6 – 67.1]	43.00 [32.2 – 53.6]	27.12 [18.2 – 39.0]	1166.18	54.20 [45.8 – 62.6]	14.96 [9.4 – 23.5]	14.40 [8.4 – 24.0]	215.2
DEBRIS		**29.47** **[23.7 – 35.7]**	**20.46** **[14.9 – 26.2]**	**1.30** **[0.3 – 3.2]**	**-**	**33.59** **[26.0 – 42.0]**	**11.64** **[7.2 – 18.3]**	**1.46** **[0.4 – 3.1]**	**-**
Plastic debris		19.81 [14.5 – 25.6]	13.90 [9.3 – 18.8]	<0.01	-	18.12 [12.2 – 25.2]	6.50 [3.5 – 10.8]	<0.01	-
Unidentified organic matter and sediment debris		14.98 [10.1 – 19.8]	6.56 [3.5 – 10.2]	1.30 [0.3 – 3.2]	-	18.84 [12.2 – 26.0]	5.07 [2.7 – 8.8]	1.45 [0.4 – 3.1]	-

The diet of both species varied according to the estuary, regardless the level of prey identification applied ($p < 0.002$). Specifically, differences between estuaries were found only for Suape (Suape – Santa Cruz: $p < 0.015$; Suape – Sirinhaém: $p < 0.027$). In this estuary, *C. hippos* presented the most different diet, composed mainly of fish prey ($F_i = 60.0$; $N_i = 33.8$; $W_i = 81.4\%$). The diets of the two species were similar between Santa Cruz and Sirinhaém, either when considering all prey items ($p = 0.060$) or only those identified to at lowest taxonomic level ($p = 0.204$). Moreover, interspecific differences in diet composition were only significant in Santa Cruz, independently of the level of prey identification applied ($p < 0.025$). In this estuary, Gobiidae fish prevailed in the diet of *C. latus* and decapod shrimps in that of *C. hippos* (Supplementary Table S1). Although the two species had similar overall diets in the two remaining estuaries (Suape: $p > 0.236$; Sirinhaém: $p > 0.113$), they presented slight spatial variations in their prey preferences. In Suape, the diet of the two species only differed in terms of the type of fish consumed, with higher contributions of Clupeidae and Engraulidae for *C. hippos*, and of Gobiidae and Gerreidae for *C. latus* (Supplementary Table S2) while, in Sirinhaém, significantly higher proportions of crustaceans (Penaeidae shrimps) were found in the diet of *C. hippos* than in that of *C. latus* (Supplementary Table S3).

3.4.2. Stable isotopes analysis

The juveniles from the two species had very variable $\delta^{13}C$ and $\delta^{15}N$ values irrespective of their estuary of capture, ranging from -24.36 to -15.73‰ and from 8.00 to 13.66‰, respectively (Table 2; Fig. 3). Due to this variability, $\delta^{13}C$ values were not significantly different among estuaries ($p = 0.088$) nor between species, with average values of -19.10 ± 1.82‰ for *C. latus* and -19.35 ± 2.10‰ for *C. hippos*. Differences in $\delta^{13}C$ values between the two species were not significant either within each given estuary ($p = 0.147$). Conversely, significant differences in $\delta^{15}N$ were found according to both the estuary ($p < 0.001$) and the species ($p < 0.001$). Indeed, although $\delta^{15}N$ values for both species did not differ significantly between Suape and Sirinhaém ($p = 0.790$; Fig. 3), they were consistently higher in Santa Cruz ($p < 0.001$). Similarly, although the $\delta^{15}N$ values of the two species were similar within each estuary ($p = 0.804$; Fig. 4), the juveniles of *C. hippos* exhibited higher $\delta^{15}N$ values in overall (11.03 ± 1.10‰) than those of *C. latus* (10.21 ± 1.21‰) due to differences in spatial distribution among them.

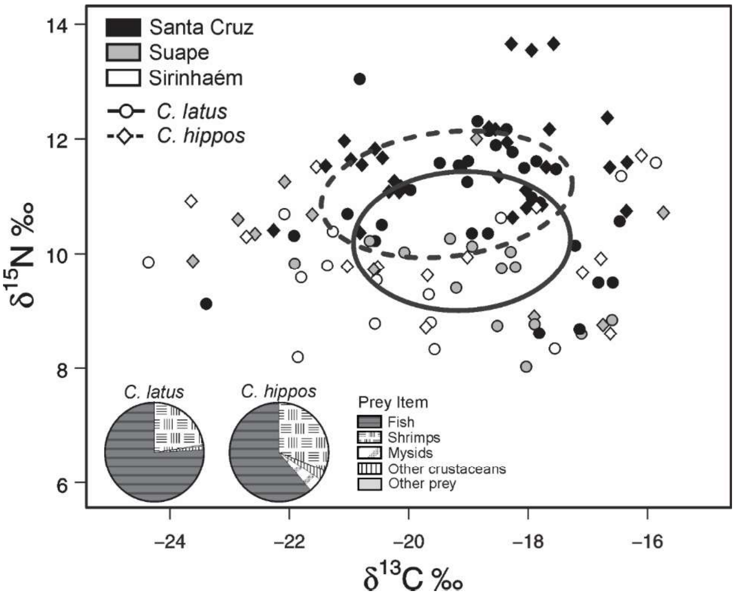


Figure 3 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of the two jack species, *Caranx latus* and *C. hippos*, in three contrasted estuaries of North-Eastern Brazil (Santa Cruz, Suape and Sirinhaém). Ellipses represent the isotopic niche (SEAc) for both species. Pie charts present the global diet of each species based on prey relative weights (W_i, see Table 3).

The global trophic (isotopic) niches of the two species were similar in size, with areas (SEA_C) of 7.3 and 7.0 ‰² for *C. latus* and *C. hippos* respectively. They largely overlapped, with 68.4% ($CI_{95\%}$ 54.1 – 82.6%) of their total area in common. However, both the SEA_C sizes and their overlaps varied according to the estuary (Fig. 3). Juvenile *C. latus* exhibited slightly wider isotopic niches than *C. hippos* in both Santa Cruz (SEA_C = 5.6‰² for *C. latus* and 4.5‰² for *C. hippos*) and Sirinhaém (SEA_C = 7.9‰² for *C. latus* and 7.1 ‰² for *C. hippos*), with high isotopic niche overlaps at both sites (57.5%, $CI_{95\%}$ 40.1 – 73.8%, in Santa Cruz and 54.3%, $CI_{95\%}$ 32.3 – 77.4%, in Sirinhaém). Conversely, in Suape, where the two species had the most different isotopic niches, niche area was much wider in *C. hippos* (SEA_C =9.5 ‰²) than in *C. latus* (SEA_C =2.7 ‰²). At this particular site, juvenile niche overlap between the two species was only of 27.13% ($CI_{95\%}$ 11.5 – 45.0%), but the isotopic niche area (SEA_C) of *C. hippos* covered up to 94.6% of that of *C. latus*. In the two remaining estuaries (Santa Cruz and Sirinhaém), the two species shared between 63 to 87% of their isotopic niche areas.

$\delta^{13}C$ and $\delta^{15}N$ values for the organic matter sources at the base of the food webs ranged from -29.25 to -14.50‰ and from -1.03 to 10.11‰, respectively, in the estuaries studied (Supplementary Table S4, Fig. 4). However, the variability in C and N isotopic ratios in the estuarine food webs depended greatly on the location: for example, the range in $\delta^{15}N$ values for organic matter source was the widest, but that in $\delta^{13}C$ values the lowest, in Santa Cruz (Fig. 4).

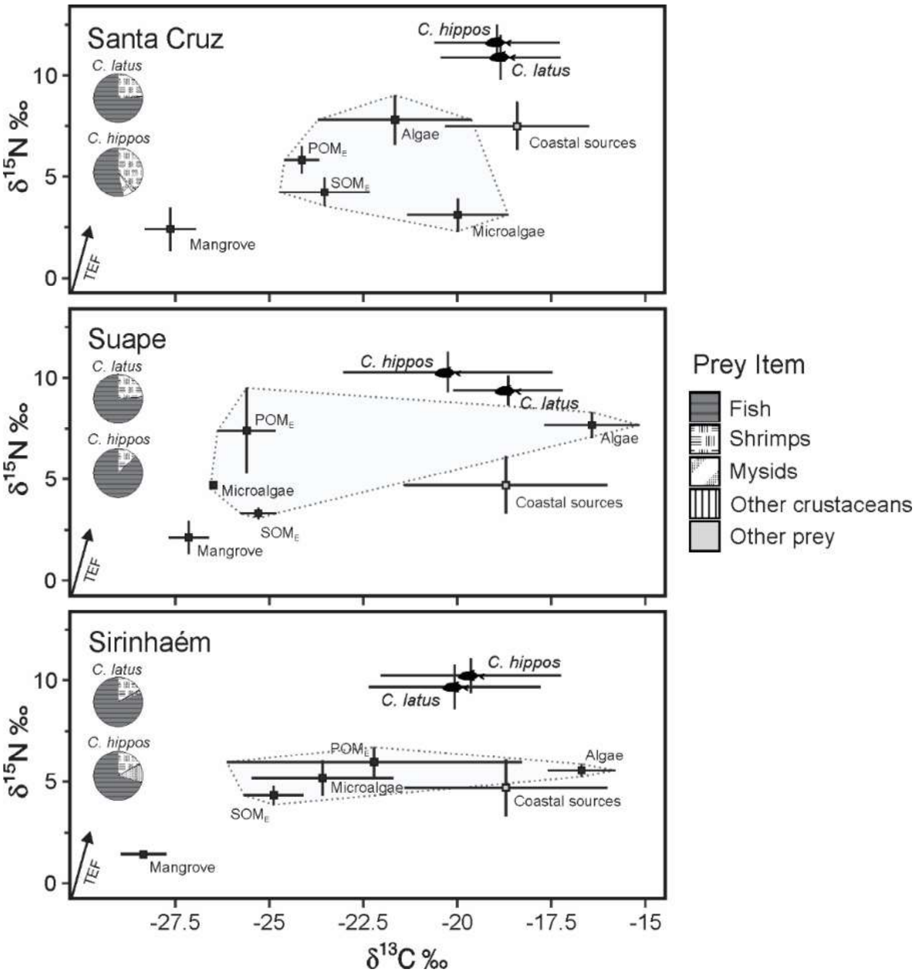


Figure 4 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios (mean ± standard deviation) of *Caranx latus* and *C. hippos* and the main available organic matter sources in three contrasted estuaries of North-Eastern Brazil (Santa Cruz, Suape and Sirinhaém). Isotopic signatures for the organic matter sources sampled in the estuaries and in adjacent coastal zones are represented by black and grey squares, respectively. Light grey polygons show the range of isotopic ratios of all estuarine organic matter sources except mangrove trees (*R. mangle*). Arrows in the bottom left corner of each panel illustrate the average isotopic enrichment per trophic level (+ 0.47 ± 1.23 ‰ for $\delta^{13}C$ and + 2.54 ± 0.11 ‰ for $\delta^{15}N$) usually applied in aquatic environments (Vander Zanden and Rasmussen, 2001; Vanderklift and Ponsard, 2003). Pie charts present the local diets of each species based on prey relative weights (W_i, see Supplementary Tables S1, S2 and S3).

3.5. Discussion

While differences in resource use within estuarine fish assemblages are thought to be largely modulated by species' functional traits (Albouy et al. 2011), closely related species are expected to display contrasted diets to allow their populations to co-exist in the wild (Ross 1986). However, very few cross-sites comparisons were carry out so far to investigate diet plasticity for closely related fish species co-occurring in diverse biotic and environmental settings (*e.g.*, Mariani et al. 2011). Our results bring new insights on this matter, by revealing site-related variations in the trophic ecology of the juveniles of two commercially important species from the *Caranx* genus with similar ecological features. Indeed, *Caranx latus* and *C. hippos* not only have similar shapes and growth trajectories (Viana et al. 2016), but also reproduce on deep reefs along the shelf (Heyman & Kjerfve 2008), and mostly colonize estuaries as juveniles, before moving to deeper waters when adults (Smith-Vaniz 2002). In the estuaries, their juveniles have been similarly reported to feed on a broad diversity of fish and crustaceans (Vasconcelos Filho et al. 2010, Medeiros et al. 2017), including key species in estuarine food webs (Ferreira 2018, Lira et al. 2018). The present study however showed that, although gobies and decapod shrimps are the main food items ingested by both species, *C. latus* juveniles have a more piscivorous diet than those of *C. hippos*. These benthic prey represent a substantial part of the diet of juvenile jack species in general (Blaber & Cyrus 1983, Smith & Parrish 2002, Figueiredo & Pessanha 2015, Medeiros et al. 2017) and are commonly eaten by other estuarine fish (Blaber 1986, Vasconcelos Filho et al. 2003, Lira et al. 2017). The juveniles of the two species were also found to largely prey on pelagic fish like engraulids and clupeids in the three estuaries studied, as already reported from visual census studies in these ecosystems (Cermak 2002). This indicates that, at least in estuaries, *C. latus* and *C. hippos* juveniles forage both at mid-water and directly above the substrate, feeding on a mix of pelagic and benthic prey.

3.5.1. Variation in food sources during juvenile life

Body size plays a central role in determining the type and size of the prey consumed by fish (Shelton et al. 1977), particularly in species like jacks that display schooling behaviors (Figueiredo & Menezes 1980, Graham & Castellanos 2005). Although a marked increase in piscivory has been reported for jacks at sizes above 200 mm SL (Blaber & Cyprus 1983, Sudekum et al. 1991, Smith & Parrish 2002), in this study, significant changes in diet composition due to increasing body size were only found for juvenile *C. latus*, and only consisted in small differences in the prey species ingested. The relatively low taxonomic precision for prey identification in the stomachs (particularly for small fish prey) may have hampered the power of our analysis. Yet, for both species, juvenile fish size did not seem to significantly be related to the size of the prey ingested. The diet of the two species thus seems to be fairly stable over the size range studied here (35 – 157 mm SL). However, as major morphological changes in fish take place between the post-larval and juvenile stages (Nunn et al. 2012), dietary shifts in the two species might occur in smaller fish, *i.e.* before and during estuary colonization (Cocheret de la Morinière et al. 2003, Usmar 2012). These dietary shifts can reflect either an increase in fish foraging ability as they grow, or changes in prey availability (Nunn et al. 2012). They probably also take place in larger fish, when they move towards offshore habitats (Cocheret de la Morinière et al. 2003).

Differences in environmental characteristics are also a major source of variation in the diet of fish, as they influences both the type and the availability of local food resources (Dineen et al. 2007, Jensen et al. 2008, Evangelista et al. 2014). Given the differences in food web structure and fish assemblages among the three estuaries studied, we expected the juveniles of the two species to display different food preferences and isotopic ratios among locations (Merigot et al. 2017, Silva-Júnior et al. 2017). However, although their prey preferences and isotopic niches varied from one estuary to the other, spatial differences in diet composition were surprisingly small, with only a greater consumption of fish (particularly of the Clupeidae and Engraulidae families) by *C. hippos* in Suape. As fish from different years and seasons were pooled in this work and because inter and intra-annual variations in food web composition and food availability may be significant in estuaries (*e.g.* Garcia et al. (2012) and Boucek & Rehage (2013)), seasonal processes might partly bias the results presented here, especially regarding the average isotopic compositions of jacks at each location. However, the $\delta^{13}C$ and $\delta^{15}N$ values observed are within the ranges reported in other tropical estuaries, both for primary producers and for juvenile jacks (Abrantes et al. 2014, Claudino et al. 2015, Dolbeth et al. 2016). Their high variabilities suggest that the amplitude in $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions of the jacks at each estuary largely reflects those at the base of local food chains. Thus, in Suape and Sirinhaém, the wide range of $\delta^{13}C$ values observed for organic matter sources is reflected in a greater range of $\delta^{13}C$ values for the two jack species. Similarly, the higher $\delta^{15}N$ ratios of the juvenile jacks in Santa Cruz may partly reflect the incorporation of enriched ^{15}N organic matter from coastal marine sources into the food web in this estuary, which has important connections with the marine realm (Flores Montes et al. 1998), although we cannot rule out this could indicate slightly higher trophic levels. Other sources may contribute to the local ^{15}N enrichments such as agricultural and domestic wastes (Morris et al. 2015) given the proximity in the region of highly urbanized areas (CPRH 2003).

Potential biases in diet composition obtained from SCA may arise from the caveats inherent to the technique. In particular, differences in digestion rates among prey and the difficulty to identify some of them when partly digested can lead to an over-estimation of the contribution of the food items with low digestion rates and to greater proportions of unidentified prey in the diet of carnivorous species (Hyslop 1980). This could partly be the case in our study, as fish and crustaceans (*i.e.* relatively big prey with hard skeletons) are less easily digested than soft-bodied organisms (Buckland et al. 2017). Moreover, sampling for SCA requires to match predators' local feeding strategies across time and space in order to produce a realistic image of their diets. Although this is yet to be demonstrated, feeding in juvenile jacks might also take place at times of the day not sampled during our survey. This would explain the high level of prey digestion in some of the stomachs analyzed and might have contributed to bias our results, by further precluding identification of the prey items with high digestibility. Within estuarine systems, the types and abundances of the prey available for foraging fish strongly vary according to habitat type (Svanbäck & Eklöv 2002, Lecomte & Dodson 2005, Cardozo et al. 2020), which partly contributes to diet changes in the predators exhibiting seasonal or size-related shifts in habitat use (Stevens et al. 2007, Ferreira et al. 2016, 2019). However, juvenile jacks are highly mobile within estuaries, using a wide diversity of estuarine habitats irrespective of their age (Medeiros et al. 2017). Moreover, the sampling design in this study attempted to capture most of the spatial and temporal variation in habitat use by the two species, by capturing juvenile jacks in all their main estuarine habitats (*e.g.* mangrove creeks, river banks) at each date, over multiple seasons and years. Because our sub-sampling strategy for SCA accounted for spatiotemporal differences in the abundances of the two species, among and within locations, the image of the global diet provided here should be rather realistic. Indeed, it reflects their habitat use but also the inter-annual and inter-seasonal variations in food source availability and food web structure in the three estuaries sampled, which are also likely to modulate fish diet composition (Boucek & Rehage 2013, Garcia et al. 2017, Possamai et al. 2018).

3.5.2. Possibility for trophic competition

In estuaries, physico-chemical gradients (*e.g.* in salinity) drive food web structure and determine habitat suitability for fish (Barletta et al. 2008, da Silva et al. 2018). However, food abundance also modulates interactions between potential competitors (Sánchez-Hernández et al. 2017, Costa-Pereira et al. 2019). As a result, co-existing species tend to either share abundant food resources or differ in one or more dimensions of their environmental niche (Ross 1986). One major caveat when evaluating resource partitioning between coexisting species is the measurement of only one dimension of their ecological niche (Costa-Pereira et al. 2019). With this regard, stable isotope analysis is a valuable complementary approach to common dietary methods (Silveira et al. 2020), calculating the isotopic niche as a proxy of the trophic niche (Newsome et al. 2007). However, although the position and the size of the isotopic niche of a species are primarily driven by variations in its diet, they can be influenced by its biology and physiology (Gorokhova 2018, Karlson et al. 2018), and by habitat-driven differences in the isotope ratios of local food webs (Flaherty & Ben-David 2010). In this study, SCA and SIA presented opposing results, especially in the Santa Cruz estuary where the greater difference in diet between the two species did not result in a reduction in their isotopic niche overlap. Moreover, the variability in $\delta^{13}C$ values for both species at each site largely followed that of the organic matter sources present in the estuary. This suggests that the position and size of the isotopic niches for juvenile jacks in our study area largely reflect local variation in the isotopic signatures of their prey caused by local differences in food web structure. This confirms that the isotopic niche approach should be interpreted with caution, and does not necessarily provide accurate information to evaluate food partitioning between co-existing species (Flaherty & Ben-David 2010, Petta et al 2020, Shipley & Matich 2020). Because tropical estuaries often exhibit a wide variety of organic matter sources and consumers, isotopic signals may be mixed along their food webs (Layman 2007). Therefore, the isotopic niche approach might prove less valuable in these complex environments than in lakes or on land, where its application has been successful in elucidating biological processes at inter and intraspecific scales within food webs (Pettitt-Wade et al. 2015, Mumby et al. 2018, Sheppard et al. 2018, Costa-Pereira et al. 2019).

Resource partitioning has been reported for many fish species, and in diverse types of estuaries, including tropical ones (Pimentel & Joyeux 2010, Le Loc'h et al. 2015, Moulton et al. 2017, Stevens et al. 2020). In the three estuaries studied here, although the two jack species had very similar prey and isotopic niches in overall, they exhibited slight spatial differences in their diet composition, which contributed to reduce the actual overlap in their niches at each studied location. This supports the idea that juvenile jacks adapt their feeding strategies to local food resources' availability in order to reduce trophic competition among them. This seems to occur in different ways though, depending on local environmental conditions.

Indeed, although prey abundance was never directly assessed in any of the three estuaries studied, previous work concluded that Santa Cruz is that with the greatest fauna biodiversity in the area (Silva-Júnior et al. 2017). In particular, it sustains a wide variety of secondary consumers (Vasconcelos Filho et al. 2010, Ferreira 2018), many of which are prey for juvenile jacks. In this rich environment, both *C. latus* and *C. hippos* juveniles occur at higher densities than in other estuaries (Paiva & Araújo 2010, Silva-Júnior et al. 2017). They exhibit the most contrasting diets, but surprisingly also the most similar isotopic niches. Because the high diversity of secondary consumers in Santa Cruz allows many carnivores to feed upon both pelagic and benthic prey (Vasconcelos Filho et al. 2003), the local similarity in juvenile jacks' isotopic niches likely reflects the isotopic ratios of their fish and crustacean prey, as most of these are small predators feeding on both food chains. Thus, it appears that, when the diversity and availability of food is high like in Santa-Cruz, the juveniles of the two species avoid trophic competition by exploiting different prey, matching their respective diet preferences. Nonetheless, they apparently have to adapt these latter and partially compete for food in less favorable environments. Indeed, in the Suape and Sirinhaém estuaries, where the diversity of available prey is limited, the two species focus on the same food resources. The greatest variability in their $\delta^{13}C$ ratios at these sites indicates that they rely on a broader number of food chains though, including those based on allochthonous sources of organic matter, like freshwater inputs (Abrantes & Sheaves 2010). This diversification of carbon sources can be seen as an ecological response to reduce competition between species (Lecomte & Dodson 2005). It might allow *C. latus* and *C. hippos* to co-exist in Suape and Sirinhaém in spite of their similarities in diet. The fact that the abundances of both *C. latus* and *C. hippos* juveniles are lower in these two estuaries suggests that the higher trophic niche overlap observed at these sites result in an increased competition for food among them. However, further information on the temporal fluctuations in prey abundance and the timing of their consumption is needed before one can conclude about the actual intensity of this phenomenon. First, trophic competition between fish species with similar global diets can be reduced when these latter largely reflect an opportunistic use of seasonal peaks in the abundances of the most shared prey (Lucena et al. 2000, Boucek & Rehage 2013). This might very well be the case here, especially as this kind of opportunistic feeding behavior would explain the variability in $\delta^{13}C$ ratios observed for both species. Differences in feeding rhythms between *C. latus* and *C. hippos* may also reduce the intensity of the trophic competition among their juveniles at the daily scale, as already observed for other jack species (Blaber & Cyrus 1983). Lastly, competition for food is also often avoided through differences in the periods for juvenile occurrence in the estuaries, as observed in local snook species with similar diets but distinct spawning periods (Stevens et al. 2020). However, this does not really apply here as *C. latus* and *C. hippos* in North-Eastern Brazil both are expected to spawn from April to June (Heyman & Kjerfve 2008), and their juveniles are mostly fished in local estuaries during the late summer (McBride & McKown 2000, Vilar et al. 2011, da Silva et al. 2018).

3.6. Conclusion

This study contributes to better understanding the drivers of juvenile trophic ecology and its variation in tropical estuaries. Although the two close species of jacks studied here apparently globally rely on similar prey during their juvenile estuarine life, our results revealed some plasticity in their resource use, supporting the idea that resource partitioning processes between sympatric species are locally dependent (Costa-Pereira et al. 2019). Such plasticity in resource use according to local food web structure may not only favor the coexistence of a larger number of species but also provide greater stability for estuarine food webs (Kondoh 2003). In order to evaluate it, cross-sites comparisons should be systematically undertaken when investigating the trophic ecology of sympatric fish species, particularly in tropical estuaries that show a high diversity of food sources (Layman 2007). As spatial variation in the trophic ecology of predators like *C. latus* and *C. hippos* may not only influence the growth and survival of their juveniles, but also modulate their respective roles in the functioning of estuarine food webs, such cross-sites comparisons could be key for evaluating the implications of different co-existence scenarios, not only on the maintenance of coastal fish stocks but also on the composition and functioning of estuarine systems. This should be undertaken keeping in mind that both anthropic pressures and Climate Change may displace the environmental boundaries of estuaries or alter the composition and productivity of their food webs (Araújo et al. 2016, Chevillot et al. 2019), thereby affecting the way fish species exploit estuarine resources and modifying their roles in food webs.

3.7. Supplementary Material

Supplementary Table S1 Frequency of occurrence (F_i), relative abundance (N_i) and weight (W_i) and alimentary coefficient (Q) of prey items of *Caranx latus* and *C. hippos* in the Santa Cruz estuary. The number of fish specimens (n) is presented for each species. For each prey item, confidence interval estimates (95% CI) are displayed between brackets. Values for major taxonomic groups are shown in bold.

Item	Species							
	Caranx latus (n = 70)				*Caranx hippos* (n = 70)			
	F_i (%)	N_i (%)	W_i (%)	Q	F_i (%)	N_i (%)	W_i (%)	Q
ALGAE	**4.29** **[0 – 10.0]**	**5.05** **[0 – 12.8]**	**0.08** **[0 – 0.2]**	**0.30**	**1.43** **[0 – 4.3]**	**0.15** **[0 – 0.6]**	**0.22** **[0 - 0.9]**	**0.03**
Chlorophyta (Unidentified)	1.43 [0 – 4.3]	0.85 [0 – 2.7]	0.04 [0 – 0.1]	0.03	-	-	-	-
Unidentified Algae	2.86 [0 – 7.1]	5.13 [0 – 13.6]	0.04 [0 – 0.2]	0.20	1.43 [0 – 4.3]	0.15 [0 – 0.6]	0.23 [0 – 1.0]	0.03
NEMATODA (Unidentified)	**-**	**-**	**-**	**-**	**1.43** **[0 – 4.3]**	**0.15** **[0 – 0.6]**	**<0.01**	**0.01**
	-	-	-	-	1.43 [0 – 4.3]	0.15 [0 – 0.6]	<0.01	0.01
BIVALVIA (Unidentified)	**1.43** **[0 – 4.3]**	**1.44** **[0 – 4.4]**	**<0.01**	**0.01**	-	-	-	-
	1.43 [0 – 4.3]	1.71 [0 – 4.9]	<0.01	0.01	-	-	-	-
POLYCHAETA (Unidentified)	**1.43** **[0 – 4.3]**	**0.36** **[0 – 1.3]**	**<0.01**	**0.01**	**1.43** **[0 – 4.3]**	**0.44** **[0 – 1.7]**	**0.01** **[0 – 0.1]**	**0.01**
	1.43 [0 – 4.3]	0.43 [0 – 1.4]	<0.01	0.01	1.43 [0 – 4.3]	0.46 [0 – 1.7]	0.01 [0 – 0.1]	0.01
CRUSTACEA	**41.43** **[30.0 – 52.9]**	**26.35** **[16.7 – 37.3]**	**24.35** **[12.3 – 41.4]**	**632.66**	**67.14** **[55.7 – 78.6]**	**78.10** **[62.6 – 86.0]**	**45.97** **[24.3 – 76.5]**	**3526.05**
Cirripedia (Unidentified)	-	-	-	-	1.43 [0 – 4.3]	1.08 [0 – 4.0]	<0.01	0.01

Supplementary Table S1 Continued.

Copepoda (Unidentified)				2.86 [0 – 7.1]	3.42 [0 – 10.0]	<0.01	0.01	7.14 [1.4 – 12.9]	1.23 [0.3 – 2.8]	<0.01	0.01
Malacostraca	Decapoda	Brachyura (Unidentified)		-	-	-	-	1.43 [0 – 4.3]	0.15 [0 – 0.6]	0.44 [0 – 1.8]	0.06
		Caridea	Alpheidae	1.43 [0 – 4.3]	0.43 [0 – 1.5]	0.11 [0 – 0.4]	0.04	1.43 [0 – 4.3]	0.15 [0 – 0.6]	1.68 [0 – 6.8]	0.25
			Unidentified Caridea	1.43 [0 – 4.3]	0.43 [0 – 1.4]	0.72 [0 – 2.8]	0.30	-	-	-	-
		Dendrobranchiata	Penaeidae	15.71 [7.1 – 24.3]	7.69 [3.2 – 12.8]	19.27 [8.7 – 34.6]	148.10	27.14 [17.1 – 38.6]	4.76 [2.2 – 9.5]	23.29 [10.9 – 44.6]	110.86
		Unidentified Decapoda		10.00 [4.3 – 17.1]	4.27 [1.3 – 8.1]	3.44 [0.7 – 8.1]	14.68	31.43 [21.4 – 42.9]	17.36 [7.7 – 33.3]	12.35 [3.6 – 29.0]	214.39
	Isopoda (Unidentified)			-	-	-	-	2.86 [0 – 7.1]	0.31 [0 – 0.9]	0.02 [0 – 0.1]	0.01
	Mysida (Unidentified)			1.43 [0 – 4.3]	0.43 [0 – 1.5]	0.02 [0 – 0.1]	0.01	8.57 [2.9 – 15.7]	48.08 [16.3 – 64.3]	6.37 [1.2 – 16.1]	306.26
	Stomatopoda (Unidentified)			-	-	-	-	1.43 [0 – 4.3]	0.15 [0 – 0.6]	0.04 [0 – 0.1]	0.01
Ostracoda (Unidentified)				2.86 [0 – 7.1]	5.98 [0 – 15.1]	<0.01	0.01	-	-	-	-
Unidentified Crustacea				14.29 [7.1 – 22.9]	8.55 [3.3 – 14.8]	0.89 [0.2 – 2.0]	7.60	11.43 [4.3 – 20.0]	8.91 [1.6 – 18.2]	1.89 [0.1 – 6.2]	16.83
VERTEBRATA				**80.00** **[70.0 – 88.6]**	**51.26** **[39.8 – 63.7]**	**75.14** **[57.9 – 87.3]**	**3724.73**	**74.29** **[64.3 – 84.3]**	**16.20** **[10.1 – 27.7]**	**53.56** **[22.8 – 75.4]**	**870.58**
Teleostei	Clupeiformes		Clupeidae	1.43 [0 – 4.3]	0.85 [0 – 2.8]	1.81 [0 – 5.7]	1.53	1.43 [0 – 4.3]	0.15 [0 – 0.6]	0.26 [0 – 1.1]	0.03
			Engraulidae	8.57 [2.9 – 15.7]	3.85 [0.9 – 7.7]	2.99 [0.2 – 8.1]	11.51	1.43 [0 – 4.3]	0.15 [0 – 0.6]	0.75 [0 – 3.1]	0.11
	Gobiiformes		Eleotridae	2.86 [0 – 7.1]	0.85 [0 – 2.2]	0.95 [0 – 2.9]	0.80	-	-	-	-
			Gobiidae	31.43 [21.4 – 42.9]	14.96 [9.2 – 20.9]	48.35 [22.0 – 67.6]	723.31	20.00 [11.4 – 30.0]	3.53 [1.5 – 7.2]	41.69 [6.5 – 67.5]	147.16

Supplementary Table S1 Continued.

Perciformes	Carangidae	-	-	-	-	4.29 [0 – 10.0]	2.76 [0 – 8.2]	1.02 [0 – 3.6]	2.81
	Gerreidae	4.29 [0 – 8.6]	1.28 [0 – 3.0]	1.17 [0 – 4.0]	1.49	-	-	-	-
Unidentified teleostei		47.14 [35.7 – 58.6]	38.89 [24.9 – 50.5]	20.20 [10.4 – 35.8]	785.57	55.71 [44.3 – 67.1]	10.45 [5.8 – 19.3]	9.96 [4.4 – 21.5]	104.08
DEBRIS		**17.14** **[8.6 – 25.7]**	**15.52** **[5.1 – 27.7]**	**0.43** **[0.1 – 1.1]**	**-**	**27.14** **[17.1 – 37.1]**	**4.96** **[2.2 – 10.1]**	**0.23** **[0 – 0.6]**	**-**
Plastic debris		11.43 [4.3 – 20.0]	13.36 [2.8 – 25.6]	<0.01	-	10.00 [2.9 – 17.1]	2.63 [0.6 – 6.5]	<0.01	-
Unidentified organic matter and sediment debris		8.57 [2.9 – 15.7]	2.17 [0.7 – 4.2]	0.43 [0.1 – 1.1]	-	17.14 [8.6 – 25.7]	2.34 [1.0 – 5.0]	0.23 [0 – 0.6]	-

Supplementary Table S2 Frequency of occurrence (F_i), relative abundance (N_i) and weight (W_i) and alimentary coefficient (Q) of prey items of *Caranx latus* and *C. hippos* in the Suape estuary. The number of fish specimens (n) is presented for each species. For each prey item, confidence interval estimates (95% CI) are displayed between brackets. Values for major taxonomic groups are shown in bold.

Item				Species							
				Caranx latus (n = 67)				*Caranx hippos* (n = 20)			
				F_i (%)	N_i (%)	W_i (%)	Q	F_i (%)	N_i (%)	W_i (%)	Q
ALGAE				**17.91** **[9.0 – 26.9]**	**5.03** **[2.2 – 9.4]**	**0.52** **[0.1 – 1.7]**	**1.78**	**5.00** **[0 – 15.0]**	**1.47** **[0 – 5.7]**	**<0.01**	**0.01**
Chlorophyta (Unidentified)				1.49 [0 – 4.5]	0.58 [0 – 2.1]	<0.01	0.01	-	-	-	-
Unidentified Algae				16.42 [7.5 – 25.4]	5.85 [2.1 – 10.6]	0.54 [0.1 – 1.7]	3.15	5.00 [0 – 15.0]	2.70 [0 – 10.0]	<0.01	0.01
CRUSTACEA				**40.30** **[28.4 – 52.2]**	**21.05** **[10.7 – 35.4]**	**24.44** **[9.4 – 47.3]**	**903.64**	**35.00** **[15.0 – 55.0]**	**19.12** **[5.1 – 37.1]**	**12.14** **[1.9 – 42.9]**	**232.11**
Malacostraca	Decapoda	Brachyura (Unidentified)		1.49 [0 – 4.5]	0.29 [0 – 1.0]	0.29 [0 – 1.0]	0.08	-	-	-	-
		Caridea	Alpheidae	4.48 [0 – 9.0]	2.63 [0.5 – 7.2]	3.11 [0 – 10.9]	8.17	-	-	-	-
		Dendrobranchiata	Aristeidae	1.49 [0 – 4.5]	0.58 [0 – 1.0]	0.13 [0 – 0.5]	0.07	-	-	-	-
			Penaeidae	8.96 [3.0 – 16.4]	2.92 [0.6 – 6.6]	14.85 [3.1 – 31.9]	43.36	15.00 [0 – 30.0]	8.11 [0 – 21.2]	7.96 [0 – 35.7]	64.55
		Unidentified Decapoda		14.93 [7.5 – 23.9]	14.91 [3.6 – 30.2]	5.86 [0.9 – 14.4]	87.37	15.00 [0 – 30.0]	24.32 [0 – 51.5]	4.70 [0 – 23.6]	114.30
	Isopoda (Unidentified)			5.97 [1.5 – 11.9]	1.46 [0.2 – 3.4]	0.02 [0 – 0.1]	0.02	5.00 [0 – 15.0]	2.70 [0 – 11.1]	0.31 [0 – 2.0]	0.83
Ostracoda				2.99 [0 – 7.5]	1.46 [0 – 4.0]	<0.01	0.01	-	-	-	-
Unidentified Crustacea				11.94 [4.5 – 20.9]	2.92 [0.9 – 5.6]	0.94 [0.1 – 2.7]	2.74	-	-	-	-

Supplementary Table S2 Continued.

VERTEBRATA			**86.57** **[77.6 – 94.0]**	**52.17** **[34.7 – 67.9]**	**72.57** **[49.2 – 88.2]**	**3167.20**	**60.00** **[40.0 – 80.0]**	**33.82** **[16.0 – 55.3]**	**81.48** **[44.5 – 94.2]**	**2755.65**
Thaliacea	Salpida	Salpidae	1.49 [0 – 4.5]	0.29 [0 – 1.0]	0.02 [0 – 0.1]	0.01	-	-	-	-
Teleostei	Clupeiformes	Clupeidae	4.48 [0 – 10.4]	1.46 [0.2 – 3.8]	4.39 [0 – 13.5]	6.40	10.00 [0 – 25.0]	18.92 [0 – 43.2]	41.93 [0 – 59.5]	793.31
		Engraulidae	2.99 [0 – 7.5]	0.58 [0 – 1.6]	2.38 [0 – 9.0]	1.38	15.00 [0 – 30.0]	8.11 [0 – 17.9]	23.34 [0 – 49.3]	189.28
	Gobiiformes	Eleotridae	1.49 [0 – 4.5]	0.29 [0 – 1.1]	0.19 [0 – 0.8]	0.05	-	-	-	-
		Gobiidae	8.96 [3.0 – 16.4]	2.92 [0.7 – 6.6]	37.32 [3.4 – 65.3]	108.97	-	-	-	-
	Perciformes	Gerreidae	16.42 [7.5 – 25.4]	8.48 [2.2 – 17.2]	4.84 [0.2 – 13.1]	41.04	-	-	-	-
		Scianidae	1.49 [0 – 4.5]	0.29 [0 – 1.0]	0.54 [0 – 2.1]	0.15	-	-	-	-
	Unidentified teleostei		71.64 [61.2 – 82.1]	52.05 [27.2 – 68.4]	24.59 [12.2 – 45.7]	1279.90	50.00 [30.0 – 70.0]	35.14 [20.0 – 55.6]	21.77 [13.2 – 43.6]	764.99
DEBRIS			**34.33** **[22.4 – 46.3]**	**21.74** **[11.2 – 34.4]**	**2.47** **[0.3 – 7.5]**	**-**	**40.00** **[20.0 – 60.0]**	**45.59** **[24.2 – 66.7]**	**6.38** **[1.0 – 16.5]**	**-**
Plastic debris			25.37 [14.9 – 35.8]	16.70 [8.6 – 27.6]	<0.01	-	30.00 [10.0 – 50.0]	23.53 [9.2 – 40.0]	0.01 [0 – 0.1]	-
Unidentified organic matter and sediment debris			16.42 [7.5 – 25.4]	5.03 [1.8 – 9.5]	2.47 [0.3 – 7.5]	-	30.00 [10.0 – 50.0]	22.06 [7.1 – 37.7]	6.38 [0.9 – 16.4]	-

Supplementary Table S3 Frequency of occurrence (F_i), relative abundance (N_i) and weight (W_i) and alimentary coefficient (Q) of prey items of *Caranx latus* and *C. hippos* in the Sirinhaém estuary. The number of fish specimens (n) is presented for each species. For each prey item, confidence interval estimates (95% CI) are displayed between brackets. Values for major taxonomic groups are shown in bold.

	Species							
Item	*Caranx latus* (*n* = 70)				*Caranx hippos* (*n* = 41)			
	F_i (%)	N_i (%)	W_i (%)	Q	F_i (%)	N_i (%)	W_i (%)	Q
ALGAE	**14.29** **[7.1 – 22.9]**	**3.08** **[1.1 – 5.9]**	**0.16** **[0 – 0.4]**	**0.26**	**4.88** **[0 – 12.2]**	**2.68** **[0 – 7.2]**	**0.16** **[0 – 0.5]**	**0.34**
Unidentified Algae	14.29 [7.1 – 22.9]	3.94 [1.2 – 6.9]	0.16 [0 – 0.4]	0.63	4.88 [0 – 12.2]	3.37 [0 – 8.4]	0.16 [0 – 0.5]	0.53
FORAMINIFERA (Unidentified)	**1.43** **[0 – 4.3]**	**0.18** **[0 – 0.6]**	**<0.01**	**0.01**	-	-	-	-
	1.43 [0 – 4.3]	0.23 [0 – 0.7]	<0.01	0.01				
NEMATODA (Unidentified)	**15.71** **[7.1 – 24.3]**	**2.54** **[1.2 – 4.3]**	**<0.01**	**0.01**	**7.32** **[0 – 17.1]**	**1.53** **[0 – 3.6]**	**<0.01**	**0.01**
	15.71 [8.4 – 24.3]	3.25 [1.9 – 4.9]	<0.01	0.01	7.32 [0 – 17.1]	1.92 [0 – 3.9]	<0.01	0.01
BIVALVIA (Unidentified)	-	-	-	-	**2.44** **[0 – 7.3]**	**0.38** **[0 – 1.3]**	**0.02** **[0 – 0.1]**	**0.01**
					2.44 [0 – 7.3]	0.48 [0 – 1.5]	0.02 [0 – 0.1]	0.01
GASTROPODA (Unidentified)	**8.57** **[2.9 – 15.7]**	**2.90** **[0.7 – 6.0]**	**0.06** **[0 – 0.2]**	**0.12**	-	-	-	-
	8.57 [2.9 – 15.7]	3.71 [0.7 – 6.8]	0.06 [0 – 0.2]	0.22				
POLYCHAETA (Unidentified)	-	-	-	-	**2.44** **[0 – 7.3]**	**1.15** **[0 – 4.0]**	**<0.01**	**0.02**
					2.44 [0 – 7.3]	1.44 [0 – 4.8]	<0.01	0.01

Supplementary Table S3 Continued.

OLIGOCHAETA (Unidentified)				**1.43** **[0 – 4.3]**	**0.18** **[0 – 0.6]**	**<0.01**	**0.01**	**7.32** **[0 – 17.1]**	**1.15** **[0 – 2.7]**	**<0.01**	**0.01**
				1.43 [0 – 4.3]	0.23 [0 – 0.7]	<0.01	0.01	7.32 [0 – 14.6]	1.44 [0 – 3.3]	<0.01	0.01
CRUSTACEA				**65.71** **[54.3 – 75.7]**	**29.89** **[20.3 – 40.5]**	**18.44** **[10.7 – 28.1]**	**462.93**	**60.98** **[46.3 – 75.6]**	**45.59** **[28.4 – 61.0]**	**28.96** **[9.8 – 48.4]**	**1613.92**
Cirripedia (Unidentified)				1.43 [0 – 4.3]	1.39 [0 – 4.3]	<0.01	0.01	-	-	-	-
Copepoda (Unidentified)				1.43 [0 – 4.3]	2.32 [0 – 6.9]	<0.01	0.01	12.20 [2.4 – 22.0]	5.29 [1.2 – 9.8]	0.01 [0 – 0.1]	0.05
Malacostraca	Decapoda	Brachyura	Portunidae	1.43 [0 – 4.3]	0.23 [0 – 0.7]	0.53 [0 – 1.8]	0.12	4.88 [0 – 12.2]	0.96 [0 – 2.0]	0.50 [0 – 1.2]	0.48
			Sesarmidae	1.43 [0 – 4.3]	0.23 [0 – 0.7]	0.27 [0 – 0.9]	0.06	-	-	-	-
			Unidentified Brachyura	1.43 [0 – 4.3]	1.39 [0 – 4.3]	0.05 [0 – 0.2]	0.06	2.44 [0 – 7.3]	0.96 [0 – 3.3]	<0.01	0.01
		Caridea	Alpheidae	8.57 [2.9 – 15.7]	2.32 [0.4 – 4.3]	0.81 [0 – 1.9]	1.87	2.44 [0 – 7.3]	0.48 [0 – 1.5]	<0.01	0.01
			Unidentified Caridea	7.14 [1.4 – 14.3]	2.09 [0.4 – 4.0]	5.97 [1.3 – 12.3]	12.47	-	-	-	-
		Dendrobranchiata	Penaeidae	10.00 [2.9 – 17.1]	4.87 [1.1 – 9.3]	4.64 [0.2 – 12.6]	22.59	12.20 [2.4 – 22.0]	19.71 [1.6 – 33.2]	9.47 [1.2 – 20.6]	186.65
		Unidentified Decapoda		21.43 [11.4 – 31.4]	6.50 [3.0 – 9.3]	5.33 [1.9 – 10.0]	34.64	14.63 [4.9 – 26.8]	6.25 [1.3 – 12.1]	7.51 [0.6 – 18.0]	46.93
	Isopoda (Unidentified)			2.86 [0 – 7.1]	0.70 [0 – 1.7]	0.01 [0 – 0.1]	0.01	4.88 [0 – 12.2]	0.96 [0 – 2.0]	<0.01	0.01
	Mysida (Unidentified)			4.29 [1.0 – 10.0]	1.62 [0 – 3.3]	0.03 [0 – 0.1]	0.04	9.76 [2.4 – 19.5]	7.21 [0.5 – 16.4]	0.32 [0 – 1.0]	2.30
Ostracoda (Unidentified)				7.14 [1.4 – 14.3]	2.09 [0.4 – 3.8]	<0.01	0.01	4.88 [0 – 12.2]	2.44 [0 – 5.2]	<0.01	0.01

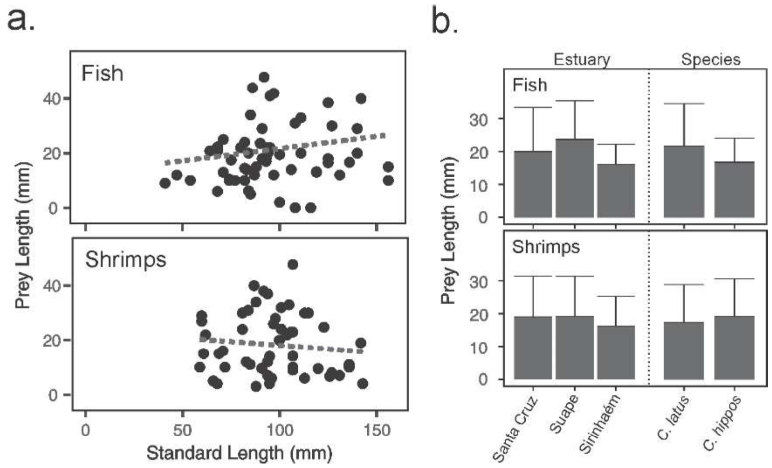
Supplementary Table S3 Continued.

Unidentified Crustacea			18.57 [10.0 – 28.6]	12.53 [4.2 – 20.3]	0.83 [0.2 – 1.8]	10.39	12.20 [2.4 – 22.0]	12.98 [1.0 – 28.4]	11.61 [0 – 32.4]	150.69
HEXAPODA			**1.43** **[0 – 4.3]**	**0.18** **[0 – 0.7]**	**<0.01**	**0.01**	**-**	**-**	**-**	**-**
Unidentified Insecta			1.43 [0 – 4.3]	0.23 [0 – 0.7]	<0.01	0.01	-	-	-	-
VERTEBRATA			**85.71** **[77.1 – 94.2]**	**39.13** **[28.6 – 49.9]**	**81.12** **[71.4 – 88.9]**	**3271.88**	**73.17** **[58.5 – 85.4]**	**27.20** **[14.9 – 40.9]**	**69.27** **[49.7 – 88.6]**	**1743.05**
Thaliacea	Salpida	Salpidae	1.43 [0 – 4.3]	0.23 [0 – 0.7]	0.46 [0 – 1.6]	0.10	-	-	-	-
Teleostei	Clupeiformes	Engraulidae	1.43 [0 – 4.3]	1.16 [0 – 3.7]	1.61 [0 – 5.5]	1.86	-	-	-	-
	Gobiiformes	Eleotridae	-	-	-	-	2.44 [0 – 7.3]	0.48 [0 – 1.6]	8.48 [0 – 25.4]	4.07
		Gobiidae	30.00 [20.0 – 41.4]	7.19 [3.7 – 9.9]	29.57 [17.4 – 42.5]	212.60	26.83 [14.6 – 41.5]	7.69 [3.2 – 11.8]	27.96 [13.0 – 44.9]	215.01
	Perciformes	Carangidae	1.43 [0 – 4.3]	0.23 [0 – 0.7]	0.85 [0 – 3.0]	0.19	-	-	-	-
		Gerreidae	8.57 [2.9 – 15.7]	2.78 [0.5 – 5.2]	0.89 [0 – 2.1]	2.47	2.44 [0 – 7.3]	0.48 [0 – 1.5]	0.78 [0 – 2.9]	0.37
	Pleuronectiformes	Cynoglossidae	1.43 [0 – 4.3]	0.23 [0 – 0.7]	0.73 [0 – 2.6]	0.16	-	-	-	-
		Paralichthyidae	1.43 [0 – 4.3]	0.23 [0 – 0.7]	0.24 [0 – 0.9]	0.05	-	-	-	-
	Unidentified teleostei		62.86 [51.4 – 74.3]	38.05 [20.9 – 46.0]	46.95 [34.1 – 59.1]	1786.44	53.66 [39.0 – 68.3]	25.48 [11.7 – 36.7]	33.16 [17.9 – 50.0]	844.91
DEBRIS			**37.14** **[25.7 – 48.6]**	**21.92** **[14.6 – 29.6]**	**0.21** **[0 – 0.6]**	**-**	**41.46** **[26.8 – 56.1]**	**20.31** **[11.5 – 32.3]**	**1.59** **[0.1 – 4.2]**	**-**
Plastic debris			22.86 [12.9 – 32.9]	11.96 [.63 – 18.3]	0.01 [0 – 0.1]	-	26.83 [14.6 – 41.5]	12.26 [5.2 – 22.4]	0.02 [0 – 0.1]	-
Unidentified organic matter and sediment debris			20.00 [11.4 – 30.0]	9.96 [3.8 – 17.4]	0.20 [0 – 0.5]	-	17.07 [7.3 – 29.3]	8.05 [2.2 – 16.0]	1.57 [0.1 – 4.1]	-

Supplementary Table S4 Number of samples (n) and isotopic means (± S.D.) of carbon (δ^{13}C), nitrogen (δ^{15}N) of organic matter sources in three estuaries of the northeast Brazilian coast: estuarine complex of Santa Cruz Channel and the estuaries of Suape and Sirinhaém. Minimum and maximum values of each variable are shown in brackets.

Species	Estuary								
	Santa Cruz			Suape			Sirinhaém		
	n	δ^{13}C (‰)	δ^{15}N (‰)	n	δ^{13}C (‰)	δ^{15}N (‰)	n	δ^{13}C (‰)	δ^{15}N (‰)
Mangrove trees									
Rhizophora mangle	12	-27.63±0.68 [-28.77 – -26.77]	2.40±1.06 [1.02 – 4.48]	6	-27.14±0.53 [-27.90 – -26.48]	2.14±0.81 [0.95 – 3.06]	6	-28.34±0.60 [-29.25 – -27.60]	1.41±1.76 [-1.03 – 3.64]
Algae									
Ulva spp.	9	-21.61±2.37 [-23.84 – -18.19]	7.44±1.19 [6.16 – 9.15]	3	-16.30±0.75 [-16.78 – -15.43]	7.78±0.54 [7.34 –8.38]	-	-	-
Gracilaria cervicornis	3	-21.84±0.60 [-22.52 – -21.37]	8.90±0.46 [8.36 –9.19]	3	-16.45±0.62 [-16.95 –-15.75]	8.25±0.20 [8.08 –8.47]	3	-16.62±0.49 [-17.11 – -16.12]	5.70±0.13 [5.58 – 5.83]
Sargassum spp.				3	-16.51±2.33 [-19.06 – -14.50]	6.99±0.21 [6.75 – 7.12]	3	-16.78±1.31 [-18.26 – -15.77]	5.40± 0.40 [5.05 – 5.84]
Microalgae									
Benthic microalgae	8	-19.99±1.34 [-21.61 – -17.59]	3.10±0.81 [1.81 – 4.34]	1	-26.48†	4.66†	6	-23.58±1.88 [-25.36 – -21.01]	5.18±0.87 [4.15 – 6.17]
Organic matter									
POM (Estuary)	10	-24.13±0.46 [-24.65 – -23.34]	5.82±0.66 [4.91 – 6.76]	5	-25.60±0.77 [-26.28 – -24.43]	7.40±2.09 [5.29 – 10.11]	6	-22.21±3.92 [-26.35 – -17.22]	5.96±0.75 [4.85 – 6.78]
SOM (Estuary)	12	-23.53±1.19 [-25.12 – -21.25]	4.22±0.68 [3.48 – 5.14]	6	-25.29±0.47 [-25.83 – -24.68]	3.32±0.26 [2.97 – 3.59]	6	-24.88±0.79 [3.84 – 5.19]	4.33±0.46 [-25.60 – -23.96]
POM (Coast)	5	-20.06±069 [-20.62 – -19.12]	8.52±0.48 [8.13 – 9.24]	5	-21.60±0.65 [-22.35 – -20.61]	6.39±0.36 [5.90 – 6.79]	5	-21.60±0.65 [-22.35 – -20.61]	6.39±0.36 [5.90 – 6.79]
SOM (Coast)	6	-17.05±1.40 [-18.85 – -14.72]	6.61±0.73 [5.43 – 7.35]	9	-17.10±1.86 [2.85 – 4.53]	3.76±0.59 [-21.83 – -15.84]	9	-17.10±1.86 [2.85 – 4.53]	3.76±0.59 [-21.83 – -15.84]

† Standard deviation was not calculated for species with less than three samples.



Supplementary Figure S1 (**a.**) Relationship between fish size and prey's length of jack species for main food items: Fish, fish species and unidentified fishes; Shrimps, decapod shrimps. (**b.**) Mean and standard deviation of the prey's length between estuaries (Santa Cruz, Suape and Sirinhaém) and the two jack species (*C. latus* and *C. hippos*).

3.8. IN A NUTSHELL

- *Caranx latus* and *C. hippos* both mostly eat fish and crustaceans during their estuarine juvenile life and their global isotopic niches in estuaries largely overlap (>68%).
- However, *C. latus* juveniles are more piscivorous than those of *C. hippos*, and combined differences in juvenile diet and food web structure at each location contribute to reduce local isotopic niche overlaps between the two species.
- Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition in the muscle tissue of juvenile jacks mainly reflect differences in the organic matter sources supporting each system.
- Variation in their diet composition among estuaries indicate that the two species partly adapt their food preferences to local prey availability.
- The plasticity in resource use observed in this work supports the idea that resource partitioning between sympatric species can largely vary depending on local settings.
- Cross-sites comparisons are therefore key for evaluating the implications of different co-existence scenarios on the growth and survival of estuarine fish, particularly in the face of currently growing anthropic and climatic pressures.

This second research axis revealed how juvenile jacks use available food resources during their estuarine life in North-Eastern Brazil. Particularly, it highlighted that *C. latus* can partially adapt its juvenile diet to match different environmental estuarine settings and different levels of interaction with coexisting fish species. Our results support the assumption that life conditions are not equal for all the juveniles of the species in North-East Brazil, and that the type of habitat they colonize during their first year of life influence their growth and the recruitment success of the local population.

CHAPTER 4: Importance of the estuaries for the exploited stock

The horse-eye jack *Caranx latus* is commonly considered to be a reef-associated marine species (Figueiredo & Menezes 1980, Smith-Vaniz 2002) but, in North-Eastern Brazil, it is frequently found in estuaries at the juvenile stage, especially during the first year of life. Nonetheless, the differences in the species' early growth among local estuarine habitats (CHAPTER 2) and the plasticity in the diet of its juveniles under varying local environmental and biological settings (CHAPTER 3) suggest that the varied estuaries spread along the coast in this area provide different life conditions to juvenile *C. latus.* This raises the question of whether, like in other jack and reef fish species, these inshore environments are nursery grounds for *C. latus*, at least in this part of the world. To investigate this, the third research axis of this study aimed to evaluate the connectivity between the local juvenile and adult habitats of the species, and quantify the respective importance of varied estuaries in sustaining the local offshore stock of *C. latus* (**Article III**). The analysis of the lifetime fingerprints in different chemical elements left in the otoliths of 183 juvenile and adult specimens captured in several estuaries and offshore allowed to unveil the local life cycle of *C. latus* and its inter-individual variability. Furthermore, this work enabled us to quantify to what degree the varied types of local estuaries contribute to sustain the exploited stock of the species in North-Eastern Brazil.

Article III

This section will be submitted during the second semester of 2021, probably to the journal *Aquatic Conservation: Marine and Freshwater Ecosystems.*

Importance of estuaries for exploited stocks of the horse-eye jack (*Caranx latus*): a case study in North-Eastern Brazil.

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4.1. Abstract

Understanding how coastal habitats may help sustaining exploited fish populations is key to delineate effective and sustainable strategies for both fishery and ecosystem management. In this study we evaluated whether the diverse types of estuaries in North-eastern Brazil are key juvenile habitats for the horse-eye jack (*Caranx latus*), supporting the local exploited population of this marine subtropical species. A total of 143 otoliths, from juvenile *C. latus* collected over 3 consecutive years in seven estuaries spread along the coasts of the Pernambuco and Alagoas states, were first used to develop a dataset of multi-elemental fingerprints for the main potential juvenile habitats used by the species in this area, namely seven estuaries and the coastal marine zone. Then the signature in the juvenile part of the otolith of 40 (sub)adults, all captured at sea, were assigned to the juvenile habitats chemically discriminated, using a Random Forest algorithm. Elemental signatures for local estuaries largely overlapped and resulted in a low overall maximum discrimination accuracy (58%) when trying to discriminate them all, even with the optimal list of elements (B, Ba, Cr, P, Rb, Sr and Zn). However, grouping estuaries according to their level of freshwater influence (*i.e.* saline *vs*. brackish ones) allowed to increase discrimination accuracy to 80%. In both cases, the correct re-assignment rate for the sea was notably high (>94%). Strontium was the element contributing most to juvenile habitat discrimination. The remaining elements enabled further distinguish estuary types, with correct re-assignment rates for otolith signature varying from 70 to 88% depending on the estuary group. Otolith elemental fingerprints in the local (sub)adult fish analysed surprisingly revealed that most of the *C. latus* specimens captured in the area (75%) have spent their first year of life in an estuary, principally a saline one (32.5%). These results stress the value of otolith microchemistry for identifying juvenile habitats for coastal fish in the tropics and indicate that estuaries play a key role in the maintenance of *C. latus* populations in North-eastern Brazil. This has strong implications for the management of the species' local stocks, but also for that of several of these estuaries.

Keywords Marine fish, transitional waters, otolith microchemistry, elemental fingerprints, juvenile habitat.

4.2. Introduction

Successful recruitment to the adult population is key for the maintenance of exploited fish stocks (Beverton & Holt 1993). With this regard, biological and environmental constraints during juvenile life represent critical bottlenecks (Chamber & Trippel 1997) and often shape the size and condition of recruiting populations (Walters & Korman 1999, Andersen et al. 2017, Poorten et al. 2018). Juvenile fish often occupy different habitats than the adults of their population, usually in search of higher food availability and lower predation risk (Dahlgren & Eggleston 2000). Among these specific juvenile habitats, some are referred to as nursery grounds, because they allow the juveniles of a given species to occur at higher densities or to benefit from (biological) processes that enhance their survival and maximize their recruitment in the adult stock (Beck et al. 2001).

Transitional coastal environments, like estuaries and lagoons, are used as nursery grounds by a diverse number of marine species, including some exploited by fisheries (Nagelkerken et al. 2008, Sheaves et al. 2015). However, they are also under constant and high levels of human pressure, ranging from eutrophication and habitat alteration to overfishing (Kennish 2002, Mitra & Zaman 2016). These latter not only threaten the health and food security of local human communities, but also the quality of coastal habitats for juvenile fish (Nagelkerken et al. 2008, Crook et al. 2014, Ogden et al. 2014). Moreover, it is becoming increasingly clear that even similar nursery grounds may not provide equivalent life conditions for juvenile fish (Isnard et al. 2015, Schloesser & Fabrizio 2019). Therefore, understanding how these coastal habitats may help sustain marine exploited fish populations is key for delineating effective strategies for species conservation and fisheries management (Nagelkerken et al. 2015, Sheaves et al. 2015). This is particularly true in the tropics, where environmental awareness is only just emerging (Prandle & Lane 2015, Mitra & Zaman 2016)), and the rapid urbanization of the littoral and the growing demand for seafood threaten local coastal fish resources in the near future (Barlow et al. 2018, FAO 2018).

In this study we evaluated whether coastal estuaries are key juvenile habitats in an exploited tropical marine fish, the horse-eye jack (*Caranx latus*). This pelagic species is widely spread along the Western Atlantic coast and constitutes a substantial source of food and income in the South-Western Atlantic (Lessa et al. 2009, Pinheiro et al. 2010, Rombenso et al. 2016). Although the biology and life history of *C. latus* are still poorly known, it is commonly referred as a reef-associated marine species. The information gathered thus far however suggests that its life cycle involves the use of a mosaic of coastal and marine environments. Large specimens of *C. latus* (up to 100 cm in length) are usually associated with deep waters (> 40 m) and offshore reefs near the shelf break (Lessa et al. 2009, Felizola-Freire et al. 2018, Novak et al. 2020), where they are expected to breed, with peaks in April and August (Figuerola-Fernández et al. 2008, Heyman & Kjerfve 2008). As a result, *C. latus* larvae are mainly present offshore, along the continental shelf (Berry 1959, Campos et al. 2010). Its juveniles however are commonly found within estuaries (Figueiredo & Menezes 1980, Medeiros et al. 2017, Silva-Júnior et al. 2017), where they feed on a broad diversity of fish and crustaceans (Flores Montes et al. 1998, Figueiredo et al. 2006), including key species in estuarine food webs (Lira et al. 2018). They apparently occupy these latter during their first year of life before moving back offshore to join the adult population (Gonzalez et al. *in prep*.). However, most of the studies so far regarding the species' lifetime habitats and the migrations between them, only investigated the abundance of *C. latus* in particular habitats, or at specific locations (Campos et al. 2010, Paiva & Araújo 2010, Felizola-Freire et al. 2018). The species' movements or migratory patterns were only assessed at the adult stage (Novak et al. 2020). Therefore, the role of coastal estuaries in supporting the species' adult populations is still unknown.

In North-Eastern Brazil, the frequent occurrence of juveniles of *C. latus* in estuarine environments (Paiva & Araújo 2010, Medeiros et al. 2017, Silva-Júnior et al. 2017) questions whether, like other jack species (Smith & Parrish 2002), it uses these inshore environments as nursery grounds rather than alternative juvenile habitats. To investigate this, otolith chemical fingerprints of juvenile and (sub)adult *C. latus* were used to estimate the relative contribution of varied estuaries in the area to the local exploited stock. Otoliths are calcified structures present in the inner ear of most bony fishes. They grow throughout fish life, by the daily accretions of concentric layers, which explains their ubiquitous use for age estimation (Panfili et al. 2002). Otolith microchemistry takes advantage from this constant growth and the inert nature of the otoliths: as the elements deposited within the otoliths are rarely reabsorbed, the fine-scale analysis of their composition allows identifying which elements were deposited at each period of the fish' life (Campana 1999, Sturrock et al. 2012). Chemical element incorporation in the otoliths is influenced by their availability in the environment and/or the physiological processes that occur throughout the fish' life (Izzo et al. 2015, 2018, Sturrock et al. 2015). If the varied habitats occupied by the fish present well established and contrasting elemental compositions, it is possible to reconstruct their past life history (Gillanders & Kingsford 2000, Gillanders 2005). Therefore, otolith microchemistry has largely been applied to investigate the movements performed by marine coastal fish at various stages of their life (Gillanders & Kingsford

2000, Gillanders 2005). It often allows estimating the relative contribution of distinct nursery grounds to recruiting adult populations (*e.g.* Gillanders et al. (2003) and Tournois et al. (2017)).

In this study, we first analyzed otolith multi-elemental composition for juvenile *C. latus* collected in several contrasted estuaries spread along the North-eastern Brazilian coast, to develop a multi-annual database of otolith chemical fingerprints for the main potential juvenile habitats used by the species in this area. We then confronted it with the multi-elemental signatures recorded in the juvenile part of the otolith of (sub)adults of the species captured at sea, to identify their past juvenile habitats and evaluate the proportion of estuarine users among them, using a Random Forest algorithm. Assessing the contribution of estuarine populations to local adult stocks of *C. latus* is particularly relevant in Brazil because the species is targeted by both inshore and nearshore fisheries, and most catches occur before the individuals reach sexual maturity and enter the adult population (Pelage 2020). Moreover, the food sources exploited by *C. latus* juveniles and their growth have recently been shown to differ among estuaries in this area (Gonzalez et al., 2021, Gonzalez et al. *in prep*.). Because both of these aspects may influence the value of estuaries as juvenile habitats, the implications of this work extend beyond providing knowledge on the local life strategies of the species. Indeed, it should also help improving local fishery and ecosystem management strategies, at least in Brazil.

4.3. Material and Methods

4.3.1. Study area

The study area for this work is located in the western South Atlantic Ocean, along the coasts of the Pernambuco and Alagoas states, in North-eastern Brazil (Fig 1). The local climate is sub-tropical, with temperatures ranging from 18 to 32 °C throughout the year (CPRH 2003, 2003a, Domingues et al. 2017). In this area, the continental shelf is ~35 km wide and has a maximum depth of 60 m near its break (Vital et al. 2010, Domingues et al. 2017). The coastal and shelf areas are characterized by the presence of numerous and relatively small estuaries across the shore and coral reefs patches in the inner and outer shelf (Paiva & Araújo 2010, Leão et al. 2016). They represent key habitats for many fish species exploited by fisheries and several other endemic and reef-associated ones (Vila-Nova et al. 2014, Aschenbrenner et al. 2016b, Eduardo et al. 2018).

Besides the fact that they are all colonized by juvenile *C. latus* each year (Ramos et al. 2011, Silva-Júnior et al. 2017, da Silva et al. 2018), the seven tropical estuarine systems investigated in this work

(Goiana, Santa Cruz, Suape, Sirinhaém, Rio Formoso, Santo Antônio and Mundaú-Manguaba) exhibit distinct morphological features and are subject to different freshwater inputs, resulting in varying environmental settings (Table 1).

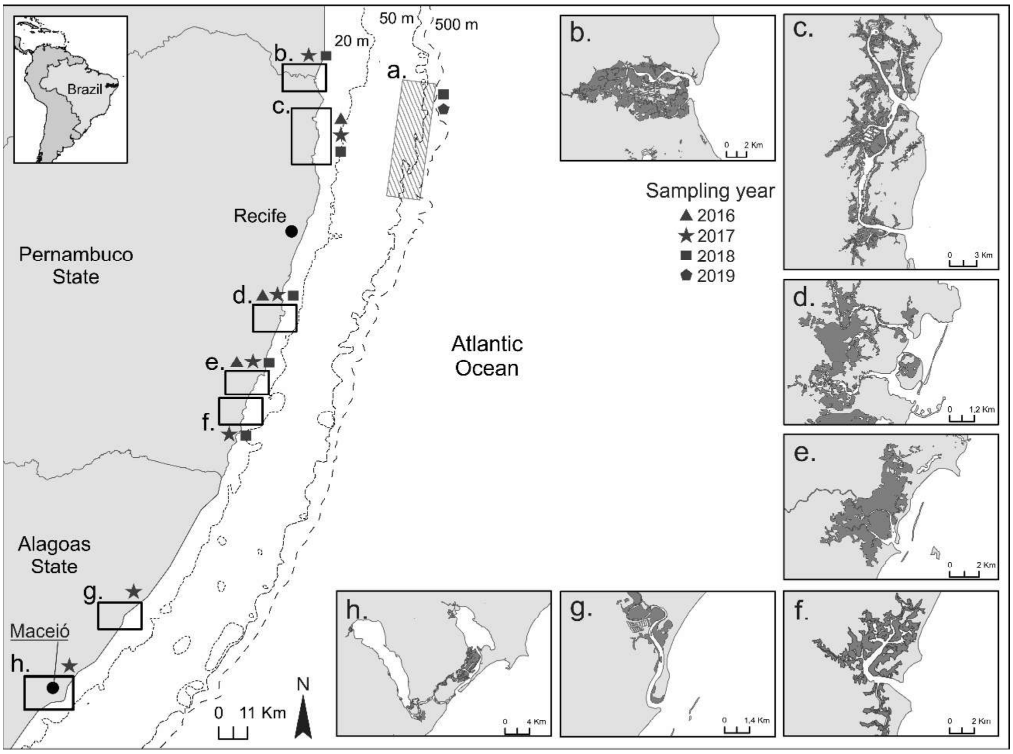


Figure 1 Fish sampling locations for this study. The offshore fishing area for *C. latus* (a) is indicated by the dashed rectangle. Inshore ones, i.e. the estuaries of Goiana (b), Santa Cruz (c), Suape (d), Sirinhaém (e), Rio Formoso (f), Santo Antônio (g) and Mundaú-Manguaba (h) are indicated by plain rectangles. The years when fish were captured in each location are represented by the different black polygons. Mangrove vegetation cover is shown in dark grey on the detailed view for each estuary.

Table 1 Morphological characteristics and environmental conditions (during the dry season) for the seven estuaries investigated along the North-eastern Brazilian coast.

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	3.1	2.6	4	-	2
N 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
Freshwater influence †	Important	Low	Low	Important	Low	Important	High
Salinity range ‡	4.2 – 36.4	24.0 – 37.0	30.0 – 37.7	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	27.2 – 31.7	27.0 – 33.4	27.0 – 29.5	28.0 – 31.0	25.0 – 31.0
Reference	(Medeiros & Kjerfve 1993, Oliveira & Kjerfve 1993, Medeiros et al. 2001, Honorato da Silva et al. 2004, Silva et al. 2009, Borges 2011, Costa et al. 2011, Otsuka et al. 2014, Lima et al. 2015, Gonzalez et al. 2019, Conti et al. 2020)						

† Freshwater influence, classification based on the amplitude of salinity range in middle and lower estuarine zones of each location: High. salinity lower than 25; Low, amplitude < 15; Important, amplitude >15. ‡ Salinity and temperature ranges during the local dry season along the middle and lower estuary.

Located in the northern part of the Pernambuco state, the estuaries of Goiana (GOI) and Santa Cruz (STC) have neighbouring hydrological basins and present high socio-economic and ecological importance (Medeiros et al. 2001, Barletta et al. 2009). While the estuary of Goiana only comprises a main river channel of 17 km long and its flooding area (Barletta et al. 2009), that of Santa Cruz is the largest estuary of Pernambuco's state and consists of a shallow U-shape channel, connected to the sea by two large entrances (Silva et al. 2011). Because the seawater inflow in the latter is high, the estuary is under a strong marine influence (Flores Montes et al. 1998, Figueiredo et al. 2006), and hypersaline conditions may occur during the driest months of the year (Medeiros & Kjerfve 1993).

The estuaries of Suape (SUA), Sirinhaém (SIR), and Rio Formoso (RIO) are all located on the southern part of the Pernambuco state (Fig 1). The former is formed by two rivers, which flow into a shallow brackish lagoon with limited connection to the sea, resulting in a strongly euryhaline system (Silva et al. 2019). The two other estuaries have similar hydrologic basins, yet, they differ in geomorphological and environmental characteristics. Located within two marine protected areas (CPRH 2003a), the Sirinhaém estuary gathers a variety of interconnected lagoons and channels and spreads on the shallow flood plain around the main bed of the Sirinhaém river, which constitutes its sole connection to the sea (CPRH 2003a). Conversely, the Rio Formoso estuary presents large tributaries and is under a greater influence from the marine environment (Silva et al. 2009).

Lastly, the estuaries of Santo Antônio (STA) and Mundaú-Manguaba (MM) are both situated in the Alagoas state. However, while the former is brackish and includes only a single small river, the latter is formed by two inland lagoons only connected to the sea through a single small channel. It is therefore largely oligohaline (Oliveira & Kjerfve 1993). Furthermore, it is under particularly high domestic and industrial contaminations because the Alagoas state's capital (Maceió) is positioned along its margins (Oliveira & Kjerfve 1993, Costa et al. 2011).

4.3.2. Fish sampling

A total of 143 young-of-the-year (YOY) of *C. latus* (56 -165 mm SL) were collected across the seven estuaries studied (b-h, Fig 1) between 2016 and 2019, using both beach seines (20 × 1.9 m, mesh 20 mm), trawled along the river banks, and block nets (350 × 2.9 m, mesh 70 mm) set close to mangrove creeks. All these juveniles were sampled during the local dry season, which spans between September to February (CPRH 2003), as it is when their densities in estuaries are the highest (da Silva et al. 2018). For simplification, all juveniles were all assigned to the year in which their dry season of capture started, *i.e.* the fish sampled between September 2016 and February 2017 were attributed to the same year (2016). For both the dry seasons starting in 2017 and 2018, up to 10 YOY with similar sizes were collected in each of the five estuaries (Goiana, Santa Cruz, Suape, Sirinhaém and Rio Formoso) spread along the coast of Pernambuco (Fig 1). These samples were complemented with 30 YOY captured in three of these estuaries (Santa Cruz, Suape and Sirinhaém) during the 2016 dry season, and with 14 YOY captured in the two estuaries located in the Alagoas state (Santo Antônio, *n* = 9, Mundaú-Manguaba, *n* = 5) during the 2017 dry season. In addition, 40 (sub)adults of the species, between 2 and 11 years old (317 - 750 mm SL, Gonzalez et al. *in prep.*), were obtained from artisanal fisheries operating on the continental shelf of Pernambuco between 2018 and 2019. All these specimens were captured by hand line fishing on the offshore reefs used as fishing spots by the artisanal fleet, at ~30 km from the coastline (Fig 1.a). Upon collection, all fish were identified following specific literature (Figueiredo & Menezes 1980, Smith-Vaniz 2002**),** measured (standard length – SL in mm) and stored frozen until further analysis.

4.3.3. Otolith preparation and elemental analysis

All the equipment used for otolith extraction and handling was acid washed in a 4% ultrapure nitric solution bath, rinsed in ultrapure water and set to dry in Class 100 laminar flow hood before use. Fish left sagittal otoliths were extracted using plastic tweezers, manually cleaned with ultrapure water to remove biological remains, sonicated for 5 minutes in separate clean vials filled with ultrapure water and set to dry under a clean class-100 laminar flow hood. The otoliths were then individually embedded in epoxy resin (Araldite 2020) 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 on the anterior side 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. Lastly, each of the final otolith sections was sonicated again for 5 minutes in ultrapure water (to decontaminate its surface), dried under the laminar flow hood and glued on a glass slide for further analysis.

All sections were photographed before and after their elemental 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- Physiks) coupled to an Element XR sector field ICPMS (ThermoFisher). To reduce the potential bias linked to variations in machine precision among analysis sessions, otoliths from different sampling locations and years were mixed on each of the analysis plate run in the LA-ICPMS system. For every otolith, the analysis was made in raster mode, along a transect following the maximum axis for otolith growth from the otolith core to its dorsal edge, thereby allowing to measure variation in otolith elemental composition throughout the fish's lifetime (Fig 2a, b). The laser beam diameter for this was set at 51 µm, and the laser was operated with an energy of 6 J/cm², a repetition rate of 7 Hz and at a speed of 20 $\mu m.s^{-1}$. The calibration of the machine and the control of the instrumental drift were made by analysing standard reference glass material (NIST 612) every five samples. Moreover, the analysis of an otolith certified reference material (MACS 3) at the beginning and the end each session of analysis was used for control of measurement quality among sessions. The calculations of the final otolith concentrations and the machine limits of detection (LOD) were made in the R software using the *ElementR* package (Sirot et al. 2017). Besides ^{43}Ca, which was used as a proxy of the otolith material ablated, a total of 22 chemical elements was analysed originally. However, only 10 of them (^{11}B, ^{138}Ba, ^{59}Co, ^{52}Cr, ^{65}Cu,

^{31}P, ^{85}Rb, ^{86}Sr, ^{66}Zn and ^{89}Y) had at least 25% of their measures above LOD in at least one of the habitat sampled and were therefore retained for subsequent analysis. All element concentrations were normalized to the respective concentrations of ^{43}Ca and 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.

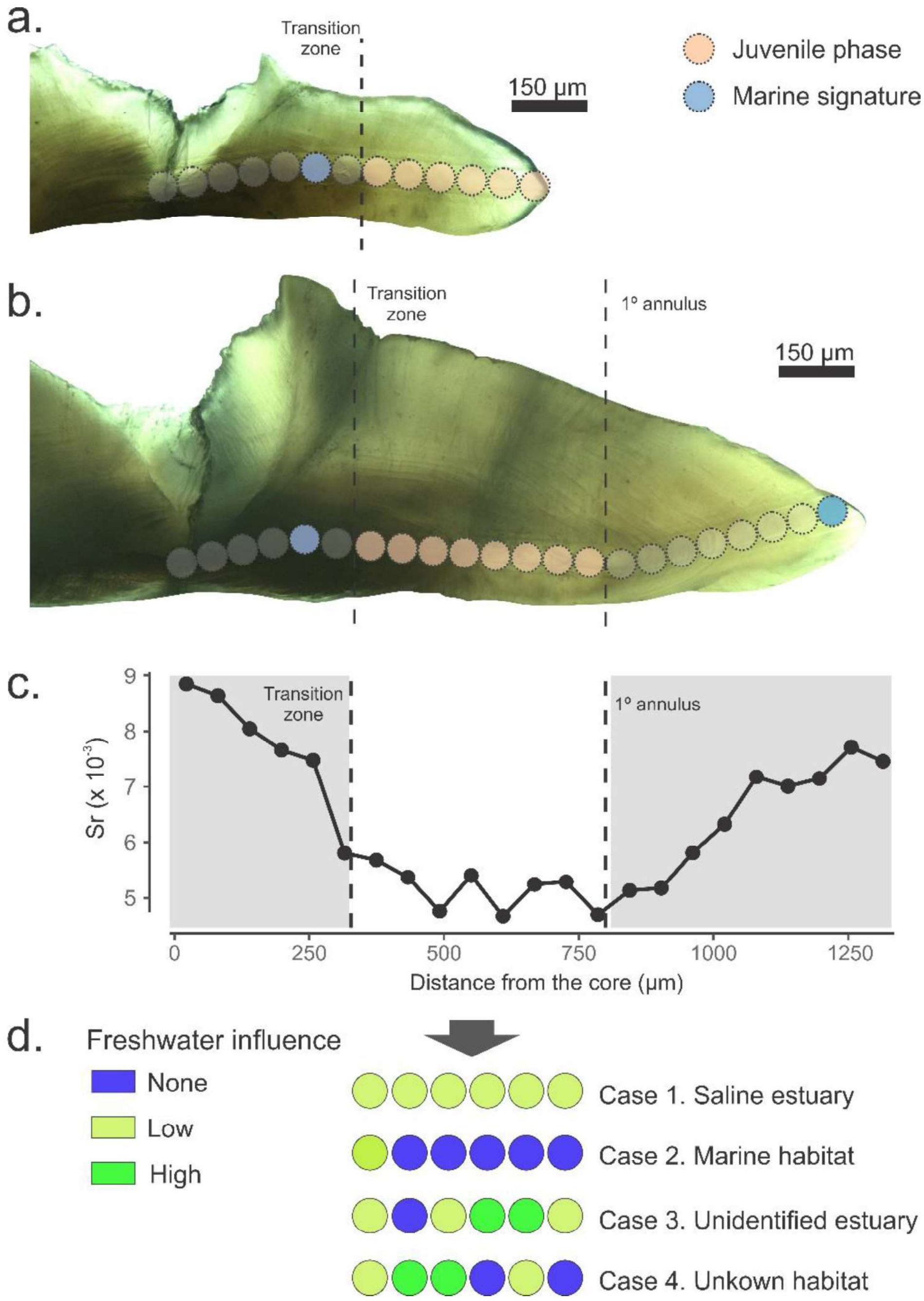


Figure 2 Otoliths sections (dorsal side, transmitted light) of a young-of-the-year (**a**) and a sub-adult (**b**) of *Caranx latus*, respectively captured in an estuary and at sea. In each case, the position of the raster analysed is indicated, together with that of the otolith structures (transition zone and first annulus) used for delineating the portions of the otolith reflecting the elemental signatures recorded during both the juvenile phase and the larval or adult life at sea. (**c**) Typical pattern of lifetime 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**) Illustration of the procedure for identifying past juvenile habitat in (sub)adult *C. latus*, based on the results of individual spot assignment using the Random Forest algorithm.

4.3.4. Signal treatment

To reduce autocorrelation bias in our otolith record of environmental signatures, the continuous record in otolith elemental concentrations obtained by each raster analysis was first filtered to retain solely sequential non-overlapping signatures (corresponding to adjacent spots of 51µm diameter) along the transect analysed. Then, the respective positions of the otolith zones corresponding to the larval, juvenile and adult phase (if any) for each fish were identified and the corresponding adjacent spots regrouped accordingly. For this, different structural marks in the otoliths were used. In the otoliths of *C. latus,* the central opaque zone extends up to 300-350 µm away from the core, with an inflexion of the otolith growth axis at its end (hereafter called transition zone, Fig 2a, b). This change in the density and structure of the otolith is observed in almost all the YOY found in local estuaries and probably reflect the change in physiology linked to their arrival in inshore systems (Gonzalez et al. *in prep*.). Examination of lifetime variations in the otolith concentrations in Sr, an element commonly used to discriminate environments under different salinity regimes (Sturrock et al. 2012), for every fish allowed to verify this assumption, bearing in mind that *C. latus* spawns offshore in the study area. As expected, in most of the otoliths analysed, Sr values decreased near the end of the transition zone, and remained low until the fish capture, except for the adult fish collected offshore, in which a later increase in Sr was observed after the first annulus (Fig 2c). This pattern was consistent with previous findings, which confirmed the annual deposition of annuli for *C. latus* in North-eastern Brazil, and demonstrated that its juveniles mainly inhabit local estuaries during their first year of life (Gonzalez et al. *in prep.*).Therefore, the position of the end of the transition zone and that of the first annulus along the transect analysed were used to delimit the portions of the otolith laid down during the larval life at sea (before the transition zone) and at the juvenile stage (after the transition zone and before the first annulus) during the first year of life in all the *C. latus* specimens studied. In the (sub)adults investigated, this latter portion of the transect comprised between 5 and 10 spots, depending on the individual.

In order to capture most of the spatio-temporal variability in elements concentration within each of the estuaries studied for building the dataset of otolith juvenile fingerprints, all the spots between the transition zone and the otolith edge (3 to 8 depending on the fish) were kept for each YOY analysed. To obtain otolith elemental signatures reflecting juvenile life at sea in *C. latus*, one single spot, corresponding to the last part of the larval life at sea (~200 µm away from the core), was selected on all the otoliths of the

YOY analysed (Fig 2a). This dataset for marine fingerprints was complemented with the otolith edge signatures (one single spot per fish) of all the (sub)adult fish below 400 mm SL (*n* = 13, age = 2 – 4 years), 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 (Figuerola-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 like gonad maturation (Sturrock et al. 2015).

4.3.5. Data analysis

4.3.5.1. Identifying local fingerprints

A total of 770 multi-elemental signatures, from 156 fish, were used to investigate the temporal stability of otolith fingerprints differences among locations. These comprehended the juvenile life of all YOY and the larval and sub-adult signatures selected as proxies for the sea (Table 2). Because the majority of the elements analysed did not meet the assumptions of normality and homoscedasticity, only non-parametric tests were applied. Spatial differences in elemental signatures were evaluated 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 differences observed. In addition, a principal component analysis (PCA) was performed on otolith multi-elemental signatures to illustrate the variability in fingerprints at each site. Temporal stability in the multi-elemental signatures between sampling years within each site was investigated by non-parametric permutational multivariate analyses of variance (PERMANOVA), based on the Euclidian distance of the *log(x+1)* transformed multi-elemental dataset. Moreover, PERMANOVA tests were applied for the locations (Goiana, Santa Cruz, Suape, Sirinhaém and Rio Formoso estuaries and the Sea) where fish were captured in more than one year. Whenever a site exhibited a significant inter-annual difference in otolith fingerprints, Mann-Whitney and Kruskal-Wallis tests, followed by *post hoc* comparisons (Dunn’s tests) when applicable, were applied to elucidate which elements contributed to the temporal differences observed.

Table 2 Mean (± SD) standard lengths (SL) of the 156 *C. latus* specimens used to build the dataset of estuarine and marine otolith elemental fingerprints in North-eastern Brazil. For each sampling site, the total number of otolith signatures gathered and the years of otolith records are indicated.

Region	Location	N. of fish	SL (mm)	N. of signatures	Year
Pernambuco state	Goiana (GOI)	20	104 ± 24	71	2017, 2018
	Santa Cruz (STC)	30	105 ± 9	137	2016, 2017, 2018
	Suape (SUA)	30	108 ± 11	140	2016, 2017, 2018
	Sirinhaém (SIR)	29	105 ± 20	122	2016, 2017, 2018
	Rio Formoso (RIO)	20	113 ± 6	100	2017, 2018
Alagoas state	Santo Antônio (STA)	9	69 ± 3	29	2017
	Mundaú-Manguaba (MM)	5	68 ± 11	15	2017
Sea	Larval life (Sea$_L$)	143	103 ± 18	143	2016, 2017, 2018
	Sub-adult (Sea$_A$)	13	353 ± 30	13	2018

A machine learning method, the Random Forest algorithm (RF, Breiman 2001), was applied to discriminate sampling sites based on the respective elemental fingerprints they leave in *C. latus* otolith. The advantage of the RF approach is that it does not require to match any assumption regarding the data distribution or normality (Breiman 2001). Moreover, it has proven very effective for discriminate fish habitats using otolith multi-elemental fingerprints (Mercier et al. 2011a, Tournois et al. 2017, Delerue-Ricard et al. 2019). Following Mercier et al. (2011), all the possible combinations of the 10 chemical elements retained after data pre-treatment (B, Ba, Co, Cr, Cu, P, Rb, Sr, Zn and Y) were tested, to identify that providing the best discrimination accuracy among the locations studied. For each element combination, 500 classification trees and 1000 iterations were used to assess the average overall discrimination accuracy of the RF classifier (Mercier et al. 2011). For this, 75% of the signatures were randomly selected to form a sub-dataset, which was used to train the RF with each possible combination of elements (RF classifiers). Then, the remaining 25% signatures were used for a cross-validation procedure to assess the accuracy of each RF classifier in re-assigning each sample to its known origin. After identifying the list of elements providing the best discrimination among locations (optimal RF classifier), the contribution of each element to the spatial discrimination was assessed by calculating the mean decrease in Gini Index (Breiman 2001) following its removal from the classifier. The higher its values for an element, the more this latter is essential for the discrimination. In addition, the respective accuracies and the True Skill Statistics (TSS, (Allouche et al. 2006)) for each location were calculated using the optimal classifier (based on 500 iterations). While the accuracy represents the average percentage of spots correctly reassigned to their actual location, the TSS represents a balance between the correct predictions and the errors in re-assignments. TSS range 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. It is calculated as $(ab-cd)/((a+d)\times(b+c))$, where a is the correct predictions of presence in re-assignment, b is the correct predictions of absence, c is the incorrect predictions of presence and d is the incorrect predictions of absence (Allouche et al. 2006).

The procedure described above was applied considering all juvenile potential habitats (*i.e.* the seven estuaries and the Sea) separately, but also after regrouping estuaries based on the similarities in their local environmental conditions revealed by the PCA. The results obtained with the two approaches were compared to identify the list of chemical elements and type of habitat grouping (optimal RF classifier) allowing the most accurate discrimination of the local juvenile habitats of *C. latus* based on its otoliths fingerprints.

4.3.5.2. Assignment (sub) adult fish

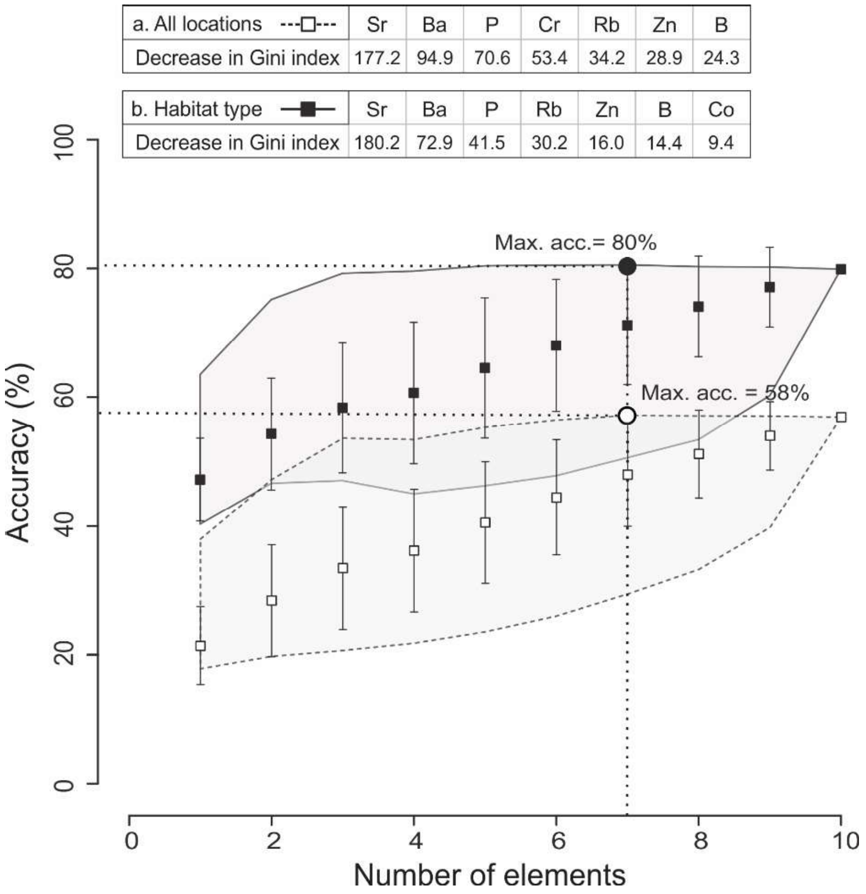
Once identified and validated, the optimal RF classifier (in terms of both element list and habitat grouping) was used to identify juvenile origin in the 40 (sub)adults captured offshore, based on the 307 multi-elemental signatures (5-10 depending on the fish) gathered from the juvenile portion in their otoliths. To limit errors in habitat assignment due to spatiotemporal variation in the environmental conditions experienced by individual fish during their juvenile life, and evaluate the reliability of the juvenile habitat prediction for each fish (Tournois et al. 2017), the most likely habitat of origin was predicted for each of the adjacent spot comprised in the juvenile portion of the otolith of a given fish (Fig 2d). An *a priori* limit of 70% of consistent spot assignment was used as the threshold to assign each fish to a given habitat. Similarly, fish was attributed to a past juvenile habitat type only when more than 70% of the spots for their juvenile phase were specifically assigned to it (Fig 2d, Case 1 and 2). Otherwise, they were assigned either to an unidentified estuary, when at least 70% of the spots for their juvenile phase were attributed to a mix of estuarine types (Fig 2d, Case 3), or to an unknown habitat, when spots in the juvenile phase were randomly assigned to any of the possible habitat types, resulting in similar assignments scores for all habitat types (Fig 2d, Case 4). All analyses were made in R software (R Core Team, 2021)

4.4. Results

Otolith elemental fingerprints in B, Ba, Co, Cr, Cu, P, Rb, Sr, Zn and Y from the 143 estuarine YOY and 40 (sub)adult *C. latus* specimens analysed in this work allowed identifying the optimal list of chemical elements for discriminating the estuarine and marine juvenile habitats of the species in North-eastern Brazil, assessing discrimination accuracies among locations and identifying past juvenile habitat for the (sub)adults stock exploited offshore in this area.

4.4.1. Spatial variation in elemental fingerprints

When all juvenile potential habitats were considered separately, discrimination accuracy was the highest when using only seven (B, Ba, Cr, P, Rb, Sr and Zn) of the 10 elements analysed (Fig 3). However, even when using this optimal RF classifier, the overall discrimination accuracy was low (58%) due to frequent errors in re-assignment among the estuaries studied (Table 3). Indeed, individual discrimination accuracy and TSS, in this case, were only high for the marine habitat (>94% and 0.94, respectively). Moreover, although 82% of the signatures for the lagoon system of Mandaú-Manguaba were correctly re-assigned, average accuracies 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), which suggested a random re-assignment of otolith signatures among several estuarine sites.



a. All locations ---□---	Sr	Ba	P	Cr	Rb	Zn	B
Decrease in Gini index	177.2	94.9	70.6	53.4	34.2	28.9	24.3

b. Habitat type —■—	Sr	Ba	P	Rb	Zn	B	Co
Decrease in Gini index	180.2	72.9	41.5	30.2	16.0	14.4	9.4

Figure 3 Effect of the number of elements included in the Random Forest procedure on the discrimination accuracy among (**a**) the seven estuaries and the Sea, and (**b**) the type of estuarine habitat (brackish, saline and the Mundaú-Manguaba lagoon system) and the Sea. The maximum accuracy obtained for the optimal RF classifier in each case is indicated (dotted lines). For each size combination and RF classifier, the minimum and maximum accuracies obtained are shown by the grey area, while the mean (± SD) is indicated by the squares. The list of elements selected for each optimal RF classifier are presented in the tables and according to their mean decrease in Gini Index.

Table 3 List of elements retained, cross-validation contingency table and True Skill Statistics (TSS) per juvenile habitat in the Random Forest classifier allowing to reach maximum discrimination accuracy (58%) among all sampling locations. Correct assignments in the contingency table are shown in bold.

Location (B, Ba, Cr, P, Rb, Sr, Zn)

		Origin							
		GOI	STC	SUA	SIR	RIO	STA	MM	Sea
Assignment (%)	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

These errors in re-assignment were mainly due to the fact that otolith multi-elemental signatures were highly variable for all habitats, and largely overlapped among estuaries (Fig 4). Hence, the first plan of the PCA, illustrating 47.1% of the total variance in multi-elemental composition (mostly driven by otolith signatures in B, Cr, P, Rb and Zn along PC1, and in Sr and Ba along PC2, Fig. 4b) revealed contrasted otolith signatures solely for the Sea and the Mundaú-Manguaba estuary (Fig 4a). The fact that Sr was the element contributing most to the discrimination among all sampling sites (mean decrease in Gini Index of 177.2) was mainly due to the significantly higher ($p < 0.001$) otolith Sr values fact that observed for the Sea (Fig 5). Sr values also varied among estuarine habitats but were surprisingly significantly higher ($p < 0.012$) in Sirinhaém (5.63 ± 0.43 mg.g^{-1}), and Goiana (5.42 ± 0.46 mg.g^{-1}) than at sites under stronger marine influence Rio Formoso (5.19 ± 0.50 mg.g^{-1}) and Santa Cruz (4.95 ± 0.46 mg.g^{-1}, Fig 5). Ba was the second element contributing most to the spatial discrimination (mean decrease in Gini Index of 94.9), mainly due to significantly higher mean Ba concentrations ($p < 0.031$, Fig 5) in the brackish estuaries of Sirinhaém (1.19 ± 0.94 µg.g^{-1}) and Goiana (1.05 ± 0.70 µg.g^{-1}) and at the Sea (0.88 ± 0.24 µg.g^{-1}). The remaining chemical elements also contributed to the spatial discrimination but to some minor extent (Fig 5). In particular, the significantly higher ($p < 0.014$) Rb concentrations (342.92 ± 104.37 pg.g^{-1}), and the absence of signal above the LOD for B in the Mundaú-Manguaba estuary (Fig 5) both contributed to the discrimination of this estuarine habitat (Fig 4) and underpinned 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 despite their high variability at most sites.

Despite the high overlap in otolith multi-elemental signatures for most estuaries, the positioning of their centroids on the first plan of the PCA (Fig. 4) indicated that similarity in otolith signatures among them were mostly based on their respective degree of freshwater influence, irrespective of their geographical proximity (Fig 4a). This, supported grouping them according to an increasing gradient in freshwater influence (low to high, Table 1), resulting in three estuarine habitat types: saline (Santa Cruz, Suape and Rio Formoso) or brackish ones (Goiana, Sirinhaém and Santo Antônio) and the lagoon system of Mundaú-Manguaba (MM). Despite that the Mundaú-Manguaba system can be characterized as a brackish estuary, it accounted for unique otolith signatures and was considered as a separate estuary group (MM). The second plan of the PCA (combining PC2 and PC3 and representing 30.3% of the total variance) confirmed this pattern, further illustrating the differences in multi-elemental signatures between the brackish estuaries and the Sea (Fig 4c).

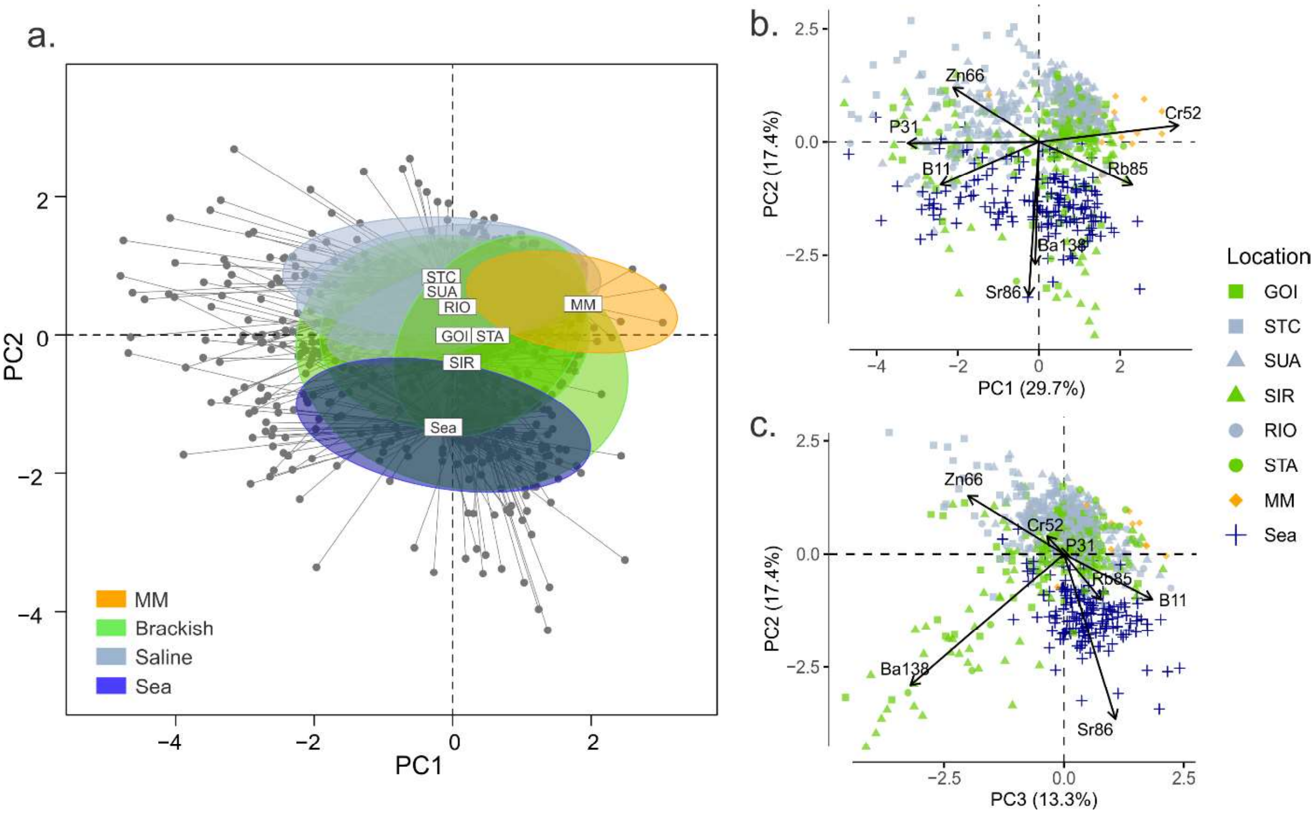


Figure 4 Score plots for the first three principal components (PC1, PC2 and PC3) of the PCA based on the 770 otolith multi-elemental signatures (from 156 individuals) gathered for the eight juvenile habitats of *C. latus* investigated in North-Eastern Brazil. Projection of the position of the juvenile elemental signatures for all habitats on the plan PC1 × PC2 (**a**). For each habitat, the position of the centroid is indicated in the white box (see Table 1 for habitat acronyms). Projections of the correlation for all the variables (elements) driving the distribution of multi-elemental signatures in the plan PC1 × PC2 (**b)** and plan PC2 × PC3 (**c)**. The black arrows represent the correlation of each variable (element) with the two respective principal components. Colours represent the three types of estuaries and the Sea.

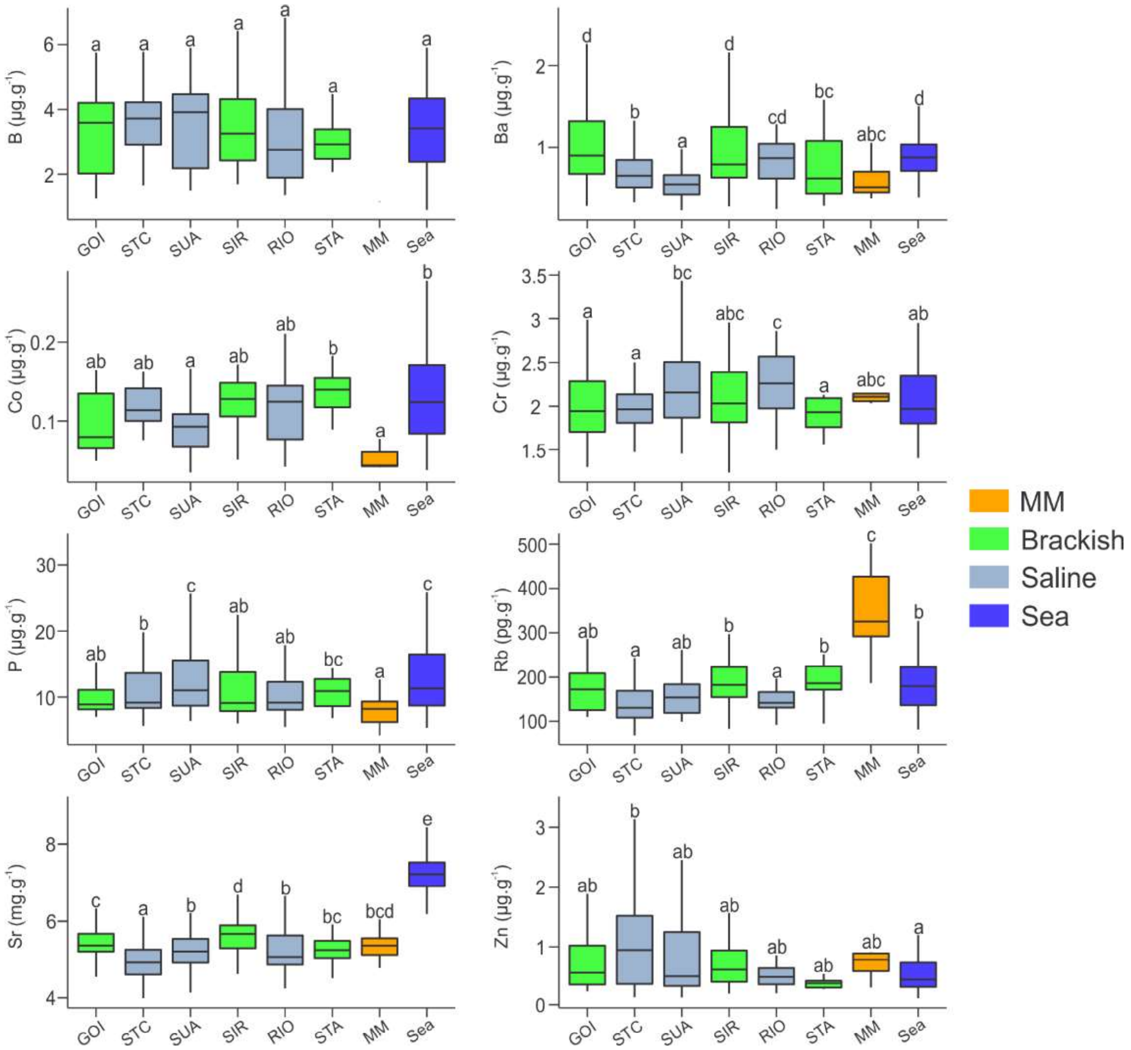


Figure 5 Boxplot of elemental fingerprints recorded in the otoliths of *C. latus* during life in the seven estuaries studied and at Sea (see Table 2). Elemental signatures for the Sea include those recorded during the larval life (Sea$_L$) and the otolith edge signature of sub-adult specimens captured at sea (Sea$_A$). Elements concentration 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. Colours represent the three types of estuaries (brackish, saline and the Mundaú-Manguaba lagoon system) and the sea.

Regrouping estuaries based on their similarities in environmental conditions, to consider only three big types of estuarine habitats (brackish, saline and the Mundaú-Manguaba lagoon system) and the Sea allowed to increase overall discrimination accuracy to 80%, but changed the composition of the RF classifier by replacing Cr by Co in the list of optimal elements (Fig 3, Table 4). Differences in elemental compositions among estuary types largely reflected those found when considering all locations separately.

As expected, Sr and Ba were still the most important elements in the discrimination, with respective decreases in Gini Index of 180.2 and 72.9 (Fig 3). This was due to the fact that, on average, mean Sr and Ba were significantly higher ($p < 0.001$) in brackish lagoons (5.51 ± 0.45 $mg.g^{-1}$, 1.13 ± 0.86 $\mu g.g^{-1}$, respectively) than in saline ones (Sr: 5.11 ± 0.48 $mg.g^{-1}$; Ba: 0.68 ± 0.27 $\mu g.g^{-1}$).

Table 4 List of elements retained, cross-validation contingency table and True Skill Statistics (TSS) per juvenile habitat type in the Random Forest classifier allowing to reach maximum overall discrimination accuracy (80%) among the three retained estuarine habitat types (brackish, saline and the Mundaú-Manguaba lagoon system - MM) and the Sea.

Estuary type (B, Ba, Co, P, Rb, Sr, Zn)

		Origin			
		Brackish	Saline	MM	Sea
Assignment (%)	Brackish	**70.10**	19.47	5.26	2.43
	Saline	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

This new grouping allowed to reach a discrimination accuracy above 70% for all potential juvenile habitat types (Table 4), although corresponding TSS did not surpass 0.64. Errors in re-assignment were still observed, especially among the brackish and saline estuary groups, with more than 19% of the signatures from the saline estuaries incorrectly re-assigned to the brackish one (19.47%), and vice versa (25.30%). These errors were probably linked to the high amplitude of elements concentration found across locations. In particular, the average difference in Sr signature between brackish and saline estuaries (~0.40 $mg.g^{-1}$ in mean values) was relatively small, although significant ($p < 0.001$). Re-assignment accuracies for the estuary of Mundaú-Manguaba (*i.e.* the single-estuary habitat type, 88%) and the Sea (95%) remained roughly the same, indicating that they hold unique elemental fingerprints that contrast with other coastal environments in North-eastern Brazil. The slight increase in the discrimination accuracy of these two latter habitat types with this new classifier was partly due to the addition of Co, for which signatures were significantly higher at Sea (0.13 ± 0.05 $mg.g^{-1}$) than in the Mundaú-Manguaba estuary (0.05 ± 0.02 $mg.g^{-1}$,

$p = 0.039$). This element did not however contribute to the discrimination of the brackish and saline estuaries, as Co signatures were similar between these two habitat types ($p = 0.179$).

4.4.2. Temporal variation in elemental fingerprints and prediction of adult habitat origin

A partial bias in the otolith fingerprints database for some of the juvenile habitat types investigated cannot be excluded due to our uneven sampling design (Table 2). Indeed, as both the Santo Antônio and Mundaú-Manguaba estuaries were only sampled in one year (2017), the temporal stability in their elemental fingerprints in B, Ba, Co, P, Rb, Sr and Zn (*i.e.* in the elements included in the optimal RF classifier for discriminating the four types of potential juvenile habitats) could not be evaluated. However, for the Sea, significant differences in otolith fingerprints were found for 2018 ($p < 0.001$), with higher Sr ($p < 0.001$), Cr ($p < 0.001$) and Ba ($p = 0.048$) signatures in that year, while otolith compositions in Zn ($p < 0.001$) and P ($p = 0.002$) showed the opposite trend. Inter-annual variation in otolith signatures was also significant for saline estuaries ($p = 0.001$), with significant differences in Sr ($p < 0.001$), P ($p < 0.001$), Rb ($p = 0.001$), Co ($p < 0.001$) and B ($p = 0.018$). It was mainly due the inter-annual variation found in both Suape ($p = 0.012$) and Rio Formoso ($p = 0.001$) estuaries. In particular, significantly higher Sr values ($p < 0.005$) were observed in 2017 (5.35 ± 0.44 µg.g^{-1}, $p < 0.001$) than in 2016 (5.08 ± 0.47 µg.g^{-1}) and 2018 (4.95 ± 0.44 µg.g^{-1}). Suape showed significantly different multi-elemental fingerprints for 2017 ($p < 0.009$) but not for the remaining years (2016 and 2018, $p = 0.474$). In both locations, higher concentrations of P ($p < 0.001$) and Cr ($p < 0.001$) were found in 2017 and 2018, respectively. Moreover, lower values in Zn ($p = 0.004$) were found in 2018 at Rio Formoso. Lastly, inter-annual differences in otolith multi-elemental signatures were not significant for the brackish estuarine habitats ($p = 0.372$), but they were probably partially obscured by the high intra-annual variability in the otolith signatures observed in both Goiana and Sirinhaém.

Despite this limitation, the assignment of the 307 juvenile multi-elemental signatures recorded in the otoliths of the (sub)adult fish to the four juvenile habitat types identified revealed an important variability in juvenile habitat origin for the *C. latus* specimens fished offshore the Pernambuco state (Fig 6). Surprisingly, no fish in this adult sample was assigned to the estuary of Mundaú-Manguaba, despite the unique elemental fingerprints found for this latter. In turn, the majority of the specimens analysed (75%) were found to have spent their first year of life in a local estuary. Saline estuaries seemed to be the main juvenile habitat source for the fish captured offshore (32.5%), whereas only 12.5% of them had spent their first year in a brackish estuary (Fig 6). Moreover, 30% of the (sub)adults analysed exhibited a dominant mixture of saline and brackish estuarine fingerprints and were therefore assigned to an unidentified type of estuary. In total, 20.2% of the 307 multi-elemental fingerprints recorded in the juvenile part of the otoliths of the (sub)adult fish were assigned to the Sea. However, only very few fish (5%) were purely assigned to the marine habitat during their first year of life (Fig 6). Indeed, most of these marine signatures were observed in the fish assigned to an estuary; as they were usually observed at the end of the juvenile transect, representing 1-2 individual spot signatures before the annulus for most fish, they were assumed to reflect fish return at sea at the end of their first year. However, 20% of the fish exhibited a complex mixture of marine and varied estuarine elemental signatures during their juvenile life. They were therefore assigned to an “unknown" juvenile habitat.

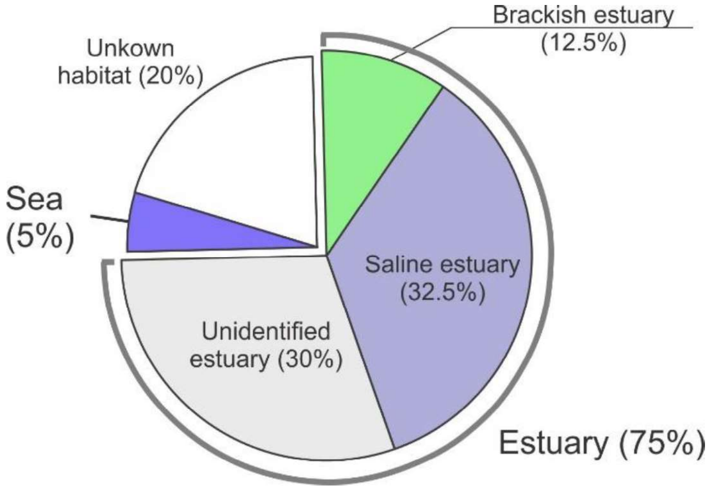


Figure 6 Relative contribution of juvenile habitats to the exploited population of *Caranx latus* in North-eastern Brazil.

4.5. Discussion

Assessing the connectivity between fish costal habitats and their respective importance in supporting exploited populations is key to delineate fishery management and conservation strategies (Nagelkerken 2009, Sheaves et al. 2015). This study provides valuable insights on this matter by elucidating the use of inshore habitats by an exploited yet poorly studied fish species in North-eastern Brazil. Although the elemental fingerprints in the estuaries studied largely overlapped, they were fairly different from the sea. Otolith elemental compositions of (sub)adult fish revealed that a considerable part of the *C. latus* specimens fished off the shore of the Pernambuco state inhabit local estuaries during their first year of life, suggesting that these habitats may play a significant role in sustaining the local exploited stock.

4.5.1. Spatiotemporal variations in elemental fingerprints

Re-assignment accuracy was the highest (94-95%) for the sea, regardless of the RF classifier selected and despite the strong marine influence in the seven estuaries studied (Table 1). This discrimination efficiency was mainly due to the contrasting Sr values recorded in *C. latus* otoliths during their life at sea. Indeed, significantly higher otolith Sr values were found both in the portion of the otolith representing the larval life and on the otolith edge for the (sub)adult fish at the sea, probably in link with the higher salinities found at sea (Kafemann et al. 2000, Sturrock et al. 2012, Izzo et al. 2015). This supports the reliability of Sr for evaluating lifetime migrations of *C. latus* among marine and inshore coastal habitats in North-eastern Brazil, as already suggested by previous studies with other migratory fish species (Aschenbrenner et al. 2016a, Santana et al. 2018). On the other hand, although Ba is commonly used to reconstruct fish migrations across transitional environments (Elsdon & Gillanders 2005, Walther & Thorrold 2006, Sturrock et al. 2012), in the present work, it was better suited for distinguishing among the estuaries studied than between estuarine and marine environments. However, while Ba concentrations in the portion of the otolith representing the larval life at Sea were globally similar to those recorded in the estuaries, they were significantly lower on the edge of the otoliths of the sub-adults captured offshore (0.57 ± 0.16 $\mu g.g^{-1}$). This signal was compensated by high Ba concentrations in the portion corresponding to larval life in all fish (0.91 ± 0.22 $\mu g.g^{-1}$), similar to those observed in brackish estuaries. This could indicate that *C. latus* post-larvae inhabit nearshore reefs under freshwater influence before entering the estuaries, as observed in several coral reef species (Hamilton & Warner 2009). However, physiological processes during the early stages of life can modulate Ba incorporation in the otolith (*e.g.* Hicks et al. (2010) and Miller (2011)), where a negative effect of fish somatic growth on Ba uptake has been reported (Miller 2011, Hüssy et al. 2020). This likely to happen in *C. latus* because Ba concentrations continuously decreased from the larval to the juvenile portion of the otoliths while the opposite would be expected during fish colonization of estuaries. However, Ba incorporation might also be affected by more complex processes such as salinity, temperature, growth and the mixed effects of all of them (Sturrock et al 2012, Izzo et al. 2018, Hüssy et al 2020).

The characteristics of specific regions or hydrological basins often yield unique fingerprints as element loads are likely to vary among locations (Moore & Simpfendorfer 2014, Delerue-Ricard et al. 2019). However, in our case, otolith elemental compositions of *C. latus* juveniles largely overlapped among the estuaries studied. Interestingly, distant locations (*e.g.* Goiana and Sirinhaém estuaries) had more similar otolith fingerprints than neighbouring ones (*e.g.* Goiana and Santa Cruz). Environmental conditions, in particular in terms of hydrological regime, seemed to largely drive differences in elemental fingerprints of estuaries. Sr and Ba, which are commonly used to discriminate environments under different salinity regimes (Miller 2011, Sturrock et al. 2012), were the main drivers distinguishing the studied locations. However, while Sr signatures for the estuaries sampled were more variable and notably lower on average than those recorded at sea, differences among estuarine sites were low. Surprisingly, brackish estuaries had significantly higher Sr concentrations on average than saline ones, which contrasts with the usual trend observed among estuarine environments (Miller 2011, Sturrock et al. 2012, Izzo et al. 2015). This suggests that other factors, alongside the chemistry of waterbodies, may intervene in the incorporation of Sr. One possible cause for this is the effect of temperature on Sr uptake. Indeed, under high temperature scenarios, Sr uptake and incorporation in the otoliths may decrease with increasing salinity (Webb et al. 2012). This might be the case in the Santa Cruz, Suape and Rio Formoso estuaries, which exhibited the lowest average Sr values in our study area despite their elevated salinity ranges (Table 1). In turn, in accordance with previous studies (Elsdon & Gillanders 2005, Gillanders 2005, Sturrock et al. 2012), the estuaries under strong freshwater influence, like Goiana and Sirinhaém showed higher Ba concentrations. The only exception was the lagoon system of Mundaú-Manguaba, for which Ba signatures were intermediate despite very low minimum salinities (Table 1). This might be due to the low number of fish collected at this site. However, this latter was characterized by markedly distinct otolith elemental fingerprints, in particular Rb concentrations. Although the main drivers for Rb uptake in fish otoliths are not yet fully understood (Sturrock et al. 2012), previous studies suggest that it might be linked to local freshwater inputs (Hicks et al. 2010). As the estuaries under important freshwater influence in this work tended to show higher Rb concentrations (Fig 5), high freshwater inputs might explain the particularly high Rb otolith values observed for the Mundaú-Manguaba estuary, which was the only oligohaline environment investigated. This hypothesis is in apparent contradiction with the low otolith Ba concentrations observed for this latter site. However, other environmental features might explain the particularity in the otolith signatures recorded in the Mundaú-Manguaba estuary. Indeed, among all the estuaries studied, it is the sole to experience eutrophic conditions during the dry season, as a result of high domestic and industrial nutrient loads and low water exchange with the sea (Oliveira & Kjerfve 1993). Stecher & Kogut (1999) found a rapidly, and nearly complete, removal of dissolved Ba in the water following seasonal algal blooms in a temperate estuary. Therefore, the low Ba concentrations observed in *C. latus* otoliths in this lagoon could be somehow associated with its eutrophic status, in an analogous way to what has been suggested for bivalve shells

(Thébault et al. 2009). Although the exact processes modulating water chemistry in the Mundaú-Manguaba are not fully understood, it is possible that the unique elemental fingerprints in this estuary result from a mix of environmental and anthropogenic factors.

Reliable reconstruction of fish life history using otolith microchemistry requires that differences in elemental fingerprints among 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 observed in these environments usually result in fluctuating chemical fingerprints within otoliths (Elsdon & Gillanders 2006, Walther & Thorrold 2009). In this study, inter-annual stability in otolith signatures was relatively high within estuaries, and only two estuaries (Suape and Rio Formoso) presented significant temporal shifts in their otolith signatures. Because these were similar and concerned the same year (2017), they may reflect similar responses to inter-annual changes in local environmental conditions. In Suape, otolith elemental compositions were similar for the two other years investigated, which supports the reliability of the otolith elemental fingerprints obtained in this study to identify the juvenile origin for (sub)adults of *C. latus.* Juvenile sampling for this study occurred at the end of the dry season, *i.e.* after several months during which the marine influence is the strongest in all estuaries. However, given juvenile jacks in these environments can be found earlier in the late rainy season (Gonzalez et al. 2021), it is likely that the juvenile portions of the otoliths analysed also included some elemental signatures deposited during periods of high freshwater inputs. This explains the highly variable otolith elemental signatures observed for some locations, especially in the brackish ones and probably blurred inter-annual differences in average fingerprints at each site. However this use of sequential otolith signatures increases the inter-annual stability of the elemental fingerprints database by covering most of the spatio-temporal variability in elements recorded within the estuarine juvenile life of specimens (Tournois et al. 2017).

4.5.2. Contribution to coastal fisheries

Estimating the relative importance of varied nursery grounds for stock recruitment implies that all potential juvenile habitats are considered and adequately characterized (Campana 1999). In this study, elemental signatures from *C. latus* pelagic larval life at sea and from the otolith edge of young sub-adults captured offshore were used as a proxy of those of the marine habitats occupied by the species' juveniles, like sandy beaches and nearshore shallow reefs (Mazzei et al. 2011, Silva et al. 2011, Medeiros et al. 2017), since these latter could not be sampled. Because these signatures might not reflect the life in these specific areas, we might lack some specific elemental fingerprints linked to the species' marine habitats, *e.g.* the unique concentrations in Ba or in other elements observed on some coral reefs (Hamilton & Warner 2009). Nevertheless, the juvenile part of the otolith of a few of our adult sample were assigned to the sea, suggesting that at least some of the local juvenile marine habitats have been correctly characterized in our analysis. Moreover, a particular subset of offshore fish (20%) were attributed to an unknown habitat as they exhibited a balanced mixture of elemental signatures, assigned to several estuaries and the sea. As in any other classification approach, errors in fish assignment may arise since otolith signatures are all allocated to one of the previously determined classification subsets (Campana 1999, Tournois et al 2017). However, the use of sequential elemental signatures allows to reduce this error by assigning fish to a unknown location when they present a mixture of signatures attributed to two or more habitats analysed (Tournois et al. 2017). This subset of offshore adults could thus reflect the fact that some *C. latus* individual might inhabit several estuaries for short periods of time during their juvenile life and performed varying migrations across the inshore areas of North-eastern Brazil (*e.g.* Schilling et al. (2018)), but could also indicate residency in an habitat not described in our juvenile fingerprints dataset. In this latter case, the 20% fish that were not reassigned to any habitat in this work might have grown at Sea, either offshore the states sampled or in other areas along the Brazilian coast.

Previous studies have highlighted the value and versatility of the RF algorithm for identifying fish past habitats using otolith elemental fingerprints from different life stages (Tournois et al. 2013, Delerue-Ricard et al. 2019), both in temperate (Mercier et al. 2011, Tournois et al. 2017, Prichard et al. 2018) and (sub)tropical regions (Paillon et al. 2014, Teichert et al. 2018). Here, the overall accuracy obtained with the optimal RF classifier (80%) is in the range of the values found by these authors and confirms the value of this approach for identifying juvenile habitats for tropical coastal fishes. Moreover, the use of sequential elemental signatures offers the advantage of identifying habitats within ranges of those described in the juvenile fingerprints dataset, such as for estuaries, and reduce the probability of generating false positives for a given location (Tournois et al. 2017). This was the case for a considerable part of offshore fish attributed to an unidentified estuary, *i.e.* those that exhibited a mixture of saline and brackish elemental signatures (30%). In view of the numerous small estuaries spread along the North-eastern Brazilian coast, up to 15 only in the Pernambuco state (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. Surprisingly, no individual element signature was attributed to the Mundaú-Manguaba estuary, the southernmost location investigated, indicating that there may exist some geographical or hydrological constraints on the contribution of estuaries to the offshore population of *C. latus* in Pernambuco.

Overall, estuaries were found to be the local juvenile habitats contributing most to the *C. latus* exploited population, with 75% of the specimens analysed originating from one of them. This indicates that *C. latus* might help export the organic matter produced in these inshore habitats, acting as a biological vector linking distinct coastal environments across the shelf, like other transient estuarine fish (*e.g*. Oliveira et al. (2014) and Pelage et al. (2021)). Although the duration of the estuarine life for *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 the most variable (Gonzalez et al *in prep*.). As such, estuarine use by the juveniles of *C. latus* may have important consequences in terms of organic matter transfer from the continent to the sea. These results, complement what was known on the local ecology of the species, but further highlight that inshore environments play a key role in the maintenance of its stocks.

Among the estuaries studied, those under stronger marine influence (*i.e.* the saline ones) showed to have greater relative contributions to the exploited stock (32.5%), which is in accordance with the ecology of the species, described as a marine migrant (Elliott et al. 2007). Brackish estuaries and juvenile habitats at sea had notably lower contributions, of 12.5% and 5% respectively. Even when considering that part of fish attributed to an unidentified estuary (30%) or an “unknown habitat” (20%) came from these environments, saline estuaries still surpassed the other juvenile habitats in terms of *C. latus* juvenile provision. This is probably partly due to the fact that juvenile *C. latus* present faster growth rates at these locations (Gonzalez et al *in prep*.), and occur in higher numbers in at least some of them, suggesting that saline estuaries might provide better environmental conditions for juvenile survival and growth in the species. However in deep and complementary studies are needed before one can conclude about the actual factors underpinning the importance of different estuarine settings for *C. latus* population in this area, as they may comprehend both biological and environmental constrains that affect the life condition of juveniles (Vasconcelos et al. 2009, Isnard et al. 2015, Litvin et al. 2018).

Much has been done that Beck et al. (2001) formalized the concept of nursery ground and provided a comprehensive description of when a habitat should be considered as such. Following this definition, habitats may be considered as nursery grounds if they allow the juveniles of a given species to occur at higher densities or to benefit from (biological) processes that enhance their survival (Beck et al. 2001).

However, our understanding on the role of coastal habitats for fisheries and the drivers of this function still requires further improvement (Nagelkerken et al. 2015, Litvin et al. 2018, Lefcheck et al. 2019). With these regards, only a few offshore adult specimens are expected to rely on juvenile habitats at Sea and (5%), even when considering that part of fish attributed to an “unknown habitat” (20%) can also have grown at Sea, it is still inferior to the 75% of fish originating from the estuaries and indicate that estuarine habitats might provide better life conditions for juvenile *C. latus*. In theory, this suggests that estuaries could be characterized as nursery grounds for *C. latus* (Dahlgren et al. 2006). However, the similarity in otolith elemental signatures of juvenile *C. latus* among estuaries studied hampered our capacity to correctly discriminate them, and thereby, a more precise estimate of the contribution of each location. Further studies using different chemical element or more detailed approaches may help fulfil this gap by comparing the results obtained here with other criteria that take into account the area of the estuaries to estimate their value as juvenile habitats (*e.g.* Beck et al. (2001)). This information is essential for improving local fishery management and conservation strategies like the design and evaluation of marine protected areas along the coast, for *C. latus* but also other species that undergo through ontogenetic migrations across the shelf (Aschenbrenner et al. 2016).

4.6. Conclusion

This study provides valuable knowledge on the local variation in life strategies for an exploited yet poorly studied tropical fish species. The analysis of otolith chemistry of juvenile and adult individuals of *C. latus* indicates that, like in other coastal and reef species, estuaries may play a significant role in the maintenance of the population of the crevalle jack in North-eastern Brazil. Indeed, up to 75% of the adult of the species fished offshore seem to have spent their first year of life in one of these inshore environments. However, the variation observed in the contribution of estuaries according to their environmental conditions indicate that the value of estuaries is not homogenous and local environmental settings modulate their respective quality as juvenile habitats. These findings are key for improving local fishery but also ecosystem management, especially given the recurrent anthropogenic pressures to which estuarine habitats are subjected to. These latter threaten estuary quality for juvenile fish growth and survival, with potential implications on stock recruitment success. Furthermore, the unexpected responses to local environmental settings found for some chemical elements (*e.g.* Sr and Ba) in this study reinforce previous calls for a more comprehensive investigation of the factors influencing element uptake and composition in fish otoliths (Reis-Santos et al. 2018), particularly in the tropics.

4.7. IN A NUTSHELL

- Multi-annual otolith elemental fingerprints were assessed for the main potential juvenile habitats for *C. latus* in North-Eastern Brazil, namely seven estuaries spread along the coast and the sea.
- Habitat fingerprints mainly differed in terms of Strontium (Sr) and Barium (Ba) concentrations, but Phosphorus (P), Chromium (Cr), Rubidium (Rb), Zinc (Zn), Bromium (B) and Cobalt (Co) also contributed to discriminate locations.
- Differences in otolith elemental fingerprints were maximum between the estuaries and the sea, particularly due to noticeably higher Sr values at sea.
- Elemental fingerprints largely overlapped for most of the estuaries studied, resulting in a low overall habitat discrimination accuracy (58%). Grouping estuaries according to their level of freshwater influence however allowed increasing it up to 80%.
- Otolith elemental compositions of the juvenile portion of the otoliths of large *C. latus* specimens from offshore fisheries revealed that most of them (75%) spend their first year of life in local estuaries, particularly those under the stronger marine influence (32.5% of the fish analysed).
- This indicates that estuaries play a prominent role in the maintenance of the local exploited stock of *C. latus*, acting as nursery sites for the species in North-Eastern Brazil.

This third research axis contributed to the general question of this thesis by evaluating the importance of estuaries for the *C. latus* population exploited in North-Eastern Brazil. Given the considerable part of fish that originate from a local estuary, these habitats could be considered as nursery grounds in this area. However, in agreement with the results from CHAPTER 2 and 3, the results obtained here indicate that estuaries are not equivalent: local variations in environmental or biological settings likely modulate their value as nursery grounds for *C. latus*.

CHAPTER 5: General discussion

Estuaries and other transitional coastal habitats are nursery grounds for a large number of marine species (Nagelkerken et al. 2008, Sheaves et al. 2015). Understanding how these habitats support the adult populations of exploited fish species is key to maintain marine fishery resources and forecast their evolution in future scenarios. In this study, combining natural tags (stable isotopes and otolith microchemistry) and empirical techniques (*e.g.* stomach content analysis and sclerochronology) allowed to (i) uncover the life-history traits of an exploited yet poorly studied jack species and (ii) highlight the importance of coastal estuaries for the maintenance of the population of this marine fish in North-Eastern Brazil. The results obtained indicate that *C. latus* specimens can reach up to 22% of their final size by the end of their first year of life but may live up to 13 years old (CHAPTER 2) . Moreover, they reach sexual maturity when 2-3 years old, *i.e.* only one year after they enter the local exploited stock. Thus, the local population is under the threat of an increasing fishing pressure targetting its individuals before they are even able to reproduce (Pelage 2020). This not only affect the local stock renewal, but probably also the functioning of local food webs, in which *C. latus* play a key regulating role (Lira et al. 2018). This study also revealed that estuaries unexpectedly play a predominant role in the maintenance of the *C. latus* population in North-Eastern Brazil (CHAPTER 4). The information gathered confirmed previous reports of the presence of *C. latus* juveniles in local estuaries (Figueiredo & Menezes 1980, Smith-Vaniz 2002) but provided further understanding on the life strategies of the species in this area. In particular, the results gathered here pointed out that local differences in the abiotic and biotic environmental conditions that juvenile jacks experience in the estuaries (CHAPTERS 2 and 3) strongly modulate the respective value of these inshore habitats for the renewal of the (sub)adult stock fished at Sea (CHAPTER 4).

5.1. Improvement of the knowledge on *C. latus* life-history traits

Previous information on *C. latus* life-history traits suggested that the species uses a mosaic of coastal habitats throughout its life span (Smith-Vaniz 2002). The results obtained here support this assumption in North-Eastern Brazil but substantially improve knowledge on the local life-history strategies of the species. The first main contribution with this regard is the disclosure of distinct age structures for the species in the estuaries and offshore (CHAPTER 2): whereas all age classes are found at sea, the *C. latus* specimens inhabiting the estuaries are almost exclusively yearlings. Older specimens might enter large and deep estuaries, as observed for another local jack species (*C. hippos*) during our sampling surveys.

However, our estuarine sampling, spanning over five years in seven estuaries, gives a rather realistic image of the age structure of *C. latus* estuarine sub-populations. In our study area, *C. latus* yearlings seem to colonize the estuaries when 3-4 months old, at sizes below 50 mm SL (CHAPTER 2). This timing was confirmed by changes in *C. latus* otolith microchemistry, as a marked decrease of Sr concentrations in the corresponding otolith section was observed in most of the specimens analysed (CHAPTER 4). Indeed, Sr signatures in the portions of the otoliths deposited during the larval and early juvenile phases for all individuals were similar to those measured on the edge of the otoliths of the sub-adult fish captured offshore, and markedly higher than in any local estuary. Thus, although *C. latus* larvae were not collected in this study, the chemical composition of *C. latus* otoliths suggests that this phase of life takes place at sea, corroborating previous assumptions regarding the fact that *C. latus* is an offshore spawner (Heyman & Kjerfve 2008). It also indicates that combined analysis of otolith structure and chemistry might allow estimating the time spent in estuarine habitats by *C. latus* individuals, as already done for other speices (Mercier et al. 2012).

The factors triggering juvenile *C. latus* arrival and departure in the estuaries are still poorly understood. This is in part due to the breeding period of *C. latus* that may span throughout the year (Figuerola-Fernández et al. 2008), although peaks of spawining occur in April and in August (Figuerola-Fernández et al. 2008, Heyman & Kjerfve 2008). Thus, post-larvae individuals are able to colonize inshore areas the entire year and which precludes a precise identification of the drivers of their estuarine residency. However, the data obtained in this study may provide some hints for a better understanding. We suppose that estuary colonization by juvenile jacks is modulated both by the local ecology of the species and by variations in local environmental settings. Indeed, juvenile *C. latus* occurrence in North-Eastern Brazilian estuaries is rather low during the rainy season (da Silva et al. 2018). This is not surprising as this particular period is that when peaks of reproduction of adult specimens occur at sea (in April and August), and post-larvae only colonize local estuaries when 3-4 months old (CHAPTER 2). Based on this larva life duration, peaks of post-larvae arrival are expected in the late rainy (July – August) and the early dry (October to November) seasons. Moreover, a likely reason for the colonization of inshore areas by *C. latus* post-larvae is the seek for more favourable conditions for growth (Beck et al. 2001). Therefore, the timing for this process each year is probably linked to that of the increase in estuarine productivity following the pulses in continental inputs observed during the rainy season (Eskinazi-Leça et al. 1999). Indeed, jack species seem to positively respond to chemical compounds (*e.g.* Dimethylsulfoniopropionate, DMSP) produced by marine algae and which are released in the water when they are predated by zooplankton and fish species (DeBose et al. 2010). Therefore, times of high estuarine secondary productivity, which are mainly observed at the end of the rainy season, could act as chemosensory clues for the settlement of *C. latus* yearlings in the estuaries spread along the shore each year. Bearing in mind that most *C. latus* juveniles spend only their first year of life within the estuaries (CHAPTER 2), fish may occupy these areas from the moment of their colonization up to the next period of high rainfalls. Indeed, altough juvenile *C. latus* are are capable to use the whole extent of estuarine environments, including riverine habitats (Figueiredo & Menezes 1980, Smith-Vaniz 2002), their occurrence is higher at the lower reaches of the estuaries (Medeiros et al. 2017), where the salinity is close to that found at sea. Morevoer, estuaries under stronger marine influence (*i.e.* saline ones) contributed the most to the local *C. latus* population in North-Eastern Brazil (CHAPTER 4). This indicates that life conditions found during periods of high salinity are the most beneficial for juvenile *C. latus* in estuarine systems, in agreement with the expected marine life history strategy of the species (Elliott et al. 2007). In turn, the annual cycle of freshwater inputs in the estuaries may represent a physiological driver casting away the yearlings and limiting their residence time in estuaries to the drier period of the year.

Another key aspect of the life cycle of *C. latus* highlighted by this study is the high degree of connectivity between its juvenile (inshore) and adult (offshore) habitats. Connectivity between coastal habitats has been extensively addressed (*e.g.* Sheaves (2009) and Ogden et al. (2014)) and results from both physical (freshwater discharges and marine currents) and biological processes (movements of migratory species). However, identifying the exact role of coastal fish in supporting this connectivity can be particularly challenging due to the complex environmental dynamics of estuaries and the mobile nature of migratory species (Sheaves 2009). For *C. latus*, most studies with this regard so far used artificial tags and failled to identify the patterns of habitat use in the species due to the high mobility of the large specimens tagged (Randall 1962, Chapman & Kramer 2000, Novak et al. 2020). In this study, the indirect assessment of the connectivity between inshore and offshore areas in North-Eastern Brazil obtained through the study of otolith microchemistry (CHAPTER 4) demonstrated that *C. latus* contributes to biomass exchanges at the land-sea interface in this area, as shown for other species worldwide (Aschenbrenner et al. 2016, Tournois et al. 2017, Toledo et al. 2019). During their estuarine stay, spanning from 5 to 9 months of their first year of life (CHAPTER 2), juvenile *C. latus* incorporates the organic matter produced locally, including from continental inputs (CHAPTER 3). Then, they export it to the sea, where it constitutes a large part of the fish biomass captured by local fisheries (CHAPTER 4). These results indicate that *C. latus* significantly takes part in the local land-sea connectivity in North-Eastern Brasil, with important implications for the fishery productivity of this oligotrophic marine area (Ekau & Knoppers 1999). Nevertheless, a finer investigation of the local spatiotemporal movements performed by the species is still needed to elucidate its potential estuarine use at older ages and the potential movements of its invividuals among the diverse estuaries spread along the shore.

5.2. The value of estuaries for the *C. latus* population in North-Eastern Brazil

Habitats may be considered as nursery grounds for a given species if they allow its juveniles to occur at higher densities or to benefit from (biological) processes that enhance their survival (Beck et al. 2001). In this study, recruitment success, *i.e.* the final contribution of each (group of) habitat to the exploited population (Dahlgren et al. 2006), was used to infer the value of estuaries as nursery sites for *C. latus*. The results obtained indicate that estuaries play a major role in the maintenance of the exploited population of *C. latus* in North-Eastern Brazil, contributing to a large (75%) portion of the specimens captured by the fisheries offshore the Pernambuco state (CHAPTER 4). This suggests that, just like for other jack (*C. ignobilis* (Smith & Parrish 2002)) and reef species (*e.g. Lutjanus* sp. (Mateo et al. 2010, Gerard et al. 2015)), estuaries may constitute nursery grounds for *C. latus*, at least in North-Eastern Brazil.

Only a limited portion of the exploited stock seem to originate from coastal marine habitats (CHAPTER 4). This was unexpected because juvenile *C. latus* are commonly found along the coast of the Pernambuco state, on sandy beaches and nearshore shallow reefs, which were therefore pointed out so far as potential juvenile habitats for the species (Mazzei et al. 2011, Medeiros et al. 2017). The results obtained in this study challenge this assumption. However, we cannot exclude that juvenile habitats at sea might have a non-negligible contribution to the local population. Indeed, we were not able to assign 20% of the sub(adult) specimens captured offshore to any of the habitats described in our database of otolith fingerprints. As this group of fish exhibited a mixture of signatures attributed to the estuaries and the sea in the juvenile portion of their otolith, and otolith elemental signatures of fish from the Sea had the highest re-assignment rate (~95%), this mixed re-assignement might reflect actual frequent movements between the coastal marine zone and varied estuaries during the first year of life. Alternatively, these fish might originate from specific habitats at Sea leaving otolith fingerprints distinct from those characterized using the larval or sub(adult) protions of the otoltihs. If this is the case, then the importance of marine habitats for the local exploited stock would increase to 25%. This is still inferior to the 75% of fish originating from the estuaries, which apparently provide better life conditions for juvenile *C. latus*. Although distinct locations can serve as juvenile habitats for a species, they may differently impact the growth and maintenance of the overall population (Fodrie et al. 2009). Indeed, the fact that fish abundantly settle in a given habitat does not determines its quality for the subsequent growth and survival of the yearlings (Ils & Beverton 2000). This might be the case for coastal marine habitats at sea, where a lower availability of food and/or shelter from predators might result in higher mortalitiy rates for juvenile *C. latus*, thereby reducing the value of these ecosytems for the exploited population.

The intra-populational differences in juvenile habitat evidenced here (CHAPTER 4) have strong implications regarding the size-at age structure of the local exploited stock. Indeed, the first year of life is the period where the growth of the species is the fastest, but also the most variable (CHAPTER 2). Variations in environmental or biological settings in estuaries may influence the growth and condition of juvenile fish, and thereby, their value as nursery grounds (Vasconcelos et al. 2009, Escalas et al. 2015, Schloesser & Fabrizio 2019). Although the similarities in otolith elemental compositions among estuaries precluded a precise estimate of the sites colonized by the fish during their first year of life, the estuaries under strong marine influence seem to contribute more to the local adult population (32.5%) in North-Eastern Brazil (CHAPTER 4). Because juvenile fish also appear to have faster growth rates in these estuaries (*e.g.* in Santa Cruz and Suape estuaries, CHAPTER 2), the life conditions experienced by *C. latus* specimens in this type of habitat may increase the recruitment success to the adult population, by improving either the survival or the fitness of juvenile *C. latus*. This contrasts with the slower growth observed in Sirinhaém and may explain the lower contribution of brackish estuaries to the local stock. The varying life conditions for juvenile *C. latus* in estuaries might primarily be in link with the physiological constrains of the species, where the reduction of energy cost for osmoregulation processes can be addressed to its growth, and thereby, their preference for more saline habitats (Medeiros et al. 2017). Nonetheless, it can also be influenced by the food resources exploited by juveniles (*e.g.* Escalas et al. (2015) and Isnard et al. (2015)).

During their estuarine life, *C. latus* juveniles were found to mostly eat fish and crustaceans (CHAPTER 3), feeding on a mix of pelagic and benthic prey. However, the results obtained suggest that they partly adapt their diet to varying local environmental and biological settings, in particular regarding organic matter sources and prey availability. Indeed, variations in muscle carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions for *C. latus* juveniles mainly reflect the organic matter sources supporting the food webs in each estuary (CHAPTER 3). Moreover, although their main prey categories remain the same at all locations, the food preferences of *C. latus* juveniles differ among estuaries. This plasticity in diet is also driven by how they interact with other sympatric species at each site, as illustrated by our findings regarding the juveniles of crevalle jack, *Caranx hippos* (CHAPTER 3). Altough juvenile *C. latus* and *C. hippos* have very similar prey and isotopic niches in overall, combined differences in their diet and in food web structure at each location result in much-reduced local isotopic niche overlaps between the two species (from 27% in Suape to 57% in Santa Cruz). In particular, the estuary of Sirinhaém is amongst the smallest estuary studied in terms of surface area (CHAPTER 4), and its where juveniles of *C. latus* and other co-existing species apparently relies on the most diverse number of food sources (CHATPER 3). The more diverse the food sources, the less likely they all have simlar nutritional qualities and equally influence the growth of individuals (Zandonà et al. 2011, Brooker et al. 2013). As a result, the greater diversity of prey exploited at this site may promote more variable growth and survival among individuals and reduce the overall growth of the juveniles when compared to more stable enviornments (*i.e.* Santa Cruz and Suape, CHAPTER 2). These spatial differences might influence the growth and condition of *C. latus* juveniles and thus modulate their size and fitness at the end of their first year of life, when they begin their migration offshore. Lower growth rates during the first year of life can also result in fish reaching maturity at smaller sizes, and thus, being more susceptible to unfavourable events for their reproduction success (Hixon et al. 2014).

Altogether, this support that the value of estuaries for juvenile fish is not homogenous and variations in estuarine settings are likely to affect their quality as nursery grounds (Isnard et al. 2015, Schloesser & Fabrizio 2019). Although the exact drivers of juvenile growth and survival success of *C. latus* are still unkown, they seem to be in link to more saline habitats, either by these exhibiting higher availibity of (preferential) prey (CHAPTER 3) or lower physiological constrains for the species. In the latter case, freshwater inputs in local estuaries could act as a physiological forcing factor limiting the distribution and growth of juvenile *C. latus* in these habitats.

5.3. Implications for local management strategies

Besides being key habitats for coastal wildlife, estuaries provide many services for human populations (Barbier et al. 2011). This study highlights their importance for sustaining coastal offshore fisheries in the tropics. Even if *C. latus* stocks are not at any risk of overexploitation in the Atlantic, specific threats may still arise at the local scale (Smith-Vaniz et al. 2019), particularly those associated with human activities in estuarine and nearshore environments. This is particularly true in North-Eastern Brazil, where

C. latus is targeted by fishermen in both inshore and nearshore areas, and most captures occur before the individuals enter the adult population (Pelage 2020). In addition, the local small-scale artisanal fisheries that target this species are rarely reported, which prevents adequate assessment of their status and gives no option for their management (FAO 2020). Thus, incomplete information on the stock exploited in North-Eastern Brazil limits our understanding of how environmental pressures in estuaries might affect the overall local *C. latus* population. In this context, this study provided key information, by producing the first assessment of its growth based on detailed size-at-age data for most life-stages (CHAPTER 2).

Bearing in mind that *C. latus* is not a primary target of fisheries in the area, it is likely that the foremost threats to the maintenance of its stock occur during its juvenile life in inshore and nearshore areas. Indeed, habitat alteration due to land use and pollution occur at all studied locations, which are all affected by intense urbanization, aquaculture, and industrial development (Muniz et al. 2005, Guimarães et al. 2010, Pelage et al. 2019). These latter strongly affect the quality of inshore environments for juvenile fish (Nagelkerken et al. 2008, Crook et al. 2014, Ogden et al. 2014). In particular, habitat alterations that affect the hydrological regime of estuaries may have significant effects on the distribution and growth of juvenile *C. latus*, with potential implications on their respective nursery value. Adopting management strategies for preserving the environmental quality of these habitats is crucial to maintain their value for juvenile *C. latus.* These may comprise actions aiming to maintain the biodiversity of local macrobenthic communities, but also some to maintain the diversity of the organic matter sources supporting local food webs (Nunn et al. 2012), and the environmental features responsible for fish estuarine colonization and emigration (Sheaves 2009). In this context, the results obtained here provide precious information for the design and evaluation of marine protected areas along the North-Eastern Brazilian coast, bearing in mind that *C. latus* is only one of the many marine fish species that undergo ontogenic migrations across the local continental shelf (Aschenbrenner et al. 2016).

Finally, although the impact of ungoing exploitation rates on the status of the local *C. latus* stock is unkown, fishery management strategies discouraging the capture of specimens before they reach sexual maturity (*e.g.* setting a minimum size of capture or forbidding the species capture in inshore or nearshore areas) could favor the maintenance of the local population. However, to be effective, such strategies must be taken in consensus with both local communities (*i.e.* fishermen) and decision makers (Reis & Incao 2000, Jablonski & Filet 2008). Although their applicability in North-Eastern Brazil is uncertain, there is much room for improvement with this regard, particularly given that most of the fishermen we met during our sampling surveys were reluctant to capture *C. latus* (and *C. hippos*) yearlings in estuaries, in order to capture them when older (*i.e.* at larger sizes).

5.4. Perspectives

This study provides a better understanding of the life-history traits of an exploited yet poorly studied jack species. The results obtained indicate that estuaries play a significant role in the life-cycle of the C. latus population in North-East Brazil, where these inshore ecosystems, especially those under strong marine influence, sustain a considerable part of the stock exploited by offshore fisheries. This information confirms previous knowledge on the life-history strategies of the species and supports the assumption that estuaries do not provide equal life conditions for juvenile fish species. However, it also leads to several further questions, which open up varied research perspectives.

Although this study shed light on the potential effect of estuarine environmental settings on the growth of juvenile C. latus and the importance of estuaries for its local population, the exact drivers of the value of these habitats for C. latus juvenile growth and survival are still unknown. Identifying the factors controlling fish early survival and recruitment success is key to address the importance of juvenile habitats for fish populations (Sheaves et al. 20105), but it is challenging because both biological and environmental constrains modulate the quality of life conditions of fish juveniles (Vasconcelos et al. 2009, Isnard et al. 2015, Litvin et al. 2018). Therefore, more work is needed to validate the drivers of the variability in C. latus juvenile growth and survival observed in this study. This has to be done bearing in mind that environmental settings, like the physico-chemical gradients in estuaries, are likely to modulate food web structure and determine habitat suitability for fish (Barletta et al. 2008, da Silva et al. 2018). For C. latus, it is possible that a combined effect of spatial (estuarine settings) and temporal factors (timing of colonization) modulate the life conditions experienced by the yearlings. Indeed, juveniles colonizing the estuaries at distinct seasons of the year (i.e., in the late rainy or the early dry season) are less likely to experience similar life conditions, which can result in different survival, but also different body sizes at the time they migrate back at sea (Tournois et al. 2017, Jørgensen et al. 2020). In addition, as the present study only focussed on the first year of life of C. latus, fully addressing the role of estuaries in the local stock maintenance requires further research on the ecology and migratory behaviour of older specimens. In particular, assessing the successive habitats occupied by the species sub-adults during their first two years of life and their movements in the nearshore marine area they occupy after they leave the estuaries would improve our understanding on the drivers of individual fitness, as it is when C. latus specimens are targeted most by local fisheries, before entering the adult population (Pelage 2020). This information might also help to position marine protected areas along the coast or evaluate their efficiency, as nearshore marine habitats probably also play a significant role in the maintenance of the population, acting as ecological corridors linking inshore and offshore areas (Nagelkerken 2009, Sheaves et al. 2015).

Much work has been done worldwide since the conceptualization of the nursery value by Beck et al. (2001). However, our understanding of the importance of coastal habitats for fisheries and the drivers of the nursery function still requires further improvement (Litvin et al. 2018, Lefcheck et al. 2019), particularly in Brazil (Blaber & Barletta 2016). This study provides a first step towards this goal. However, the similarity in otolith elemental signatures for juvenile C. latus among the estuaries studied hampered our capacity to correctly discriminate them. This study would therefore benefit from a more accurate discrimination of the studied locations, either by the incorporation of additional markers of fish origin, from fish otolith (i.e. other trace elements or stable isotopic ratios (Hauser et al. 2019, Thomas et al 2020)) or from other tissues (e.g. muscle composition in isotopic ratios or pollutants (Herzka 2005, Agah et al. 2009)). Tagging experiments using acoustic and/or data storage tags could also be undertaken to infer the potential movements of the species' juveniles among estuarine sites until they reach the adult stage (Moulton et al. 2017, Rooker et al. 2018). This would allow to complete the results obtained here and match the contributions to the adult stock with other important criteria, like the respective surface area of the estuaries, in order to actually estimate their value as nursery or essential juvenile habitats (Beck et al. 2001). It is worth noting that habitat contributions to the exploited stock provide valuable information for maintaining local recruitment success, but do not directly allow evaluating how each habitat affects the global growth and fitness features of the population (Fodrie et al. 2009). Thus, complementary approaches that incorporate both the contribution of the varied habitats to the adult stock and their respective impact on individual growth and condition would help identifying the key areas sustaining the population (Fodrie & Levin 2008, Fodrie et al. 2009). Altogether, this knowledge can help improving local management strategies by feeding asvanced ecosystem-based models that consider connectivity between coastal habitats (Sheaves et al. 2015).

Lastly, the value of inshore areas for coastal marine fish is expected to vary according to the biology and the life-history strategies displayed by each species (Nagelkerken et al. 2015, Lefcheck et al. 2019). Therefore, the results obtained here cannot be extrapolated to all jacks species: some might not be estuarine dependent at all (*e.g. C. crysos* (Smith-Vaniz 2002)), while other might reside in the estuaries for even longer periods or at different life stages (*e.g. C. hippos*). However, this study stresses the lack of knowledge on the actual life cycle of many tropical coastal fish, even exploited ones. In these species, usually associated to coral reefs and the marine zone, estuarine use might be far more generalized that previously thought. Therefore, the approach used here could be applied to other exploited coastal tropical species regularly found in estuaries at the juvenile stage, in Brazil (*e.g.*, snappers *Lutjanus* sp. and barracudas *Sphyraena* sp.) or elsewhere, to locate their lifetime key habitats, and thereby identify the environmental pressures threatening their populations in the coming decades.

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