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

3

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12 **Abstract**

13 In this study, we investigated the size-at-age structure and growth of the horse-eye jack (*Caranx latus*), a
14 highly mobile neritic species with significant commercial value in many parts of the tropical southwest
15 Atlantic. For this, we combined size (standard length – SL) data and otolith readings from 282 juvenile
16 and adult specimens of the species captured across a range of inshore (estuaries) and offshore habitats
17 spread along the Brazilian coast between 2017 and 2019. Both otolith edge-type interpretation and
18 marginal-increment width analysis suggested that annuli are deposited only once a year for *C. latus* in this
19 part of the world, the opaque band being formed between May and August. The growth parameters
20 estimated by the growth model that fitted best our size-at-age data (von Bertalanffy) were 782.37 mm for
21 L_{inf} , 0.179 for k and -0.436 years for t_0 . Interestingly, fish ages differed between local inshore and offshore
22 habitats : 91.8% of the individuals captured in the estuaries (36-223 mm SL) were age-0 fish, while all
23 age groups (0-13 years) were found in the offshore marine area, where sizes ranged from 155 to 760 mm
24 SL. Growth is apparently the fastest in the first year of life, allowing to reach up to 22.75% of the local
25 maximum size expected for the species at one year. These results can inform fishery and ecosystem
26 management strategies in Brazil but also elsewhere, as the present study provides the first assessment of
27 *C. latus* growth in the South-Western Atlantic based on detailed size-at-age data for most life stages and
28 lifetime habitats.

29 **Keywords:** Marine fish; Coastal habitats; Otolith; Size-at-age; von Bertalanffy.

30 1. Introduction

31 Jacks (*Caranx* spp.) are highly prized marine fish, exploited by sport and artisanal fisheries in
32 many tropical and subtropical regions (Smith-Vaniz, 2002; FAO, 2003; Arra et al., 2020). Considerable
33 effort has been made to study their biology around the globe (Berry, 1959; Smith-Vaniz, 2002; Heyman
34 and Kjerfve, 2008). However, basic knowledge is still lacking for several species in this genus (Froese
35 and Pauly, 2021). This is notably the case for the horse-eye jack (*Caranx latus*), a species widely spread
36 along the West Atlantic coast of America, with catches spanning from the New Jersey state in the US to
37 Rio Grande do Sul in southern Brazil (Figueiredo and Menezes, 1980). Populations of *C. latus* are also
38 found around oceanic islands in the Western (St. Peter and St. Paul archipelago, Vaske Jr et al. (2005))
39 and Eastern (Ascension Island, Smith-Vaniz (2002)) Atlantic. This pelagic fish can reach up to 100 cm in
40 length and constitutes an important source of food and income in the South-Western Atlantic (Lessa et al.,
41 2009; Arra et al., 2020). In Brazil, for example, more than 3400 tons of *C. latus* were caught by artisanal
42 fisheries each year between 2009 and 2011, representing 45% of the total local landings of jacks (MPA,
43 2011).

44 Despite its commercial importance, the biology and population dynamics of *C. latus* is still largely
45 unknown in Brazil and elsewhere. The species' lengths at 50% maturity (L_{50}) are of 325 and 345 mm FL,
46 for males and females respectively, and its L_{100} (*i.e.* the length at which all individuals are mature) of 420
47 mm FL for both sexes (Figuerola-Fernández et al., 2008). However, there is no information on local
48 sizes-at-age so far, and previous growth studies have been limited to exploring length-weight
49 relationships of individuals (Figuerola-Fernández et al., 2008; Viana et al., 2016). Available information
50 on the local life cycle of the species indicates that it uses a mosaic of coastal and marine environments
51 (Smith-Vaniz, 2002), among which its growth rates are likely to vary. Indeed, large specimens of *C. latus*
52 are usually associated with deep waters (> 40 m) and offshore reefs near the shelf break (Lessa et al.,
53 2009; Felizola-Freire et al., 2018; Novak et al., 2020), where they are expected to breed, mainly in April
54 and August (Figuerola-Fernández et al., 2008; Heyman and Kjerfve, 2008). As a result, *C. latus* larvae are
55 mostly found offshore along the continental shelf (Berry, 1959; Campos et al., 2010). Juveniles, however,
56 are commonly found within estuaries or along sand beaches (Figueiredo and Menezes, 1980; da Silva et
57 al., 2018), which they apparently occupy for a few months or years before joining the offshore adult
58 population (Figueiredo and Menezes, 1980; Smith-Vaniz, 2002). This potential for habitat-specific

59 differences in growth calls for a more comprehensive description of *C. latus* growth, encompassing the
60 diversity of habitats used throughout their life (Lessa et al., 2009; Novak et al., 2020).

61 To fill this knowledge gap, we investigated the size-at-age and growth parameters of *C. latus* in
62 north-east Brazil using size data and otolith readings from specimens captured at most life stages across
63 different coastal and offshore habitats, including several estuaries where yearlings of the species are
64 commonly found (Paiva and Araújo, 2010; Silva-Júnior et al., 2017). The timing for local seasonal otolith
65 ring deposition was investigated before using otolith growth patterns to specify the ages in all the
66 environments colonized at each life stage and infer the species' global growth features in the area.

67

68 **2. Material and Methods**

69 *2.1 Study area and fish sampling*

70 The study was carried out along the coast of the Pernambuco state, in north-east Brazil (Fig.1).
71 The local climate is sub-tropical, with temperatures ranging from 18 to 32 °C throughout the year (CPRH,
72 2003a, 2003b; Domingues et al., 2017). As a result of the northward displacement of the Intertropical
73 Convergence Zone (ITCZ) in the Atlantic and the presence of strong winds blowing from the south-east
74 in the area (CPRH, 2003a, 2003b; Hounsou-gbo et al., 2015), precipitation along the coast peaks in late
75 autumn and winter (May to August). The driest period lasts from late spring to early summer (October to
76 December).

77 The coastline of Pernambuco state is 187 km long. Its continental shelf is ~35 km wide and has a
78 maximum depth of 60 m near its break (Vital et al., 2010; Domingues et al., 2017). The presence of
79 fringing reefs in the outer region and upper slope of the shelf led to its recognition as an Ecologically or
80 Biologically Significant Marine Area (CBD, 2014). This particular configuration provides favourable
81 habitats for many residents and migratory fish species (CBD, 2014), including *C. latus*. In the present
82 work, *C. latus* specimens from the continental shelf were obtained from artisanal fisheries landings. All
83 were captured by hand line fishing on the offshore reefs used as fishing spots by the artisanal fleets, at
84 ~30 km from the coastline. Based on previous exploratory surveys on *C. latus* distribution in the area
85 (Paiva and Araújo, 2010; Ramos et al., 2011; Silva-Júnior et al., 2017), five local coastal estuaries
86 (Goiana, Santa Cruz, Suape, Sirinhaém and Rio Formoso) were selected to represent the variety in the
87 inshore environments colonized by the species. Besides their geographical proximity, they exhibit distinct
88 morphological features and are subject to different freshwater inputs, resulting in varying environmental

89 settings (Table S1). At all these sites, *C. latus* specimens were mainly caught using beach seines trawled
90 along the river banks and block nets set close to mangrove creeks. The specimens were collected monthly
91 between August 2017 and August 2019 in inshore and offshore areas. All individuals were identified
92 according to the specialized literature (Figueiredo and Menezes, 1980; Smith-Vaniz, 2002), measured
93 (standard length, SL, in mm) and weighed (eviscerated weight, EW, in g). As most of the fish obtained
94 from offshore fisheries were eviscerated onboard, and those collected in the estuary were all immature,
95 the variable 'sex' could not be included in our analyses.

96

97 2.2 Otolith preparation and annuli reading

98 Every month during the period of study, a maximum of 25 fish, with mixed sizes, were selected
99 from those collected to provide a balanced design between size classes. For this, all the fish sampled in
100 the offshore region were usually kept and added to those collected in the estuaries until the desired sample
101 size was reached. The resulting final fish sample included a total of 282 *C. latus* individuals, with sizes
102 (SL) ranging from 36 to 760 mm and weights (EW) between 1 to 7090 g. Of these, 238 specimens were
103 juveniles or sub-adults and 44 were above the L_{100} reported for the species (420 mm SL, Figuerola-
104 Fernández et al. (2008)). Unfortunately, during the two years sampled, *C. latus* was almost absent from
105 the local catches from April to July: only a few individuals were caught in the estuaries studied during
106 this period, and none were captured at sea between June and July. This explains the low numbers of fish
107 analysed for these months.

108 The sagittal otoliths of each individual were extracted and used for age estimation. The left
109 otoliths were embedded in epoxy resin (Araldite 2020) and cut transversally to produce thin sections
110 containing the core (500 μm width) using a precision saw (Buehler, Isomet 1000). Sections were then
111 polished on the anterior side using sandpapers (800, 1200 and 2400 grit) and diluted alumina powder
112 (particle size 1 to 0.3 μm) until the core was exposed on the surface, resulting in thin sections of 200 to
113 300 μm width. All sections were then cleaned with water, dried and kept in individual clean vials until
114 further processing. The otolith sections were etched with EDTA 5% for 1 minute and then stained with
115 Toluidine Blue 1% during 1 min 30 s to enhance growth marks' visibility following the protocol from
116 Panfili et al. (2002). All sections were photographed before and after the staining process, under both
117 transmitted and reflected lights, using a stereomicroscope (Olympus SZX12, $\times 12.5$ to $\times 40$ magnification,
118 depending on the size of the otolith) equipped with a computer-linked camera (Jenoptik Prog Res C5,

119 software Progress capture). The seasonal growth increments were visible in both the ventral and dorsal
 120 regions of the otoliths of *C. latus*, under both transmitted and reflected light. Moreover, the presence of
 121 thin coloured rings within each translucent zone complicated growth mark interpretation, especially the
 122 identification of the first seasonal growth increment.

123 Fish ages were estimated separately by two distinct readers. Stained sections were observed
 124 under the stereomicroscope using reflected light to assess the type (translucent or opaque) of the edge of
 125 the otolith for each fish. Seasonal growth marks on the otolith (annuli), comprising one translucent and
 126 one opaque zone, were identified and counted by each reader from the core to the outer edge. Differences
 127 in age estimates between the two readers were assessed using the coefficient of variation index (CV):

$$128 \quad CV_j = 100 \times \frac{\sqrt{\frac{\sum_{i=1}^R (X_{ij} - X_j)^2}{R - 1}}}{X_j}$$

129 where R is the number of times that each fish was aged, X_{ij} is the i th age estimation for the j th fish and X_j
 130 is the mean age obtained for the j th fish (Chang, 1982). Although there is no *a priori* value for CV
 131 estimates, the average coefficient of variation (CV) between readers for individual counts was 2.92%,
 132 lower than the criteria of 7.6% provided by Campana (2001). Otolith samples that presented high CV
 133 estimates were reanalysed by the two readers until consensus was reached, otherwise the sample was
 134 removed from further analysis.

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

142 The timing for annulus formation in *C. latus* was investigated by two complementary
 143 approaches: by evaluation the type of the otolith edge (opaque or translucent) for all fish, and by
 144 estimating the relative marginal increment width (*WMI*) for all specimens with more than one identified
 145 annulus. The formula used for this was:

$$146 \quad WMI = 100 \times (M \times D_{(n,n-1)}^{-1})$$

147 where M is the distance from the last annulus to the edge of the otolith and D is the distance between the
148 last two annuli. In principle, it is recommended to use only group 2+ fish for this, as D should represent a
149 full year of growth, which is rarely the case for the birth year. However, to fill in the gaps in our sample
150 for some months, we chose to include group 1 fish in the analysis. To avoid bias in their WMI values, the
151 average distance between the otolith core and the first annulus for all group 2+ fish was used as an
152 estimate for their individual value of D in the formula.

153 The periodicity in annulus formation was investigated through circular-linear regression models
154 with random effects, using the WMI of individuals and their capture dates (Okamura et al., 2013) to fit
155 three distinct models, each one with a different assumption on the periodicity of annulus formation: (1)
156 annuli are formed anytime along the year (no cycle); (2) they are formed on an annual basis (one cycle) or
157 (3) they are formed twice per year (two cycles). The three models were applied separately using every
158 fish with at least one annulus (group 1+) and using only those exhibiting two or more annuli (group 2+),
159 allowing us to evaluate whether the inclusion of group 1 fish, and thereby the particular I_{MR} estimation
160 approach used for them, improved the identification of the time of annulus deposition. In each case, the
161 model that best fitted the data was selected based on the Akaike Information Criteria (AIC, Akaike
162 (1974)).

163

164 2.3 Micro-increment analysis

165 Based on a previous work on *Caranx melampygus* (Sudekum et al., 1991), it is reasonable to
166 assume that otolith micro-increments are formed daily in *C. latus*. To clarify this however and estimate
167 growth during the first year of life in the species, 40 individuals without any visible annulus (group 0
168 fish), with sizes ranging from 36 to 170 mm (SL) and from three distinct estuaries (Santa Cruz, Suape and
169 Sirinhaém, Fig. 1), were selected among the *C. latus* specimens collected. Their right otoliths were
170 prepared for micro-increments analysis following the same protocol as for annuli reading. In this case
171 however, each transverse section was polished until the otolith core was $\sim 5 \mu\text{m}$ below the surface. All
172 sections were then glued to glass slides with the core facing down. The opposite side was polished down
173 until the final width of the section was 10-30 μm . The thin sections obtained were photographed using a
174 camera (Olympus ProgRes C5) linked to a microscope (Olympus BX41, magnification $\times 100$ and $\times 400$;
175 software Image Pro Plus). Fish ages (in days) were estimated separately by two distinct readers. For this,
176 each thin section was analysed under a microscope, and the micro-increments were counted along the

177 dorsal axis of the otolith, from the core to the outer edge. As for annuli counts, differences in age
178 estimates between the two readers were evaluated using the coefficient of variation index (CV, see
179 above).

180

181 2.4 Growth modelling

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

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

$$191 \quad AIC_c = AIC + \frac{2k \times (k + 1)}{n - k - 1}$$

$$192 \quad \Delta_i = AIC_{C,i} - AIC_{C,min}$$

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

198 All analyses were carried out in R (R Core Team, 2021), using the packages *ggplot2* (Wickham,
199 2016), *fishmethods* (Nelson, 2019) and *AICcmodavg* (Mazerolle, 2020).

200

201 3. Results

202 Although all four types of otolith radius measurements investigated showed a good linear
203 relationship with fish body length ($p < 0.001$, $r^2 = 0.895$ to 0.965), those following the axes of maximum
204 otolith growth on the dorsal and ventral sides (Z_{S1} and Z_{S2} , Fig. 2) consistently presented the best fits, with
205 respective r^2 coefficients of 0.950 and 0.965 (Fig. S1). Among these later, Z_{S1} was retained for otolith

206 radius measurement because annuli (particularly the first one) proved to be easier to locate on the dorsal
207 side of *C. latus* otoliths. The pertinence of the choice of this otolith radius for age evaluation and/or back-
208 calculation of size in *C. latus* was confirmed by the results from group 0 fish. In these later, marks
209 assumed to be daily rings were clearly visible on all the otoliths analysed, especially on the dorsal side of
210 the sections (Fig. 3). The average CV between readers for daily ring count on this axis was low (3.33%).
211 Therefore, we recommend using Z_{S1} for age and growth evaluation using otoliths in *C. latus*, irrespective
212 of the approach retained (annual or daily ring count).

213

214 3.1 Timing of annulus deposition

215 Otolith edge type was reliably identifiable in ~90% of the specimens analysed (252 fish,
216 including 92 group 1+ and 70 group 2+ specimens). The remaining ones (30 fish) comprised age 0
217 specimens that could not have their otolith edge type determined. Opaque and translucent margins were
218 observed irrespective of the month, but their proportions varied along the year (Fig. 4). Translucent edges
219 were predominant (in $\geq 75\%$ of the fish successfully analysed) from November to February, *i.e.* during the
220 austral summer. Conversely, a greater proportion of opaque edges were observed between May and
221 August (*i.e.* in the late autumn and winter), with a peak in August (76.9% of the fish analysed). The
222 seasonality in otolith growth band deposition was corroborated by the results from the marginal increment
223 width (*WMI*) analysis. *WMI* was more variable in group 1+ fish, but their inclusion in the *WMI* analysis
224 did not change the patterns observed (Fig. 4): irrespective of the fish sample analysed, monthly *WMI*
225 means were the highest in August (of $55.0 \pm 16.8\%$ for group 1+ fish, and $56.6 \pm 14.0\%$ for group 2+
226 fish) and the lowest in January ($21.9 \pm 3.8\%$ for both group 1+ and group 2+ fish). Moreover, the model
227 that best fitted the *WMI* data was the one assuming that ring formation occurs on an annual basis, either
228 when including all group 1+ specimens or when considering group 2+ fish only (Table 1).

229 Because estimated ages for the group 0 specimens analysed ranged from 77 (for a specimen of
230 36 mm SL captured in November) to 272 days (in a fish of 170 mm SL captured in early December),
231 annulus deposition for *C. latus* in north-east Brazil can happen up to 10 months after the fish hatch date.
232 Overall, all these results suggest that annuli in *C. latus* otoliths are only deposited once during the year in
233 this area of the globe, with opaque and translucent bands mainly deposited from May to August and from
234 November to February, respectively. Accordingly, the denser (chromophilic) mark corresponding to the

235 annulus before the start of the translucent band each year should essentially be deposited in October-
236 December each year, and annuli count in *C. latus* otoliths should provide reliable age estimation.

237

238 3.2 Sizes-at-age and growth parameters

239 Estimated ages (in years) in our fish sample ($n = 282$) varied between 0.21 and 13 years.
240 However, more than half of the *C. latus* specimens analysed (67.4%) were age-0 fish and fish ages
241 differed between inshore and offshore habitats (Fig. 5). In the estuaries, where observed sizes ranged
242 from 36 to 223 mm SL (for weights between 1 and 282 g), almost all individuals (91.8 %) were less than
243 one year old. Conversely, all age classes (0-13 years) were found at sea, where sizes (SL) ranged from
244 155 to 760 mm, and weights from 105 to 7090g. The sizes of the age-0 fish captured at sea varied from
245 155 to 195 mm SL and were thus close to the maximum size observed at this age in the estuaries (177 mm
246 SL). Based on the sizes-at-age found for the 40 group 0 specimens of *C. latus* captured in Santa Cruz (98
247 to 130 mm SL), Suape (100 to 170 mm SL) and Sirinhaém (36 to 158 mm SL), the oldest specimens in
248 the local inshore habitats could be about 10 to 11 months old, while the smallest ones caught at sea could
249 be older than 7 months.

250 Of all the growth models tested, the von Bertalanffy model presented the best fit to the size-at-
251 age data for *C. latus*, showing the lowest AIC_C (1347.9). Its estimates for local growth parameters were of
252 782.37 mm for L_{inf} , of 0.179 for k and of -0.436 years for t_0 (Fig. 6). The Gompertz ($AIC_C = 1379.0$) and
253 Logistic ($AIC_C = 1403.8$) models had significantly poorer performances ($\Delta AIC_C > 2$). Their estimates for
254 local growth parameter were: Gompertz, 701.11 mm for L_{inf} , 0.346 for G (effect on slope of the curve)
255 and 1.998 years for t_1 (age at inflexion of the curve); and Logistic, 670.10 mm for L_{inf} , 0.529 for the
256 scaling of the curve and 3.039 years for its age at inflexion. Both models predicted lower L_{inf} than the
257 maximum size observed in this study (760 mm SL), supporting that the von Bertalanffy was the most
258 suitable model for predicting *C. latus* size-at-age in our study area.

259 The von Bertalanffy equation predicted an average size of 178 mm at age 1, 277 mm at age 2, 360
260 mm at age 3, 488 mm at age 5 and 662 mm at age 10. However, the use of the relationship between Z_{S1}
261 and fish body size ($\log(SL) = -7.340 + 1.894 \times \log(Z_{S1})$, $r^2 = 0.950$) allowed gathering additional
262 information regarding *C. latus* growth and biology in the area. Using this type of measure, the first
263 annulus on the otolith was found to be deposited at an average distance of $754 \pm 85 \mu\text{m}$ from the core.
264 Increments widths for the subsequent annuli were drastically lower, ranging from $163 \pm 41 \mu\text{m}$ (for the

265 2nd annulus) to $19 \pm 2 \mu\text{m}$ (for the twelfth). This suggests that *C. latus* in north-east Brazil grows most
266 rapidly during the first year of life, with 22.75% of its local L_{inf} and around 56% of their size-at-maturity.
267 In addition, the inter-individual variation in the width of the first annulus (620 to 900 μm) represented a
268 difference of up to 130 mm in fish body size at the end of this first year of life. Variability in Z_{S1} at the
269 end of year 2 was lower (maximum of 80 mm), and negligible at the end of the 12th year (difference in
270 size < 15 mm).

271

272 4. Discussion

273 Previous studies on the growth of the horse-eye jack *C. latus* were limited to only length weight
274 relationships of individuals (*e.g.*, Figuerola-Fernández et al. (2008) and Viana et al. (2016)), which
275 hampered a proper understanding of the population dynamics of this highly mobile species (Lessa et al.,
276 2009; Novak et al., 2020). The present work provides novel insights on this matter as, to our knowledge,
277 it is the first assessment of *C. latus* growth based on detailed size-at-age data for most life-stages
278 (juveniles and adults) and lifetime habitats (estuarine and marine) in north-east Brazil.

279

280 4.1 Otolith structure

281 Cyclical variations in physiology and somatic growth have been associated with the deposition
282 of growth bands in fish, with opaque and translucent bands expected to reflect periods of slow and fast
283 growth rates, respectively (Panfili et al., 2002). While temperature can be a primary driver of fish growth
284 in temperate regions (Hoie et al., 2009), variations in fish growth in the tropics have been associated with
285 differences in life history strategies, habitat diversity and food availability (Val et al., 2005; Espino-Barr
286 et al., 2008). In this study, both edge-type and otolith marginal increments width indicated that annuli
287 deposition for *C. latus* occurs only once a year in north-east Brazil, supporting the reliability of otolith
288 methods in estimating the age of local marine fish. Because seasonal variation in otolith edge type was
289 estimated from 252 fish collected in a variety of coastal and offshore habitats, over two or three different
290 years for almost all months, these patterns reflect both the interannual variation in meteorological
291 conditions reported in our study area (Hastenrath, 2012) and the local spatial diversity in environmental
292 settings for *C. latus* (Paiva and Araújo, 2010; Medeiros et al., 2017). However, our results might partly be
293 biased by the fact that most of the fish in our sample were immature and collected in estuaries.

294 Indeed, in our *C. latus* sample, translucent bands were found to be mainly deposited from
295 November to February, *i.e.*, during the local dry period (austral spring and summer), while opaque bands
296 seem to be formed between May and August, *i.e.*, during the local rainy period (austral autumn and
297 winter) (CPRH, 2003a, 2003b). In inshore areas, both the seasonal changes in temperatures (Morrongiello
298 et al., 2014; Doubleday et al., 2015) and in freshwater inputs have been shown to mainly influence fish
299 growth (Cardona, 2000; Diouf et al., 2009; Isnard et al., 2015). Although *C. latus* juveniles inhabit
300 estuaries with varying salinities in north-east Brazil (Paiva and Araújo, 2010; Medeiros et al., 2017), their
301 global occurrence these inshore habitats is rather low in periods of high freshwater inputs (da Silva et al.,
302 2018), suggesting that they experience physiological limitations when local salinities drop. Because
303 temperature in the area also reaches its lowest values (~ 25 ° C) during the rainy season, the reduction in
304 fish metabolism and somatic growth in the estuaries at this time of the year probably explains the
305 generalized opaque band formation (associated with slowest otolith growth rates) at this time period in
306 our fish sample.

307 Unfortunately, the low numbers of group 1+ individuals in some months in this study prevented
308 a thorough understanding of the factors underlying the deposition of opaque and translucent bands in the
309 otoliths of sub-adult and adult *C. latus* at sea. Because both water temperature (26 – 29.5 ° C) and salinity
310 (36.5 – 37.0) are quite stable over the year in the marine offshore area (Domingues et al., 2017), other
311 processes probably drive local seasonal changes in metabolism and otolith growth band formation. As in
312 other tropical species (Gallardo-Cabello et al., 2007; Espino-Barr et al., 2008), the formation of the
313 translucent growth band in the otoliths of local *C. latus* adults could be associated with a fastest growth
314 due to enhanced food availability, as the secondary production along the north-eastern Brazilian shelf is
315 maximum at the end of the austral summer (Hazin, 2009). However, opaque growth bands deposition in
316 sub-adult and adult tropical fish might also be linked to physiological endogenous cycles associated to
317 biological processes (Val et al., 2005; Fowler, 2009), including gonad development (Nóbrega and Lessa,
318 2009; Freitas et al., 2019) and breeding (Fowler, 2009; Wootton and Smith, 2014). This call for further
319 studies investigating the timing of growth band deposition for *C. latus* in north-east Brazil, with a more
320 balanced sampling between juveniles and adults (from both sexes) and between months and years, to
321 allow identification of the environmental and biological factors responsible for the deposition of opaque
322 and translucent growth bands throughout fish life. In particular, although very little information is
323 available on the breeding period of *C. latus* in our study area, studies on *C. latus* populations at the

324 Caribbean suggest that it may occur throughout the year, with two main peaks, in April and in August
325 (Figuerola-Fernández et al., 2008; Heyman and Kjerfve, 2008). Therefore, opaque edges might be more
326 frequent at these times of the year in the adults of the species, and the formation of a false annulus cannot
327 be excluded, especially in the females.

328

329 4.2 Size-at-age and growth modelling

330 Like in most fish species, growth in *C. latus* is the highest during the first year of life, with an
331 estimated gain in size of 178 mm on average in our study area, which represents 22.75% of the local L_{inf}
332 for the species. Based on previous findings by Figuerola-Fernández et al. (2008), age at first maturity is
333 expected to take place after the second year of life (L_{50} of 305 mm and 325 mm SL for males and
334 females, respectively). The growth parameters obtained here for the species ($L_{inf} = 782.37$ mm, $k = 0.179$)
335 were within the range reported for other *Caranx* species around the globe and present comparable values
336 to those found in other large sized species of jacks (Table S3), which all reach between 60 and 75% of
337 their maximum sizes during their 7th year of life (Sudekum et al., 1991; Kishore and Solomon, 2005;
338 Espino-Barr et al., 2008). However, among them, *C. latus* is one of the species with the lowest L_{inf} .
339 Interestingly, growth parameters for *C. latus* are very similar to those reported for local specimens of the
340 closely related species *C. hippos* (Table S3). Since both species have similar life cycles and coexists in
341 inshore and offshore areas across the Brazilian coast (Paiva and Araújo, 2010; Silva-Júnior et al., 2017),
342 variations in growth rates among large size jacks might be largely caused by small differences in lifetime
343 strategies and local environmental conditions. Conversely, small sized jacks (e.g. *C. crysos*, *C. caballus*
344 and *C. ronchus*) with higher growth rates may achieve >75% of their maximum size on their 5th year of
345 life (FAO, 1979; Goodwin and Johnson, 1986; Gallardo-Cabello et al., 2007).

346 Because of its versatility in estimating key growth parameters and comparison with indirect
347 growth assessment methods (e.g. length frequency analysis) the von Bertalanffy model has been applied
348 for a diverse number of fish species, including some of the *Caranx* genus (Kishore and Solomon, 2005;
349 Gallardo-Cabello et al., 2007). However, an increasing number of studies have suggested that it may not
350 provide realistic size-at-age estimates for some species or life stages (Charnov, 2008; Mercier et al.,
351 2011; Sirot et al., 2015). In our case, the von Bertalanffy was the best model fitting the size-at-age data of
352 *C. latus*. Considering that jack species may live up to 20 years old and above (Goodwin and Johnson,
353 1986; Pardee et al., 2021), the low number of old specimens (age 12+) in our sample might have biased

354 the performance of the von Bertalanffy model and led to an under-estimation of the actual local values of
355 L_{inf} . Nonetheless, the sizes of the specimens in our adult sample reflect those in local landings (Lessa et
356 al., 2009). Moreover, the growth parameters obtained here for *C. latus* are within the range found for
357 other *Caranx* species and the L_{inf} suggested by the model is close to the maximum size (858 mm FL and
358 ~812 mm SL) reported for the species in Brazilian coastal waters (Lessa et al., 2009).

359 Precise and reliable age estimation is key information for consistent assessment of growth in
360 fish. When evaluating fish age by annulus counts, specific ages can be interpreted as years or months
361 depending on the complementary information available on life history processes, namely the expected
362 date of birth (Panfili et al., 2002). Indeed, fish age in number of months or subdivisions within a year (1.5,
363 2.5, etc.) can provide more detailed information on the growth of species though their life and has being
364 successfully applied in tropical (*e.g.*, Sirot et al. (2015) and Soeth et al. (2019)) and temperate regions
365 (*e.g.*, Moore et al. (2007) and Mercier et al. (2011)). However, in our case, age was determined in years
366 due the inconclusive knowledge on the date of birth of *C. latus*. Accordingly, reproduction for this species
367 takes place mainly in April and August, but spawning may extends from February to October and even
368 occurs year-round at different locations in the Atlantic (Figuerola-Fernández et al., 2008; Heyman and
369 Kjerfve, 2008). Although the decision to estimate *C. latus* age in years rather than months was oriented
370 by precaution, it can influence the slope of the growth curve and thereby the parameter obtained for the
371 species. Therefore, further studies addressing older fish and at different aging scales (*e.g.* months) are
372 needed to improve the assessment of *C. latus* growth parameters in north-east Brazil and also elsewhere
373 in the Atlantic where it is exploited by fisheries.

374

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390

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548 **Figure captions**

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

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

557 **Fig 3** Transverse section (dorsal side) of the otolith of a juvenile of *Caranx latus* (SL = 85 mm, age = 154
558 days) prepared for micro-increment (black arrows) analysis. The position of the otolith core and the
559 growth axis are indicated by the white arrow and dashed line, respectively.

560 **Fig 4** Monthly proportions of opaque edges in the otoliths of 252 specimens of *Caranx latus* (56 -760
561 mm) captured in north-east Brazil between 2017 and 2019, and corresponding marginal increment widths
562 (*WMI*, mean \pm standard deviation) in the otoliths of the group 1+ ($n = 92$) and group 2+ ($n = 70$)
563 specimens among them. For each month, the number of individuals analysed for the type of otolith edge
564 is indicated between brackets. For each variable, results are shown only if at least three fish were
565 available.

566 **Fig 5** Age class and length (SL, in mm) frequency distribution of the *Caranx latus* specimens collected
567 for this work along the north-east Brazilian coast, based on the type of habitat (estuary or sea) where they
568 were collected.

569 **Fig 6** Von Bertalanffy growth curve (dashed line) obtained for *Caranx latus* in north-east Brazil ($n = 132$,
570 including 40 group 0 and 92 group 1+ fish). For each age-class, observed lengths are represented by grey
571 points, the horizontal light grey bar representing the size range for local sexual maturity and the vertical
572 one the corresponding ages estimated by this equation.

573

574 **Tables**

575 **Table 1** Akaike information criterion (AIC) of the three distinct circular-linear regression models fitted to

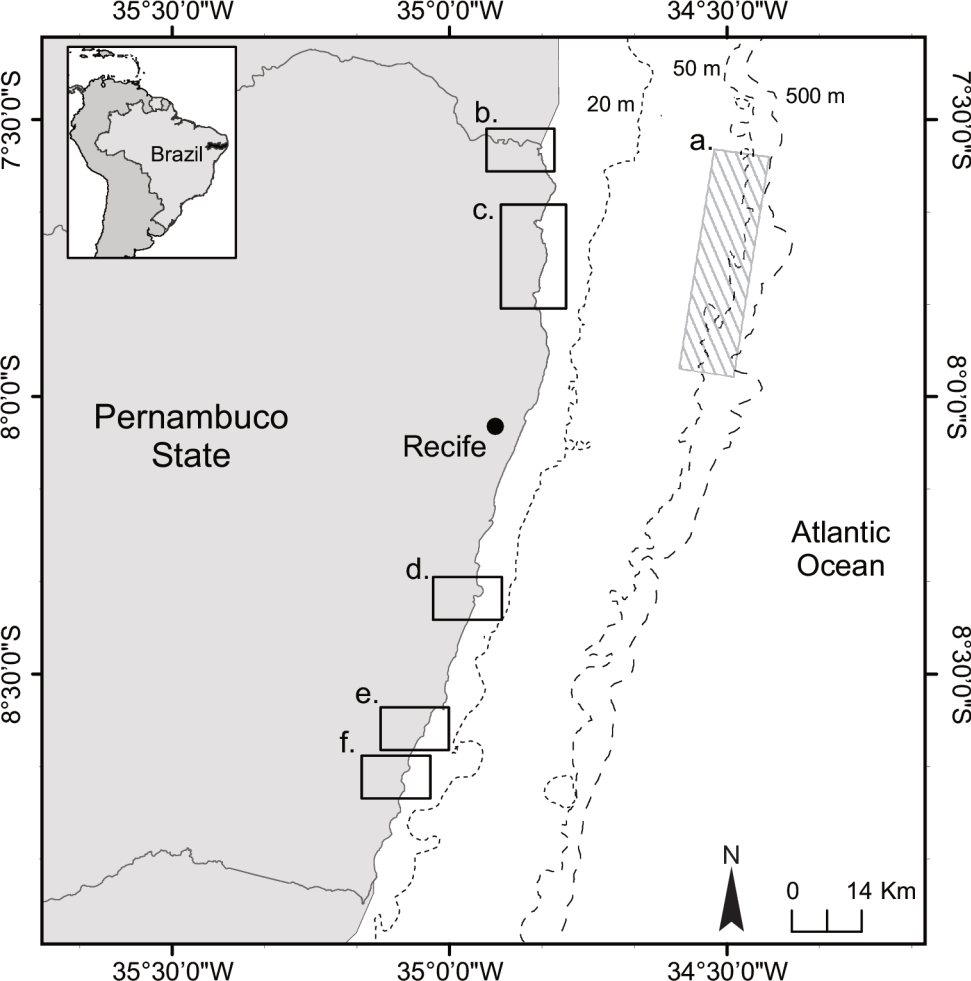
576 the two groups of fish (group 1+ and group 2+, see section 2.2.) to evaluate the periodicity of annulus

577 formation of *Caranx latus* in north-east Brazil. The number of individuals in each group is presented (n).

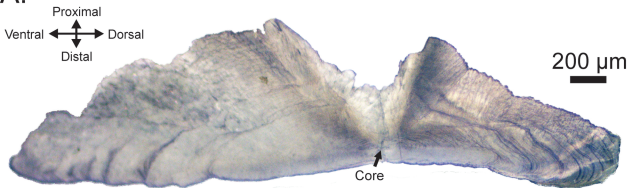
Fish	n	AIC		
		No cycle	1 cycle	2 cycles
Group 1+	92	-50.46	-56.53	-51.22
Group 2+	70	-42.41	-45.01	-39.97

578

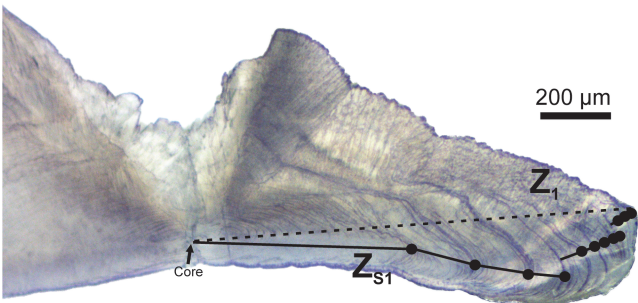
579

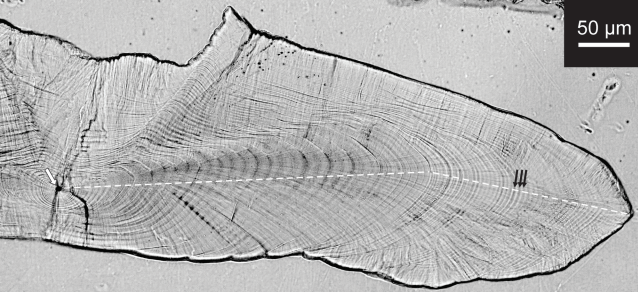


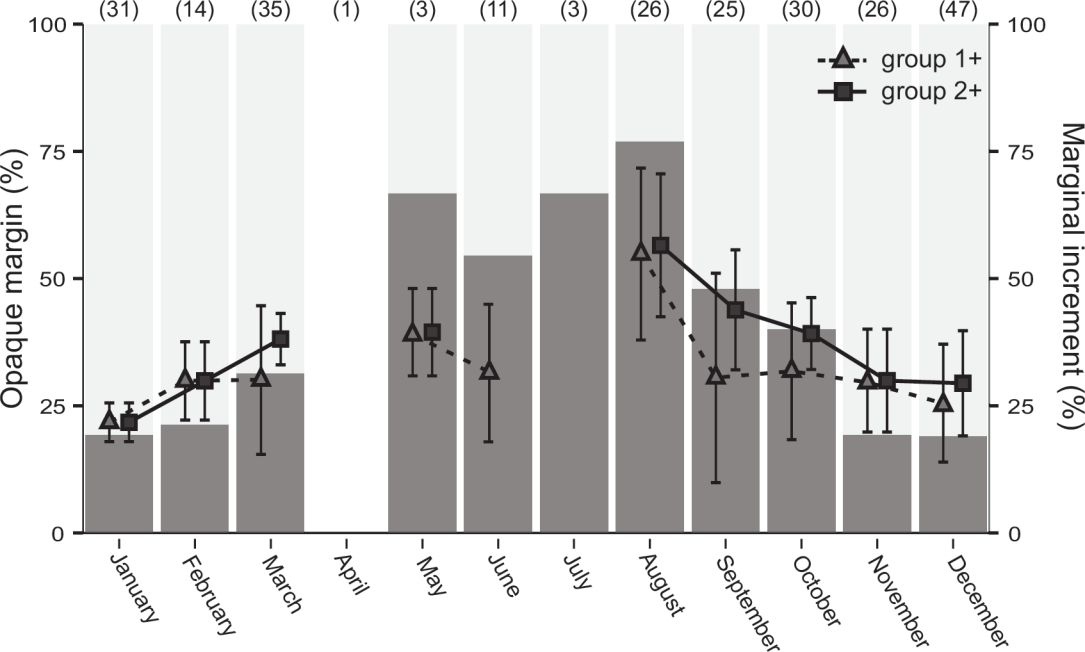
A.



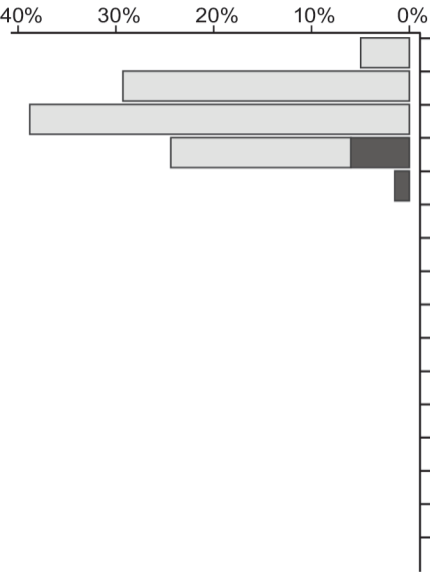
B.







Estuary (n = 196)



Sea (n = 86)

