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Reconstructing freshwater fishing seasonality in a neotropical savanna: first application of swamp eel (*Synbranchus marmoratus*) sclerochronology to a pre-Columbian Amazonian site (Loma Salvatierra, Bolivia)

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2 **Reconstructing freshwater fishing seasonality in a neotropical savanna: first**
3 **application of swamp eel (*Synbranchus marmoratus*) sclerochronology to a pre-**
4 **Columbian Amazonian site (Loma Salvatierra, Bolivia)**

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22 **ABSTRACT**

23 Sclerochronology is a method used to estimate the season of death (season of capture) of
24 archaeological individuals based on a modern growth model. This method has been
25 increasingly accepted in South America and has mainly been applied to coastal
26 archaeological sites (on the Atlantic and Pacific Ocean). This is the first time that this method
27 has been applied to a freshwater species, the marbled swamp eel (*Synbranchus marmoratus*),
28 in archaeology. Excavations undertaken at Loma Salvatierra, a human-built platform located
29 in the Bolivian Amazon and occupied from 500 until 1400 AD, have yielded 111
30 zooarchaeological vertebrae of the marbled swamp eel, which is one of the most widely
31 distributed species recovered in South American continental archaeological sites. In order to
32 estimate the fishing season for these archaeological individuals, we developed a modern
33 osteological reference collection, made up of 61 specimens with known capture dates
34 sampled monthly over a one-year period, about 60 km from Loma Salvatierra. The vertebrae
35 present periodic growth patterns with a succession of dark and light bands alternately.
36 Consequently, the vertebrae are a reliable basis for the estimation of the marbled swamp eel
37 fishing season. The analysis of the marginal increments of vertebrae in present-day fish

38 allowed us to elaborate a modern growth model showing that the seasonal growth of the
39 marbled swamp eel is related to the hydrological cycle, whereby the fast growth period
40 coincides with the onset of rainfall in the region. On the basis of this modern-based model,
41 the analysis of zooarchaeological vertebrae demonstrates that fish were captured over several
42 seasons. Demonstrating that human groups occupied villages year-round does not mean that
43 they were not mobile but shows year-round fishing in the savanna. This year-round fishing
44 practice raises questions concerning the generalized idea of fishing as an exclusively dry-
45 season activity. As wild resources are generally seasonal, the evidence of the year-round
46 fishing of swamp eels might suggest year-round fishing at Loma Salvatierra and contributes
47 to the understanding of late-Holocene mobility patterns in pre-Columbian times.

48 **Keywords:** Sclerochronology, Zooarchaeology, Llanos de Mojos, *Synbranchus*
49 *marmoratus*, freshwater fishing

50 1. INTRODUCTION

51 One of the most accurate methods to estimate the season of occupation of riverine or
52 coastal archaeological sites is the study of fish or mollusk growth structures, which allows
53 for an estimation of the ontogenetic age, growth and season of death (capture period) of
54 archaeological individuals (Casteel, 1974, 1972; Desse and Desse-Berset, 1992; Guillaud et
55 al. 2017; Van Neer, 1993). In American archaeology, such studies have been increasingly
56 applied to coastal environments (Hales and Reitz, 1992; Scartascini et al., 2015; Torres,
57 2006; Torres et al., 2020). However, very few studies have attempted to apply this approach
58 to freshwater contexts (Cahiza, 2003; Svoboda, 2013). Despite the increasing interest in age
59 determination and seasonality markers of modern freshwater tropical species, the analysis of
60 growth-increment structures has been underexploited in South American archaeological
61 contexts (Prestes-Carneiro et al. 2019, 2020).

62 Fishing was claimed to be a seasonal activity by the first scholars who studied the
63 subsistence strategies adopted by pre-Columbian Amazonian groups (Moran, 1993;
64 Roosevelt, 1980). Due to the scarcity of seasonality indicators, archaeological research
65 carried out in the Amazon region frequently uses indirect evidence to indicate the seasonality
66 of occupations. For example, Schaan (2008) carried out investigations within sites of the
67 Amazon River estuary on Marajo Island that revealed a system of artificial temporary ponds
68 that were filled by higher water levels during the rainy season. Associated overbank flooding
69 led the author to suggest that fishing was mainly a dry-season activity. Similarly, in the

70 Venezuelan Llanos, where Garson (1980) described systems of water-retention dikes and
71 ponds across extensive savannas, dry-season fishing was suggested by aspects of fish
72 ecology, such as the size of recovered fish communities and the dominance of drought-
73 tolerant fish. In the absence of biological evidence, the dry season character of fishing in
74 both examples was only supported by indirect corroboration of periodicity.

75 In the 1950's and 1960's, the "sedentary versus nomadic" character of the strategies
76 adopted by pre-Columbian Amazonian groups fueled a lively debate among the first
77 archaeologists working in the region (Lathrap, 1968; Meggers, 1954). Around AD 1000
78 several regions of the Amazon were occupied by large societies with villages. There is
79 evidence of monumentality in the form of earthworks, such as the roads that connected
80 villages in the Xingu region, the mounds, defensive ditches, and circular villages in the
81 central Amazon, the great extensions of black earth in the Santarém region, and the
82 monumental platforms in the southwestern Amazon (Heckenberger et al., 2003; Neves et al.,
83 2004; Prümers, 2004; Moraes and Neves, 2012). It is, however, difficult to understand the
84 seasonality of resource use and occupations of these groups since the seasonality of past
85 occupations is commonly inferred from density and extent of the archaeological settlements.

86 These suggestions may be refined by direct study of archaeological remains (such as
87 biorecorders) that contain markers of seasonality. Sclerochronology addresses ontogenetic
88 age estimation, which refers to the time elapsed after birth, and growth, and can be used to
89 explore a range of other themes such as the impact of human action on local ecology. This
90 term is derived from the Greek, *sclêros* "hard", *chronos* "time", and *logos* "study" that
91 together, mean the estimation of time by way of the growth marks on organisms' calcified
92 (hard) structures. Sclerochronology is analogous to dendrochronology (the study of tree
93 rings) in postulating that, as an animal grows, skeletal hard tissue records changes that are
94 linked to environmental conditions and physiological processes. Thus, sclerochronology
95 permits investigation of life-histories as well as environmental and climatic change across
96 space and time. In calcified tissues, growth patterns can be seen under a reflected light, as a
97 succession of alternately dark and light bands. A light band ("zone") represents a fast-
98 growing period and a dark band ("annulus") represents a slowdown in growth (see Fig 6). In
99 many taxa, a couplet of one light and one dark band typically represents one annual growth
100 cycle, although this may differ between tissue types (e.g., bone, otoliths, teeth, scales,
101 vertebrae) (Beamish and McFarlane, 1983; Quitmeyer et al., 1997; Van Neer et al., 1999;
102 Andrus et al., 2011; Meunier, 2012; Vitale et al., 2019).

103 The presence of an annulus does not imply that an animal stopped growing, but it
104 indicates a decrease in growth rate and metabolic activity (Quitmeyer et al., 1997; Panfili et
105 al., 2002). The deposition of calcified tissue (increments) is commonly driven by factors
106 related to temperature, such as seasonal contrasts, and the availability of water (Andrus et
107 al., 2011). There are, however, many other potential factors related to internal rhythms
108 (reproduction, sex reversal, migration, maturation) or external conditions (lack of food or
109 water, water quality, salinity) that can affect growth and thus the increments formed. As
110 such, sclerochronology can be used to study anthropogenic or naturally occurring impacts
111 on natural resources and anthropogenic impacts on the local ecology (Campana, 1990;
112 Panfili et al., 2002; Schone et al., 2008; Vitale et al., 2019).

113 Since the vast majority of fish are poikilothermic (organisms that do not control their
114 internal temperatures), they are sensitive to external environmental variations, and are
115 therefore potential bio-indicators of seasonal fluctuations. The increment for the last period
116 of growth is used to estimate the season of death. Its measurement is made from the last
117 annulus to the margin of the bone or otolith, which shows how much the individual has
118 grown and lived since the last annulus formed (Casteel, 1972; Mahé, 2009; Torres et al.,
119 2020).

120 As each type of calcified structure has a particular chemical composition and
121 biomineralization process, specific studies are necessary to observe how each calcified
122 structure records growth (Castanet et al., 1992; Panfili et al., 2002). The great majority of
123 studies applying the sclerochronological approach to archaeological contexts are based on
124 bivalve shells and fish otoliths (Andrus, 2011; Carré et al., 2005; Casteel, 1974; Hales and
125 Reitz, 1992; Van Neer et al., 2004). Sclerochronological studies based on scale, pectoral
126 spine, opercle, cleithrum, and vertebra are also possible, depending on the species and on
127 the condition that increments are visible, regular and readable, although these studies are
128 less common (Brewer, 1987; Desse and Desse-Berset, 1992; Morey, 1983; Guillaud et al.,
129 2017).

130 Over the past decades, great efforts have been made to document the age and growth
131 of South American freshwater fish based on calcified structures (Boujard et al., 1991; Cutrim
132 and Batista, 2005; Fabr e and Saint-Paul, 1998; Martins et al. 2009; Mateus and Petrere,
133 2004; Santos and Barbieri, 1993; Ponton et al., 2001). Baseline or proxy studies of modern
134 living taxa need to be conducted to establish a model of growth relevant to the location of
135 the archaeological site (Deith, 1983; Quitmeyer et al., 1997; Butler et al., 2019).
136 Archaeological studies also require good preservation of the bone material, exhaustive

137 sampling of archaeological remains using fine screen recovery, and modern comparative
138 collections (Casteel, 1972; Rojo, 1988; Deith, 1983). The large majority of
139 sclerochronological studies carried out with modern and archaeological samples have been
140 developed in temperate latitudes, where the formation of growth increments is strongly
141 related to winter versus summer contrasts (variations of temperature and photoperiodicity),
142 even though the hard tissue formation is a complex phenomenon and not necessarily
143 temperature-driven (Guillaud et al., 2017; Panfili et al., 2002). In tropical areas, where
144 temperature gaps are less disparate, factors driving growth increment formation are complex
145 and, for this reason, the impact of seasonality in archaeological assemblages requires careful
146 modeling (Meunier, 2012).

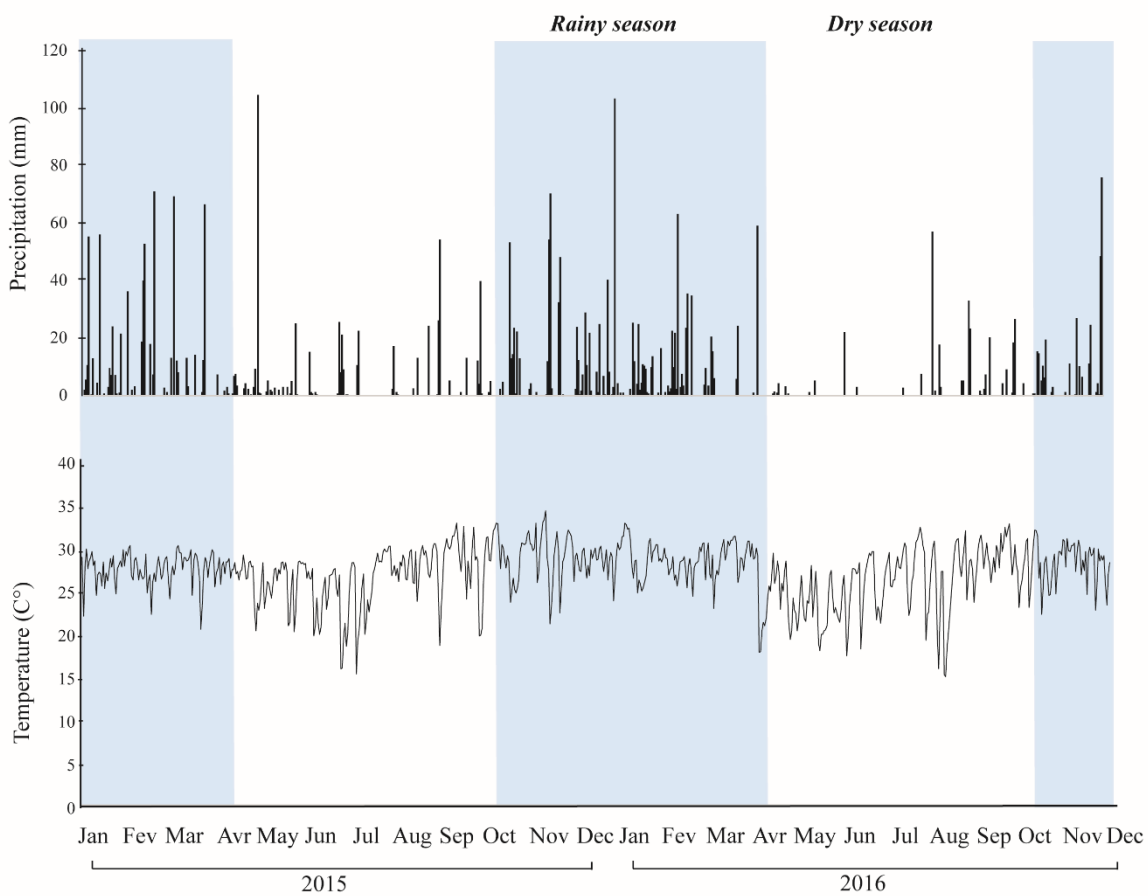
147 Archaeological taxa with large sample sizes generate more accurate sclerochronological
148 estimates of seasonality. Therefore, here we focus on the South American marbled swamp
149 eel (*Synbranchus marmoratus*), which is one of the most abundant and widely distributed
150 synbranchid species in Central and South America and a common taxon recovered in
151 archaeological assemblages in the Amazon Basin, Pantanal wetlands and estuarine zones of
152 Rio Grande do Sul (Prestes-Carneiro and Béarez, 2017; Prestes-Carneiro et al., 2018; Rosa,
153 2000, 2006). In south-western Amazonia, *Synbranchus marmoratus* comprises more than
154 70% of the fish remains recovered at Loma Salvatierra (Trinidad, Bolivia), a site was
155 occupied from AD 500 to AD 1400 (Béarez and Prümers, 2005; Von den Driesch and
156 Hutterer, 2012). Loma Salvatierra is an earthen platform mound that extends over 2 ha and
157 reaches a height of 20 m. In the Llanos de Mojos there are more than 100 human-built earthen
158 mounds (Jaimes Betancourt and Prümers, 2018). These sites are frequently associated with
159 other earth works, such as canals, ponds, and kilometers of causeways that radiate from the
160 mounds and connect the sites together. The monumentality of these earth works raises
161 questions about mobility and the interconnections between other groups, although no
162 specific studies on mobility patterns or seasonality have been carried out. In order to address
163 seasonality, we developed a modern reference collection of 61 *S. marmoratus* skeletons
164 collected monthly over a year. We established a growth increment model for the species
165 based on the vertebrae, and applied it to the 111 vertebrae recovered at Loma Salvatierra.
166 Here, we present the possible factors driving the formation of the annulus and use the model
167 to estimate the seasonality of fishing activities and mobility in pre-Columbian times.

168

169

170 **2. ECOLOGICAL OVERVIEW OF THE STUDY AREA**

171 Llanos de Mojos is the largest savanna in South America, extending over more than
172 200 000 km², between the Bolivian Andes and the southernmost border of the Amazonian
173 rainforest. The monthly average temperature oscillates between 27 and 28°C from
174 September until March. Temperatures slowly decrease from April to May and the lowest
175 average values are reached in June-July (23-24°C). They are highly affected by cold fronts
176 (wet or dry) of wind coming from the south, the well-known *surazos*. These wind currents
177 can lead to drastic decreases in temperatures, which can fall below 15°C for a few days (Fig
178 1) (Loubens et al., 1992).



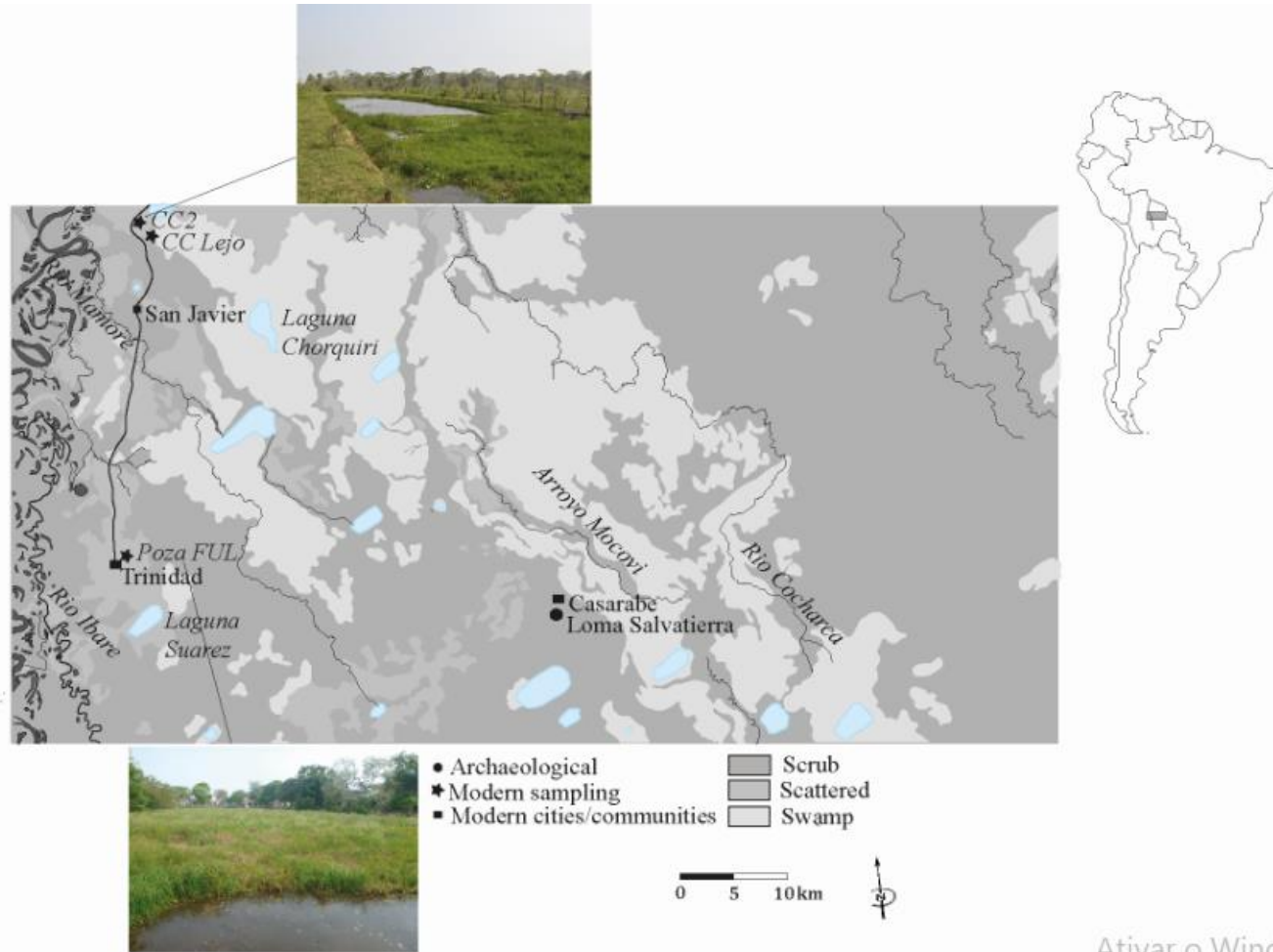
179
180 Fig 1: Temperatures and precipitation levels recorded at Trinidad (STLR station) in 2015
181 and 2016 (AASANA database available on www.aasana.bo).

182 In typical tropical areas, contrasts in temperatures are less extreme than in temperate
183 regions, and major year-round changes in the landscape are therefore driven by precipitation
184 fluctuations. In the study area more than 60-80% of rainfall coincides with the highest
185 temperatures, occurring from December to March, and the annual average precipitation

186 oscillates around 1 200 mm. From April, precipitation levels decrease and the dry season
187 can last for over six months. The combination of rainfall and temperature defines a wet
188 season running from November to April, and a dry season, which lasts from May to October
189 (Hanagarth, 1993). These extensive low-altitude areas of Llanos de Mojos are drained by
190 four main rivers: Madre de Dios, Beni, Itenez/Guaporé and its central axis, the Mamoré
191 River. A combination of torrential rainfall and poor drainage of the soils drives the overflow
192 of the main rivers, tributaries and shallow depressions. Denevan (1966: 11) estimates that
193 over 50 percent of the territory of the Llanos de Mojos savannas is under water during
194 maximum precipitation.

195 These flooding events had a huge impact on the management strategies adopted by
196 the first Mojos groups settling in the region. Many artificial platforms of raised fields and
197 canals (called *lomas*), identified in many areas of the Llanos de Mojos are indicative of the
198 ability of such populations to deal with flooding and water constraints. Such is the case in
199 Loma Salvatierra, a monumental platform located about 50 km to the east of Trinidad (Fig
200 2). The top of the platform contains three mounds laid out in a “U” shape, with the highest
201 point reaching 7 meters. Loma Salvatierra is surrounded by a polygonal causeway encircling
202 an area of 21 ha. Two sets of canals (about 300 m long) run from the main platform to an
203 excavated pond which is itself connected to other ponds (Prümers, 2007). Far from the area
204 of flooding of the Mamoré River, these ponds were probably supplied by precipitation water.
205 A set of radiocarbon dates indicates that the site was built and occupied by five cultural
206 groups between 500 and 1400 AD (Jaimes Betancourt, 2012; Prümers, 2007). Recent
207 zooarchaeological studies carried out at Loma Salvatierra indicate that a high diversity of
208 fishes, with species from at least 35 genera, were exploited and consumed, suggesting that,
209 even in an interfluvial area, humans managed to exploit and deal with seasonal contrasts
210 (Prestes-Carneiro et al., 2019).

211



214 Fig 2: Map of Llanos de Mojos showing the distance between archaeological sites (Loma Salvatierra) and modern sampling areas (Poza FUL, CC2
 215 and CC Lejo).

216

217 3. ECOLOGICAL OVERVIEW OF MARBLED SWAMP EEL

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219 The marbled swamp eel, *Synbranchus marmoratus* Bloch, 1795, is the most widely
220 distributed Synbranchidae in the neotropics. Its present-day distribution encompasses the
221 freshwater and estuarine areas of Central and South America (from Argentina to Guatemala
222 and Mexico) (Lo Nostro and Guerrero, 1996). Genetic and systematic studies have yet to be
223 developed and it is very likely that *S. marmoratus* is a complex of species (Perdices et al.,
224 2005; Torres et al., 2005; pers. obs.). In order to avoid identification bias, we decided to
225 sample individuals collected as near as possible to the archaeological site (Deith, 1983).

226 There are two recognized swamp eel species in the Llanos de Mojos (Rosen and
227 Rumney, 1972), *Synbranchus madeirae* Rosen & Rumney, 1972, and *S. marmoratus*.
228 Synbranchids have a mucous-covered, scaleless, cylindrical eel-like body, and lack pelvic
229 and pectoral fins. Their average length is 50 cm but the largest individuals reach up to 150
230 cm. The form and skin patterns of *S. marmoratus* are highly variable compared to *S.*
231 *madeirae* (pers. obs.) (Fig 3b). Swamp eels are very tolerant of high temperatures, even
232 though they can also occur in subtropical regions (Rosen and Rumney, 1972), and can
233 inhabit a variety of aquatic environments where shallow waters prevail (river shores, marshy
234 areas, shallow ponds or lakes). Synbranchids have mechanisms of accessorial aerial
235 breathing, and in the absence of water they can dig defined channels in the earth where they
236 stay throughout the dry season (Bicudo and Johansen, 1979). As they are non-migratory fish,
237 synbranchids are probably good indicators of local environmental fluctuations.

238 The marbled swamp eel is a protogynous diandric species where a high percentage
239 of females change into males in the terminal phase. According to Lo Nostro and Guerrero
240 (1996), there are therefore two types of males: 1) males born with reproductive male organs
241 (primary males) and 2) females who, by sex reversal, have gonads transformed into
242 functional testes. Lo Nostro and Guerrero (1996) estimate that sex reversal occurs when
243 individuals reach between 56 and 91 cm. It is expected that this process requires great
244 energy. It is not known, however, whether this physiological process generates a false
245 annulus in calcified structures.

246 Except for semi-arid Brazil (Rio Grande do Norte), where the reproductive period
247 runs from July to August, the reproduction of marbled swamp eel seems to be highest during
248 the austral summer, from November until March. On the Argentinean coast (province of
249 Corrientes), females are mature by the end of summer (December to March). In São Paulo

250 State (Americana, Brazil), maturation is reached at a total length of about 47 cm and
251 reproduction takes place mainly from December to February (Barros et al., 2013; Gathaz,
252 2012; Lo Nostro and Guerrero, 1996). Age-based studies of *S. marmoratus* otoliths from
253 northeastern Brazil have been carried out to characterize the dynamics of sex reversal
254 (Barros et al., 2017). In the Llanos de Mojos, the age and period of maturation have not yet
255 been studied.

256 Marbled swamp eel is mainly a generalist carnivore, feeding on detritus, protozoans,
257 nematodes, insects, shrimps, crabs, mollusks, and fish. A case-study in the marshes of the
258 Paraná River (Argentina) demonstrates that food intake seems to be related to rainfall levels,
259 with higher food intake values during the rainfall period. This does not seem to be the case
260 in Rio Grande do Norte (Brazil), where higher food intakes were observed during the low
261 water period (Braga et al., 2009; Montenegro et al., 2011; Rodriguez, 1999).

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263 4. MATERIALS AND METHODS

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265 *4.1. Present-day sampling*

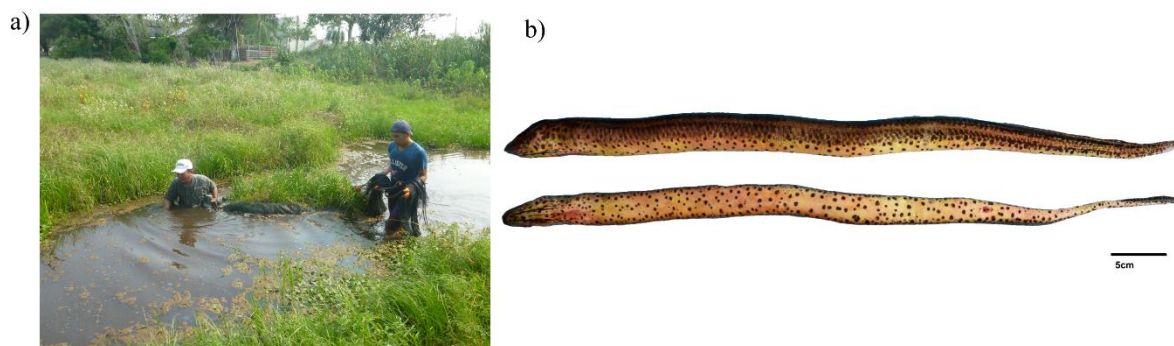
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267 Precipitation and temperature conditions may have slightly changed over the last
268 1,500 years in the Llanos de Mojos (Carson et al., 2014), however, we selected three ponds
269 close to archaeological site (Fig 2) as the best proxies. “Poza FUL” is a pond located inside
270 the University campus of the Universidad Autonoma del Beni (UABJB) in Trinidad (20S
271 295423 8361689); “CC2” (20L 298744 8406265) and “CC Lejo” (20L 297871 8408452) are
272 ponds located between San Javier and San Pedro Nuevo, about 40 km to the north on the
273 east side of the road connecting Trinidad and San Ramon (Fig 2). The three ponds are
274 artificial and located about 60 km from the Loma Salvatierra archaeological site. These
275 ponds are more than a dozen kilometers from the Mamoré River (and its floodplain), and are
276 almost exclusively supplied by local precipitation. The fish community of these ponds is
277 composed of wild populations adapted to seasonal periods of drought and flood events
278 (Yunoki et al., 2018). Ponds measured about 50 m x 15 m and swamp eels were dispersed
279 under floating vegetation, predominantly *Pontederia subovata* and *Cyperus luzulae*. The
280 aquatic vegetation partially covering the ponds was cut and brought to the edge of the pond
281 with the aid of a seine net (5 mm mesh size), and eels were then caught by hand (Fig 3a).

282 The modern reference collection includes 61 individuals captured at the end of each
283 month from July 2015 to July 2016, except for the month of February 2016. Information on
284 specimens (size, fishing capture date, and sex) is available in Supplemental Table 1.

285 Specimens were kept frozen at the *Centro de Investigaciones de Recursos Acuaticos*
286 (Trinidad) and two fieldwork campaigns were carried out to prepare the osteological
287 material. To prepare the skeletons, frozen specimens were defrosted, cooked in boiling water
288 and then macerated in water for 5 days. It is possible that a preparation at 100°C may have
289 altered the microcrystalline structure of the vertebrae as has been observed for otoliths
290 (Andrus and Crowe, 2002), however, we are assuming that this had no impact on the
291 distribution of the annuli. Head length (HD) was measured from the tip of the snout to the
292 posterior end of the branchial opening, total length (TL) was measured from the tip of the
293 snout to the tip of the caudal fin, and pre-anal length (PAL) was measured from the tip of
294 the snout to the anal vent. Sex identification was undertaken following the criteria described
295 by Lo Nostro and Guerrero (1996). Growth increment analysis was then performed on the
296 third precaudal vertebra at the Sclerochronology Centre of the *Institut Français de*
297 *Recherche pour l'exploitation de la Mer* (IFREMER, Boulogne-sur-Mer, France). The
298 skeletons are now part of the modern comparative collections of the Curt Nimuendaju
299 Archaeological laboratory of the Federal University of Western Pará (UFOPA-Santarém).
300 The zooarchaeological samples were sorted at the Muséum national d'histoire naturelle
301 (MNHN) in Paris (France), brought to IFREMER for reading, and are now housed at the
302 Deutsches Archäologisches Institut, Kommission für Archäologie Außereuropäischer
303 Kulturen (KAAK, Bonn, Germany).

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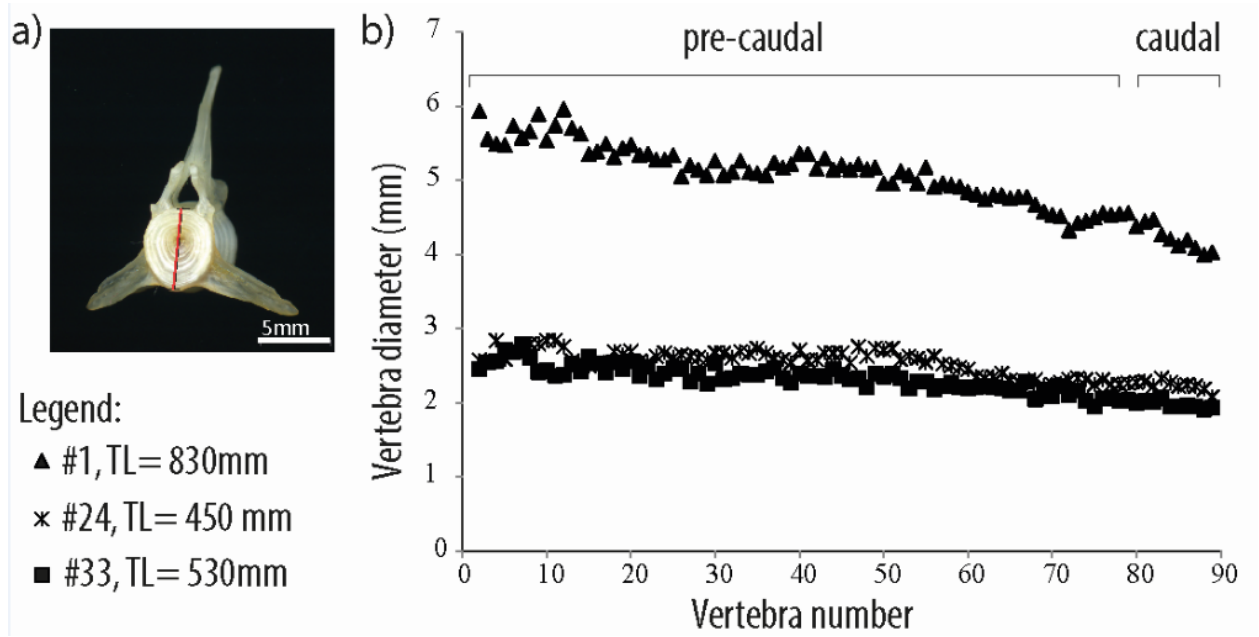
306 Fig 3: (a) The swamp eels were captured from under the floating vegetation of shallow ponds
307 (b) *Synbranchus marmoratus* in lateral and ventral view

4.2. Selection of vertebrae

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Although the majority of sclerochronological studies on fish are carried out on otoliths or scales, archaeological scales were absent at Loma Salvatierra and otoliths presented a porous consistency, which prevented us from obtaining good quality, readable anatomical specimens. We thus decided to work on vertebrae, where increments were visible and readable. To compare zooarchaeological and modern samples, it is appropriate to work with vertebrae that are always located at the same place along the spine. We therefore constructed the global rachidian profile to test whether there was significant variation in size between pre-caudal and caudal vertebrae (Desse et al., 1989). The first 80 vertebrae of three different individuals were placed in a scanner and their diameters were analyzed and compared using the *Traitement Numérique des Pièces Calcifiées* (TNPC) software (<https://www.seanoe.org/data/00320/43117/>) (Mahé et al., 2011) (Fig 4). This software was developed specifically for analysis of calcified parts through sclerochronology. It can be noted that vertebra size decreases in relation to the position in the vertebral column (the diameter decreases gradually towards the caudal vertebrae), especially for larger specimens (Fig 4b).

After verifying the constancy of size variations, we selected a vertebra with an easily recognizable position in the vertebral column. The first, second and third precaudal vertebrae (v1, v2 and v3) are easily distinguishable from each other; however, annuli in v1 are too constricted. The diagnostic criteria distinguishing v2 from v3 are: a) v2 is shorter and flatter compared to v3; b) v2 presents a linear foramen in ventral view; c) the parapophyses are straight in v2 vs. curved in v3 (Fig 5). These criteria were used to identify the archaeological vertebrae, and the separation of v3. Between vertebrae 2 and 3, the latter is dominant in the archaeological assemblage, which justified our choice to model growth from v3. Only zooarchaeological samples where conservation preserved the criteria mentioned above were used in this study.

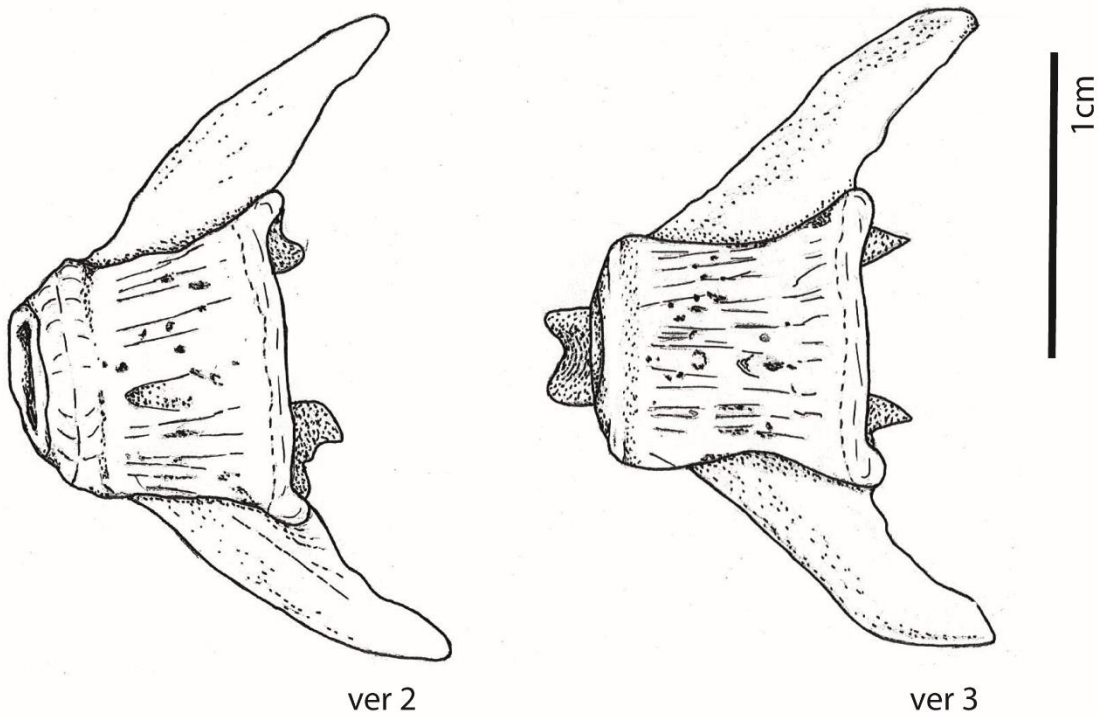


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337 Fig 4: (a) In cranial view, the dorso-ventral diameter of each vertebra was measured in order
 338 to elaborate the rachidian profile and evaluate size variation in vertebrae along the vertebral
 339 column; (b) global rachidian profile showing pre-caudal and caudal vertebral diameters of
 340 individuals of different sizes where (#) is the specimen number and (TL) is the total length.
 341 The caudal vertebrae of the larger specimen presented a more pronounced decrease in size.

342



343

344 Fig 5: Ventral view of vertebrae 2 and 3 of marbled swamp eel (*Synbranchus marmoratus*)
345 (© K. Dillenseger).

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347

4.3. Growth and Marginal Increment analysis

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349 In contrast to the great majority of teleostean fishes, marbled swamp eel vertebrae
350 resemble more the opisthocoele than the amphicoele type, i.e., the vertebrae present a flat
351 surface anteriorly (cranial view) and a concave, cone-shaped one, posteriorly (caudal view).
352 Although the flat surface provides a better view of the increments, on this surface they are
353 superposed. In the cone, the increments are more spaced out and readable, hence the caudal
354 view was the most suitable for growth increment reading. Modern and archaeological v3
355 vertebrae were photographed using a stereomicroscope connected to a video camera and an
356 image-analysis system (TNPC software). We used reflected light and a magnification of 1.25
357 for modern specimens and 1.6 for archaeological specimens. The reading axis (radius) was
358 placed at the level of the right parapophysis of each vertebra from the center of the chordal
359 centrum (focus) to the greatest distant margin (Fig 6). Measurements between each annulus
360 were taken from the focus to the marginal edge of each vertebra. Readings were taken twice
361 by the same expert to limit bias. With image analysis, we validated the annual periodicity
362 of the annulus as shown by the sinusoidal regression (Supplemental Fig 1).

363 In order to estimate the season of capture, we used the Marginal Increment (MI), a ratio
364 that expresses the state of completion of the forming growth increment in relation to the last
365 completed increment, based on measurements of the distances between the focus and: 1) the
366 marginal edge of the vertebral cone, 2) the outermost (ultimate) annulus, and 3) the
367 penultimate annulus (Fig 6). MI also normalizes the sizes between individuals to be able to
368 compare them (Beamish and McFarlane, 1983):

369

370

$$MI = (R - r_n) / (r_n - r_{n-1})$$

371

372 where:

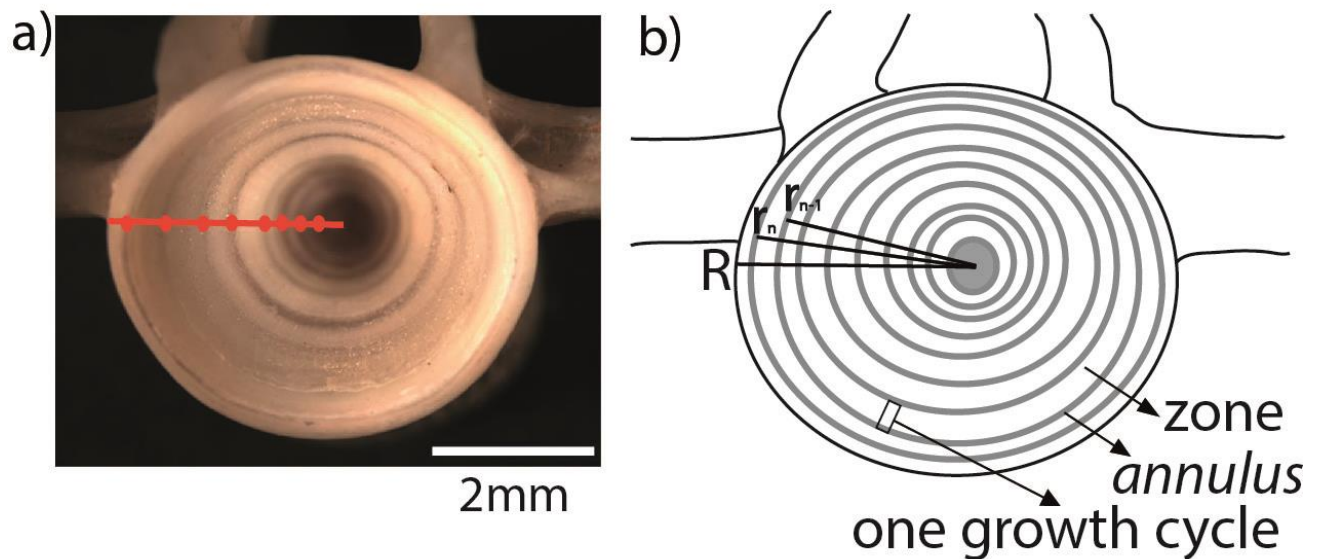
373 R = vertebra radius from the focus to the marginal edge

374 r_n = distance from the focus to the outermost annulus

375 r_{n-1} = distance from the focus to the penultimate annulus

376 In modern samples, the marginal edge of the vertebra is covered by an intervertebral
377 ligament that can be confounded with a zone (fast growth increment). In order to avoid this
378 bias, we measured the radius to slightly before this false dark increment. It is worth noting

379 that this phenomenon has also been described among *Pseudoplatystoma fasciatum* vertebrae
 380 (Panfili, 1992). The Kruskal-Wallis test was used to test the differences of MI among months
 381 at a 0.05 significance level as MI were not normally distributed. Tests of linear relationship
 382 between fish length and weight were made after logarithmic transformation of the data. Each
 383 linear relationship between two descriptors of fish (length and weight) or otolith (radius) was
 384 tested (Reitz et al., 1987). Statistical analyses were performed using the open-source
 385 statistical package environment R (R Core Team, 2016). Differences were considered
 386 significant at $p < 0.05$.



387
 388 Fig 6: Caudal view under reflected light of (a) modern specimen and (b) schematic vertebra.
 389 The reading axis was placed in front of the paraphophysis, from (grey area) the focus to the
 390 marginal edge of the vertebral cone. R = distance from the focus to the marginal edge
 391 (radius); r_n = distance from the focus to the outermost annulus; r_{n-1} = distance from the focus
 392 to the penultimate annulus. Annuli corresponding to periods of slow growth are marked by
 393 dots on the reading axis (in red).

394 395 **4.4. Archaeological sampling**

396
 397 Archaeofaunal material was recovered from Loma Salvatierra by wet sieving with
 398 meshes of 2 mm, 1 mm, and 0.5 mm (Pretes-Carneiro and Béarez, 2017). Taxonomic
 399 identification was carried out using modern comparative collections in order to identify the
 400 zooarchaeological specimens. The reference collection is housed at the Zooarchaeology

laboratory (UMR 7209) of the MNHN (Paris). From remains of *Synbranchus* spp. we sorted 111 precaudal vertebrae (v3) representing 111 individuals. These vertebrae came from the five different periods or occupation phases of the site that have calibrated radiocarbon dates ranging between AD 500 and AD 1400 (Jaimes Betancourt, 2012). The sampling distribution of individuals sampled from the oldest to the most recent phase was: Phase 1 (N= 14), Phase 2 (N = 9), Phase 3 (N= 42), Phase 4 (N= 43) and Phase 5 (N=2). Since we were not able to distinguish *S. marmoratus* from *S. madeirae* on the basis of the vertebrae, taxonomic identification was based on the dentary and ectopterygoid bones. From these data, we observed that *S. marmoratus* corresponds to about 94% of the identified *Synbranchus* species at Loma Salvatierra (Prestes-Carneiro *et al.*, 2019). We therefore assume here that the great majority of the archaeological samples correspond to this species and a model for *S. marmoratus* can be applied.

413

414 5. RESULTS

415

416 *5.1. The annual growth increment pattern of modern specimens*

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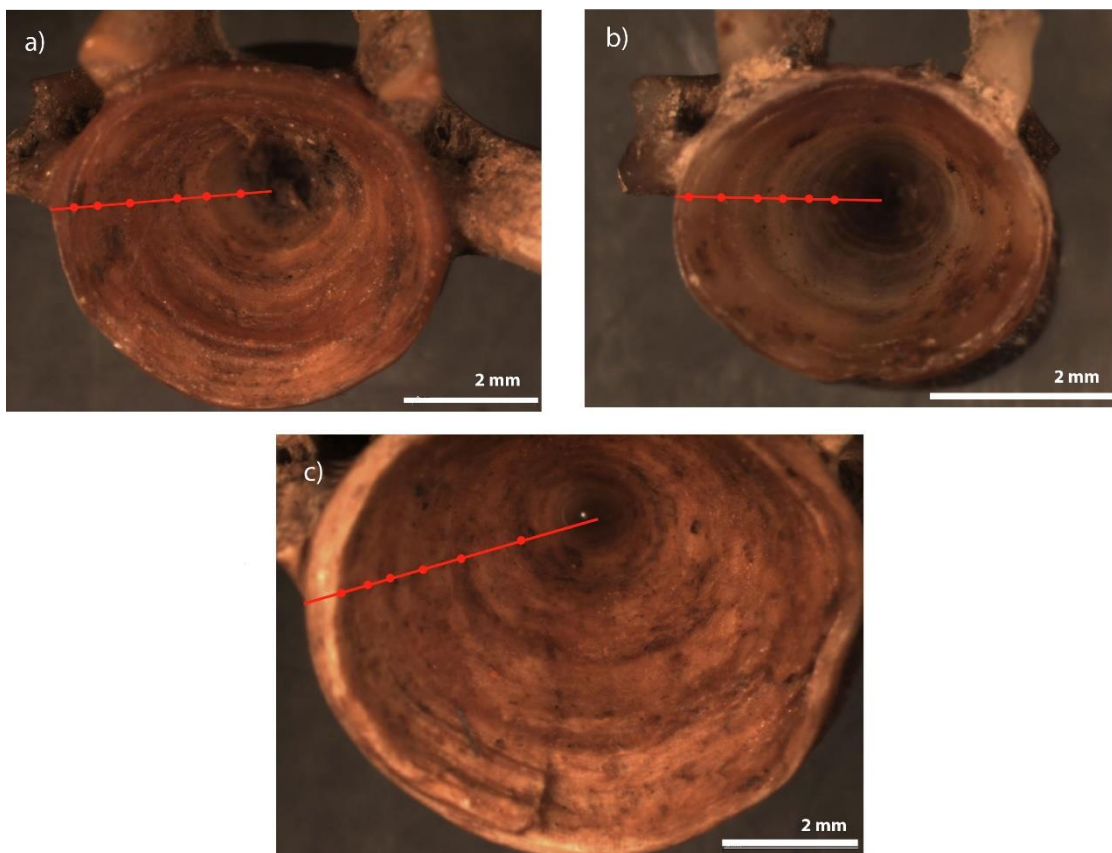
The modern reference collection consists of 61 individuals of *Synbranchus marmoratus* with total lengths (TL) distributed between 145 and 740 mm and net weights (W) ranging from 3 to 811 g. The species showed slightly positive allometric growth, where a significant relationship is given by the formula: $W = 6 \cdot 10^{-7} \cdot TL^{3.134}$ (N = 61, $r^2 = 0.9382$, $P < 0.05$). Furthermore, there was a significant relationship between measurements (radius) of the third vertebra and the total length of individuals, where $TL = 315.72 \cdot radius^{0.669}$ (N = 61, $r^2 = 0.88$, $P < 0.05$). This result means that vertebral development is closely related to the growth of the individual, which is a condition for incremental analysis.

Growth increments of *S. marmoratus* are regularly spaced and distinctly developed for the 61 modern vertebrae analyzed. Under reflected light, a dark zone with a diameter of around 0.81 mm surrounds the centrum of the vertebra. Panfili *et al.* (2002) attribute this zone to hatching, a hypothesis that should be further investigated. This first increment is followed by a broad and light increment (= zone) that probably corresponds to a fast growth period and a dark increment (= annulus), corresponding probably to a low growth period (Fig 7). Marbled swamp eel vertebrae present regular annuli with an annual periodicity (Supplemental Fig 1).

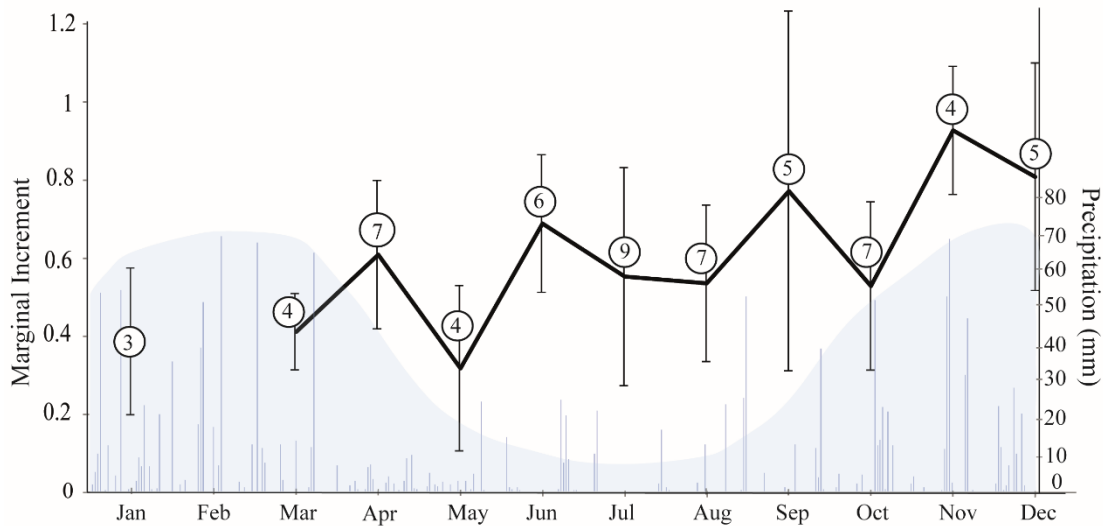
434 Marginal Increment (MI) varies between 0.3 and 1.2. The zone starts to form in October;
435 higher values of marginal increment are reached between November and December, which
436 corresponds to the beginning of rainfall (Fig 8). There is a decrease in MI in January (0.4).
437 The Kruskal-Wallis test and Pairwise Wilcoxon Rank Sum test were used to test the
438 differences of MI among months at a 0.05 significance level as MI were not normally
439 distributed. We see differences, but these differences are not significant at the 5% threshold.

440 We observed that individuals with a total length of no more than 30 cm had mature eggs,
441 and that the vast majority of specimens carrying mature eggs were recovered in October, just
442 before the first rainfall. Data from January and February must be interpreted with caution
443 given the small number of individuals sampled during this period (Fig 8).

444 The slow growth period starting in January continues during the first semester of the year
445 (until June) with the lowest marginal increment recorded in May (0.2). It is interesting to
446 note that the slow growth in May corresponds to the drop in precipitation levels and the
447 beginning of the cool period with temperatures recorded for Trinidad reaching 15°C (see Fig
448 1). From June to October, growth increments are less regular and therefore difficult to
449 interpret.



451 Fig 7: Zooarchaeological whole vertebrae of *Synbranchus marmoratus*. Annuli
452 corresponding to periods of slow growth are marked by dots on the reading axis (in red).



453

454 Fig 8: Marginal increment variation per month (solid line: mean \pm standard deviation) of
 455 modern specimens. Blue area indicates approximate levels of precipitation, encircled
 456 numbers represent the number of modern specimens per month. Marginal increments
 457 indicate that fast growth occurs from November until December, at the beginning of the
 458 rainy season.

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5.2. Archaeological application

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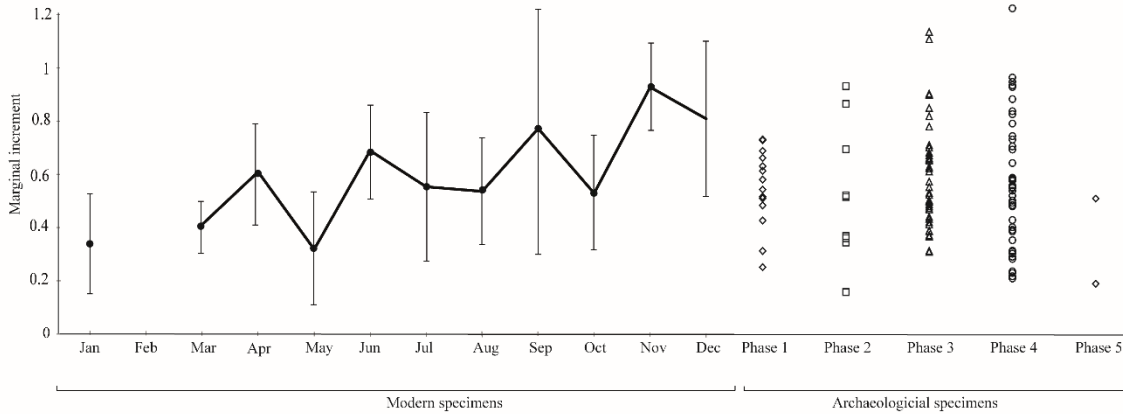
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The archaeological material recovered from Loma Salvatierra shows relatively little taphonomical deterioration. One hundred and eleven of the 138 vertebrae (v3) were preserved in good condition, showing visible annuli and thus considered suitable for age estimation, vertebrae were rejected when growth increments were not visible. We observed that some vertebrae presenting burning marks (white/grey/black colors) and deformed configuration, the measurements between annuli had lower values compared to the expected values (in relation to their corresponding class sizes). These vertebrae were also excluded. The marginal edges of the archaeological specimens were different: some of them were placed right on the annulus location, while for others, the edge was placed on zones. The marginal increments of vertebrae from distinct archaeological phases varied from 0.2 to 1.4. This is the case for phases 1 to 4, however, this cannot be proven for phase 5, where the number of preserved vertebrae is too low (N = 2) (Fig 9).



471
 473 Fig 9: Marginal increment (MI) values of the archaeological assemblage compared to the
 474 modern reference. As MI values of archaeological samples are well distributed between 0.2
 475 and 1.2, we infer that individuals were captured during different seasons of the year.

476 **6. DISCUSSION**

477 The Llanos de Mojos aquatic environments and fauna are greatly affected by
 478 hydrological cycles. As water recedes, the fish fauna is concentrated in shallow water bodies
 479 and food availability decreases (Loubens et al., 1992; Panfili, 1992). As both modern and
 480 archaeological assemblages are from ponds mainly supplied by precipitation, the increase in
 481 marginal increments during the last months of the year (October, November and December)
 482 suggests that growth rates increase with the onset of heavy rainfall and the consequent food
 483 availability. As for many other tropical fishes, the marbled swamp eel growth pattern is
 484 influenced by the alternation of wet and dry seasons more than by the oscillation between
 485 summer and winter (Fabr e and Saint-Paul, 1998; Junk et al., 1997; Lowe-McConnell, 1964;
 486 Meunier, 2012; Panfili, 1992; Silva and Stewart, 2006).

487 In this study, as the vast majority of female specimens were carrying eggs in October;
 488 as for many other tropical species, marbled swamp eel seems to present a gonadal maturation
 489 process synchronized with the beginning of the rainy season, but this should be verified since
 490 reproduction was not the focus of this study (Vazzoler and Menezes, 1992).

491 To date, near Trinidad, growth increment models have been established for five fish
 492 species: barred catfish (*Pseudoplatystoma fasciatum*), sabalo (*Prochilodus nigricans*),
 493 tambaqui-pacu (*Colossoma macropomum*), Amazon pella (*Pellona castelnaeana*) and
 494 red-bellied piranha (*Pygocentrus nattereri*) (Duponchelle et al., 2007; Le Guennec and
 495 Loubens, 2004; Loubens and Panfili, 2000, 1997, 1992). In all these cases, the annulus is
 496 formed during the period of receding waters or the dry season (somewhere between August

497 and November), whereas the light zone is formed during periods of rising waters. These data
498 suggest that water level stress and the isolation of water bodies are the main drivers of
499 annulus formation.

500 In our case, the annulus formation still needs to be validated with larger sample sizes.
501 Despite the fact that many authors suggest that temperature fluctuations do not (or hardly)
502 influence the growth pattern of Amazonian fish fauna (Fabr e and Saint-Paul, 1998; Loubens
503 and Panfili, 1992), our lower values of marginal increments coincide with the period when
504 lowest temperatures are recorded (June and July). As commented above, such discrepancies
505 in temperature values are driven by the arrival of cold windy fronts (*surazos*), when
506 temperatures can drop as low as 6 C (albeit low mean temperatures do not drop below 15 C).
507 The low temperature of the *surazos* is explained by the origin of air masses: during the
508 summer, the region is subject to humid winds from the northeast (Bolivian and Central
509 Amazon region). In contrast, during the winter, cold fronts from the South Pole and the
510 southernmost areas of South America reach the Llanos de Mojos, causing a drastic fall of 10
511 to 15 C from one day to another (Hanagarth, 1993).

512 These cold winds have been described since the first missionaries arrived in Mojos.
513 By the end of the 18th century, the Jesuit missionary Francisco Eder quoted “*the winter is*
514 *replaced by winds (...) before the waters start to recede, the new rains are blocked by these*
515 *winds, which mark the end of the rainfall, they draw and dry the standing water spread*
516 *throughout the savannas (...) With the exception of the surazo days, the heat is extreme,*
517 *however, with the arrival of these winds, an extreme dryness overcomes the territory,*
518 *followed by intense cold* (Eder, 1985). The impact of the drop in temperature on faunal
519 communities (mainly fish) has been also described by these first missionaries: “*on the*
520 *strength of the heat, the sudden wind from the south is so cold that it kills the fish in the*
521 *rivers. They start in March and end in August-September*” (Altamirano, 1979; Matthei and
522 Jeria, 2001). Although the periods of slow growth coincide with the period when *surazos*
523 occur, the impact of such drops in temperature, that could lower the water temperature, on
524 incremental growth structures has yet to be investigated.

525 As postulated by Meunier (2012), growth increments can be driven by factors involving
526 external environmental conditions and internal metabolic activity, which makes the
527 interpretation of growth patterns difficult (Silva and Stewart, 2006). Therefore, our study is
528 a first step and requires further investigation by enlarging the modern reference collection to
529 include individuals of both species and of various age classes, investigating other calcified

530 structures, and undertaking validation procedures, such as mark-recapture and rearing
531 studies (Beamish and McFarlane, 1983; Campana, 2001; Hales and Reitz, 1992).

532

533 6.1. *Year-round fishing?*

534 The first scholars visiting the Mojos region described fishing as an important
535 subsistence activity practiced not only by groups settling along major rivers but also in
536 interfluvial areas (Métraux, 1942). As for fishing seasonality, fishing seemed to be mainly a
537 dry season activity, at least for groups settled along the rivers, practiced as soon as water
538 levels receded and schools were concentrated in water bodies (Métraux, 1942; Nordenskiöld,
539 2002 [1912], 2001 [1924]). For groups inhabiting interfluvial areas, however, the seasonality
540 of fishing is less clear. At the beginning of the 20th century, Mojos groups, who were among
541 the groups living closest to the areas where Loma-type sites have been recovered, seemed to
542 take advantage of the receding water period. Métraux (1942: 60) described fishing in Mojos
543 as follows “*Throughout the large Plains of Mojos (...) fishing was the most productive*
544 *economic activity. Recession of floods left millions of fish stranded on the dry land or*
545 *concentrated in small pools (...)*”.

546 To date, little is known about the functioning of pre-Columbian fisheries in Mojos.
547 In spite of that, great efforts have been made to document the ancient fish weir systems
548 observed near Baures (about 150 km northeast of Loma Salvatierra). Due to the lack of
549 biological information, Erickson (2000) and McKey et al. (2016) assumed that fishes were
550 trapped as water receded, and thus presumed that fishing was a dry period activity. In Loma
551 Salvatierra, however, as marginal increment analysis demonstrates that specimens were
552 caught all year round, fishing may not have been an exclusively seasonal activity.

553 Evidence of year-round fishing is backed up by the presence of twisted pectoral fins
554 in about 3% of the armored catfish *Hoplosternum littorale* specimens (total N = 437)
555 recovered in Loma Salvatierra (Prestes-Carneiro et al., 2019). According to Reis (1998), in
556 mature males, pelvic fin tips twist into a hook shape during the reproductive period.
557 Therefore, if environmental conditions have not drastically changed during the last 1 000
558 years, our observations indicate that some fishing of armored catfish could have taken place
559 at the beginning of the rainy season (from December to March).

560 The modified landscape around the *lomas* in Llanos de Mojos can provide
561 supplementary information about seasonality of the occupation of these sites. The density of
562 villages concentrated in the territory, the architecture, and the monumentality of earth works

563 led the archaeologists working on the region to suggest that these mounds were occupied by
564 organized and densely populated societies that were inhabiting the sites throughout different
565 periods of the year (Jaimes Betancourt and Prümers, 2018). If the ponds and canals were
566 used during the dry season, it is probable that people did not abandon the site during this
567 period. Furthermore, Loma Salvatierra is composed of dozens of successive, thin layers of
568 sediment filled with archaeological material. Since no stratigraphic layer lacks
569 archaeological material, there are no documented events of abandonment. This continuity
570 reinforces the idea that people occupied the site permanently.

571 Archaeological evidence of a year-round occupation of Loma Salvatierra is also
572 consistent with archaeobotanical evidence since this is another indicator of seasonality as
573 some plants can have seasonal behaviors. The presence of chili peppers, sweet potatoes, jack
574 beans, peanuts, squash, and other cultivars suggests that agricultural activities were probably
575 practiced by sedentary groups living in Llanos de Mojos (Bruno, 2010). Another indicator
576 of human groups dealing with seasonality in their agriculture comes from the soil
577 engineering of raised fields. These systems were able to drain water related to overflowing
578 during the rainy season and also to prolong the presence of water, turning the dry season into
579 an additional cultivation period (Rodrigues et al., 2017, 2018).

580 The possibility of year-round fishing might be related (and explained) by the
581 presence of artificial ponds near Loma Salvatierra. Mapping of the surroundings of Loma
582 Salvatierra (Prümers, 2007, 2004) revealed a system of canals supplying excavated ponds
583 that have a diameter of 35 m and a depth of 2 m. The existence of continual fishing of
584 marbled swamp eel indicates that fish were available during both dry and rainy seasons,
585 supporting the hypothesis that some type of fishing management associated with earth works
586 and ponds could have taken place at Loma Salvatierra and that ponds could have ensured the
587 availability of these animals for a longer period of time (Prestes-Carneiro *et al.*, 2019). This
588 new evidence of year-round exploitation calls into question the general assumption that
589 fishing was a seasonal activity (Roosevelt, 1980). We do not exclude the possibility that
590 fishing could have been more intensive during the dry season, but our data reinforce the idea
591 that fishing involves the ability to deal with seasonal constraints through the development of
592 techniques, methods, and practices that take into account species behaviors and distribution
593 in the environment (Gragson, 1992). Hence, as the complex network of natural and artificial
594 depressions seems to have captured surplus seasonal rainfall and retained water during the
595 dry season, Loma Salvatierra demonstrates that the construction of managed aquatic
596 landscapes could have provided year-round resources.

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**6.2. Methodological issues concerning the application of growth increment
analysis to archaeological contexts**

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The application of a growth model to an archaeological assemblage is accompanied by a certain number of potential biases that could have compromised the accuracy of the analysis if they had not been taken into account: 1) The use of vertebrae raised taxonomic and rank identification problems; thus, it is of interest to verify the constancy of size along the vertebral column. 2) Despite the fact that vertebrae are solid bony structures, in some cases the marginal edges, which are essential for marginal increment analysis, can be eroded and unreadable. In the future, it would be interesting to use sections of vertebrae since the marginal edge can then be interpreted more easily on a flat structure than on a conic one (Desse and Desse-Berset, 1992; Rojo, 1988). 3) Since modern and archaeological fish may have been cooked or grilled at different temperatures and culinary practices, this could engender modifications in the form and size of the vertebrae and, therefore, we strongly recommend excluding clearly charred or deformed samples from the assemblage. A similar problem has also been pointed out by Andrus and Crowe (2002) for the analysis of over-cooked archaeological otoliths.

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Sclerochronological research should fundamentally comply with and verify this checklist of pre-requisites: archaeological specimen conservation, presence of readable not-eroded increments, species level identification for the archaeological elements, verifying that the zooarchaeological element chosen for the study represents different individuals, collection of modern specimens from as close as possible to the archaeological site (Deith, 1983), carrying out collections every month of the year with the largest possible number of specimens. These are time-consuming tasks, albeit necessary for study quality.

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A further consideration for the application of modern growth models to archaeological contexts is the assumption that environmental conditions (temperature, rainfall) have not changed so modern fish can be the model. Paleoclimatic data from southwestern Amazonia, such as the carbon isotope record of soil organic matter collected in the state of Rondônia (Brazil), indicate that the rainforest expanded over the savanna around 3,000 BP (De Freitas et al., 2001; Mayle et al., 2000; Taylor et al., 2010). This southward expansion, according to analysis of fossil pollen and macroscopic charcoal, appears to reach the Llanos de Mojos around 2,000 BP (Carson et al., 2014). The start of the construction of monumental platforms, around AD 300 or 1,650 BP (Jaimes Betancourt and

630 Prümers, 2018) is contemporary with the rain forest reaching stability at a level comparable
631 to the modern canopy rainforest. Forest expansion is compatible with evidence of increased
632 water levels in Lake Titicaca (Cross et al., 2000). A visible change in the pollen record occurs
633 during the occupation of the Llanos de Mojos, around the year AD 1000, when signs of
634 anthropogenic fire are linked to small scale-deforestation and slash-and-burn agriculture
635 (Urrego et al., 2013; Carson et al., 2014, Watling et al., 2017). This reinforces that humans
636 were shaping landscapes and modestly changing forest ecology. It remains to be seen
637 whether these changes have had an impact on animal populations (Henry and Cerrato, 2007).

638 The final issue about bias is related to the locations of ancient *versus* modern
639 captures. The model presented here is based on swamp eels inhabiting ponds all year long,
640 yet it is known that, in the absence of water, synbranchids burrow channels (Bicudo and
641 Johansen, 1979). As the location of ancient captures is unknown, we have assumed that the
642 archaeological specimens also came from ponds, which might not be the case. The growth
643 pattern of swamp eels living in buried channels is not yet known and should be further
644 investigated.

645

646 7. CONCLUSIONS

647 This study examined fishing seasonality in Amazonian archaeological contexts from
648 marbled swamp eel (*Synbranchus marmoratus*) vertebrae. Despite the fact that the great
649 majority of sclerochronological studies on fish are based on the analysis of otoliths, in
650 Amazonian archaeological sites, these remains have not been found to be well-preserved.
651 This led us to use sclerochronological techniques adapted to vertebrae. The anatomical
652 identification of the second and third vertebrae permits the differentiation and quantification
653 of individuals and the observation of the vertebrae in caudal view (conic part) provides a
654 better visualization of growth increments. Vertebrae are therefore the most suitable calcified
655 structures for age reading for this species. Based on a modern reference collection, we
656 developed a model to estimate the fishing season of the marbled swamp eel. Their vertebrae
657 present regular annuli suggesting that growth increments are related to environmental
658 fluctuations. Our observations point to the existence of one growth cycle per year and
659 confirm the results of Barros et al. (2017). The greatest fish growth occurred during the wet
660 season when waters were rising, as for many other species in the Bolivian Amazon. The
661 period of slowed growth (annulus formation) appears to have occurred simultaneously with

662 the fall in precipitation levels and drop in temperatures, somewhere between May and
663 October.

664 The analysis of 111 archaeological swamp eel vertebrae from the Loma Salvatierra
665 site (Bolivia), spanning occupations from AD 500 to AD 1400, demonstrated that the fishing
666 of swamp eels occurred all year-round. This supports the hypothesis that people living on
667 this seasonally flooded savanna fished during all seasons either as permanent residents or as
668 groups of people continually coming and going over the millennium, and whose activities
669 left no signs of abandonment. While large expanses of water are present during the wet-
670 season, dry-season fishing may have been enhanced by the use of permanent water
671 management systems, such as those that have been recorded at Loma Salvatierra.

672 Demonstrating that human groups occupied villages year-round does not mean that
673 these groups were not mobile. The presence of causeways is a great indicator of inter-site
674 mobility as they could function as sidewalks. Furthermore, mobility is inherent to the
675 exploitation of some seasonal Amazonian resources such as Brazil nuts and most palm trees
676 as well as the hunting of certain animals. In other words, to understand human occupation in
677 the Amazon it is necessary to break with the paradigms that hunter-fisher-gatherers did not
678 return to places they previously used and that ceramic possessing farmers did not have
679 practices that depended on mobility to acquire resources from beyond their own settlements.
680 These categories of sedentarism or nomadism are external and should be questioned,
681 especially within debates about seasonality of occupation, as suggested by Mongeló (2013)
682 and Shock and Moraes (2019).

683 While the seasonal differences in fish growth are less pronounced in South American
684 fresh waters than in the ocean, it was possible to investigate human fishing strategies in
685 relation to the hydraulic cycle. This contributes to the conclusion that, for seasonality studies,
686 indications from multiple proxies such as landscape transformations, study of plant remains,
687 malacofauna, vertebrate animals, etc. should be taken into account (Sanger et al., 2019).
688 These concerns are especially relevant for understanding the use of resources in the context
689 of the dense human occupation of the Amazon, which is suggested by the large
690 archaeological sites, especially around AD 1000 (Moraes and Neves, 2012).

691 Studies that seek to describe the ontogenetic age and growth of Amazonian fishes
692 have been expanded in biology, while in archaeology the importance of fishing among pre-
693 Columbian Amazonian societies is increasingly recognized. These two areas of study can
694 continue to complement each other. The application of sclerochronology to other Amazonian
695 archaeological contexts will be an opportunity to combine biological and archaeological

696 data. Like fish, many other biological resources may inform on seasonality (e.g. mollusks,
697 amphibians, reptiles). The analysis of seasonality based on archaeological remains can
698 contribute to the understanding of how pre-Columbian groups dealt with Amazonian
699 ecosystems, the seasonality of resources, and the impacts of human exploitation on a local
700 scale.

701

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718 modern comparative collections are housed at the Curt Nimuendaju Archaeological
719 laboratory of the Federal University of Western Pará (UFOPA-Santarém) and the
720 zooarchaeological specimens are housed at the Deutsches Archäologisches Institut,
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730

731 REFERENCES

732 Altamirano, D.F., 1979 [1700]. Historia de la mision de los Mojos. Instituto Boliviano de
733 Cultura Biblioteca Jose Agustin Palacios, La Paz, Bolivia.

734 Andrus, C.F.T., Crowe, D.E., 2002. Alteration of otolith aragonite: effects of prehistoric
735 cooking methods on otolith chemistry. *Journal of Archaeological Science* 29, 291–
736 299. <https://doi.org/10.1006/jasc.2001.0694>

737 Andrus, C.F.T., 2011. Shell midden sclerochronology. *Quaternary Science Reviews* 30,
738 2892–2905. <https://doi.org/10.1016/j.quascirev.2011.07.016>

739 Barros, N.H.C., Nascimento, W.S., Araújo, A.S., Souza, A.A., Chellappa, S., 2013. Biologia
740 reprodutiva do muçum, *Synbranchus marmoratus* Bloch, 1795 no açude Marechal
741 Dutra, Rio Grande do Norte, Brasil. *Biota Amazônia* 3, 39–47.
742 <http://dx.doi.org/10.18561/2179-5746/biotaamazonia.v3n1p39-47>

743 Barros, N.H.C., de Souza, A. A., Peebles, E. B., Chellappa, S., 2017. Dynamics of sex
744 reversal in the marbled swamp eel (*Synbranchus marmoratus* Bloch, 1795), a
745 diandric hermaphrodite from Marechal Dutra Reservoir, northeastern Brazil. *Journal*
746 *of Applied Ichthyology* 33(3), 443-449.

747 Beamish, R., McFarlane, G.A., 1983. The forgotten requirement for age validation in
748 fisheries biology. *Transactions of the American Fisheries Society* 112, 735–743.
749 [https://doi.org/10.1577/1548-8659\(1983\)112<735:TFRFAV>2.0.CO;2](https://doi.org/10.1577/1548-8659(1983)112<735:TFRFAV>2.0.CO;2)

750 Béarez, P., Prümers, H., 2005. Prehispanic fishing at Loma Mendoza, Llanos de Moxos,
751 Bolivia, in: Plogmann, H. (Eds.), Proceedings of the 13th Meeting. Internationale
752 Archäologie: Arbeitsgemeinschaft, Symposium, Tagung, Kongress, Band 8 of the
753 ICAZ Fish Remains Working Group. Presented at the The Role of Fish in Ancient
754 Time, Verlag Marie Leidorf, Basel, pp. 3–10.

755 Bicudo, P.W., Johansen, K., 1979. Respiratory gas exchange in the airbreathing fish,
756 *Synbranchus mamoratus*. *Environmental Biology of Fishes* 4 (1), 55-64.
757 <https://doi.org/10.1007/BF00005928>

758 Boujard, T., Lecomte, F., Renno, J.-F., Meunier, F., Neveu, P., 1991. Growth in four
759 populations of *Leporinus friderici* (Bloch, 1794) (Anostomidae, Teleostei) in French

760 Guiana. *Journal of Fish Biology* 38, 387–397. [doi:10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.1991.tb03128.x)
761 [8649.1991.tb03128.x](https://doi.org/10.1111/j.1095-8649.1991.tb03128.x)

762 Butler, P.G., Freitas, P.S., Burchell, M., Chauvaud, L., 2019. Archaeology and
763 sclerochronology of marine bivalves, in: Smaal, A.C., Ferreira, J.G., Grant, J.,
764 Petersen, J.K., Strand, O. (Eds.), *Goods and Services of Marine Bivalves*. Springer,
765 Cham, pp. 413–444. Braga, A.L.C., dos Santos Pompeu, P., Carvalho, R.F., Ferreira,
766 R.L., 2009. Dieta e crescimento de *Synbranchus marmoratus* (Bloch, 1975) (Pisces,
767 Synbranchiformes) durante período de pré-estivação em uma lagoa marginal da bacia
768 do São Francisco, Minas Gerais. *Revista Brasileira de Zootecias* 10, 133–138.

769 Brewer, D.J., 1987. Seasonality in the prehistoric Faiyum based on the incremental growth
770 structures of the Nile catfish (Pisces: *Clarias*). *Journal of Archaeological Science* 14,
771 459–472. [doi.org/10.1016/0305-4403\(87\)90032-X](https://doi.org/10.1016/0305-4403(87)90032-X)

772 Bruno, M., 2010. Carbonized plant remains from Loma Salvatierra, Department of Beni,
773 Bolivia. *Zeitschrift für Archäologie Außereuropäischer Kulturen* 3, 153–208.

774 Cahiza, P.A., 2003. Ictioarqueología de las Lagunas de Guanacache (Mendoza, Argentina).
775 *Relaciones de la Sociedad Argentina de Antropología* 28, 167–183.

776 Campana, S.E., 1990. How reliable are growth back-calculations based on otoliths?
777 *Canadian Journal of Fisheries and Aquatic Sciences* 47, 2219–2227.
778 doi.org/10.1139/f90-246

779 Campana, S.E., 2001. Accuracy, precision and quality control in age determination,
780 including a review of the use and abuse of age validation methods. *Journal of Fish*
781 *Biology* 59, 197–242. doi.org/10.1111/j.1095-8649.2001.tb00127.x

782 Carré, M., Bentaleb, I., Blamart, D., Ogle, N., Cardenas, F., Zevallos, S., Kalin, R.M.,
783 Ortlieb, L., Fontugne, M., 2005. Stable isotopes and sclerochronology of the bivalve
784 *Mesodesma donacium*: potential application to Peruvian paleoceanographic
785 reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 228, 4–25.
786 doi.org/10.1016/j.palaeo.2005.03.045

787 Carson, J.F., Whitney, B.S., Mayle, F.E., Iriarte, J., Prümers, H., Soto, J. D., Watling, J.,
788 2014. Environmental impact of geometric earthwork construction in pre-Columbian
789 Amazonia. *Proceedings of the National Academy of Sciences* 111(29), 10497–
790 10502.

791 Castanet, J., Meunier, F.J., Francillon-Vieillot, H., 1992. Squelettochronologie à partir des
792 os et des dents chez les vertébrés, in: Baglinière, J.L., Castanet, J., Meunier, F.J.,
793 Conand, F. (Eds.), *Tissus durs et âge individuel des vertébrés*. Colloque

794 National, Bondy, France, 4–6 Mars 1991. Colloque et séminaire ORSTOM–
795 INRA, pp. 257–280.

796 Casteel, R.W., 1972. Some archaeological uses of fish remains. *American Antiquity* 37,
797 404–419. <https://doi.org/10.2307/278439>

798 Casteel, R.W., 1974. On the remains of fish scales from archaeological sites. *American*
799 *Antiquity* 39, 557–581. <https://doi.org/10.2307/278905>

800 Cross, S., Baker, P., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., 2000. A new estimate of the
801 Holocene lowstand level of Lake Titicaca, central Andes, and implications for
802 tropical palaeohydrology. *Holocene* 10(1), 21–32.

803 Cutrim, L., Batista, V.S. 2005. Determinação de idade e crescimento do mapará
804 (*Hypophthalmus marginatus*) na Amazônia Central. *Acta Amazon* 35, 85–92.
805 <http://dx.doi.org/10.1590/S0044-59672005000100013>

806 Deith, Margaret R., 1983. Molluscan calendars: the use of growth-line analysis to establish
807 seasonality of shellfish collection at the Mesolithic site of Morton, Fife, *Journal of*
808 *Archaeological Science* 10(5), 423-440.

809 De Freitas, H. A., Pessenda, L. C. R., Aravena, R., Gouveia, S. E. M., de Souza Ribeiro, A.,
810 Boulet, R., 2001. Late Quaternary vegetation dynamics in the southern Amazon basin
811 inferred from carbon isotopes in soil organic matter. *Quaternary Research*, 55(1), 39-
812 46.

813 Denevan, W.M., 1966. The aboriginal cultural geography of the Llanos de Mojos Bolivia.
814 University of California Press, Berkley.

815 Desse, J., Desse-Berset, N., Rocheteau, M., 1989. Les profils rachidiens globaux.
816 Reconstitution de la taille des poissons et appréciation du nombre minimal
817 d'individus à partir des pièces rachidiennes. *Revue de paléobiologie* 8, 89–94.

818 Desse, J., Desse-Berset, N., 1992. Age et saison de mort des poissons: applications à
819 l'archéologie, in: Baglinière, J.L., Castanet, J., Conand, F., Meunier, F.J. (Eds.), .
820 Presented at the Tissus durs et âge individuel des vertébrés. Colloque National,
821 Bondy, France, 4–6 Mars 1991, Colloque et séminaire ORSTOM– INRA, pp.
822 341–353.

823 Duponchelle, F., Lino, F., Hubert, N., Panfili, J., Renno, J.-F., Baras, E., Torrico, J.-P.,
824 Dugué, R., Nunez, J., 2007. Environment-related life-history trait variations of the
825 red-bellied piranha *Pygocentrus nattereri* in two river basins of the Bolivian
826 Amazon. *Journal of Fish Biology* 71, 1113–1134. [https://doi.org/10.1111/j.1095-
827 8649.2007.01583.x](https://doi.org/10.1111/j.1095-8649.2007.01583.x)

828 Eder, F.J., 1985 [1791]. Breve descripción de las reducciones de Mojos. Historia boliviana,
829 Cochabamba.

830 Fabré, N.N., Saint-Paul, U., 1998. Annulus formation on scales and seasonal growth of the
831 Central Amazonian anostomid *Schizodon fasciatus*. Journal of Fish Biology 53, 1–
832 11. <https://doi.org/10.1111/j.1095-8649.1998.tb00103.x>

833 Garson, A.G., 1980. Comment upon the economic potential of fish utilization in riverine
834 environments and potential archaeological biases. American Antiquity 45, 562–567.
835 <https://doi.org/10.2307/279874>

836 Gathaz, R.J., 2012. Condição relacionada ao hermafroditismo protogínico diândrico em
837 *Synbranchus marmoratus* (Bloch, 1975) (Teleostei, Synbranchiformes,
838 Synbranchidae) na represa de Salto Grande, Americana-SP (Master dissertation).
839 Universidade Estadual Paulista Júlio de Mesquita Filho, Rio Claro, Brazil.
840 <http://hdl.handle.net/11449/99517>

841 Gragson, T.L., 1992. Fishing the waters of Amazonia: Native subsistence economies in a
842 tropical rain forest. American Anthropologist 94, 428–440.
843 www.jstor.org/stable/680469

844 Guillaud, E., Elleboode, R., Mahé, K., Béarez, P., 2017. Estimation of age, growth and
845 fishing season of a Paleolithic population of grayling (*Thymallus thymallus*) using
846 scale analysis. International Journal of Osteoarchaeology 27, 683–692.
847 <https://doi.org/10.1002/oa.2595>

848 Hales, L.S., Reitz, E.J., 1992. Historical changes in age and growth of Atlantic croaker,
849 *Micropogonias undulatus* (Perciformes: Sciaenidae). Journal of Archaeological
850 Science 19, 73–99. [https://doi.org/10.1016/0305-4403\(92\)90008-Q](https://doi.org/10.1016/0305-4403(92)90008-Q)

851 Hanagarth, W., 1993. Acerca de la geocología de las sabanas del Beni en el noreste de
852 Bolivia. Instituto de Ecología de La Paz, La Paz.

853 Heckenberger, M.J., Kuikuro, A., Kuikuro, U.T., Russell, J.C., Schmidt, M., Fausto, C.,
854 Franchetto, B., 2003. Amazonia 1492: Pristine forest or cultural parkland? Science
855 301, 1710–1714. <https://doi.org/10.1126/science.1086112>

856 Henry, K. M., Cerrato, R.M., 2007. The annual macroscopic growth pattern of the northern
857 quahog hard clam *Mercenaria mercenaria* in Narragansett Bay, Rhode Island.
858 Journal of Shellfish Research 26(4), 985-993.

859 Jaimes Betancourt, C., Prümers, H. 2018. A la sombra de los Andes. Arquitectura
860 monumental en los Llanos de Mojos, in: Ghezii, I., Camacho, L.E.S. (Eds.), La
861 Cooperación Científica Francesa en Latinoamérica: Avances Recientes en Datación

862 y Arqueometría en los Andes. Institut Français d'Études Andines (IFEA), Plural, La
863 Paz, pp. 253-273. Jaimes Betancourt, C., 2012. La cerámica de la Loma Salvatierra
864 (Beni-Bolivia). Editora Plural, La Paz.

865 Junk, W.J., Soares, M.G., Saint-Paul, U., 1997. The fish, in: Junk, W.J. (Eds) The Central
866 Amazon Floodplain. Springer, Berlin, pp. 385–408.

867 Lathrap, D.W., 1968. The “Hunting” economics of the Tropical Forest Zone of South
868 America: An attempt at Historical perspective, in: Lee, R., Devore, I. (Eds.), Man the
869 Hunter. Aldine Transaction, Chicago, pp. 23–29.

870 Le Guennec, B., Loubens, G., 2004. Biologie de *Pellona castelnaeana* (Teleostei:
871 Pristigasteridae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyological
872 Exploration of Freshwaters 15, 369–383. [http://horizon.documentation.ird.fr/exl-](http://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers10-12/010034660.pdf)
873 [doc/pleins_textes/divers10-12/010034660.pdf](http://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers10-12/010034660.pdf)

874 Lo Nostro, F.L., Guerrero, G.A., 1996. Presence of primary and secondary males in a
875 population of the protogynous *Synbranchus marmoratus*. Journal of Fish Biology 49,
876 788–800. <https://doi.org/10.1111/j.1095-8649.1996.tb00079.x>

877 Loubens, G., Lauzanne, L., Le Guennec, B., 1992. Les milieux aquatiques de la région de
878 Trinidad (Béni, Amazonie bolivienne). Revue d'hydrobiologie tropicale 25, 3–21.

879 Loubens, G., Panfili, J., 1992. Estimation de l'âge individuel de *Prochilodus nigricans*
880 (Teleostei, Prochilodidae) dans le Béni (Bolivie): protocole d'étude et application.
881 Aquatic Living Resources 5, 41–56. [http://horizon.documentation.ird.fr/exl-](http://horizon.documentation.ird.fr/exl-doc/pleins_textes/cahiers/hydrob-trop/37736.pdf)
882 [doc/pleins_textes/cahiers/hydrob-trop/37736.pdf](http://horizon.documentation.ird.fr/exl-doc/pleins_textes/cahiers/hydrob-trop/37736.pdf)

883 Loubens, G., Panfili, J., 1997. Biologie de *Colossoma macropomum* (Teleostei:
884 Serrasalmodae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyological
885 Exploration of Freshwaters 8, 1–22.

886 Loubens, G., Panfili, J., 2000. Biologie de *Pseudoplatystoma fasciatum* et *P. tigrinum*
887 (Teleostei: Pimelodidae) dans le bassin du Mamoré (Amazonie Bolivienne).
888 Ichthyological Exploration of Freshwaters 11, 13–34.

889 Lowe-McConnell, R.H., 1964. The fishes of the Rupunini savanna district of British Guiana,
890 Pt 1. Groupings of fish species and effects of the seasonal cycles on the fishes.
891 Journal of the Linnean Society (Zoology) 45, 103–144.
892 <https://doi.org/10.1111/j.1096-3642.1964.tb00490.x>

893 Mahé, K., Fave, F., Couteau, J., 2011. TNPC user guide. France: IFREMER (accessed
894 December 9, 2019). <https://archimer.ifremer.fr/doc/00032/14288/>.

895 Mahé, K., Bellail, R., Dufour, J. L., Boiron-Leroy, A., Dimeet, J., Duhamel, E., Elleboode,
896 R., Felix, J., Grellier, P., Huet, J., 2009. Synthèse française des procédures
897 d'estimation d'âge. Programme SIDEPECHE, Projet Système d'Informations
898 Halieutiques Sous-Action Scélérochronologie. Vol. 1. IFREMER, Paris.
899 <https://archimer.ifremer.fr/doc/00000/7294/>.

900 Man-Wai, R., Quignard, J.-P., 1982. Les sars *Diplodus sargus* (Linnée 1758) du Golfe du
901 Lion: croissance et caractéristiques des débarquements aux criées de Sète et du Grau-
902 du-Roi. Revue des Travaux de l'Institut des Pêches Maritimes 46, 173–194.

903 Mateus, L.A.F., Petrere, M., 2004. Age, growth and yield per recruit analysis of the pintado
904 *Pseudoplatystoma corruscans* (Agassiz, 1829) in the Cuiabá River basin, Pantanal
905 Matogrossense, Brazil. Brazilian Journal of Biology 64, 257–264.
906 <http://dx.doi.org/10.1590/S1519-69842004000200011>

907 Matthei, M., Jeria, R.M., 2001. Cartas e informes de misioneros jesuitas extranjeros en
908 Hispanoamérica: selección, traducción, introducción y notas (1751-1778). Pontificia
909 Universidad Católica de Chile, Santiago.

910 Martins, J.M.E., Rego, A.C.L., Pinese, J.F. 2009. Determinação da idade e crescimento
911 de *Hoplias malabaricus* (Bloch, 1794) (Characiformes, Erythrinidae) na represa de
912 Campim Branco I, Rio Araguari, MG. Rev Bras Zool 11, 261–268.

913 Mayle, F.E., Burbridge, R., Killeen, T.J., 2000. Millennial-scale dynamics of southern
914 Amazonian rain forests. Science 290(5500), 2291–2294.

915 McKey, D.B., Durécu, M., Pouilly, M., Béarez, P., Ovando, A., Kalebe, M., Huchzermeyer,
916 C.F., 2016. Present-day African analogue of a pre-European Amazonian floodplain
917 fishery shows convergence in cultural niche construction. Proceedings of the
918 National Academy of Sciences 113, 14938–14943.
919 <http://doi:10.1073/pnas.1613169114>

920 Meggers, B.J., 1954. Environmental limitation on the development of culture. American
921 anthropologist 56, 801–824. <https://www.jstor.org/stable/663814>

922 Métraux, A., 1942. The native tribes of eastern Bolivia and western Matto Grosso,
923 Smithsonian Institution Bureau of American Ethnology. US Government Printing
924 Office, Washington.

925 Meunier, F., 2012. Skeletochronological studies of cyclical growth of freshwater fishes in
926 French Guiana. A review. Cybium 36, 55–62. <http://sfi-cybium.fr/en/node/68>

927 Mongeló, G., 2013. O formativo e os modos de produção: ocupações pré-ceramistas no
928 Alto Rio Madeira-RO. PhD Thesis, Universidade de São Paulo, Brazil.

929 Montenegro, L.A., Damasceno, D.N.F., Almeida, R.G., Chellappa, S., 2011. Biologia
930 alimentar do mussum, *Synbranchus marmoratus* (Bloch, 1795)(Osteichthyes:
931 Synbranchidae) no açude Marechal Dutra localizado no semi-árido brasileiro. Biota
932 Amazônia 1, 45–52. [http://dx.doi.org/10.18561/2179-5746/biotaamazonia.v1n2p45-
933 52](http://dx.doi.org/10.18561/2179-5746/biotaamazonia.v1n2p45-52)

934 Moraes, C.P., Neves, E. G., 2012. O ano 1000: adensamento populacional, interação e
935 conflito na Amazônia Central. Amazônica-Revista de Antropologia 4(1), 122-148.

936 Moran, E.F., 1993. Through Amazonian eyes: The human ecology of Amazonian
937 populations. University of Iowa Press, Iowa City.

938 Morey, D.F., 1983. Archaeological assessment of seasonality from freshwater fish remains:
939 a quantitative procedure. Journal of Ethnobiology 3, 75–95.
940 <https://www.jstor.org/stable/20170168>

941 Neves, E.G., Petersen, J.B., Bartone, R.N., Heckenberger, M.J., 2004. The timing of terra
942 preta formation in the Central Amazon: archaeological data from three sites, in:
943 Glaser, B., Woods, W.I. (Eds.), Amazonian Dark Earths: Explorations in Space and
944 Time. Springer-Verlag, Heidelberg, pp. 125–134.

945 Nordenskiöld, E., 2001 [1915]. Exploraciones y aventuras de Sudamérica. APCOB, La Paz.

946 Nordenskiöld, E., 2002 [1912]. La vida de los indios: El gran Chaco (Sudamérica). APCOB,
947 La Paz.

948 Panfili, J., 1992. Estimation de l'âge individuel des poissons: méthodologies et applications
949 à des populations naturelles tropicales et tempérées. PhD Thesis, Université
950 Montpellier II, Montpellier, France.

951 Panfili, J., De Pontual, H., Troadec, H., Wrigh, P.J., 2002. Manual of fish sclerochronology.
952 Ifremer-IRD coedition, Brest, France. <https://archimer.ifremer.fr/doc/00017/12801/>

953 Perdices, A., Doadrio, I., Bermingham, E., 2005. Evolutionary history of the synbranchid
954 eels (Teleostei: Synbranchidae) in Central America and the Caribbean islands
955 inferred from their molecular phylogeny. Molecular Phylogenetics and Evolution 37,
956 460–473. <http://doi:10.1016/j.ympev.2005.01.020>

957 Ponton, D., Mol, J.H., Panfili, J., 2001. Use of otolith microincrements for estimating the
958 age and growth of young armoured catfish *Hoplosternum littorale*. Journal of Fish
959 Biology 58, 1274–1285. <http://doi:10.1111/j.1095-8649.2001.tb02285.x>

960 Pouilly, M., Beck, S.G., Moraes, R., Ibanez, C., 2004. Diversidad biológica en la llanura de
961 inundación del Río Mamoré: importancia ecológica de la dinámica fluvial. Centro de
962 Ecología Simón, Santa Cruz de la Sierra.

963 Prestes-Carneiro, G., Béarez, P., 2017. Swamp-eel (*Synbranchus* spp.) fishing in Amazonia
964 from pre-Columbian to present times. *Journal of Ethnobiology* 37, 380–397.
965 <https://doi.org/10.2993/0278-0771-37.3.380>

966 Prestes-Carneiro, G., Béarez, P., Dillenseger, K., Yunoki, T. 2018. Size estimation of
967 *Synbranchus marmoratus* and *Synbranchus madeirae* based on isolated cranial and
968 post-cranial bones. *Cybium* 42, 201–207.

969 Prestes-Carneiro, G., Béarez, P., Shock, M.P., Prümers, H., Jaimes Betancourt, C. 2019. Pre-
970 Hispanic fishing practices in interfluvial Amazonia: zooarchaeological evidence
971 from managed landscapes on the Llanos de Mojos savanna. *PLoS ONE* 14(5):
972 e0214638. <https://doi.org/10.1371/journal.pone.0214638>

973 Prestes-Carneiro G., Béarez, P., Pugliese, Shock, M.P., Zimpel C.A., Pouilly, M., Neves
974 E.G., 2020. Archaeological history of Middle Holocene environmental change from
975 fish proxies at the Monte Castelo archaeological shell mound, Southwestern
976 Amazonia. *The Holocene*, 0959683620941108.
977 <https://doi.org/10.1177/0959683620941108>

978 Prümers H., Jaimes Betancourt C., 2014. 100 años de investigación arqueológica en los
979 Llanos de Mojos. *Arqueoantropológicas* (4), 11–53.

980 Prümers, H., 2007. Der Wall führt zum See. Die Ausgrabungen 2005–2006 in der Loma
981 Salvatierra (Bolivien). *Zeitschrift für Archäologie Au\’s sereuropäischer Kulturen* 2,
982 371–379.

983 Prümers, H., 2004. Charlatanocracia en Mojos, investigaciones arqueológicas en la Loma
984 Salvatierra, Beni, Bolivia. *Boletín de arqueología PUCP*, 103–116.

985 Quitmyer, I. R., Jones, D. S., Arnold, W. S., 1997. The sclerochronology of hard clams,
986 *Mercenaria* spp., from the south-eastern USA: A method of elucidating the
987 zooarchaeological records of seasonal resource procurement and seasonality in
988 prehistoric shell middens. *Journal of Archaeological Science*, 24(9), 825-840.

989 Rodrigues, L., Lombardo, U., Veit, H., 2018. Design of pre-Columbian raised fields in the
990 Llanos de Moxos, Bolivian Amazon: Differential adaptations to the local
991 environment?. *Journal of Archaeological Science: Reports*, 17, 366-378.

992 Rodrigues, L., Lombardo, U., Canal Beeby, E., Veit, H., 2017. Linking soil properties and
993 pre-Columbian agricultural strategies in the Bolivian lowlands: the case of raised
994 fields in Exaltación. *Quaternary International* 438 (Part B), 143–155.

995 Rodriguez, M., 1999. El espectro trófico de juveniles de *Synbranchus marmoratus*
996 (*Synbranchiformes*, *Synbranchidae*). *Iheringia*, sér. Zool 86, 137–143.

- 997 R Core Team 2016. R: A language and environment for statistical computing. Foundation
998 for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- 999 Rojo, A., 1988. Excavated fish vertebrae as predictors in bioarchaeological research. North
1000 American Archaeologist 8, 209–226. [https://doi.org/10.2190/QTDW-T2A0-P7G6-](https://doi.org/10.2190/QTDW-T2A0-P7G6-QX2V)
1001 [QX2V](https://doi.org/10.2190/QTDW-T2A0-P7G6-QX2V)
- 1002 Roosevelt, A.C., 1980. Parmana: Prehistoric maize and manioc subsistence along the
1003 Amazon and Orinoco. New York Academic Press, New York.
- 1004 Rosa, A., 2000. Zooarqueologia de alguns sítios do Pantanal Sul-matogrossense. Revista
1005 Clio de Arqueologia 14, 327–342.
- 1006 Rosa, A.O., 2006. Caçadores de cervídeos no Litoral Central: o sítio RS-LC-96. Pesquisas.
1007 Antropologia, 223–248.
- 1008 Rosen, D.E., Rumney, A., 1972. Evidence of a second species of *Synbranchus* (Pisces,
1009 Teleostei) in South America. American Museum Novitates 2497, 1–
1010 45. <http://hdl.handle.net/2246/2704>
- 1011 Sanger, M.C., Quitmyer, I.R., Colaninno, C.E., Cannarozzi, N., Ruhl, D.L., 2019. Multiple-
1012 proxy seasonality indicators: An integrative approach to assess shell midden
1013 formations from Late Archaic shell rings in the coastal southeast North America. The
1014 Journal of Island and Coastal Archaeology 15.3, 333-363.
- 1015 Santos, G.B., Barbieri, G., 1993. Idade e crescimento do “piau gordura”, *Leporinus piau*
1016 Fowler, 1941, na represa de Três Marias (estado de Minas Gerais) (Pisces,
1017 Ostariophysi, Anostomidae). Braz J Biol 53, 649–658
- 1018 Scartascini, F.L., Sáez, M., Volpedo, A.V., 2015. Otoliths as a proxy for seasonality: The
1019 case of *Micropogonias furnieri* from the northern coast of San Matías Gulf, Río
1020 Negro, Patagonia, Argentina. Quaternary International, Archaeology of coastal
1021 hunter-gatherer occupations in the Southern Cone 373, 136–142.
1022 <https://doi.org/10.1016/j.quaint.2014.11.046>
- 1023 Schaan, D.P., 2008. The nonagricultural chiefdoms of Marajó Island, in: Silverman, H.,
1024 Isbell, W. (Eds.), The Handbook of South American Archaeology. Springer, New
1025 York, pp. 339–357.
- 1026 Shock M.P., Moraes, C.P., 2019. A floresta é o domus: A importância das evidências
1027 arqueobotânicas e arqueológicas das ocupações humanas amazônicas na transição
1028 Pleistoceno/Holoceno. Boletim do Museu Paraense Emílio Goeldi. Ciências
1029 Humanas 14(2), 263–289.

- 1030 Schone, B., 2008. The curse of physiology—challenges and opportunities in the
1031 interpretation of geochemical data from mollusk shells. *Geo-Marine Letters* 28 (5-
1032 6), 269-285.
- 1033 Silva, E.A., Stewart, D.J., 2006. Age structure, growth and survival rates of the commercial
1034 fish *Prochilodus nigricans* (bocachico) in North-eastern Ecuador. *Environmental*
1035 *Biology of Fishes* 77, 63–77. <https://doi.org/10.1007/s10641-006-9055-y>
- 1036 Svoboda, A., 2013. Método para determinar la estacionalidad de ocupación de sitios
1037 arqueológicos de ambientes fluviolacustres de Patagonia a partir de la observación
1038 de otolitos de percas. *La Zaranda de Ideas, Revista de Jóvenes Investigadores en*
1039 *Arqueología* 9, 145–153. <http://hdl.handle.net/11336/1279>
- 1040 Taylor, Z.P., Horn, S.P., Mora, C.I., Orvis, K.H., Cooper, L.W., 2010. A multi-proxy
1041 palaeoecological record of late-Holocene forest expansion in lowland Bolivia.
1042 *Palaeogeogr Palaeoclimatol Palaeoecol* 293(1-2), 98–107.
- 1043 Torres, R.A., Roper, J.J., Foresti, F., Oliveira, C., 2005. Surprising genomic diversity in the
1044 Neotropical fish *Synbranchus marmoratus* (Teleostei: Synbranchidae): how many
1045 species? *Neotropical Ichthyology* 3, 277–284. [http://dx.doi.org/10.1590/S1679-](http://dx.doi.org/10.1590/S1679-62252005000200005)
1046 [62252005000200005](http://dx.doi.org/10.1590/S1679-62252005000200005)
- 1047 Torres, J.E. 2016. La pêche chez les chasseurs-cueilleurs marins de la région du détroit de
1048 Magellan et des mers adjacentes, de l'Holocène moyen aux temps ethnographiques :
1049 rôle, technologie et stratégies saisonnières. PhD thesis, Université Paris 1 Panthéon
1050 Sorbonne.
- 1051 Torres J., Mahé K., Dufour J.-L., Béarez P., San Román M., 2020. Characterizing seasonal
1052 fishing patterns and growth dynamics during the Middle and Late Holocene in the
1053 Strait of Magellan (Chilean Patagonia): Sclerochronological analysis of *Salilota*
1054 *australis* (Teleostei: Moridae) vertebrae. *Journal of Island and Coastal Archaeology*,
1055 1-20. [10.1080/15564894.2020.1755393](https://doi.org/10.1080/15564894.2020.1755393)
- 1056 Urrego, D. H., Bush, M. B., Silman, M. R., Niccum, B. A., De La Rosa, P., McMichael, C.
1057 H., Hagen, S., Palace, M., 2013. Holocene fires, forest stability and human
1058 occupation in south- western Amazonia. *Journal of biogeography*, 40(3), 521-533.
- 1059 Van Neer, W., Löugas, L., Rijnsdorp, A. D., 1999. Reconstructing age distribution, season
1060 of capture and growth rate of fish from archaeological sites based on otoliths and
1061 vertebrae. *International Journal of Osteoarchaeology*, 9(2), 116-130.

1062 [https://doi.org/10.1002/\(SICI\)1099-1212\(199903/04\)9:2<116::AID-](https://doi.org/10.1002/(SICI)1099-1212(199903/04)9:2<116::AID-)
1063 [OA465>3.0.CO;2-H](https://doi.org/10.1002/(SICI)1099-1212(199903/04)9:2<116::AID-OA465>3.0.CO;2-H)

1064 Van Neer, W., 1993. Limits of incremental growth in seasonality studies: The example of
1065 the clariid pectoral spines from the Byzantino-Islamic site of Apamea (Syria; sixth
1066 to seventh century AD). *International Journal of Osteoarchaeology* 3, 119–127.
1067 <https://doi.org/10.1002/oa.1390030209>

1068 Van Neer, W., Ervynck, A., Bolle, L.J., Millner, R.S., 2004. Seasonality only works in
1069 certain parts of the year: the reconstruction of fishing seasons through otolith
1070 analysis. *International Journal of Osteoarchaeology* 14, 457–474.
1071 <https://doi.org/10.1002/oa.727>

1072 Vazzoler, A., Menezes, N.A., 1992. Síntese de conhecimentos sobre o comportamento
1073 reprodutivo dos Characiformes da América do Sul (Teleostei, Ostariophysi). *Revista*
1074 *Brasileira de Biologia* 52, 627–640.

1075 Vitale, F., Worsøe Clausen, L., Ní Chonchúir, G. (Eds.), 2019. Handbook of fish age
1076 estimation protocols and validation methods. ICES Cooperative Research Report
1077 346. 180 pp. <http://doi.org/10.17895/ices.pub.5221>

1078 Von den Driesch, A., Hutterer, R., 2012. Mazamas, patos criollos y anguilas de lodo. Restos
1079 de subsistencia del asentamiento precolombino “Loma Salvatierra”, Llanos de
1080 Mojos, Bolivia. *Zeitschrift für Archäologie Außereuropäischer Kulturen* 4, 341–367.

1081 Watling, J., Iriarte, J., Mayle, F. E., Schaan, D., Pessenda, L. C., Loader, N. J., Street-
1082 Perrottf, F.A., Dickau, E.G., Damascenod, A., Ranzi, A. 2017. Impact of pre-
1083 Columbian “geoglyph” builders on Amazonian forests. *Proceedings of the National*
1084 *Academy of Sciences*, 114(8), 1868-1873.

1085 Yunoki, T., Torres, L. V., Cholima, R. B., 2018. A metacommunity ecological approach to
1086 understanding the community organization of fish in artificial ponds of the Mamoré
1087 River floodplain in the Amazonian lowlands of Bolivia. *Environmental Biology of*
1088 *Fishes*, 101(9), 1329-1341.

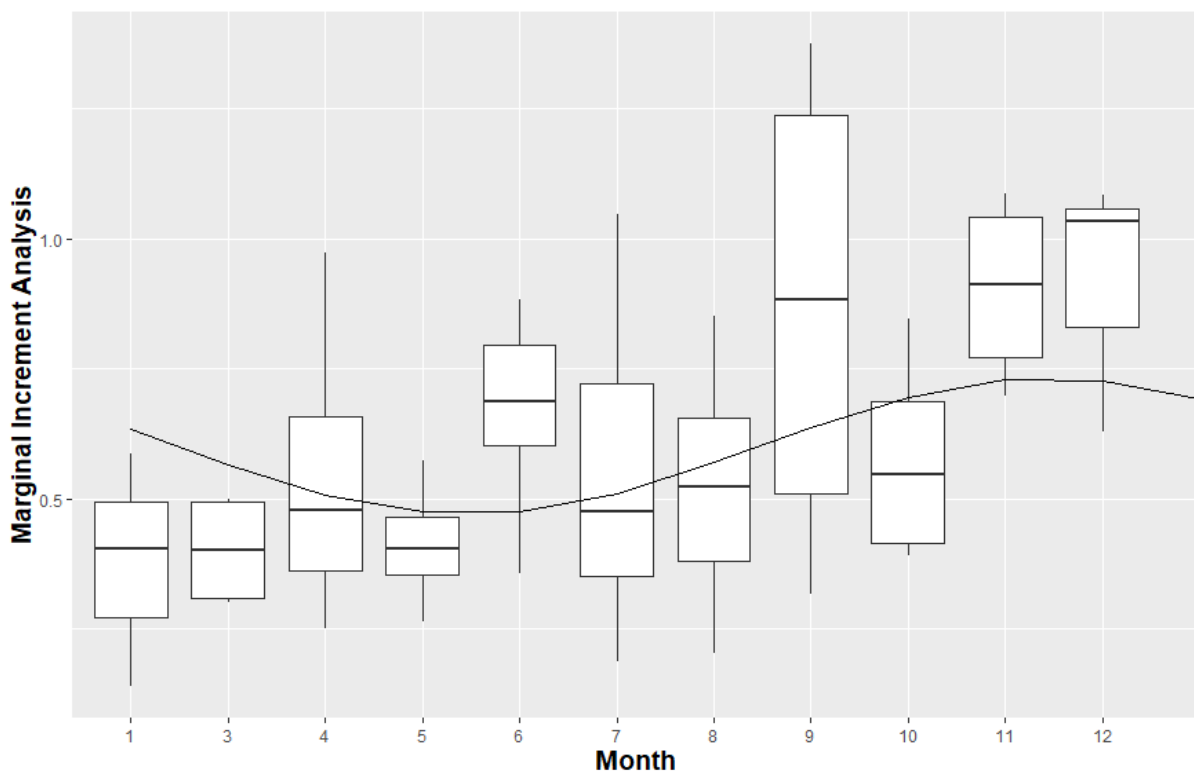
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1094 **Supplemental material for Reconstructing freshwater fishing seasonality in a**
1095 **neotropical savanna: first application of swamp eel (*Synbranchus marmoratus*)**
1096 **sclerochronology to a pre-Columbian Amazonian site (Loma Salvatierra, Bolivia)**

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1098 **Béarez Philippe¹**

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1100 Supplemental Figure 1: Temporal dynamics of monthly marginal increments on vertebrae
1101 of swamp eel (n = 61) with sinusoidal regression showing the annual periodicity of the
1102 annulus.



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1112 Supplemental Table 1: Information of each modern specimen. During the first months of
 1113 collection, it was not possible to record the sex of individuals. During the subsequent months,
 1114 sex was identified by Takayuki Yunoki based on Lo Nostro and Guerrero (1996). Collections
 1115 were made on the last days of each month, except for the April collections that were made
 1116 during the first days of May (03/05/2016).

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Specimen number	Pre-Anal length (mm)	Total length (mm)	Weight (g)	Date of capture	Sex
4	105	145	3	31/07/2015	No data
5	121	143	5	31/07/2015	No data
1	600	830	811	23/08/2015	No data
10	385	465	185	31/08/2015	No data
16	215	312	34	31/08/2015	No data
15	230	320	36	31/08/2015	No data
13	252	360	48	31/08/2015	No data
12	310	425	88	31/08/2015	No data
14	245	350	50	31/08/2015	No data
11	345	470	135	31/08/2015	No data
34	350	485	162	31/08/2015	No data
28	250	351	53	30/09/2015	No data
27	269	372	64	30/09/2015	No data
25	305	449	106	30/09/2015	No data
24	310	450	107	30/09/2015	No data
31	229	310	72	21/10/2015	No data
37	162	235	14	23/10/2015	No data
36	254	350	58	23/10/2015	No data
35	325	450	127	23/10/2015	No data
33	385	530	196	23/10/2015	No data
00-8	295	435	94	23/11/2015	Female 1
00-10	269	391	65	23/11/2015	Female 1
00-12	226	328	34	23/11/2015	Female 1
00-13	252	350	33	23/11/2015	Male 1
12-08	316	466	87	23/12/2015	Female 3
12-09	315	441	94	23/12/2015	Female 1
12-10	226	325	33	23/12/2015	Female 2
12-11	228	313	32	23/12/2015	Female 3
12-12	207	299	26	23/12/2015	Female 1
0-8	290	415	71	26/01/2016	Female 1
0-9	296	412	79	26/01/2016	Female 3
0-10	247	355	31	26/01/2016	Female 1
03-1	362	502	155	29/03/2016	Male 1

03-2	315	446	103	29/03/2016	Male 1
03-3	286	412	85	29/03/2016	Female 2
03-4	267	392	76	29/03/2016	Male 1
03-5	170	242	14	29/03/2016	Male 1
05-17	323	460	118	03/05/2016	Male 1
05-18	320	450	105	03/05/2016	Male 1
05-19	303	434	112	03/05/2016	Male 1
05-20	301	390	70	03/05/2016	Male 1
05-21	215	300	30	03/05/2016	Female 1
05-22	203	255	19	03/05/2016	Male 1
05-24	380	520	203	03/05/2016	Male 1
05-25	245	342	60	03/05/2016	Female 1
05-1	186	261	26	30/05/2016	Female 1
05-2	279	384	65	30/05/2016	Male 1
05-3	272	395	79	30/05/2016	Female 1
05-4	299	405	72	30/05/2016	Male 1
06-5	385	534	276	30/06/2016	Male 1
06-6	365	501	178	30/06/2016	Male 1
06-7	306	432	165	30/06/2016	Female 2
06-8	323	443	109	30/06/2016	Female 1
06-9	232	321	78	30/06/2016	Female 1
06-10	262	350	82	30/06/2016	Female 1
07-1	497	680	460	28/07/2016	Female 1
07-2	323	419	126	28/07/2016	Female 1
07-3	334	457	157	28/07/2016	Male 1
07-4	247	358	57	28/07/2016	Female 1
07-5	244	342	50	28/07/2016	Female 1
07-6	240	340	51	28/07/2016	Female 1
07-7	220	305	28	28/07/2016	Male
07-8	186	260	20	28/07/2016	Female 1
07-9	229	410	91	28/07/2016	Female 1
07-10	254	347	44	28/07/2016	Female 1

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