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Ontogenetic Development of Hyperostosis in the Crevalle Jack *Caranx hippos* (Linnaeus, 1766) and New Records of Affected Bone Regions

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ABSTRACT

Hyperostosis is a non-pathological condition widely reported in marine teleosts, yet its developmental dynamics and underlying drivers remain poorly understood. This study investigates the ontogenetic progression and anatomical distribution of hyperostosis in *Caranx hippos* based on a growth series of 39 specimens collected along the Brazilian coast. Individuals were categorised into two size classes (class 1 < 400 mm and class 2 ≥ 400 mm), and skeletal alterations were assessed through radiographic imaging, morphometric analyses and histology. Hyperostosis was detected in 87.2% of specimens and affected nine skeletal regions, including dorsal and anal pterygiophores, cleithrum, ribs, pelvic bones, neural and hemal spines and for the first dorsal fin pterygiophore, preopercle and opercle. The dorsal pterygiophores were the earliest and most consistently affected elements, with detectable changes in individuals as small as 184 mm TL, suggesting an early onset of the condition. Other regions exhibited a size-dependent pattern, with hyperostosis appearing sequentially and increasing in frequency and extent with growth. Morphological variation among skeletal elements indicates region-specific expression, with pronounced differences in thickness, width and mass between hyperostotic and non-hyperostotic bones. Comparisons with previous studies confirm a species-specific pattern of hyperostotic distribution in *C. hippos*, with minor variation in the onset and extent of affected regions. The observed ontogenetic progression supports the hypothesis that hyperostosis develops sequentially across skeletal elements rather than simultaneously. These findings, combined with ecological and biomechanical considerations, suggest that hyperostosis results from multiple interacting factors, including growth-related mechanical loading and environmental variability. Overall, this study provides a comprehensive characterisation of hyperostotic development in *C. hippos*, highlighting the importance of ontogenetic approaches for understanding the biological and functional significance of this condition in marine fishes.

1 | Introduction

Anomalies can be defined as irregularities or deviations from the expected morphological or physiological pattern of a given species. In an ichthyological context, such alterations may manifest in two forms, distinguished by their consequences: severe

anomalies, which significantly impair individual survival, and mild anomalies, which appear to exert no negative effects on viability (Jawad and Akylol 2018). Regarding their origin, Yilmaz et al. (2024) proposed that these anomalies can be classified into four categories: environmental, biological, ecological and those resulting from pressures associated with fishing activities.

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Hyperostosis is not considered a pathological condition; rather, it is generally interpreted as a natural biological phenomenon (Smith-Vaniz et al. 2024; Ahnelt et al. 2025). This interpretation is supported by evidence indicating that it does not negatively affect fish fitness and is commonly observed in adult individuals (Aguilera et al. 2017; Mahmoud and Ibrahim 2021; Ahnelt et al. 2025). Several hypotheses have been proposed to explain its origin, including genetic and environmental factors; however, no consensus has yet been reached regarding the mechanisms responsible for triggering this condition (Paig-Tran et al. 2016; Fjellidal et al. 2021; Smith-Vaniz et al. 2024).

The family Carangidae is among the teleost groups in which hyperostosis has been most extensively documented, comprising 55 affected species distributed across 19 genera (Smith-Vaniz and Carpenter 2007; Smith-Vaniz et al. 2024; de Sá et al. 2025; Tuna et al. 2026). Members of this family are of considerable commercial importance, with virtually all species exploited as food resources. Carangids are widely distributed throughout the Atlantic, Indian and Pacific Oceans (Nelson et al. 2016) and represent one of the teleost lineages in which hyperostosis is most frequently reported (Smith-Vaniz and Carpenter 2007; Smith-Vaniz et al. 2024).

The genus *Caranx* Lacepède, 1801 is broadly distributed in the Atlantic Ocean, with most species occurring from the northern United States to southeastern Brazil. Species within this genus are primarily carnivorous, feeding on fishes, shrimps and other invertebrates, and are recognised as important top predators in tropical marine ecosystems (Smith-Vaniz and Carpenter 2007). All species are targeted by both commercial and recreational fisheries throughout their distribution and are commonly captured using a variety of fishing gears. Despite their ecological and economic importance, taxonomic and geographic uncertainties persist within the genus, with potential implications for fisheries management and conservation (Smith-Vaniz and Carpenter 2007).

Caranx hippos (crevalle jack) is a pelagic carangid commonly found in shallow coastal waters over the continental shelf, occurring at depths of up to 350 m (Carpenter 2002; WoRMS Editorial Board 2026). The species is distributed on both sides of the Atlantic Ocean. In the Western Atlantic, it is more abundant from Nova Scotia, throughout the Gulf of Mexico and the Caribbean Sea, extending southward to Uruguay. It is considered rare in the West Indies and the Bahamas and is absent from Bermuda (Carpenter 2002).

Throughout its life cycle, *C. hippos* exhibit marked habitat shifts. Larvae are pelagic, juveniles are primarily associated with estuarine systems, and adults occupy a wide range of coastal and offshore habitats (Berry 1959; Johnson 1978; McBride and McKown 2000; Mohan et al. 2017). Ecologically, the species is predominantly diurnal and commonly forages in schools near the surface, often generating conspicuous surface disturbances while pursuing schooling prey; larger individuals, however, may adopt more solitary behaviour (Kwei 1978; Carpenter 2002; Correia et al. 2017). Diet composition varies ontogenetically: post-larvae feed mainly on copepods, juveniles consume a mixture of small fishes and shrimps and adults prey primarily on

clupeid fishes (Fagade and Olaniyan 1973; Kwei 1978; Correia et al. 2017). The species can attain large body sizes, reaching up to 30 kg, and may live for at least 14 years (Caiafa et al. 2011; Jefferson et al. 2022).

Although hyperostosis has long been recognised across multiple marine teleost lineages, its developmental onset and progression remain poorly understood (Smith-Vaniz et al. 2024). Even in species where hyperostosis is recurrent, it is typically more prevalent in larger, often mature individuals and less frequent in smaller size classes (Aguilera et al. 2017; Smith-Vaniz et al. 2024; Tuna et al. 2024). This pattern complicates efforts to determine its onset and to describe how the distribution of affected skeletal elements expands during growth. This gap is particularly relevant in carangids, a family that includes several species with reported hyperostosis, in which the condition may develop sequentially across skeletal elements rather than simultaneously (Tuna et al. 2026). Such a pattern suggests potential variation across body sizes and life stages.

In this context, *Caranx hippos* represents a suitable model for investigating these ontogenetic dynamics, given the lack of detailed descriptions of when hyperostosis first becomes detectable and how its skeletal distribution expands across size classes. Accordingly, the present study analyses a size series from the Brazilian coast to characterise this developmental trajectory.

This study aims to document and describe the sequence and progression of hyperostotic development across skeletal regions in *C. hippos*, both overall and within defined size classes, and to identify regions exhibiting consistent developmental patterns. Additionally, histological analyses of the dorsal pterygiophores, preopercle and opercle from specimens collected along the southeastern coast of Brazil (Western Atlantic) were conducted to characterise tissue alterations and to confirm the presence of hyperostosis in those regions.

2 | Material and Methods

2.1 | Fish Material

A total of 39 specimens of *Caranx hippos* were analysed (4 males, 9 females and 26 of undetermined sex), obtained from artisanal fishers and local markets in Rio de Janeiro between September 2025 and January 2026. To cover smaller individuals which are not usually available in the fish trade, specimens from the ichthyological collection of the Chondrichthyes Laboratory at the Federal University of Rio de Janeiro were also examined. These specimens were not dissected, as they belong to the collection; instead, radiographic imaging was performed, and all analyses were based on the resulting X-ray images. The corresponding specimen lots were LCD50, LCD51 and LCD71.

Based on the available data on first maturation size for the genus *Caranx* (Kwei 1978; Sudekum et al. 1991; Pardee et al. 2021) and preliminary data analysis using multivariate analysis (cluster analysis, simple matching index of similarity and UPGMA—Figure S1) based on the presence of hyperostosis in

different bone regions, we classified individuals in two size classes: class 1 <400 mm TL and class 2 ≥400 mm TL. This classification aimed to evaluate the behaviour of hyperostosis in mature and immature individuals, throughout different stages of growth. A Pearson correlation coefficient was used in order to verify the relationship between fish size (as a proxy of fish development stage) and the number of affected bones or skeletal regions.

2.2 | Radiography

Radiographic imaging was employed as a non-destructive method to assess variation in skeletal radiodensity, enabling the detection and characterisation of hyperostotic structures. Due to increased mineralisation, hyperostotic elements exhibit greater radiopacity relative to adjacent tissues, facilitating accurate identification and comparison across ontogenetic stages. Specimens were radiographed using an X-ray system (MAG 300 mA Collimator), operated at 160 mA and 40–60 kV. Image acquisition was performed at a standardised focal distance of 1.0–1.2 m.

2.3 | Bone Extraction and Measurements

Biometric data, including total weight (TW, g) and total length (TL, mm), were recorded for all specimens, and sex was determined when possible. Skeletal elements affected and unaffected by hyperostosis were manually extracted from 33 specimens (six museum specimens were not dissected). Bone length, width and thickness were measured using a digital calliper, following a standardised protocol in which all hyperostotic elements were measured, along with three non-hyperostotic elements per region for comparison (Figure S2). Wet weight of the bones was determined using a Shimadzu AY220 precision digital scale (0.01 g). In order to compare width and thickness of bones of the same length within the same individual, when possible, the nonparametric paired Wilcoxon test was used.

Nomenclature followed Smith-Vaniz et al. (2024), with the following abbreviations: cleithrum (CL), preopercle (POP), opercle (OP), pelvic bone (PB), ribs (R), dorsal pterygiophores (DPT), anal pterygiophores (APT), neural spines (NS) and hemal spines (HS).

2.4 | Histology

For histological analyses, samples from the first DPT of representative juvenile and adult specimens were used, along with POP and OP samples of one of the biggest individuals (TL = 536 mm). Skeletal samples were decalcified in EDTA for 72 h, rinsed in distilled water, and dehydrated through a graded ethanol series. Samples were then cleared in xylene, embedded in paraffin and sectioned at 4 µm thickness. Sections were mounted on glass slides, stained with Harris haematoxylin and eosin and examined under a trinocular Opticam 300S microscope equipped with a 10× objective and an AmScope digital camera.

3 | Results

3.1 | Hyperostosis in *Caranx hippos*

Patterns of hyperostotic development were examined in individuals of different sizes (Figure 1). The analysed specimens had a mean total length (TL) of 416 mm (range: 137–600 mm) and a mean body mass of 1070.57 g (range: 38.36–21,482.10 g). Hyperostosis was detected in 87.2% of individuals, with variation among size classes (Table 1). The smallest specimen exhibiting hyperostosis measured 184 mm TL. There is a significant correlation between fish size and number of hyperostotic bones ($r = 0.931$, $p < 0.0001$) and skeletal regions ($r = 0.914$, $p < 0.0001$) (Figure S4).

Hyperostosis affected multiple skeletal elements, including the cleithrum (CL), preopercle (POP), opercle (OP), pelvic bone (PB), ribs (R), dorsal pterygiophores (DPT), anal pterygiophores (APT), neural spines (NS) and hemal spines (HS). Mean values for length, width and thickness of each region of affected and non-affected bones are presented in Tables 2 and 3. Using the same bone length class, there were significant differences in width and thickness of neural spines, haemal spines and dorsal pterygiophores with hyperostotic and non-hyperostotic conditions (Table S1). Representative images illustrating the morphology of hyperostotic bones are provided in the Figures S2 and S3.

The DPT is the first region to exhibit visible morphological changes associated with hyperostosis, confirmed in at least one of the six smallest individuals available for analysis (184 mm TL), which was the only specimen dissected to preserve the remaining material in the collection. Hyperostotic elements in this region correspond to the 1st, 17th and 19th positions—that is, the 1st pterygiophore of the first dorsal fin and the 10th and 12th pterygiophores of the second dorsal fin. Among all affected regions, DPTs exhibited the most pronounced differences in width, thickness and mass, with minimum and maximum values of 4.69–24.15, 1.78–11.74 and 0.09–3.56 mm, respectively.

Morphology changes with position. The 1st DPT, at its highest degree of hyperostosis, exhibits width exceeding length (40.19 mm vs. 19.3 mm), an atypical condition compared with other skeletal elements, in which length generally predominates. In contrast, the 17th and 19th elements display an expanded dorsal portion and a tapered distal end, with length remaining greater than width.

Hyperostosis in the APT was restricted to the 1st element, occurring in 43.6% of individuals and confined to the posterior region of the bone base. Thickness ranged from 0.14 mm in non-hyperostotic elements to 10.51 mm in affected ones. Unlike the DPT, which occurs in the smallest individuals, APT hyperostotic bone is only observed in specimens greater than 460 mm TL.

The cleithrum (CL) is the second region to exhibit hyperostosis, being already observed in individuals from 256 mm TL. The condition is restricted to the mid-to-distal portion of the bone. In smaller individuals, hyperostosis initially produces a slight

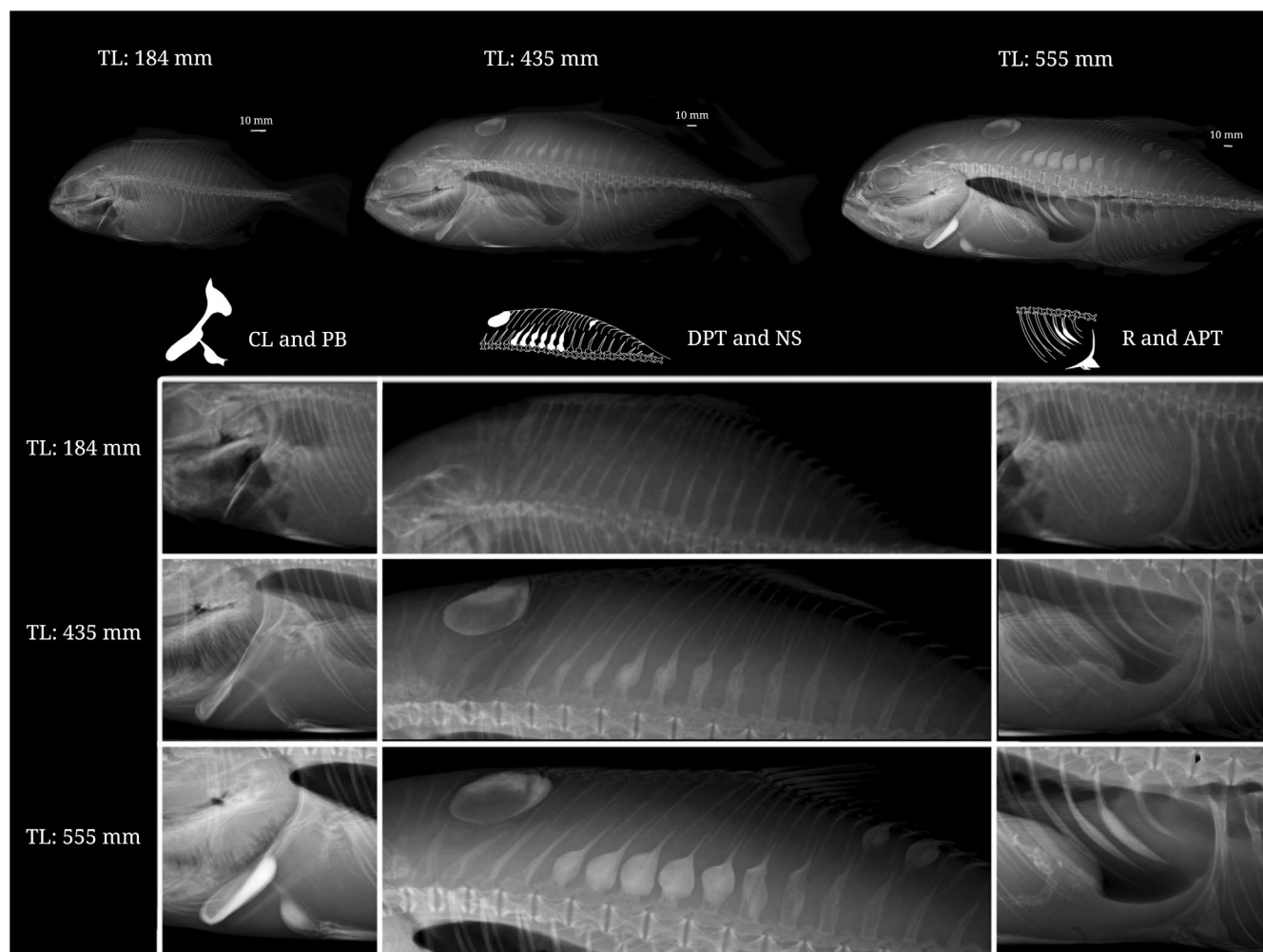


FIGURE 1 | Radiographs of *Caranx hippos* specimens of different sizes, accompanied by schematic drawings of bones affected by hyperostosis. Anal pterygiophore (APT), cleithrum (CL), dorsal pterygiophore (DPT), neural spine (NS), pelvic bones (PB), rib (R), along with magnified views of the same skeletal regions analysed in each size class.

TABLE 1 | Frequency of hyperostosis in bones of *Caranx hippos* across each size class and for all analysed specimens.

Size classes	N	FH (%)	DPT (%)	CL (%)	NS (%)	PB (%)	R (%)	APT (%)	HS (%)
Class 1 (<400 mm)	15	66.7	66.7	46.7	20	0	0	0	13.3
Class 2 (≥ 400 mm)	24	100	100	100	100	87.5	50	70.8	79.1
All individuals	39	87.2	87.2	79.5	69.2	53.9	30.8	43.6	53.9

Note: N: number of individuals per size class. FH refers to the percentage of fish exhibiting hyperostosis. Abbreviations: APT, anal-fin pterygiophores; CL, cleithrum; DPT, dorsal-fin pterygiophores; HS, hemal spines; NS, neural spine; PB, pelvic bone; R, rib.

pointed projection; as it progresses, it expands into the region between the angular margins of the cleithrum, eventually forming a more rounded structure at its most developed stage. From a given size onward, its occurrence becomes consistent: beginning with the second affected specimen (TL=335 mm), all subsequent individuals exhibited hyperostosis in the CL. The most pronounced variation was observed in width, thickness and wet weight, with minimum and maximum values of 3.11–25.62 mm, 7.38–19.22 mm and 0.35–14.42 g, respectively.

Ribs (R) exhibiting hyperostosis were recorded only in size class 2 with 30.8% of affected individuals, beginning at 475 mm TL.

The condition affected the smaller, more posterior ribs, corresponding to the 7th, 8th and 9th vertebrae. The most notable variation occurred in width, thickness and wet weight, ranging from 0.74–9.62 mm, 0.62–9.01 mm and 0.20–2.46 g, respectively. In this region, hyperostosis is characterised by a pronounced swelling in the central portion of the bone.

Pelvic bones (PB) were frequently affected (53.8%), with hyperostosis first appearing at 435 mm TL. Mean bone mass differed substantially between non-hyperostotic (0.21 g) and hyperostotic elements (0.84 g). The hypertrophic change is primarily restricted to the anterior region of the bone.

TABLE 2 | Morphometric analysis according to bone region affected by hyperostosis.

Bone region with hyperostosis	Mean height (min-max) in mm	Mean width (min-max) in mm	Mean thickness (min-max) in mm	Mean weight (min-max) in g
DPT	19.93 (9.75–38.03)	24.15 (6.41–40.19)	11.74 (3.29–31.03)	3.56 (0.15–8.67)
APT	54.93 (45.39–63.77)	24.87 (15.48–40.72)	6.80 (3.4–10.51)	3.48 (0.46–30.2)
RIB	54.87 (34.47–82.31)	5.42 (2.81–9.62)	4.75 (0.65–9.01)	0.89 (0.23–2.46)
NS	33.34 (15.59–44.56)	7.61 (1.51–14.51)	5.92 (2.14–14)	0.60 (0.11–2.22)
HS	34.56 (23.85–42.64)	8.31 (3.67–12.6)	6.09 (1.2–14.33)	0.54 (0.15–1.42)
CL	82.60 (35.23–103.6)	14.75 (2.8–47.38)	11 (3.2–19.22)	5.21 (0.68–14.42)
PB	38.89 (20.56–87.13)	10.41 (2.82–20.75)	7.39 (3.37–14.25)	0.84 (0.18–6.65)

Abbreviations: APT, anal-fin pterygiophores; CL, cleithrum; DPT, dorsal-fin pterygiophores; HS, hemal spines; NS, neural spine; PB, pelvic bone; R, rib.

TABLE 3 | Morphometric analysis by bone region not affected by hyperostosis.

Bone region without hyperostosis	Mean height (min-max) in mm	Mean width (min-max) in mm	Mean thickness (min-max) in mm	Mean weight (min-max) in g
DPT	23.95 (9.76–39.97)	4.69 (0.81–16.01)	1.78 (0.03–7.63)	0.09 (0.02–0.556)
APT	28.49 (10.79–59.24)	5.91 (0.62–34.67)	2.30 (0.14–9.48)	0.18 (0.012–2.39)
RIB	62.64 (15.15–91.83)	3.15 (0.74–20.63)	1.83 (0.62–4.2)	0.32 (0.2–1)
NS	26.67 (13.84–39.31)	4.10 (1.14–6.86)	2.42 (0.182–4.89)	0.16 (0.03–0.93)
HS	29.75 (13.15–51.02)	5.02 (0.24–29.1)	3.19 (0.38–14.09)	0.25 (0.02–2.76)
CL	52.45 (51.99–52.92)	3.21 (3.11–3.31)	7.75 (7.38–8.13)	0.36 (0.35–0.38)
PB	31.21 (24.46–71.52)	6.50 (5.43–7.57)	3.51 (2.5–4.76)	0.21 (0.14–0.30)

Abbreviations: APT, anal-fin pterygiophores; CL, cleithrum; DPT, dorsal-fin pterygiophores; HS, hemal spines; NS, neural spine; PB, pelvic bone; R, rib.

In neural spines (NS), hyperostosis originates at the base of the vertebrae and extends toward the medial portion of the spine. A total of 69.2% of individuals were affected, beginning at 340 mm TL. From the 5th to the 9th vertebrae, neural spines are markedly thickened with a rounded morphology, whereas from the 11th to the 14th vertebrae, thickening is less pronounced relative to non-hyperostotic elements. Thickness variation is the most distinctive feature in this region, ranging from 0.18 to 14 mm.

Hyperostosis in hemal spines (HS) was observed in 53.9% of individuals, affecting elements from the 12th to the 15th vertebrae. Two distinct morphological patterns were identified: in

one, hyperostosis develops as a central swelling while the lateral bases remain unmodified (e.g., 14th vertebra); in the other, the condition is concentrated at the base of the spine (e.g., 15th vertebra).

3.2 | Histological Analysis and Newly Identified Affected Regions

Three specimens measuring 184 mm TL, 340 mm TL and 555 mm were selected for histological analysis of the first dorsal pterygiophore (DPT) to confirm the presence of hyperostosis, with

particular attention given to the smallest specimen (184 mm TL), as hyperostosis had not previously been reported in individuals smaller than 250 mm TL in the literature. In addition, the preopercle and opercle were removed and examined histologically from a single specimen measuring 536 mm TL. Because only one individual was analysed for these bones, frequencies of hyperostosis in these regions could not be assessed in the present study. Besides the macroscopic identification, hyperostosis in these two newly recognised affected regions was confirmed microscopically through histological sections (Figure 2A,B), which revealed enlarged vascular canals similar to those observed in histological sections of the first dorsal pterygiophore from the other three specimens (Figure 2C–E).

4 | Discussion

Patterns of hyperostotic development within the *Caranx hippos* complex appear consistent at the species level but vary among closely related taxa, indicating strong taxonomic specificity (Smith-Vaniz and Carpenter 2007; Smith-Vaniz et al. 2024; Tuna et al. 2026; Wei et al. 2026). In an early comparative study, Smith-Vaniz et al. (1995) described the occurrence of hyperostosis in *C. hippos* (Atlantic Ocean) and *Caranx caninus* Günther,

1867 (eastern Pacific Ocean), two morphologically similar species with allopatric distributions. Their results demonstrated that hyperostotic patterns are species-specific, even among closely related taxa: *C. hippos* exhibits hyperostosis in the neural spines (NS), cleithrum (CL), dorsal and anal pterygiophores (DPT, APT) and ribs (R), whereas *C. caninus* shows the condition only in DPT, APT and R.

In the most recent review, Smith-Vaniz et al. (2024) compiled historical and contemporary records of hyperostosis in *C. hippos* e.g., (Starks 1911a, 1911b; Korschelt 1940; Kaiser 1960; Konnerth 1966; Olsen 1966; Smith-Vaniz and Carpenter 2007; Aguilera et al. 2017). This review highlights the consistent occurrence of hyperostosis across multiple skeletal elements (Table 4), reinforcing its recurrent nature in the species. Variation in the elements reported among studies likely reflects differences in sampling design, analytical methods, or population-specific responses to environmental conditions, indicating that the expression of hyperostosis in *C. hippos* remains complex and not fully resolved.

The primary method for identifying hyperostosis without initially removing bones from fish specimens is radiography, owing to the increased bone density associated with the mineralogical changes that occur during hyperostosis, including the partial dissolution

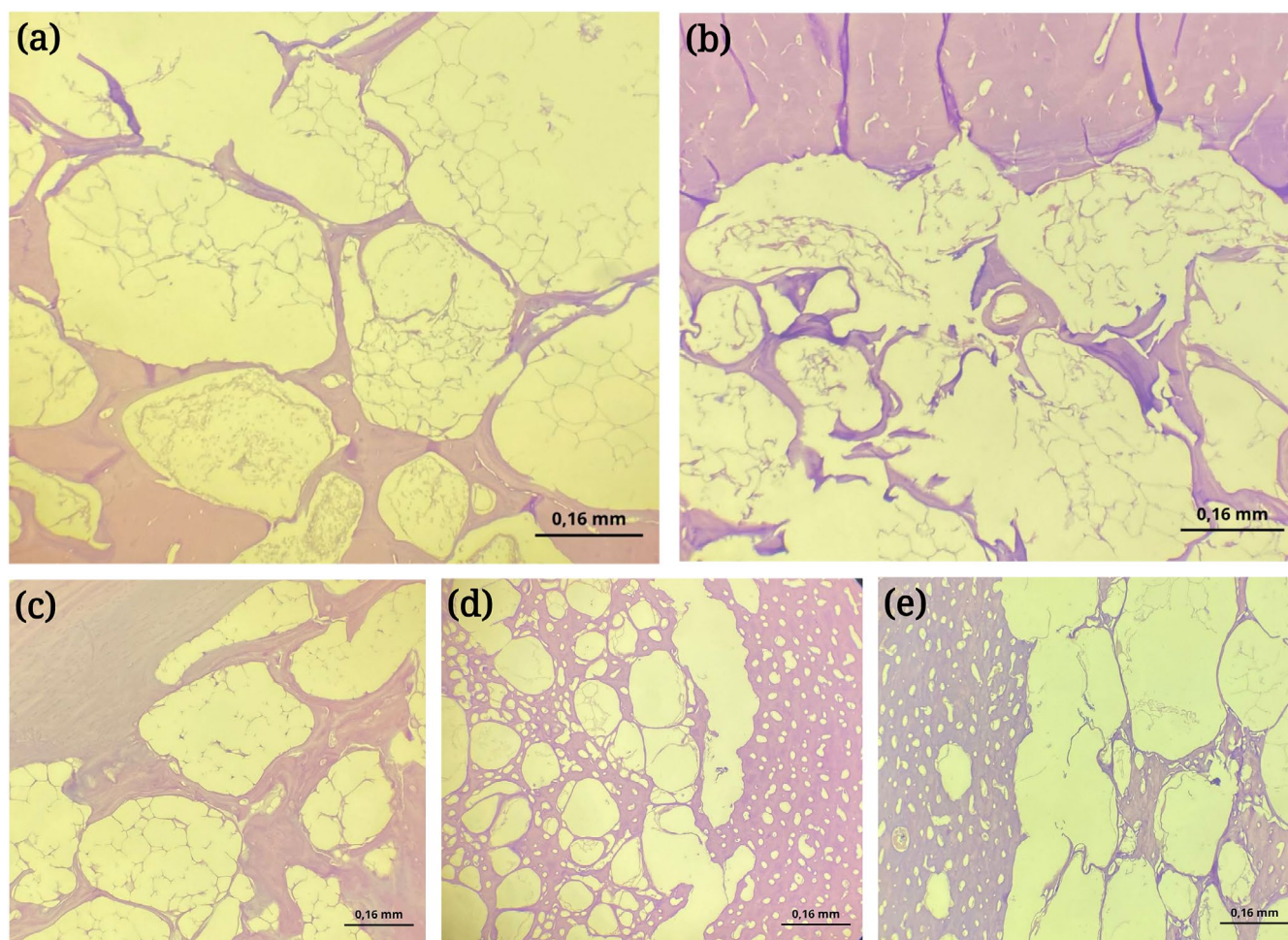


FIGURE 2 | Histological sections of: (A) preopercle and (B) opercle from a specimen measuring 536 mm TL; (C) the first dorsal pterygiophore (DPT) from a specimen measuring 184 mm TL; (D) the first DPT from a specimen measuring 340 mm TL; and (E) the first DPT from a specimen measuring 555 mm TL. Scale bar: 0.16 mm.

TABLE 4 | Occurrence of hyperostosis in *Caranx hippos* across different skeletal regions, as reported in the literature, presented in chronological order.

Authors	CL	DPT	APT	HS	NS	R	PB	SOC	POP	OP
Starks (1911a)	X	X	X	X	X	X	X			
Starks (1911b)	X	X			X		X			
Korschelt (1940)	X	X	X	X	X	X	X			
Kaiser (1960)	X	X	X	X	X	X	X	X		
Konnerth (1966)	X	X			X		X	X		
Olsen (1966)	X	X			X		X			
Smith-Vaniz et al. (1995)	X	X	X		X	X				
Smith-Vaniz and Carpenter (2007)	X	X			X		X			
Aguilera et al. (2017)					X					
Smith-Vaniz et al. (2024)	X	X	X		X	X	X			
Ahnelt et al. (2025)		X	X	X	X	X				
Present study	X	X	X	X	X	X	X		X	X

Abbreviations: APT, anal-fin pterygiophores; CL, cleithrum; DPT, dorsal-fin pterygiophores; HS, hemal spines; NS, neural spine; OP, opercle; PB, pelvic bone; POP; preopercle; R, rib; SOC, supraoccipital crest.

of hydroxyapatite and the neocrystallisation of calcite (Aguilera et al. 2017). However, histological analyses are essential to confirm the condition, as hyperostotic bones exhibit marked alterations in their normal morphology. These bones typically become highly porous as a result of increased vascularisation, characterised by numerous enlarged vascular canals and prominent trabeculae (Meunier et al. 1999; Mahmoud and Ibrahim 2021).

Our results revealed enlarged vascular canals in the first dorsal pterygiophores (DPTs) of specimens as small as 184 mm TL, demonstrating that histological changes associated with hyperostosis are already established at relatively small body sizes. In larger specimens (555 mm TL), hyperostosis was not only detected in additional skeletal regions but was also characterised by markedly enlarged vascular canals occupying most of the internal bone matrix, resulting in a highly trabecular, sponge-like architecture.

Previous studies have also described the morphology and anatomical distribution of hyperostotic bones in *C. hippos* from different regions of the eastern and western Atlantic, including Rio de Janeiro (Smith-Vaniz and Carpenter 2007; Aguilera et al. 2017). Smith-Vaniz and Carpenter (2007) noted that even in juveniles without evident hyperostosis, the first dorsal pterygiophore is laterally expanded, whereas the first anal pterygiophore is not hyperostotic in large adults.

In the present study, individuals from size class 1 exhibited the same enlarged first dorsal pterygiophore; in one specimen, histological analysis confirmed hyperostosis (TL = 184 mm). In addition, hyperostosis in the first anal pterygiophore was detected from size class 2 onward, beginning at 482 mm TL.

Overall, our results are consistent with previous reports, with only minor differences. Hyperostosis in the cleithrum was observed from 335 mm TL onward, compared to an approximate

size of 350 mm reported in the literature. Affected ribs were associated with the 7th–9th vertebrae, consistent with previous reports indicating involvement from the 6th to the 9th vertebrae. Similarly, affected neural spines ranged from the 5th to the 14th vertebrae, within the previously reported range of the 5th to the 16th vertebrae (Smith-Vaniz and Carpenter 2007; Ahnelt et al. 2025).

In the present study, *C. hippos* exhibited hyperostosis in nine skeletal regions (CL, POP, OP, PB, R, DPT, APT, NS and HS). These results corroborate previous reports, although the supraoccipital (SOC) was not observed in the analysed specimens. Nevertheless, the pattern described here expands the anatomical characterisation of hyperostosis in *C. hippos* and suggests that this species may be among those with the highest number of affected regions reported to date. For comparison, *Chaetodipterus faber* has been reported to exhibit hyperostosis in up to 12 skeletal elements (Smith-Vaniz et al. 2024).

Hyperostosis is considered a condition with a strong genetic component (Smith-Vaniz et al. 2024), exhibiting an ontogenetically programmed pattern of bone development that becomes more pronounced with age (Smith-Vaniz et al. 1995, 2024; Aguilera et al. 2017). Fierstine (1968) described its development across skeletal regions as sequential rather than simultaneous. This pattern has also been documented in ontogenetic studies (Tuna et al. 2023), in which individuals exhibit not only species-specific patterns reported in the literature but also element-specific progression. In these cases, certain skeletal elements develop hyperostosis at smaller body sizes, with frequency increasing progressively in adjacent regions as growth proceeds. This interpretation is further supported by comparative studies on closely related taxa, contributing to a better understanding of interspecific variability and potential evolutionary implications (Yasuda and Mizuguchi 1969; von den Driesch 1994; Tuna et al. 2023, 2025).

Although hyperostosis in *Caranx hippos* has been reported since Starks (1911a), relatively few studies have examined variation among size classes, particularly regarding external bone morphology, as illustrated for selected elements by Smith-Vaniz and Carpenter (2007). Ontogenetic approaches are essential not only to provide a temporal framework for osteological changes but also to determine whether hyperostotic development follows a sequential pattern across skeletal regions—as suggested by previous studies (Smith-Vaniz et al. 1995, 2024; Smith-Vaniz and Carpenter 2007; Ahnelt et al. 2025)—or may occur simultaneously in some taxa. Smith-Vaniz et al. (1995) and Smith-Vaniz et al. (2024) emphasised the importance of analysing specimens across size series to establish ontogenetic trajectories of hyperostosis.

Along the Brazilian coast, the present study indicates that *C. hippos* exhibits one of the most extensive patterns of hyperostosis among carangids, with a high number of affected skeletal regions. Within the genus *Selene*, hyperostosis has been reported in *S. vomer* and *S. setapinnis*, affecting multiple skeletal elements with variable frequencies (Tuna et al. 2021, 2023). Studies on *Trachinotus* species from the western Atlantic (Tuna et al. 2026; de Sá et al. 2025) show that hyperostosis occurs in only a subset of species, while others lack evidence of the condition. Wei et al. (2026) suggested that hyperostosis in certain bones of *Trachinotus* may have a phylogenetic basis. In *Oligoplites*, hyperostosis has been described for multiple species (Tuna et al. 2023, 2025), with variation in both skeletal distribution and frequency. Collectively, these findings indicate that although hyperostosis is widespread in Carangidae, its anatomical distribution and degree of expression vary markedly among genera and species, and even closely related taxa may exhibit distinct patterns or complete absence of the condition (Smith-Vaniz et al. 1995, 2024; Chanet 2018).

Dorsal pterygiophores (DPT) were among the earliest and most frequently affected regions, with visible morphological changes detected in an individual measuring 184 mm TL. This finding suggests that DPTs may represent one of the initial sites of hyperostotic development in *C. hippos*. Notably, DPT was the only region exhibiting visible alterations in size class 1 (<250 mm), maintaining high frequency in subsequent classes. Furthermore, hyperostosis was restricted to specific positions along the dorsal fin, indicating a non-uniform distribution among pterygiophores.

Beyond ontogenetic progression, ecological and biological traits of *C. hippos* may help explain the observed patterns. The species undergoes pronounced habitat shifts throughout its life cycle, with juveniles typically associated with estuarine environments and adults occupying a broader range of coastal and shelf habitats (Berry 1959; Johnson 1978; McBride and McKown 2000; Mohan et al. 2017). These transitions likely expose individuals to varying environmental conditions—such as salinity, temperature and depth—that have been proposed as factors influencing hyperostosis in teleosts (Chang et al. 2002, 2008; Meunier et al. 2010; Paig-Tran et al. 2016; Chanet 2018; Gerringer et al. 2021).

In parallel, increases in body size are associated with changes in locomotion, feeding and mechanical loading, which may

promote localised bone remodelling in repeatedly stressed regions (Paig-Tran et al. 2016; Fjellidal et al. 2021). Together, these factors suggest that the higher frequency and broader distribution of hyperostosis in larger individuals of *C. hippos* result from the combined effects of habitat shifts and increasing biomechanical demands. This interpretation is consistent with both the literature and the pattern observed in the present study, in which hyperostosis becomes more frequent and more widespread with increasing body size, a trend also reported in other fish species (Gauldie and Czochanska 1990; Smith-Vaniz et al. 1995; Aguilera et al. 2017; Tuna et al. 2023; Ahnelt et al. 2025).

Despite the various hypotheses proposed, no consensus has been reached regarding the underlying drivers of hyperostosis, which has also been associated with the natural aging process in several species (Aguilera et al. 2017; Smith-Vaniz et al. 2024; Ahnelt et al. 2025). Proposed explanations include environmental conditions and life-history traits (Greenwood 1992; Schlüter et al. 1992; Schlüter and Kohring 2002; Chang et al. 2008), morphofunctional demands (Fierstine 1968; Paig-Tran et al. 2016), and temperature-related responses (Capasso 2005; Tuna et al. 2023), among others. Current evidence indicates that hyperostosis likely results from multiple interacting factors acting independently or in combination, with expression becoming more pronounced during adulthood. However, no single factor fully explains why closely or distantly related species—including those with distinct ecological traits—may exhibit species-specific patterns of hyperostotic development or a complete absence of the condition. In this context, ontogenetic studies provide a valuable framework for understanding how hyperostosis develops throughout growth and in which anatomical regions it manifests, making them essential for characterising the phenomenon and its biological implications.

5 | Conclusion

The present study shows that hyperostosis in *C. hippos* follows a structured ontogenetic pattern associated with body growth. In the material analysed, the condition was recorded in nine skeletal regions, with new indications for preopercle and opercle skeletal bones, indicating a broad anatomical distribution in the species. Dorsal pterygiophores were among the earliest and most frequently affected regions, with visible morphological changes already recorded in a specimen measuring 184 mm total length, suggesting that this region may represent one of the initial sites of hyperostotic manifestation in *C. hippos*. As body size increased, hyperostotic involvement extended to additional skeletal regions, suggesting a stepwise expansion of the condition during ontogeny. These findings expand the anatomical characterisation of hyperostosis in *C. hippos* and highlight the extensive skeletal distribution of the condition in this species.

Author Contributions

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– original draft, writing – review and editing. **Fernando Augusto Pereira Tuna:** conceptualization, investigation, funding acquisition, writing – review and editing, methodology, resources, supervision. **Ana Julia Araujo Rosa D' Almeida Lima:** conceptualization, investigation, writing – original draft, writing – review and editing. **Helena Passeri Lavrado:** conceptualization, investigation, writing – original draft, funding acquisition, methodology, writing – review and editing, supervision, resources. **Alice Barbosa Henriques:** conceptualization, investigation, writing – original draft, writing – review and editing. **Maykon Victor Rezende de Oliveira:** conceptualization, investigation, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Radiographic images are deposited at Zenodo and the files are available at: <https://doi.org/10.5281/zenodo.14675355>.

References

Aguilera, O. A., I. Rocha, M. Lopes, et al. 2017. "The Bone Degenerative Processes in Senile Fishes From Holocene Brazilian Shell Mounds." *Journal of Fish Diseases* 40: 1869–1881. <https://doi.org/10.1111/jfd.12662>.

Ahnelt, H., J. S. Klein, and V. Winkler. 2025. "Fish Skeletons With Hyperostosis in the Ichthyological Collection of the Natural History Museum Vienna (Austria)." *Annals of the Natural History Museum Vienna* 126: 5–25.

Berry, F. H. 1959. "Young Jack Crevalles (*Caranx* Species) Off the Southeastern Atlantic Coast of the United States." *Fishery Bulletin* 59: 417–435.

Caiafa, I., J. Narváez, and S. Borrero. 2011. "Algunos Aspectos de la Dinámica Poblacional Del Jurel *Caranx hippos* (Pisces: Carangidae) en Bocas de Ceniza, Caribe Colombiano." *Revista MVZ Córdoba* 16: 2324–2335.

Capasso, L. L. 2005. "Antiquity of Cancer." *International Journal of Cancer* 113, no. 1: 2–13. <https://doi.org/10.1002/ijc.20610>.

Carpenter, K. E. 2002. "The Living Marine Resources of the Western Central Atlantic. Volume 3: Bony Fishes Part 2 (Opistognathidae to

Molidae), Sea Turtles and Marine Mammals." FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. Rome: FAO.

Chanet, B. 2018. "Swollen Bones in Jacks and Relatives (Teleostei: Acanthomorpha: Carangidae)." *Cybum* 42: 99–103. <https://doi.org/10.26028/cybum/2018-421-010>.

Chang, K. H., J. S. Lee, and Y. S. Kim. 2002. "Environmental Factors Associated With Skeletal Anomalies in Marine Fishes." *Environmental Biology of Fishes* 64: 29–38. <https://doi.org/10.1023/A:1016072105614>.

Chang, M., X. Wang, H. Liu, et al. 2008. "Extraordinarily Thick-Boned Fish Linked to the Aridification of the Qaidam Basin (Northern Tibetan Plateau)." *Proceedings of the National Academy of Sciences of the United States of America* 105: 13246–13251. <https://doi.org/10.1073/pnas.0805982105>.

Correia, E., J. P. Granadeiro, A. Regalla, E. Dias, A. Almeida, and P. Catry. 2017. "Predatory Pelagic Fishes of the Bijagós Archipelago (Guinea-Bissau) Show High Overlap in Diets Dominated by *Sardinella*." *African Journal of Marine Science* 39: 389–396. <https://doi.org/10.2989/1814232X.2017.1387605>.

de Sá, A. M. C., M. C. Salomão, H. P. Lavrado, W. T. V. Machado, A. P. C. Rodrigues, and F. A. P. Tuna. 2025. "Description and Patterns of Hyperostosis in Plata Pompano, *Trachinotus marginatus* Cuvier, 1832." *Journal of Fish Diseases* 48: e14129. <https://doi.org/10.1111/jfd.14129>.

Fagade, S. O., and C. I. O. Olaniyan. 1973. "The Food and Feeding Interrelationship of the Fishes in the Lagos Lagoon." *Journal of Fish Biology* 5: 205–225.

Fierstine, H. L. 1968. "Swollen Dorsal Fin Elements in Living and Fossil *Caranx* (Teleostei: Carangidae)." *Contributions in Science* 137: 1–10.

Fjelldal, P. G., A. Madaro, M. Hvas, L. H. Stien, F. Oppedal, and T. W. K. Fraser. 2021. "Skeletal Deformities in Wild and Farmed Cleaner Fish Species Used in Atlantic Salmon *Salmo salar* Aquaculture." *Journal of Fish Biology* 98: 1049–1058. <https://doi.org/10.1111/jfb.14337>.

Gauldie, R. W., and Z. Czochanska. 1990. "Hyperostotic Bones From the New Zealand Snapper *Chrysophrys auratus* (Sparidae)." *Fishery Bulletin* 88: 201–206.

Gerringer, M. E., A. S. Dias, A. A. von Hagel, J. W. Orr, A. P. Summers, and S. Farina. 2021. "Habitat Influences Skeletal Morphology and Density in the Snailfishes (Liparidae)." *Frontiers in Zoology* 18: 1–22.

Greenwood, P. H. 1992. "A Redescription of the Uniquely Polychromatic African Cichlid Fish *Tilapia guinasana* Trewavas, 1936." *Bulletin of the British Museum of Natural History (Zoology)* 58, no. 1: 21–36.

Jawad, L. A., and O. Akyol. 2018. "Vertebral Anomalies in *Mullus barbatus* Collected From Izmir Bay, Northeastern Aegean Sea, Turkey." *International Journal of Marine Science* 8: 59–65.

Jefferson, A. E., M. B. Jargowsky, G. M. Ivec, et al. 2022. "Age, Growth and Diet of Crevalle Jack (*Caranx hippos*) in the Gulf of Mexico." *Fisheries Management and Ecology* 29: 608–626. <https://doi.org/10.1111/fme.12550>.

Johnson, G. D. 1978. "*Caranx hippos* (Linnaeus), crevalle jack." In *Development of Fishes of the Mid-Atlantic Bight: An Atlas of Egg, Larval, and Juvenile Stages*, edited by G. D. Johnson, vol. 4, 35–38. Chesapeake Biological Laboratory.

Kaiser, H. E. 1960. "Untersuchungen zur vergleichenden Osteologie der fossilen und rezenten Pachyostosen." *Paleontographica (A)* 114: 113–196.

Konnerth, A. 1966. "Curious Swollen Bones Found in Fossil Deposits and in Kitchen Middens Appear in the Skeleton of Some Fishes." *Oceanus* 12, no. 2: 6–9.

- Korschelt, E. 1940. "Über die Konstanz im Auftreten von Knochenverdickungen am Fischeskelett." *Marburger Sitzungsbericht* 73, no. 2: 2–14.
- Kwei, E. A. 1978. "Food and Spawning Activity of *Caranx hippos* Off the Coast of Ghana." *Journal of Natural History* 12: 195–215.
- Mahmoud, M. A., and M. Ibrahim. 2021. "Overview on Pathogenesis and Histopathological Observations of Hyperostosis in Two Fish Species." *Bulletin of the European Association of Fish Pathologists* 41: 111–117. <https://doi.org/10.48045/001c.31528>.
- McBride, R. S., and K. A. McKown. 2000. "Consequences of Dispersal of Subtropically Spawned Crevale Jacks, *Caranx hippos*, to Temperate Estuaries." *Fishery Bulletin* 98: 528–538.
- Meunier, F. J., P. Béarez, and H. Francillon-Vieillot. 1999. "Some Morphological and Histological Aspects of Hyperostosis in the Eastern Pacific Marine Fish *Prionotus Stephanophrys* Lockington, 1880 (Triglidae)." In *5th Indo-Pacific Fish Conference*, edited by B. Séret and J. Y. Sire, 125–133.
- Meunier, F. J., J. Gaudant, and E. Bonelli. 2010. "Morphological and Histological Study of the Hyperostoses of *Lepidopus albyi* From the Tortonian (Upper Miocene) of Piedmont (Italy)." *Cybio* 34: 293–301.
- Mohan, J. A., T. T. Sutton, A. B. Cook, K. M. Boswell, and R. J. D. Wells. 2017. "Influence of Oceanographic Conditions on Abundance and Distribution of Post-Larval and Juvenile Carangid Fishes in the Northern Gulf of Mexico." *Fisheries Oceanography* 26: 526–541. <https://doi.org/10.1111/fog.12214>.
- Nelson, J. S., T. C. Grande, and M. V. H. Wilson. 2016. *Fishes of the World*. 5th ed. John Wiley & Sons.
- Olsen, S. J. 1966. "Peculiar Swollen Fish Bones." *Florida Wildlife* 20, no. 3: 22–23.
- Paig-Tran, E. W. M., A. S. Barrios, and L. A. Ferry. 2016. "Presence of Repeating Hyperostotic Bones in Dorsal Pterygiophores of the Oarfish, *Regalecus russellii*." *Journal of Anatomy* 229: 560–567. <https://doi.org/10.1111/joa.12503>.
- Pardee, C., J. Wiley, and S. Springer. 2021. "Age, Growth and Maturity for Two Highly Targeted Jack Species: *Caranx ignobilis* and *Caranx melampygus*." *Journal of Fish Biology* 99, no. 4: 1247–1255. <https://doi.org/10.1111/jfb.14828>.
- Schlüter, T., R. Kohring, and J. Mehl. 1992. "Hyperostotic Fish Bones ("Tilly Bones") from Presumably Pliocene Phosphorites of the Lake Manyara Area, Northern Tanzania." *Paläontologische Zeitschrift* 66, no. 1–2: 129–136.
- Schlüter, T., and R. Kohring. 2002. "Palaeopathological Fish Bones from Phosphorites of the Lake Manyara Area, Northern Tanzania—Fossil Evidence of a Physiological Response to Survival in an Extreme Biocenosis." *Environmental Geochemistry and Health* 24, no. 2: 131–140.
- Smith-Vaniz, W. F., and K. E. Carpenter. 2007. "Review of the Crevale Jacks, *Caranx hippos* Complex (Teleostei: Carangidae), with a Description of a New Species From West Africa." *Fishery Bulletin* 105: 207–233.
- Smith-Vaniz, W. F., L. S. Kaufman, and J. Glowacki. 1995. "Species-Specific Patterns of Hyperostosis in Marine Teleost Fishes." *Marine Biology* 121: 573–580.
- Smith-Vaniz, W. F., J. Klein, and H. Ahnelt. 2024. "Hyperostosis in Fishes: An Update With New Species Records." *Journal of Morphology* 285: e21782.
- Starks, E. C. 1911a. "Osteology of Certain Scombroid Fishes. The Osteological Characters of the Scombroid Fishes of the Families Gempylidae, Lepidopidae and Trichiuridae." *Leland Stanford Junior University Publication Series* 5: 17–26.
- Starks, E. C. 1911b. "Osteology of Certain Scombroid Fishes: The Osteology and Relationships of the Fishes Belonging to the Family Carangidae." *Leland Stanford Junior University Publications* 5: 27–49.
- Sudekum, A. E., J. D. Parrish, R. L. Radtke, and S. Ralston. 1991. "Life History and Ecology of Large Jacks in Undisturbed, Shallow, Oceanic Communities." *Fishery Bulletin* 89: 493–513.
- Tuna, F. A., A. P. C. Rodrigues, G. P. Filgueira, et al. 2025. "Comparisons of Hyperostotic Bones in Two Species of the Genus *Oligoplites* Gill, 1863 in the Southern Brazilian Coast." *Journal of Fish Diseases* 48: e14117.
- Tuna, F. A. P., F. A. A. Calixto, W. L. Cordeiro, M. Luz, and E. F. M. Mesquita. 2024. "Patterns of Hyperostosis During the Ontogenetic Development of Atlantic Spadefish (*Chaetodipterus faber*) on the Brazilian Coast." *Journal of Fish Diseases* 47: e13882. <https://doi.org/10.1111/jfd.13882>.
- Tuna, F. A. P., F. A. A. Calixto, M. Luz, and E. F. M. Mesquita. 2023. "Patterns Description of Hyperostosis Observed in Atlantic Moonfish *Selene setapinnis* and Lookdown *Selene vomer*." *Journal of Morphology* 284: e21640. <https://doi.org/10.1002/jmor.21640>.
- Tuna, F. A. P., F. A. A. Calixto, M. C. Salomão, C. E. R. Coutinho, K. R. Estanek, and E. F. M. Mesquita. 2021. "The Presence of Hyperostosis in Atlantic Moonfish, *Selene setapinnis* (Mitchill, 1815), in the Brazilian Coast: Case Report." *Arquivo Brasileiro de Medicina Veterinária e Zootecnia* 73: 179–183. <https://doi.org/10.1590/1678-4162-12131>.
- Tuna, F. A. P., A. M. Cardoso de Sá, C. V. Gonçalves-Ferreira, et al. 2026. "Hyperostosis in Pompanos: The Genus *Trachinotus* Lacepède, 1801 (Carangidae), with a New Record for the Condition in a Western Atlantic Species." *Journal of Fish Diseases* 49: e70130. <https://doi.org/10.1111/jfd.70130>.
- von den Driesch, A. 1994. "Hyperostosis in Fish." In *Fish Exploitation in the Past*, edited by W. Van Neer, vol. 274, 37–46. Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques.
- Wei, J., L. Guo, J. Liu, L. A. Jawad, N. Bouriga, and A. A. Basyouny Shahin. 2026. "Ending the Decades-Long Debate: *Trachinotus anak* Ogilby, 1909 Is the Correct Scientific Name of Golden Pompano in Chinese Aquaculture." *Journal of Zoological Systematics and Evolutionary Research* 2026, no. 1: 2260154.
- WoRMS Editorial Board. 2026. "World Register of Marine Species." <https://www.marinespecies.org>.
- Yasuda, F., and K. Mizuguchi. 1969. "Specific Characters of Three Sparid Fishes Referred to the Genus *Chrysophrys* in the Indo-Pacific." *Japanese Journal of Ichthyology* 16: 24–30.
- Yılmaz, Ö., H. Cerim, S. Yapıcı, and İ. Reis. 2024. "A Review of Fish Anomalies in Türkiye's Waters." *Aquatic Sciences and Engineering* 39: 261–271. <https://doi.org/10.26650/ASE20241467944>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Cluster analysis based on hyperostosis presence data in *Caranx hippos*, using simple matching similarity index with UPGMA clustering scheme. **Figure S2:** Protocol of measurements for *Caranx hippos* (Linnaeus, 1766), while accounting for the specific characteristics of each major region exhibiting hyperostosis in the species. **Figure S3:** Protocol of measurements for *Caranx hippos* (Linnaeus, 1766), while accounting for the specific characteristics of each major region exhibiting hyperostosis in the species. **Figure S4:** Relationship between fish total length and number of hyperostotic bones (A) or number of hyperostotic skeletal regions (B). **Table S1:** Statistical results of the comparisons between hyperostotic and non-hyperostotic spines and pterygiophores of the same length size classes using paired-test of Wilcoxon (neural spines—NS, haemal spines—HS and dorsal pterygiophores—DPT).