



Baseline

Analysis of a hypersaline drought-prone estuary reveals low density and diversity of fish eggs and larvae

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ABSTRACT

We analyzed fish eggs and larvae in an estuary under severe drought conditions. We detected an inverse salinity gradient, with values increasing from the mouth to the upper estuary. Egg densities decreased from the estuarine mouth to the upstream areas following the salinity increase for all three mesh net sizes. This pattern was also found for the density of larvae, which decreased in estuarine regions with hypersalinity (38 to 62). The low diversity constituted only nine fish species, which were classified as anadromous (*Anchoa hepsetus*), estuarine and marine (*Bathygobius soporator*, *Hippocampus reidi*, *Eucinostomus* sp., and *Diapterus auratus*), marine estuarine-opportunist (*Caranx latus* and *Bardiella rochus*), and marine stragglers (*Echeneis naucrates* and *Haemulon* sp.). In addition, we observed an oversimplification of the assemblage to include stress-tolerant estuarine and marine species. Our baseline results suggest that this hypersaline estuarine ecosystem has lower densities and diversity than a healthy mangrove system.

Estuaries are key coastal ecosystems for many species of fish worldwide because of their ecological functions as feeding, spawning, and nursery habitats (Ramos et al., 2012; Potter et al., 2015; Whitfield, 2016, 2017; Kisten and Strydom, 2021; Guerreiro et al., 2021). Fish eggs and larvae, named ichthyoplankton, drift in the water column of these estuarine systems and interact with prey, predators, and a range of environmental variables (Houde, 2001; Arévalo-Frías and Mendoza-Carranza, 2015; Zhang et al., 2022). In this regard, studies on these organisms and their dynamics are of great relevance to fisheries management, especially in low-inflow or freshwater-deprived mangrove estuarine ecosystems. As the early life stages of fish are more vulnerable to mortality, the effects of extreme events in estuaries is a determinant of recruitment (Cabral et al., 2021; Colombano et al., 2022).

Tropical estuaries in arid and semi-arid regions are characterized by low freshwater inflow and high rates of evaporation, some of which are intermittently blocked from the sea by sand spits (Potter et al., 2010; Tweedley et al., 2019). The combination of these factors and human intervention can result in hypersalinization, which means that the salinity of the estuary is higher than that of the adjacent ocean (Andutta et al., 2011). This extreme phenomenon is especially important during the dry season when salinity increases. Hypersaline conditions expose

aquatic biota, such as fish eggs and larvae, to osmotic stress and metabolic changes that affect their temporal and spatial distribution as well as survival rates (Tweedley et al., 2019; Whitfield et al., 2006). Furthermore, increased salinity is an important factor that can simplify the estuarine communities, select stress-tolerant species (Barroso et al., 2018), and reduce the overall abundance and diversity of organisms (Cyrus et al., 2010; Carrasco and Perissinotto, 2012; Rosa et al., 2016; Sloterdijk et al., 2017).

The intensification of climate change effects, such as sea level rise, reduced precipitation, and high levels of evaporation (Cai et al., 2022) results in the hypersalinization of estuaries. On the Brazilian semiarid coast, short estuaries are already experiencing hypersalinity due to local impacts (e.g., multiple dams) and ongoing climate change, which makes them useful models for understanding this phenomenon (Schettini et al., 2017; Soares et al., 2021). However, few studies have analyzed these extreme mangroves and their ichthyoplankton communities (Badú et al., 2022). Using a semiarid estuary in an extreme drought year as a model, we analyzed the intra-annual distribution and density of fish eggs and larvae.

The Piranji River Estuary is located on the Ceará state coast in the Equatorial Southwestern Atlantic. The study region is located in a small,

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shallow hydrographic basin, 55 km long and 4.367 km² total area (Silva and Silva, 2012) (Fig. 1). This low-inflow estuary is located on the Brazilian semi-arid coast, and its morphology is composed of narrow, shallow channels with extensive sand and mud banks. Moreover, there is a 3.2 km long sand spit at the mouth (Silva et al., 2012) that decreases the tidal flow inside the estuary. The rainy period lasts from January to June, and the dry period from July to December (Lacerda et al., 2007) (Fig. 2). This mangrove estuarine ecosystem can experience hypersaline conditions because of several factors, such as a semi-arid climate, drought-prone area, high evaporation rate, high water residence time, and low levels of surface runoff (Schettini et al., 2017).

Natural drought cycles are characteristic of this semi-arid region and have increased between 2000 and 2020, correlated with El Niño conditions and the positive phase of the Atlantic Meridional Mode (Marengo et al., 2017). The combination of both mechanisms from 2010 to 2016 led to the most severe drought (Fig. 2) ever recorded in this region (Marengo et al., 2017).

Intra-annual sampling occurred in 2015 during the diurnal period in the rainy (February, April, and June) and dry seasons (August, October, and December). Data were collected at three different points, P1 (upstream river station), P2 (intermediate station), and P3 (downstream river station, near the river mouth), along the Piranji Estuary (Fig. 1) during the ebb tide. The depth, water temperature, salinity, and dissolved oxygen levels were measured at each station using a YSI 6600 multiparameter meter.

Horizontal surface hauls for ichthyoplankton samples were collected by boat at all three stations using conical nets of 200, 300, and 500 µm mesh (mouth diameter: 50 cm) equipped with a flowmeter (General Oceanics, Miami, FL, USA). The nets were towed at approximately 2 knots for 3 min at each station. All samples were immediately fixed in 4% formalin buffered with borax.

Ichthyoplankton density is expressed as the number of individuals/

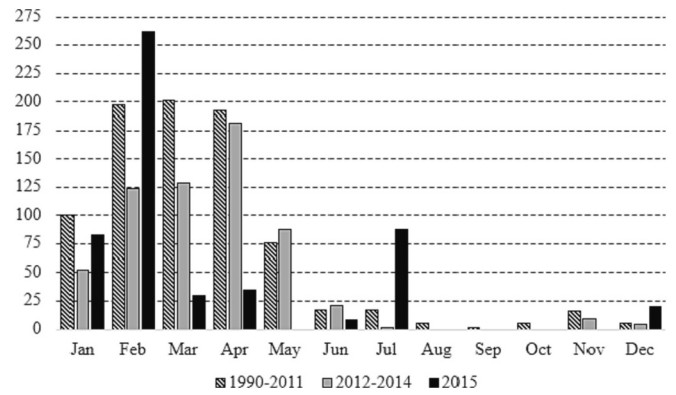


Fig. 2. Mean historical precipitation (1990–2011), precipitation during a historic drought (2012–2014), and precipitation during the study period (2015).

100m³ (Omori and Ikeda, 1984). Only the eggs of the Engraulidae family were identified and all others were classified as morphotypes A, B, C, D, and E, according to their morphometric (egg size) and morphological characteristics. Fish larvae were identified to the lowest taxonomic level (according to, (Ré, 1999; Richards, 2005) and classified into different stages of development, according to the flexion of the notochord, as pre-flexion, flexion, and post-flexion, based on Ré (1999). Ecological guild classification considers the habits of breeding adults and their migration patterns. The following characteristics were used: location of spawning, feeding, and/or refuge, which in some cases involve migratory movements between estuaries and other ecosystems (Andrade-Turbino et al., 2008; Potter et al., 2015).

The estuary depth was typical of shallow, low-inflow, short estuaries, deeper at P3, the downstream station, near the river mouth, during the

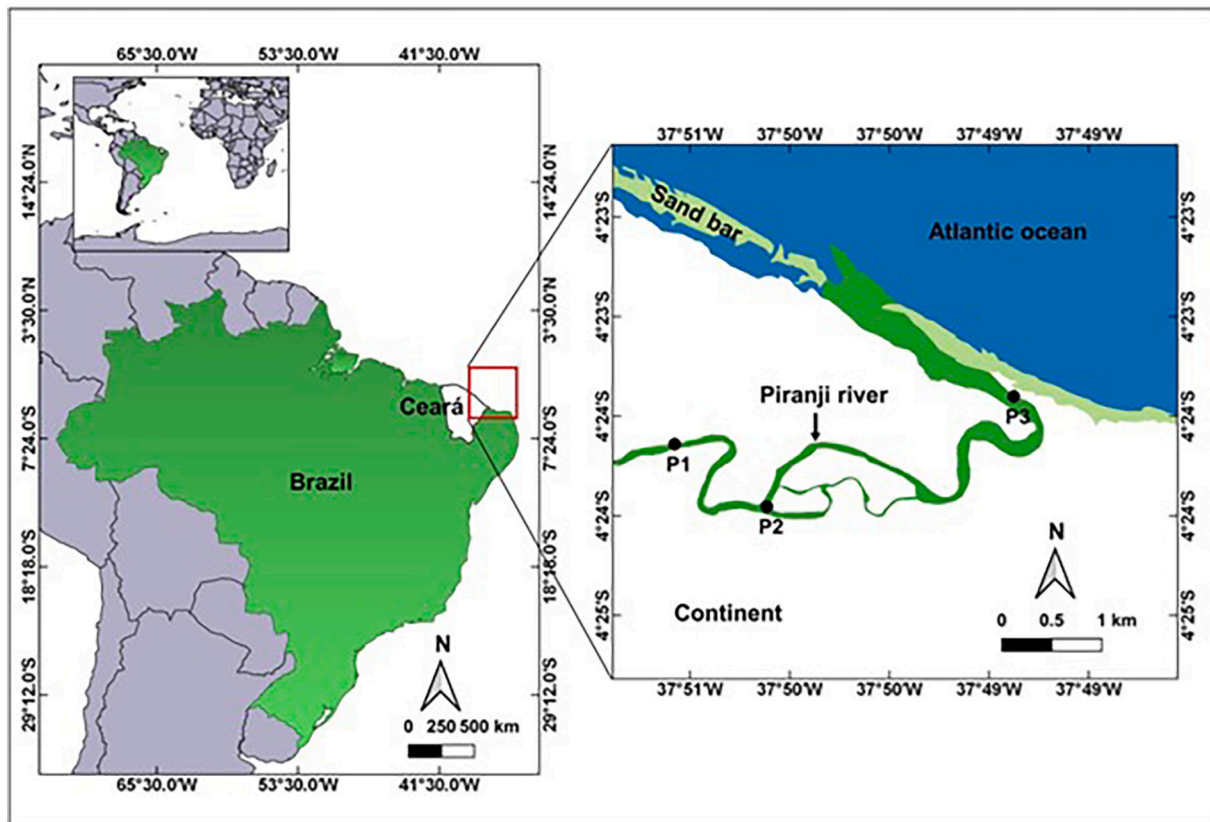


Fig. 1. Sampling points in the Piranji River Estuary, Ceará, Brazil, Equatorial SW Atlantic. P1, upstream; P2, intermediate; and P3, downstream, near the estuarine mouth and sand spit.

rainy (4.95 ± 0.67 m) and dry seasons (3.65 ± 0.28 m), and shallower at P2, the intermediate station (2.46 ± 0.18 m), and at P1, the upstream station (2.3 ± 0.37 m), during the rainy season and the dry season, respectively (Table 1). The water temperature was nearly constant during the study, as expected for low-latitude estuarine systems, at 28.4 ± 0.36 (P1), 28.2 ± 0.16 (P2) and 27.66 ± 0.32 (P3), during the rainy season, and 27.55 ± 0.43 (P1), 26.82 ± 0.68 (P2) and 26.12 ± 0.44 (P3), during the dry season (Table 1).

High levels of dissolved oxygen were found at P3 during the rainy (6 ± 0.43 mg/L) and dry seasons (6.01 ± 0.01 mg/L), but these decreased at P1 and P2 during the rainy (5.33 ± 0.36 and 5.43 ± 0.32 mg/L) and dry seasons (5.59 ± 0.21 and 5.41 ± 0.5 mg/L) (Table 1).

During the rainy season, salinity levels were high at all three sampling stations, but only P3 exceeded the salinity of the adjacent sea. During this period, the salinity was highest downstream at P3 (38 ± 0.71), followed by P2 (36 ± 7.83), and lowest at P1 (30.1 ± 15.1). In the dry season, the salinity changed drastically; it was lowest at P3 near the ocean (38.4 ± 1.08), followed by P2 (45.76 ± 5.12), and highest at P1 in the uppermost estuarine area (53.2 ± 8.38) (Table 1). Although the station closest to the sea had the highest salinity during the rainy season, in the dry period, this pattern was reversed and the estuary as a whole became hypersaline, with salinity levels increasing upstream (Fig. 3, green rectangle).

The total numbers of fish eggs were 189, 100, and 174 in the 200, 300, and 500 μ m nets, respectively. Only Engraulidae and five morphotypes (A, B, C, D, and E) comprised the estuarine egg assemblage. There was a decrease in egg density for all three mesh net sizes from the mouth to the upper estuary, i.e., downstream to upstream (Table 2). The highest egg densities were observed at P3, near the ocean (Table 2), where the total density was 124.9, 73, and 40.7 eggs/100m³ in the 200, 300, and 500 μ m net, respectively. The lowest densities were observed at P1 (Table 2) with 2.8, 0.8, and 0.5 eggs/100m³ in the 200, 300, and 500 μ m nets, respectively.

The total numbers of fish larvae were 183, 96, and 69 in the 200, 300, and 500 μ m nets, respectively. The lower fish larval diversity was composed of nine taxa distributed across eight families, nine genera, and nine species (Table 3). Considering each mesh size, the total density of fish larvae increased towards the river mouth, with the exception of the 200 μ m net when the density was higher at P1 than P2 (Table 3).

The highest total densities of fish larvae were observed at P3 with 90.9, 36.1, and 9.9 larvae/100m³ collected in the 200, 300, and 500 μ m nets, respectively. Conversely, the lowest total densities of fish larvae were observed at P2 (15.3 larvae/100m³) with the 200 μ m net, and at P1 (19.6, and 3.1 larvae/100m³) in the 300, and 500 μ m nets, respectively (Table 3).

Table 1

Physical-chemical variables measured in the Piranji Estuary, Equatorial SW Atlantic, Brazil, during the rainy and dry seasons.

	Rainy season			
	Depth (m)	Temperature (°C)	Salinity	Dissolved oxygen (mg/L)
P1	3.19 ± 0.65	28.4 ± 0.36	30.1 ± 15.1	5.43 ± 0.32
P2	2.46 ± 0.18	28.2 ± 0.16	36 ± 7.83	5.33 ± 0.36
P3	4.95 ± 0.67	27.66 ± 0.32	38 ± 0.71	6 ± 0.43
	Dry season			
	Depth (m)	Temperature (°C)	Salinity	Dissolved oxygen (mg/L)
P1	2.3 ± 0.37	27.55 ± 0.43	53.2 ± 8.38	5.41 ± 0.5
P2	3.03 ± 0.91	26.82 ± 0.69	45.76 ± 5.12	5.59 ± 0.21
P3	3.65 ± 0.28	26.12 ± 0.44	38.4 ± 1.08	6.01 ± 0.01

P1, upstream; P2, intermediate; P3, downstream.

Anchoa hepsetus was found at the highest density (mean = 16.78 larvae/100 m³) among all of the organisms collected with the 200, 300, and 500 μ m nets at the three sampling stations. *Bathygobius soporator* (mean = 4.0 larvae/100 m³), *Eucinostomus* sp. (mean = 1.74 larvae/100 m³), and *Haemulon* sp. (mean = 1.0 larvae/100 m³) were the other most representative taxa in the samples.

The assemblage of fish larvae was composed almost entirely of taxa belonging to estuarine and marine guilds (Table 3). We recorded all three developmental stages at each sampling station, with a predominance of larvae in the pre-flexion stage (18.39, 17.53, and 59.48 larvae/100m³ at P1, P2, and P3, respectively) (Fig. 4). The flexion stage was only recorded at P3 (Fig. 4).

Our baseline research evaluated the intra-annual spatial variation in fish larvae and eggs in mangroves under extreme salinity conditions. Environmental variables, such as temperature and dissolved oxygen, in the study area (Barroso et al., 2018) were similar to those of other tropical estuaries near the equator (Macedo Silva et al., 2015; Andrade et al., 2016; Bastos et al., 2016). However, there were remarkable seasonal differences in salinity in two opposing manners (Barroso et al., 2018): hyposaline and hypersaline regimes. In years of extreme drought, the combined effect of reduced annual rainfall, low water depth, and high evaporation rates promoted hypersalinity in this semiarid estuary (Schettini et al., 2017), even in the rainy season (e.g., February). The El Niño event in 2015 and 2016 was one of the most severe since 1950 (Rossi and Soares, 2017), and this phenomenon can result in prolonged periods of drought and hypersalinity in mangroves.

Our baseline assessment of ichthyoplankton density and diversity in this hypersaline estuary was unusually low compared to other estuaries without extreme salinity conditions (Balakrishnan et al., 2015; Zacardi, 2015; Correa-Herrera et al., 2017; Da Silva et al., 2020; Rousseau et al., 2017). Fish eggs and larvae are even more susceptible to variations in salinity because they cannot osmoregulate like adults, which affects the life history of the early life stages of fish (Pérez-Robles et al., 2012; Rosa et al., 2016; Santos et al., 2017).

Salinity is one of the most important factors in ichthyoplankton assemblage distribution and diversity (Jagadeesan et al., 2013; Marina et al., 2021). Extreme salinities require high energy rates for osmotic regulation; therefore, the energy that would otherwise be used for the growth and development of eggs and larvae is reduced (Kurbel, 2008). Hypersaline mangroves can impact the life cycle of fishes, including reproduction and alterations in the food web (e.g., ichthyoplankton prey), as well as causing the direct mortality of fish (Whitfield, 2021), which may be among the causes of the low density and diversity recorded in this study and the predominance of larvae in the first stage of development.

The density of fish eggs and larvae are directly influenced by the presence of favorable environmental conditions for adult spawning (Schreck et al., 2001; Servili et al., 2020). One peculiar characteristic that may have increased the salinity is the presence of a sand spit at the mouth of the estuarine-laguna system. The presence of spits in mangrove estuarine systems reduces their connectivity with the adjacent sea, blocks the entry of breeding adults, fish eggs, and larvae from coastal waters into the estuary, and negatively influences the density and diversity of ichthyoplankton (Strydom et al., 2003; Whitfield et al., 2006; James et al., 2007; Korsman et al., 2017). Other estuarine systems are influenced by the presence of sand spits at their mouths; however, because of the intensifying effects of climate change (e.g., prolonged droughts and river silting), this condition has become more frequent, which prevents the renewal of estuarine water and results in widespread hypersalinity (Whitfield, 1992; Morais and Pinheiro, 2011; Descroix et al., 2020).

Although the fish assemblage from this low-inflow estuary is composed of taxa commonly found in tropical estuarine systems (Bonecker et al., 2009; Marcolin et al., 2010; Lima et al., 2015), the number of species recorded here is considerably low, which is expected in hypersaline coastal environments (Rosa et al., 2016; Chermahini

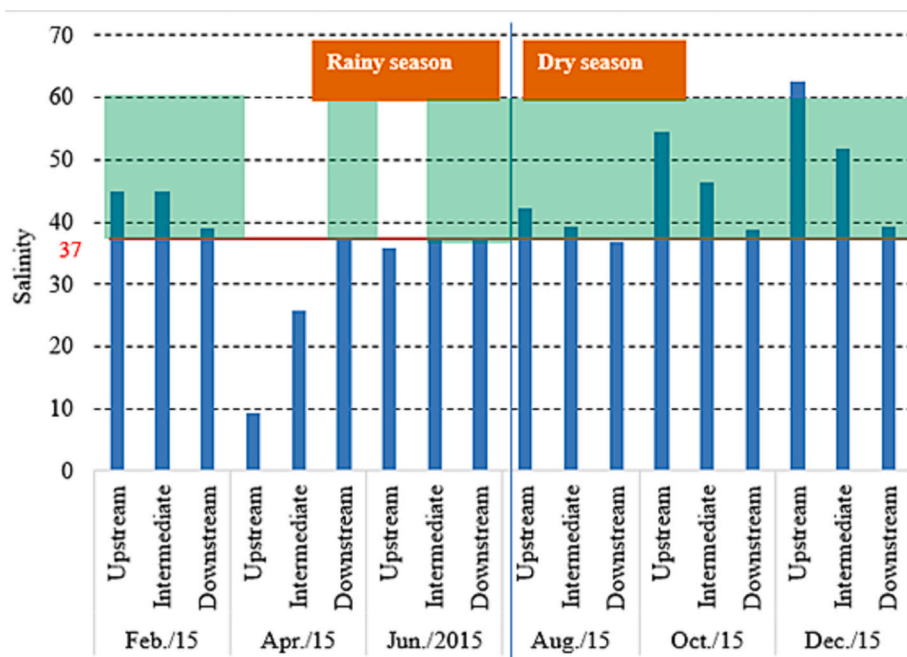


Fig. 3. Salinity levels measured at three sampling stations during the rainy and dry seasons in the Piranji Estuary, Ceará State, Equatorial SW Atlantic, Brazil. The solid red line represents the salinity of the adjacent sea, the green rectangle represents the stations and months with hypersalinity, i.e., when estuarine salinity was higher than the salinity of the adjacent sea. P1, upstream; P2, intermediate; P3, downstream. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Morphotypes of fish eggs found in the Piranji Estuary, Ceará State, Equatorial SW Atlantic, Brazil, and their respective densities at each sampling station and net mesh size.

Density (eggs/100m ³)	200			300			500		
	P1	P2	P3	P1	P2	P3	P1	P2	P3
Engraulidae	2.8	1.4	56.2	0	0	30.1	0	0	11.1
Morphotype A	0	0	18.7	0.8	0	0	0	0	5.3
Morphotype B	0	0	29.1	0	0	25.6	0	0	12.5
Morphotype C	0	2.1	20.8	0	1.5	14.3	0	0	1.2
Morphotype D	0	0	0	0	0	3.0	0	0	0.7
Morphotype E	0	0	0	0	0	0	0	0	9.9
Total	2.8	3.5	124.9	0.8	1.5	73.0	0.5	0.7	40.7

P1, upstream; P2, intermediate; P3, downstream.

Table 3

Taxa of fish larvae found in the Piranji estuary, Ceará State, Equatorial SW Atlantic, Brazil, and their respective densities at each sampling station and with each net size, and their classification according to ecological guild.

Family	Species	Mesh size (200 µm)			Mesh size (300 µm)			Mesh size (500 µm)			Ecological guild
		P1	P2	P3	P1	P2	P3	P1	P2	P3	
Gobiidae	<i>Bathygobius soporator</i> (Fillfrin Goby)	0	1.39	9.02	0	9.79	8.28	1.68	0	2.89	Estuarine and Marine
Engraulidae	<i>Anchoa hepsetus</i> (Broad-striped Anchovy)	15.27	12.49	71.48	16.57	9.79	20.33	1.20	1.20	2.65	Anadromous
Gerreidae	<i>Eucinostomus</i> sp. (Mojarra)	5.55	1.39	0	0	0	7.53	0	0.72	0.48	Estuarine and Marine
	<i>Diapterus auratus</i> (Irish Mojarra)	0	0	0	0	0	0	0	0	1.20	Estuarine and Marine
Haemulidae	<i>Haemulon</i> sp. (Scaled-fin Grunts)	0	0	10.41	0	0	0	0	0	0.72	Marine stragglers
Carangidae	<i>Caranx latus</i> (Horse-eye Jack)	0	0	0	0	0	0	0.24	0.48	0.24	Marine estuarine - opportunist
Echeneidae	<i>Echeneis naucrates</i> (Live Shark-sucker)	0	0	0	0	0	0	0	0	0.48	Marine stragglers
Sciaenidae	<i>Bairdiella</i> sp. (Ground Croaker)	0	0	0	0	0	0	0	0	0.72	Marine estuarine - opportunist
Syngnathidae	<i>Hippocampus reidi</i> (Longsnout seahorse)	0	0	0	0	0	0	0	1.20	0.48	Estuarine and Marine
Total density (larvae/100m ³)		20.8	15.3	90.9	16.6	19.6	36.1	3.1	3.6	9.9	
		P1 > P2 < P3			P1 < P2 < P3			P1 < P2 < P3			

P1, upstream; P2, intermediate; P3, downstream.

et al., 2021). According to Potter et al. (2015), these fish species are classified as anadromous (*Anchoa hepsetus*), estuarine and marine (*Bathygobius soporator*, *Hippocampus reidi*, *Eucinostomus* sp., and *Diapterus auratus*), marine estuarine-opportunists (*Caranx latus* and *Bairdiella rochus*), and marine stragglers (*Echeneis naucrates* and *Haemulon* sp.). The lack of freshwater species due to high salinity levels and the

occurrence of only marine and estuarine species is a pattern found in other hypersaline aquatic environments (Rosa et al., 2016; Badú et al., 2022), and points to an oversimplification of the fish assemblage under the influence of hypersalinity and severe drought. In addition, the mangrove fish community was composed of salinity-tolerant species.

Bathygobius soporator (Gobiidae) and *Anchoa hepsetus* (Engraulidae)

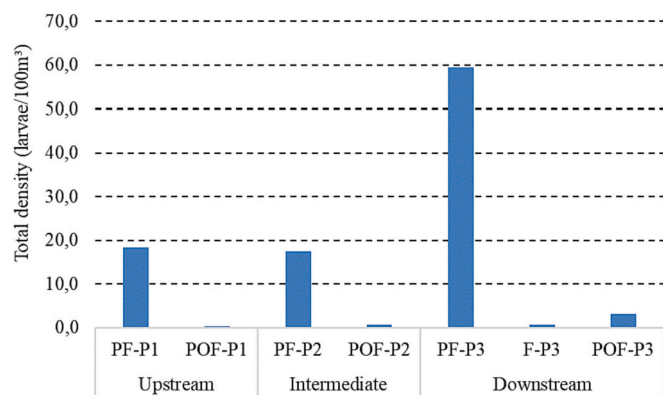


Fig. 4. Larval developmental stages found at the sampling stations along Pirangi estuary, Ceará State, Equatorial SW Atlantic, Brazil. PF, pre-flexion; F, Flexion; POF, post-flexion. P1, upstream; P2, intermediate; P3, downstream.

are euryhaline species, which means they can tolerate a wide range of salinities and occupy a great diversity of habitats (Nizinski and Munroe, 2002; Sarpedonti et al., 2013; Mangas et al., 2014; Sánchez-Ramírez and Ocaña-Luna, 2015; Merigot et al., 2017), including mangroves experiencing extreme salinity. *B. saporator* eggs are demersal, and their pelagic larvae use estuarine systems to complete their development (Joyeux et al., 2004). *A. hepsetus* spawns continuously (iteroparity), which explains the high catch of eggs and larvae during ichthyoplankton surveys in estuaries (Nizinski and Munroe, 2002; Favero et al., 2015). Another estuarine and marine larva is the near-threatened *Hippocampus reidi* (Syngnathidae) (Rosa et al., 2007) that was found at the low densities of 1.2 and 0.48 larvae/100 m³ at P2 and P3, respectively, during our study. This species occurs in habitats such as macroalgal beds and mangrove roots (Mai and Rosa, 2009). Salinity experiments with the seahorse *H. reidi* indicates that they better survive and grow at intermediate salinity levels (10–25); thus the stress caused by hypersalinity should be considered another factor that threatens their population (Hora et al., 2016) in mangroves during extreme droughts, as recorded here.

Despite inhabiting marine regions, the family Gerreidae, commonly known as mojarras or silverbiddies, seeks tropical estuaries and mangroves for feeding and reproduction (De La Cruz-Agüero et al., 2012; Ramos et al., 2016). Many species of gerreids are found from the upper to the lower zones of estuarine systems because of their broad salinity tolerance (0–35) (Franco et al., 2012); moreover, they constitute an important resource for the fishing community (Ramos et al., 2016). In this study, the Gerreidae family was represented by the estuarine and marine species, *Eucinostomus* sp. and *Diapterus auratus*.

Caranx latus (Carangidae) and *Bardiella rochus* (Sciaenidae) are marine estuarine-opportunistic species that enter estuaries to complete their life cycle and then return to the sea (Vendel and Chaves, 1998; Guazzelli et al., 2021). In contrast, *Echeneis naucrates* (Echeneidae) and *Haemulon* sp. (Haemulidae) larvae are classified as marine stragglers, meaning they enter estuaries sporadically, most commonly where salinity typically does not decline far below 35 (Potter et al., 2015).

The fish assemblage was dominated by larvae in the pre-flexion stage, with a low density of flexion and post-flexion stages. This can be indicative of spawning activity in the mangrove area, as well as the retention of these organisms in the estuary (Katsuragawa and Matsuura, 1992). Larvae in the pre-flexion stage have little or no swimming ability because their natatory structures are not yet formed, so they are threatened by hypersaline conditions, which cause increased stress (Fisher et al., 2000). In addition, larvae do not yet have osmoregulatory organs, such as gills or kidneys; therefore, they are more vulnerable to extreme salinity as more energy is required to maintain osmoregulation (Sampaio and Bianchini, 2002; Oliveira and Pessanha, 2014).

Thus, even though the semiarid mangrove in this study is an important nursery for marine fish, the lack of freshwater species and the

low densities of larvae in more advanced stages may be indicative of an ongoing loss of its nursery function. This topic requires further long-term study, as previously reported upon in other regions, for example, the loss of nursery function for fish in the Lake St. Lucia Estuary in South Africa. This lake is affected by drought and extended periods of river mouth closure, preventing the entrance of post-larvae into the estuary and the recruitment of juveniles into marine fish stocks (Cyrus and Vivier, 2006; James et al., 2007; Cyrus et al., 2011).

We found a low density and diversity of fish eggs and larvae in this mangrove system during extreme salinity. We also recorded a low number of species adapted to these extreme environmental conditions in the drought-prone mangrove ecosystem. A long time series is needed to better understand the effect of hypersalinity on ichthyoplankton assemblages in extreme estuarine environments. In this context, our results provide an important baseline for long-term ecological analyses on the loss of ecosystem functions, such as mangrove nurseries. Considering the ecological role of ichthyoplankton in mangroves and their vulnerability to global change, our study can help to better understand how this assemblage will respond to future extreme salinity due to drought and warming, with implications for fisheries and mangrove conservation.

CRediT authorship contribution statement

José Pedro Vieira Arruda Júnior: Conceptualization, Writing – original draft, Data curation, Visualization. **Érika Maria Targino Mota:** Conceptualization, Methodology, Writing – original draft, Data curation, Visualization. **Carolina Coelho Campos:** Conceptualization, Methodology, Writing – original draft, Data curation, Visualization. **Ana Cecília Pinho Costa:** Writing – original draft, Visualization. **Marcelo de Oliveira Soares:** Conceptualization, Methodology, Writing – original draft, Data curation, Visualization, Supervision, Project administration, Funding acquisition. **Tatiane Martins Garcia:** Conceptualization, Methodology, Writing – original draft, Data curation, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The authors thank the Plankton lab team (LABOMAR - UFC), the financial support provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico — CNPq (404290/2016-7; 233808/2014-0), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) for granting the scholarship during the doctoral degree, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (Research Productivity Fellowship No. 313518/2020-3, PELD Costa Semiárida do Brasil-CSB (No. 442337/2020-5), CAPES-PRINT, CAPES-Alexander Von Humboldt Foundation, and Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP - Chief Scientist Program and PELD) for their financial support.

Data availability

Data will be made available on request.

References

- Andrade, M.P., Magalhães, A., Pereira, L.C., Flores-Montes, M.J., Pardal, E.C., Andrade, T.P., Costa, R.M., 2016. Effects of a La Niña event on hydrological patterns and copepod community structure in a shallow tropical estuary (Taperaçu, northern Brazil). *J. Mar. Syst.* 164, 128–143. <https://doi.org/10.1016/j.jmarsys.2016.07.006>.
- Andrade-Turbino, M.F., Ribeiro, A.L.R., Vianna, M., 2008. Organização espaço-temporal das ictiocenoses demersais nos ecossistemas estuarinos brasileiros: uma síntese. *Oecol. Aust.* ISSN: 1981-9366 12 (4), 640–661.
- Andutta, F.P., Ridd, P.V., Wolanski, E., 2011. Dynamics of hypersaline coastal waters in the great barrier reef. *Estuar. Coast. Shelf Sci.* 94 (4), 299–305. <https://doi.org/10.1016/j.ecss.2011.06.009>.

- Arévalo-Frías, W., Mendoza-Carranza, M., 2015. Influence of temporal and spatial factors on abundance and richness of fish early stages in shallow tropical estuaries. *Environ. Biol. Fish* 98 (3), 891–904. <https://doi.org/10.1007/s10641-014-0324-x>.
- Badú, M.L.A., Lima, C.S.S., Pessanha, A.L.M., 2022. Environmental influences on the ichthyoplankton in hypersaline estuaries located in a semiarid northeastern Brazilian coast. *Neotropical Ichthyology* 20. <https://doi.org/10.1590/1982-0224-2021-0081>.
- Balakrishnan, T., Sundaramanickam, A., Shekhar, S., Muthukumaravel, K., Balasubramanian, T., 2015. Seasonal abundance and distribution of ichthyoplankton diversity in the coleroon estuarine complex, southeast coast of India. *Biocatal. Agric. Biotechnol.* 4 (4), 784–794. <https://doi.org/10.1016/j.bcab.2015.09.006>.
- Barroso, H.S., Tavares, T.C.L., Soares, M.O., Garcia, T.M., Rozendo, B., Vieira, A.S.C., Viana, P.B., Pontes, T.M., Ferreira, T.J.T., Pereira Filho, J., Schettini, C.A.F., Santaella, S.T., 2018. Intra-annual variability of phytoplankton biomass and nutrients in a tropical estuary during a severe drought. *Estuar. Coast. Shelf Sci.* 213, 283–293. <https://doi.org/10.1016/j.ecss.2018.08.023>.
- Bastos, R.B., Feitosa, F.A.N., Muniz, K., 2016. Variabilidade espaço-temporal da biomassa fitoplantônica e hidrologia no estuário do rio una (Pernambuco-Brasil). *Tropical Oceanography* 33 (1), pp. <https://doi.org/10.5914/tropocean.v33i1.5066>.
- Bonecker, F.T., Castro, M.S., Bonecker, A.C., 2009. Larval fish assemblage in a tropical estuary in relation to tidal cycles, day/night and seasonal variations. *Pan-Am. J. Aquat. Sci.* 4 (2), 239–246.
- Cabral, H., Drouineau, H., Teles-Machado, A., Pierre, M., Lepage, M., Lobry, J., Reis-Santos, P., Tanner, S.E., 2021. Contrasting impacts of climate change on connectivity and larval recruitment to estuarine nursery areas. *Prog. Oceanogr.* 196, 102608. <https://doi.org/10.1016/j.pocean.2021.102608>.
- Cai, W., Ng, B., Wang, G., Santoso, A., Wu, L., Yang, K., 2022. Increased ENSO sea surface temperature variability under four IPCC emission scenarios. *Nat. Clim. Chang.* 12 (3), 228–231. <https://doi.org/10.1038/s41558-022-01282-z>.
- Carrasco, N.K., Perissinotto, R., 2012. Development of a halotolerant community in the st. Lucia estuary (South Africa) during a hypersaline phase. *PLoS one* 7 (1), e29927. <https://doi.org/10.1371/journal.pone.0029927>.
- Chermahini, M.A., Shabani, A., Naddafi, R., Ghorbani, R., Rabbaniha, M., Noorinejad, M., 2021. Diversity, distribution, and abundance patterns of ichthyoplankton assemblages in some inlets of the northern Persian gulf. *J. Sea Res.* 167, 101981. <https://doi.org/10.1016/j.seares.2020.101981>.
- Colombano, D.D., Carlson, S.M., Hobbs, J.A., Ruhi, A., 2022. Four decades of climatic fluctuations and fish recruitment stability across a marine-freshwater gradient. *Glob. Chang. Biol.* <https://doi.org/10.1111/gcb.16266>.
- Correa-Herrera, T., Barletta, M., Lima, A.R.A., Jiménez-Segura, L.F., Arango-Sánchez, L.B., 2017. Spatial distribution and seasonality of ichthyoplankton and anthropogenic debris in a river delta in the Caribbean Sea. *J. Fish Biol.* 90 (4), 1356–1387. <https://doi.org/10.1111/jfb.13243>.
- Cyrus, D., Vivier, L., 2006. Fish breeding in, and juvenile recruitment to, the st Lucia estuarine system under conditions of extended mouth closure and low lake levels. *Afr. J. Aquat. Sci.* 31 (1), 83–87. <https://doi.org/10.2989/16085910609503874>.
- Cyrus, D.P., Vivier, L., Jerling, H.L., 2010. Effect of hypersaline and low lake conditions on ecological functioning of st Lucia estuarine system, South Africa: an overview 2002–2008. *Estuar. Coast. Shelf Sci.* 86 (4), 535–542. <https://doi.org/10.1016/j.ecss.2009.11.015>.
- Cyrus, D., Jerling, H., MacKay, F., Vivier, L., 2011. Lake St Lucia, Africa's largest estuarine lake in crisis: combined effects of mouth closure, low levels and hypersalinity. *South African Journal of Science* 107 (3), 1–13. <https://hdl.handle.net/10520/EJC97138>.
- Da Silva, P.S., Celestino, L.F., de Assumpção, L., Makrakis, S., Dias, J.H.P., Kashiwaqui, E.A.L., Makrakis, M.C., 2020. Ichthyoplankton drift through fishway in large dam: effect of hydrology, seasonal patterns and larvae condition. *Journal of Ecohydraulics* 5 (2). <https://doi.org/10.1080/24705357.2020.1762128>, p. 165–17.
- De La Cruz-Agüero, J., García-Rodríguez, F.J., De la Cruz-Agüero, G., Díaz-Murillo, B.P., 2012. Identification of gerreid species (Actinopterygii: perciformes: Gerreidae) from the Pacific coast of Mexico based on sagittal otolith morphology analysis. *Acta Ichthyol. Piscat.* 42 (4), pp. <https://doi.org/10.3750/AIP2012.42.4.03>.
- Descroix, L., Sané, Y., Thior, M., Manga, S.P., Ba, B.D., Mingou, J., Mendy, V., Coly, S., Diéye, A., Badiane, A., Senghor, M.J., Diedhiou, A.B., Sow, D., Bouaita, Y., Soumaré, S., Diop, A., Faty, B., Sow, B.A., Machu, E., Montoroj, J.P., Andrieu, J., Vanderveere, J.P., 2020. Inverse estuaries in West Africa: evidence of the rainfall recovery? *Water* 12 (3), 647. <https://doi.org/10.3390/w12030647>.
- Favero, J.M., Katsuragawa, M., Zani-Teixeira, M.L., Turner, J., 2015. Using new tools to identify eggs of *Engraulis anchoita* (Clupeiformes, Engraulidae). *J. Fish Biol.* 86 (2), 822–826. <https://doi.org/10.1111/jfb.12594>.
- Fisher, R., Bellwood, D.R., Job, S.D., 2000. Development of swimming abilities in reef fish larvae. *Mar. Ecol. Prog. Ser.* 202, 163–173. <https://doi.org/10.3354/meps202163>.
- Franco, T.P., Neves, L.M., Teixeira, T.P., Araújo, A.F.G., 2012. Patterns of spatial distribution of five species of mojarras (Actinopterygii: Gerreidae) in a small tropical estuary in South-Eastern Brazil. *J. Mar. Biol. Assoc. U. K.* 92 (5), 1217–1225. <https://doi.org/10.1017/S0025315411000609>.
- Guazzelli, J.G., Darnaude, A.M., Duarte-Neto, P.J., Le Loch, F., Lima, M.C., Menard Frédéric, M., Ferreira, V., Fredou, F.L., Munaron, J., Frédou, T., 2021. Trophic ecology of the juveniles of two jack species (*Caranx latus* and *C. hippos*) in contrasted tropical estuaries. *Estuar. Coast. Shelf Sci.* 255, 107370. <https://doi.org/10.1016/j.ecss.2021.107370>.
- Guerreiro, M.A., Martinho, F., Baptista, J., Costa, F., Pardal, M.Á., Primo, A.L., 2021. Function of estuaries and coastal areas as nursery grounds for marine fish early life stages. *Mar. Environ. Res.* 170, 105408. <https://doi.org/10.1016/j.marenvres.2021.105408>.
- Hora, M.S.C., Joyeux, J.C., Rodrigues, R.V., Sousa-Santos, L.P., Gomes, L.C., Tzuzuki, M. Y., 2016. Tolerance and growth of the longsnout seahorse *Hippocampus reidi* at different salinities. *Aquaculture* 463, 1–6.
- Houde, E.D., 2001. Fish larvae. In: Steele, J., Thorpe, S., Turekian, K. (Eds.), *Encyclopedia of Ocean Sciences*. Academic Press, Cambridge, Massachusetts, pp. 928–932.
- Jagadeesan, L., Jyothibabu, R., Anjusha, A., Mohan, A.P., Madhu, N.V., Muraleedharan, K.R., Sudheesh, K., 2013. Ocean currents structuring the mesozooplankton in the Gulf of Mannar and the Palk Bay, southeast coast of India. *Prog. Oceanogr.* 110, 27–48. <https://doi.org/10.1016/j.pocean.2017.07.004>.
- James, N.C., Cowley, P.D., Whitfield, A.K., Lamberth, S.J., 2007. Fish communities in temporarily open/closed estuaries from the warm-and cool-temperate regions of South Africa: a review. *Rev. Fish Biol. Fish.* 17 (4), 565–580. <https://doi.org/10.1016/j.ecss.2007.09.010>.
- Joyeux, J.C., Pereira, B.B., de Almeida, H.G., 2004. The flood-tide ichthyoplanktonic community at the entrance into a Brazilian tropical estuary. *J. Plankton Res.* 26 (11), 1277–1287. <https://doi.org/10.1093/plankt/fbh119>.
- Katsuragawa, M., Matsuura, Y., 1992. Distribution and abundance of carangid larvae in the southeastern Brazilian bight during 1975–1981. *Bol. Instit. Oceanogr.* 40 (1–2), 55–78.
- Kisten, Y., Strydom, N.A., 2021. Diel and tidal periodicity in the responses of early life stages of marine fishes to an estuary opening event in temperate South Africa. *Afr. J. Aquat. Sci.* 46 (1), 22–32. <https://doi.org/10.2989/16085914.2020.1796574>.
- Korsman, B.M., Kimball, M.E., Hernandez, F.J., 2017. Spatial and temporal variability in ichthyoplankton communities ingressing through two adjacent inlets along the southeastern US Atlantic coast. *Hydrobiologia* 795 (1), 219–237. <https://doi.org/10.1007/s10750-017-3131-5>.
- Kurbel, S., 2008. Are extracellular osmolality and sodium concentration determined by Donnan effects of intracellular protein charges and of pumped sodium? *Journal of Theoretical Biology* 252 (4), 769–772. ISSN 0022-5193.
- Lacerda, L.D., Menezes, M.O.T., Molisani, M.M., 2007. Changes in mangrove extension at the Pacoti River estuary, CE, NE Brazil due to regional environmental changes between 1958 and 2004. *Biota Neotropica* 7 (3), 67–72. ISSN 1676-0603.
- Lima, A.R.A., Barletta, M., Costa, M.F., 2015. Seasonal distribution and interactions between plankton and microplastics in a tropical estuary. *Estuar. Coast. Shelf Sci.* 165, 213–222. <https://doi.org/10.1016/j.ecss.2015.05.018>.
- Macedo Silva, M.A.A., Souza, M.F.L., Abreu, P.C., 2015. Spatial and temporal variation of dissolved inorganic nutrients, and chlorophyll-a in a tropical estuary in northeastern Brazil: dynamics of nutrient removal. *Braz. J. Oceanogr.* 63 (1), pp. ISSN 1678-8759.
- Mai, A.C.G., Rosa, I.M.D.L., 2009. Aspectos ecológicos do cavalo-marinho *Hippocampus reidi* no estuário Camurupim/Cardoso, Piauí, Brasil, fornecendo subsídios Para a criação de uma Área de Proteção Integral. *Biota Neotrop.* 9 (3), 85–91. <https://doi.org/10.1590/S1676-06032009000300007>.
- Mangas, A.P., da Silva, A.C., Ferreira, S.C.G., Palheta, G.D.A., de Melo, N.F.A.C., 2014. Ictioplâncton da baía do Guajará e do estuário do rio Pará, ilha do Marajó, Pará, Brasil. *Boletim Técnico Científico do CEPNOR* 13 (1), 43–54.
- Marcolin, C.R., da Conceição, B.L., Nogueira, M.M., Júnior, P.M., Johnsson, R., 2010. Mesozooplankton and Ichthyoplankton composition in two tropical estuaries of Bahia, Brazil. *Check List* 6 (2), 210–216. ISSN 1809-127X.
- Marengo, J.A., Alves, L.M., Alvala, R.C.S., Cunha, A.P., Brito, S., Moraes, O.L.L., 2017. Climatic characteristics of the 2010–2016 drought in the semiarid Northeast Brazil region. *An. Acad. Bras. Cienc.* 90, 1973–1985. <https://doi.org/10.1590/0001-3765201720170206>.
- Marina, B., Svetlana, K., Francesco, F., 2021. The long-term ichthyoplankton abundance summer trends in the coastal waters of the Black Sea under conditions of hydrometeorological changes. *Estuar. Coast. Shelf Sci.* 258, 107450. <https://doi.org/10.1016/j.ecss.2021.107450>.
- Merigot, B., Frédou, F.L., Viana, A.P., Ferreira, B.P., Junior, E.D.N.C., da Silva Júnior, C. B., Frédou, T., 2017. Fish assemblages in tropical estuaries of Northeast Brazil: a multi-component diversity approach. *Ocean Coast. Manag.* 143, 175–183. <https://doi.org/10.1016/j.ocecoaman.2016.08.004>.
- Morais, J.O., Pinheiro, L.S., 2011. The effect of semi-aridity and damming on sedimentary dynamics in estuaries-northeastern region of Brazil. *J. Coast. Res.* 1540–1544. <http://www.jstor.org/stable/26482433>.
- Nizinski, M.S., Munroe, T.A., 2002. Order Clupeiformes, Engraulidae. In: Carpenter, K.E. (Ed.), *The Living Marine Resources of the Western Central Atlantic*. Volume 2: Bony Fishes Part 1 (Acipenseridae to Grammatidae), FAO Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No 5. FAO, Rome, pp. 601–1374.
- Oliveira, R.E., Pessanha, A.L., 2014. Fish assemblages along a morphodynamic continuum on three tropical beaches. *Neotrop. Ichthyol.* 12, 165–175. <https://doi.org/10.1590/S1679-62252014000100018>.
- Omori, M., Ikeda, T., 1984. *Methods in Marine Zooplankton Ecology*. John-Wiley and Sons, Inc, New York.
- Pérez-Robles, J., Re, A.D., Giffard-Mena, I., Díaz, F., 2012. Interactive effects of salinity on oxygen consumption, ammonium excretion, osmoregulation and Na⁺/K⁺-ATPase expression in the Bullseye puffer (*Sphoeroides annulatus*, Jenyns 1842). *Aquac. Res.* 43 (9), 1372–1383. <https://doi.org/10.1111/j.1365-2109.2011.02940.x>.
- Potter, I.C., Chuwen, B.M., Hoeksema, S.D., Elliott, M., 2010. The concept of an estuary: a definition that incorporates systems which can become closed to the ocean and hypersaline. *Estuar. Coast. Shelf Sci.* 87 (3), 497–500. <https://doi.org/10.1016/j.ecss.2010.01.021>.
- Potter, I.C., Tweedley, J.R., Elliott, M., Whitfield, A.K., 2015. The ways in which fish use estuaries: a refinement and expansion of the guild approach. *Fish Fish.* 16 (2), 230–239. <https://doi.org/10.1111/faf.12050>.

- Ramos, S., Amorim, E., Elliott, M., Cabral, H., Bordalo, A.A., 2012. Early life stages of fishes as indicators of estuarine ecosystem health. *Ecol. Indic.* 19, 172–183. <https://doi.org/10.1016/j.ecolind.2011.08.024>.
- Ramos, J.A.A., Barletta, M., Dantas, D.V., Costa, M.F., 2016. Seasonal and spatial ontogenetic movements of gerreidae in a Brazilian tropical estuarine ecocline and its application for nursery habitat conservation. *J. Fish Biol.* 89 (1), 696–712. <https://doi.org/10.1111/jfb.12872>.
- Ré, P.M.A.B., 1999. Ictioplâncton estuarino da península ibérica: guia de identificação dos ovos e estados larvares planctônicos. Lisboa.
- Richards, W.J., 2005. Early life stages of Atlantic Fishes: an identification guide for the western Central Atlantic. CRC Press, Florida, USA.
- Rosa, J.C.L., Alberto, M.D., Ribas, W.M.M., Neves, M.H.C.B., Fernandes, L.D.A., 2016. Spatial variability in the ichthyoplankton structure of a subtropical hypersaline lagoon. *Braz. J. Oceanogr.* 64, 149–156. <https://doi.org/10.1590/S1679-87592016109406402>.
- Rosa, I.L., Oliveira, T.P.R., Castro, A.L.C., Moraes, L.E.S., Xavier, J.H.A., Nottingham, M. C., Dias, T.L.P., Bruto-Costa, L.V., Araújo, M.E., Birolo, A.B., Mai, A.C.G., Monteiro-Neto, C., 2007. Population characteristics, space use and habitat associations of the seahorse Hippocampus reidi (Teleostei: Syngnathidae). *Neotrop. Ichthyol.* 5, 405–414. <https://doi.org/10.1590/S1679-62252007000300020>.
- Rossi, S., Soares, M.O., 2017. Effects of El Niño on the coastal ecosystems and their related services. *Mercator (Fortaleza)* 16, e16030. <https://doi.org/10.4215/rm2017.e16030>.
- Rousseau, Y., Blanchard, F., Gardel, A., 2017. Spatiotemporal dynamics of larval fish in a tropical estuarine mangrove: example of the Mahury River estuary (French Guiana). *Can. J. Fish. Aquat. Sci.* 75, 235–246. <https://doi.org/10.1139/cjfas-2016-0267>.
- Sampaio, L.A., Bianchini, A., 2002. Salinity effects on osmoregulation and growth of the euryhaline flounder *Paralichthys orbignyanus*. *J. Exp. Mar. Biol. Ecol.* 269 (2), 187–196. [https://doi.org/10.1016/S0022-0981\(01\)00395-1](https://doi.org/10.1016/S0022-0981(01)00395-1).
- Sánchez-Ramírez, M., Ocaña-Luna, A., 2015. Estructura y variación estacional de la comunidad ictioplanctónica en una laguna hipersalina del oeste del Golfo de México: Laguna Madre, Tamaulipas. *Hidrobiológica* 25 (2), 175–186.
- Santos, R.V.S., Ramos, S., Bonecker, A.C.T., 2017. Environmental control on larval stages of fish subject to specific salinity range in tropical estuaries. *Reg. Stud. Mar. Sci.* 13, 42–53. <https://doi.org/10.1016/j.rsma.2017.03.010>.
- Sarpedonti, V., Anunciação, É.M.S.D., Bordalo, A.O., 2013. Spatio-temporal distribution of fish larvae in relation to ontogeny and water quality in the oligohaline zone of a north brazilian estuary. *Biota Neotrop.* 13, 55–63. <https://doi.org/10.1590/S1676-06032013000300007>.
- Schettini, C.A., Valle-Levinson, A., Truccolo, E.C., 2017. Circulation and transport in short, low-inflow estuaries under anthropogenic stresses. *Reg. Stud. Mar. Sci.* 10, 52–64. <https://doi.org/10.1016/j.rsma.2017.01.004>.
- Schreck, C.B., Contreras-Sanchez, W., Fitzpatrick, M.S., 2001. Effects of stress on fish reproduction, gamete quality, and progeny. In: *Reproductive Biotechnology in Finfish Aquaculture*. Elsevier, pp. 3–24. <https://doi.org/10.1016/B978-0-444-50913-0.50005-9>.
- Servili, A., Canario, A.V.M., Mouchel, O., Muñoz-Cueto, J.A., 2020. Climate change impacts on fish reproduction are mediated at multiple levels of the brain-pituitary-gonad axis. *Gen. Comp. Endocrinol.* 291, 113439 <https://doi.org/10.1016/B978-0-444-50913-0.50005-9>.
- Silva, J.M.O., Silva, E.V., 2012. Análise geoambiental do baixo curso da bacia hidrográfica do rio Pirangi – Ce. In: *Revista Geonorte, Edição Especial*, 3, pp. 593–605 n. 4.
- Silva, D.F., de Sousa, A.B., Maia, L.M., Rufino, L.L., 2012. Efeitos da associação de eventos de ENOS e ODP sobre o Estado do Ceará. *Revista de Geografia (Recife)* 29 (2), 114–135. ISSN 2238-6211.
- Sloterdijk, H., Brehmer, P., Sadio, O., Müller, H., Döring, J., Ekau, W., 2017. Composition and structure of the larval fish community related to environmental parameters in a tropical estuary impacted by climate change. *Estuar. Coast. Shelf Sci.* 197, 10–26. <https://doi.org/10.1016/j.ecss.2017.08.003>.
- Soares, M.O., Rossi, S., Gurgel, A.R., Lucas, C.C., Tavares, T.C.L., Diniz, B., Feitosa, C.V., Rabelo, E.F., Pereira, P.H.C., Kikuchi, R.K.P., Leão, Z.M.A.N., Cruz, I.C.S., Carneiro, P.B.M., Alvarez-Filipe, L., 2021. Impacts of a changing environment on marginal coral reefs in the tropical southwestern Atlantic. *Ocean Coast. Manag.* 210, 105692 <https://doi.org/10.1016/j.ocecoaman.2021.105692>.
- Strydom, N.A., Whitfield, A.K., Wooldridge, T.H., 2003. The role of estuarine type in characterizing early stage fish assemblages in warm temperate estuaries, South Africa. *African Zoology* 38 (1), 29–43.
- Tweedley, J.R., Dittmann, S.R., Whitfield, A.K., Withers, K., Hoeksema, S.D., Potter, I.C., 2019. Hypersalinity: global distribution, causes, and present and future effects on the biota of estuaries and lagoons. In: *Coasts and Estuaries*. Elsevier, pp. 523–546. <https://doi.org/10.1016/B978-0-12-814003-1.00030-7>.
- Vendel, A.L., Chaves, P.T.C., 1998. Alimentação de Bairdiella ronchus (Cuvier) (Perciformes, Sciaenidae) na Baía de Guaratuba, ParanáBrasil. *Revista Brasileira de Zoologia* 15, 297–305. <https://doi.org/10.1590/S0101-81751998000200003>.
- Whitfield, A.K., 1992. A characterization of southern African estuarine systems. *South Afr. J. Aquat. Sci.* 18 (1–2), 89–103. <https://doi.org/10.1080/10183469.1992.9631327>.
- Whitfield, A.K., 2016. Biomass and productivity of fishes in estuaries: a south african case study. *J. Fish Biol.* 89 (4), 1917–1930. <https://doi.org/10.1111/jfb.13110>.
- Whitfield, A.K., 2017. The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Rev. Fish Biol.* 27 (1), 75–110. <https://doi.org/10.1007/s11160-016-9454-x>.
- Whitfield, A.K., Taylor, R.H., Fox, C., Cyrus, D.P., 2006. Fishes and salinities in the st Lucia estuarine system—a review. *Rev. Fish Biol.* 16 (1), 1–20. <https://doi.org/10.1007/s11160-006-0003-x>.
- Whitfield, A.K., 2021. Estuaries—how challenging are these constantly changing aquatic environments for associated fish species? *Environ. Biol. Fish* 104 (4), 517–528. <https://doi.org/10.1007/s10641-021-01085-9>.
- Zacardi, D.M., 2015. Variação e abundância do ictioplâncton em canais de maré no Extremo Norte do Brasil. *Biota Amazônia (Biote Amazonie, Biota Amazonia, Amazonian Biota)* 5 (1), 43–52. <https://doi.org/10.18561/2179-5746/biotaamazonia.v5n1p43-52>.
- Zhang, H., Wang, Y., Liang, C., Liu, S., Xian, W., 2022. Estuarine ichthyoplankton studies—a review. *Front. Mar. Sci.* 9, 794433 <https://doi.org/10.3389/fmars.2022.794433>.