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Environmental influences on the ichthyoplankton in hypersaline estuaries located in a Semiarid Northeastern Brazilian coast

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Hypersaline estuaries are commonly found in the Semiarid Northeast Brazilian coast. However, the utilization of these estuaries by early life stages of fishes is less well documented. This study aimed to evaluate the effects of environmental factors on the ichthyoplankton, and to describe their spatial and temporal variation in two estuaries (Tubarão and Casqueira). The sampling were diurnally in four excursions carried out during two dry-season months (November and December 2017) and two rainy-season months (May and July 2018). A total of 423 larvae representing 30 species (14 families) and 2,762 eggs (five families) were collected. Although the community structures were similar in both estuaries, there was strong seasonal variation, with higher abundances observed during the dry season. Low rainfall was the primary environmental driver affecting ichthyoplankton in both estuaries. Other environmental factors, such as depth, water temperature, and channel width, were also predictor variables for the distribution of eggs and larvae. The ichthyoplankton was dominated by marine estuarine-dependent species in both estuaries, accounting for 76% of individuals. The presence of the early life stages of typically marine species suggests that hypersaline environments provide important nursery areas and play an essential role for some coastal fish species.

Keywords: Environmental factors, Larvae fish, Nursery, Salinity, Tropical estuary.

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Os estuários hipersalinos são comumente encontrados na região semiárida da costa nordestina brasileira. No entanto, a utilização desses estuários pelos primeiros estágios de vida dos peixes é pouco documentada. O objetivo deste estudo foi avaliar os efeitos de fatores ambientais sobre o ictioplâncton e descrever sua variação espacial e temporal em dois estuários (Tubarão e Casqueira). As amostragens foram diurnas em quatro excursões realizadas em dois meses da estação seca (novembro e dezembro de 2017) e dois meses da estação chuvosa (maio e julho de 2018). Um total de 423 larvas representando 30 espécies (14 famílias) e 2.762 ovos (cinco famílias) foram coletadas. Embora as estruturas das comunidades fossem semelhantes em ambos os estuários, houve fortes diferenças de variação sazonal, com maiores abundâncias observadas durante a estação seca. A baixa precipitação foi o principal fator ambiental que afetou o ictioplâncton em ambos os estuários. Outros fatores, como profundidade, temperatura da água e largura do canal, também foram preditoras para a distribuição de ovos e larvas. O ictioplâncton foi dominado por espécies marinhas dependentes em ambos os estuários, representando 76% dos indivíduos. A presença de estágios iniciais de espécies tipicamente marinhas sugere que ambientes hipersalinos fornecem áreas de berçário importantes e desempenham um papel essencial para algumas espécies de peixes costeiros.

Palavras-chave: Berçário, Estuário tropical, Fatores ambientais, Larvas de peixes, Salinidade.

INTRODUCTION

Hypersaline estuaries are complex and dynamic ecosystems that are widespread in arid and semi-arid regions (Kesaulya, Vega, 2019). In these estuaries, the relatively low rainfall and high evaporation rates combined with the low freshwater supply can cause hypersaline conditions, characterized by salinities that frequently exceed 40 (Castro *et al*., 1999). However, despite the high salinity, these environments support a diverse fauna, including mostly juveniles of the fish species that are typically abundant throughout the estuarine system (Sales *et al*., 2018; Duarte *et al*., 2020). The hypersaline estuaries are attractive habitats for many fish because they provide high food availability, the low abundance of predators, and the circulation patterns that favours larval stage retention in these ecosystems (Correa-Herrera *et al*., 2017).

The Northeastern Brazilian coast includes several estuarine systems, from small and large open systems, where the importance of estuaries as nursery areas for fishes is well documented (Blaber, Barletta, 2016). Particularly, hypersaline estuaries are commonly found in the Semi-arid Northeast Coast, which have a mean annual freshwater discharge in the region of 4.3 m^3s^{-1}, and the rate of evaporation is 8.5-fold higher than the precipitation (Noriega, Araújo, 2014). Consequently, these environments are subject to an intensification of saline intrusion, and as a result, alterations of salinity gradient. This may have important consequences not only from the direct physiological effects on fishes but also potentially change the ecological drivers of the system. This encompasses the ways organisms interact with the environment, including species reproduction, survival of eggs and larval fishes (Reynalte-Tataje *et al*., 2011; Hare, Richardson, 2014). However, the utilization of hypersaline estuaries by early life stages of fishes in the Northeastern Brazilian coast is less well documented.

In this general context, it is necessary to establish that the process of the entrance of new individuals to the estuary (recruitment) is composed of several steps (*e.g*., larval dispersal, settlement, and post-settlement), where each step is influenced by biotic and abiotic mechanisms, leading to large variability of recruitment in space and time (Barletta-Bergan *et al*., 2003). Research suggests that recruitment is influenced by the constant shifts in environmental conditions in estuaries, resulting in estuaries having a central role in the distribution patterns and diversity of early life history stages of species (Solari *et al*., 2015; Dourado *et al*., 2017). Among these environmental variables, salinity is considered the best predictor because it affects the osmotic balance of eggs and larval fish (Barletta-Bergan *et al*., 2005; Rosa *et al*., 2016). Trends in larval fish studies have shown that species diversity steadily declines once hypersalinity is registered in estuaries due to larval survival (Sloterdijk *et al*., 2017; Kesaulya, Vega, 2019). This approach has been utilized to some extent in studies by Simier *et al.* (2004) on the organization and dynamics of fish assemblages in the Saloum hypersaline estuary (Senegal), Kantoussan *et al.* (2012) on the taxonomic and functional diversity of fishes in the Casamance estuary (Senegal), and Whitfield *et al.* (2006) for mortalities of fishes in St Lucia estuarine system recorded under high salinity (> 70) conditions.

Seasonal variability of the environmental conditions in the estuaries in the Semi-arid Northeast Coast is influenced by sparse and variable precipitation on annual patterns, and these variations can lead to a significant change in larval fish communities. Several studies have shown that lower larval fish densities and species richness in estuaries are supported by an increase of salinity, particularly during periods of reduced precipitation (Montoya-Maya, Strydom, 2009; Sloterdijk *et al*., 2017). There is thus considerable relation between the highest contributions of marine species in larval assemblages associated with strong saline intrusion supporting the hypothesis of a marinization. Results from Pasquaud *et al.* (2015) suggest a significant increase in the occurrence and abundance of the main marine juvenile fish species was linked to the environmental changes in the estuarine area, in particular associated with increases in both water temperature and salinity. In this context, the present study focused on the distribution and abundance of eggs and larvae of fishes in two hypersaline estuaries on the Northeastern Brazilian coast, to (1) describe the composition and structure of the ichthyoplankton, and (2) analyze the influence that environmental factors, in particular salinity, have on the distribution of fish larvae in these ecosystems.

MATERIAL AND METHODS

Study area. The ichthyoplankton was collected from two estuaries (Tubarão and Casqueira) located on the Northeastern Brazilan coast (Fig. 1). The climate is semi-arid (BSh according to the Köppen-Geiger climate classification), with very low rainfall levels (average annual ≤ 650 mm) and high temperatures means (average annual ≥ 26.5 °C) throughout the year (Alvares *et al*., 2014). The estuaries are in a region along the coast that corresponds to an area with the lowest amount of total annual rainfall on the Brazilian coast (annual mean rainfall ≤ 650 mm) (Diniz, Pereira, 2015).

The dry season runs from June to January, and a short rainy season occurs from February to May (Mattos *et al*., 2011). The estuaries are subject to strong tidal action and have a mesotidal, semi-diurnal regime with maximum heights of 2.7 and 2.0 m for the spring and neap tides, respectively (Vital, 2008). The Tubarão River estuary is located within the limits of the Ponta do Tubarão Sustainable Development Reserve (RDSEPT) (05°04’37”S 36°27’24”W) and is a 10 km long tidal channel with a depth ranging from 1.0 to 6.0 m that comprises a diversity of smaller creeks and inlets (Fig. 1). The Casqueira River estuary (05°05’37”S 36°32’21”W) main channel is approximately 20 km long, with depths ranging from 1.0 to 8.0 m (Fig. 1). Currently, this drainage basin is occupied by a few urban centers, extensive mangrove forests and intertidal sands and mudflats.

Sampling. The sampling program was conducted on four excursions carried out during two dry-season months (November and December 2017) and two rainy-season months (May and July 2018) in both estuaries. Larval fish were sampled in three zones covering all of the estuary: a lower zone (Zone 1), a middle zone (Zone 2) and an upper zone (Zone 3). Each zone was created based on distance from the mouth and channel width. Three sites were sampled in each zone of the estuaries with three replicates per excursion at each site.

At each site, prior to the collection of samples, water temperature (°C), salinity, and depth (cm) were recorded using a thermometer, an optical refractometer, and an

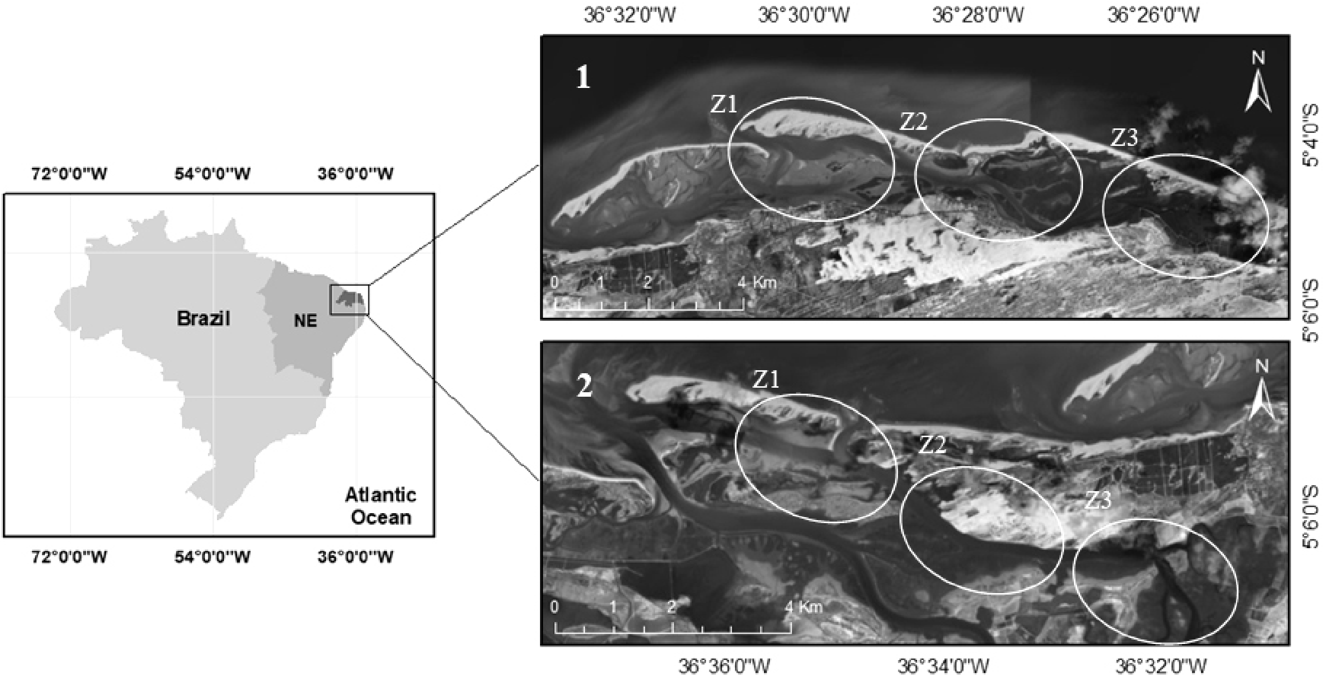

FIGURE 1 | Map of the two study areas, Tubarão (1) and Casqueira (2) river estuaries. The insert map indicates the sampling sites (zones) in both estuaries: Z1 = Lower zone, Z2 = Middle zone and Z3 = Upper zone.

Echotest depth sounder, respectively. The water transparency was measured with a Secchi disc (cm). Primary production was also quantified by analyzing the chlorophyll *a* content in the water, following the methodology proposed by Jespersen *et al.* (1987) and Wintermans, Mots (1965). Data on rainfall were obtained from Instituto Nacional de Meteorologia – INMET (http://www.inmet.gov.br/portal/), and geomorphological variables were described by distance to the mouth (defined as the distance from the sampling site to the mouth of each estuary) and channel width (defined as the horizontal distance between the estuary channel edges at each site).

Ichthyoplankton samples were collected using a conical-cylindrical plankton net (total length 1.50 m; mouth opening 60 cm; mesh size 0.2 mm). A mechanical flow meter (General Oceanic) attached to the center of the net was used to calculate the volume of filtered water. This value was used to calculate the larval density (number of larvae × 100 m^{-3}) (Lima *et al*., 2015). At each sampling site, horizontal plankton hauls were done from 1.5 m water depth to the surface and performed during the day in the middle of the main channel at spring high tides All hauls were standardized in a 5 min time with a boat speed of 1.5 knots to prevent individual escape as much as possible. All samples were stored and immediately preserved in 4% formaldehyde/seawater (Barletta-Bergan *et al*., 2002).

In laboratory, all eggs and larvae were identified counted and measured the total length (mm). Larval fish were identified to the lowest possible taxon and eggs at the family level, using keys by Kendall *et al.* (1984), Fahay (1983), and Richards (2006). To classify larvae in developmental stages, notochord flexion was used, and four stages were defined: Vitelline larval, pre-flexion, flexion and post-flexion according to Kendall *et al.* (1984) and Nakatani *et al.* (2001). Each fish species was assigned to ecological guilds based on the life history characteristics, which were developed Potter *et al.* (2015).

Data analysis. Permutational analysis of variance (PERMANOVA) was used to identify significant differences in eggs and larval fish densities and environmental variables for different estuaries, zones and sampling periods (Anderson, 2001), followed by a posteriori pairwise comparison tests (Anderson *et al*., 2008). Three fixed factors were selected: Estuary (two levels: Tubarão and Casqueira rivers), Season (two levels: Dry and Rainy), and Zone (three levels: Z1, Z2 and Z3). A resemblance matrix of densities was calculated using Bray-Curtis coefficients. Densities and environmental variables were log-transformed. The log transformation reduces or removes the skewness of our original data. Univariate permutational analysis of variance (Univariate PERMANOVA) was used to investigate significant differences among the sites and seasons. Significant factors were further analyzed using a PERMANOVA pair-wise comparison. All univariate tests were based on Euclidean distance matrices generated from 9,999 permutations.

To evaluate the influence of environmental variables on the variability of fish data and to select the best explanatory model, we used Distance-Based Linear Models (DistLMs) (Legendre, Anderson, 1999; Mcardle, Anderson, 2001), using the Akaike Information Criterion (AIC) to select the best explanatory model; models with the lowest AIC were considered the most parsimonious (Mcardle, Anderson, 2001). Distance-based redundancy analysis (dbRDA) was used to detect patterns in the spatial and temporal distribution of samples related to the predictor variables (Mcardle, Anderson, 2001).

Draftsman plots and correlation matrices were used to check for multicollinearity in the predictor variables, and redundant variables with correlations (r) > 0.7 were omitted. There was no evidence of collinearity between environmental variables, and the full set of 8 available variables was used in the analysis. The Pearson correlation was used for the selection of the most correlated variables (r > 0.2) from the axes of the dbRDA. All analyses were performed using the statistical package PRIMER v6 + PERMANOVA (Clarke, Gorley, 2006).

RESULTS

Environmental parameters. In both estuaries, salinity and transparency increased from the lower zone (Z1) to the most sheltered zone (Z3), but the depth and canal width decreased gradually (Tab. 1). The univariate PERMANOVA revealed that there were significant differences in environmental parameters between the estuaries (Pseudo-$F_{1,183}$ = 11.05; P = 0.0001), their respective zones (Pseudo-$F_{4,183}$ = 4.198; P = 0.0001) and the periods (Pseudo-$F_{2,138}$ = 5.0973; P = 0.0001) (Tab. 2). Rainfall shows that the region has two well-defined seasons, the dry season always showed the lowest rainfall values (2.5–7.5 mm), whereas the rainy season had the highest values (45.0–60.0 mm).

Among the environmental variables, the univariate PERMANOVA showed that, aside from the differences in water temperature and chlorophyll-*a*, there were no significant differences among the factors (estuary, season and zone). In contrast, transparency, depth and salinity showed significant differences for all factors. The pairwise test for each of these three parameters showed that transparency was highest during the rainy season in the Tubarão estuary, while the highest depth and salinity values were observed in the Casqueira estuary during the rainy and dry periods, respectively (Tab. **S1**).

TABLE 1 | Mean values and standard error of environmental parameters (± Standard error) for Tubarão and Casqueira river estuaries, Semiarid Northeastern Brazilian coast (Z1 = Lower; Z2 = Middle; Z3 = Upper).

			Water Temperature (°C)	Transparency (cm)	Depth (cm)	Salinity	Chlorophyll-a (μg.l^{-1})	Mouth Distance (km)	Channel Width (km)
Dry	Tubarão	**Z1**	26.6±0.59	93.8±3.72	216.2±18.15	34.0±0.55	3.52±0.58	1.83±326.70	0.99±164.20
		Z2	27.1±0.09	83.8±4.49	243.6±20.98	35.4±0.60	5.22±0.99	6.42±203.88	0.13±12.53
		Z3	27.1±0.14	93.3±4.71	181.7±24.97	36.5±0.70	7.73±1.43	8.61±526.76	0.09±13.05
	Casqueira	**Z1**	27.5±0.03	77.8±3.78	375.6±78.02	35.2±0.69	4.93±0.80	5.01±67.69	0.19±9.12
		Z2	26.8±0.07	78.9±2.46	238.9±22.74	37.3±0.47	8.88±1.68	7.82±302.99	0.24±26.9
		Z3	26.6±0.01	108.9±14.44	258.9±12.12	40.0±0.27	3.95±0.80	10.06±147.78	0.16±26.6
Rainy	Tubarão	**Z1**	27.5±0.29	120.3±6.74	264.4±29.49	37.3±0.48	4.44±0.92	2.04±379.37	0.23±31.40
		Z2	26.8±0.26	89.2±4.65	166.7±20.24	37.4±0.92	6.08±1.16	6.77±108.43	0.17±23.40
		Z3	26.6±0.22	96.1±4.54	163.9±26.95	37.7±0.41	6.74±1.23	8.46±134.05	0.49±146.26
	Casqueira	**Z1**	26.8±0.38	89.2±3.52	460.8±43.81	38.2±0.70	10.20±1.77	4.97±149.08	0.25±12.78
		Z2	26.8±0.32	97.2±2.55	435.8±31.04	37.5±0.57	8.88±1.49	8.61±277.56	0.16±10.85
		Z3	26.8±0.32	96.1±8.80	163.9±33.92	37.7±0.52	6.74±1.41	10.09±93.76	0.12±19.13

TABLE 2 | PERMANOVA results for water temperature, transparency, depth, salinity and chlorophyll-a between Tubarão and Casqueira river estuaries, as well as in their respective dry and rain periods and their different zones. Significant values in bold.

Parameters	Estuary		Zone		Period	
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p
Water temperature	0.273	0.6091	0.277	0.9071	0.053	0.9517
Transparency	**5.170**	**0.0252**	**20.620**	**0.0001**	**14.659**	**0.0001**
Depth	**62.595**	**0.0001**	**3.796**	**0.0056**	**5.557**	**0.0046**
Salinity	**13.617**	**0.0005**	**2.480**	**0.0494**	**10.132**	**0.0001**
Chlorophyll-*a*	2.618	0.1054	1.323	0.2576	0.137	0.8740
Mouth Distance	**56.337**	**0.0001**	**64.279**	**0.0001**	**7.689**	**0.0067**
Channel Width	1.517	0.2232	**15.349**	**0.0001**	0.537	0.4675

Abundance and taxonomic composition. Overall, a total of 2,762 fish eggs from five families were collected, and 423 fish larvae from 30 species (14 families) were identified in the two estuaries (Tab. 3). Engraulidae was the most dominant family, accounting for 61.3% of the total number of eggs collected, followed by Clupeidae (32.4%) and Achiriidae (2.65%). Carangidae, Clupeidae and Atherinopsidade were the dominant families, comprising 76.46% of the total number of larvae. The four dominant fish larvae species throughout the study area were *Lile piquitinga* (Schreiner & Miranda Ribeiro, 1903) (23.11%), *Caranx latus* Agassiz, 1831 (16.2%), *Atherinella brasiliensis* (Quoy & Gaimard, 1825) (12.10%) and *Oligoplites saurus* (Bloch & Schneider, 1801) (10.21%), and the remaining 23% of fish larvae belonged to the other 26 taxa (Tab. 3). In terms of ecological guilds, the larval fish composition was dominated by marine estuarine-dependent species (77%), followed by solely estuarine species (23%).

In the Tubarão estuary, *L. piquitinga*, *Achirus lineatus* (Linnaeus, 1758), *A. brasiliensis*, *O. saurus*, and *Anchoa januaria* (Steindachner, 1879) collectively constituted 71.8% of the total fish larvae caught during the dry season, while *A. brasiliensis*, *C. latus*, *O. saurus*, *L. piquitinga*, and *Oligoplites palometa* (Cuvier, 1832) dominated (82.4%) during the rainy season. In the Casqueira estuary, *A. brasiliensis*, *L. piquitinga*, *O. saurus*, *Oligoplites* sp., *Sardinella brasiliensis* (Steindachner, 1879), and *Cephalopholis cruentata* (Lacepède, 1802) were the most abundant fish larvae throughout the dry season (72.0%), whereas *A. brasiliensis*, *Mugil* sp., and *O. saurus* made up 80% of the fish larvae in the rainy season (Tab. 3). Based on composition, fish eggs from the two estuaries did not differ between seasons, and the higher abundance during the dry season was attributable to Engraulidae and Clupeidae eggs (Tab. 3).

Spatial and temporal distributions of ichthyoplankton abundances. The results of the PERMANOVA demonstrated that the density of fish larvae differed significantly between periods ($\text{Pseudo-F}_{1,120} = 2.7559$, $p = 0.0003$) and estuaries ($\text{Pseudo-F}_{1,120} = 2.8767$, $p = 0.0023$), with no differences among zones ($\text{Pseudo-F}_{4,120} = 1.1021$, $p = 0.2596$). The Tubarão estuary had the highest density of larvae than Casqueira estuary, especially in its intermediate zone (Fig. 2). The same pattern was recorded in Casqueira estuary in the intermediate zone. The highest larval density was recorded in the dry period in both estuaries (Fig. 2).

Significant differences in egg density were observed among all factors analysed: estuary (Pseudo-$F_{1,127}$ = 5.3246, p = 0.0002), zone (Pseudo-$F_{4,127}$ = 1.9047, p = 0.0113) and period (Pseudo-$F_{2,127}$ = 11.671, p = 0.0001). The Tubarão River estuary presented the highest density of eggs, and its lower and middle zones differed from its upper zone due to their higher egg densities (Tab. S2). Also a significantly higher density of eggs was observed during the dry season.

TABLE 3 | Number of fish larvae and fish eggs caught in both estuaries (Tubarão and Casqueira rivers) during dry (D) and rainy (R) periods. Zones (Z1 = Lower; Z2 = Middle; Z3 = Upper); EG = Ecological guild (MD = Marine estuarine dependent, ES = Estuarine solely); TL = Total length (min = minimum, max = maximum); Total (%) = % of all species combined.

Family/Taxa				Tubarão						Casqueira					
				Z1		Z2		Z3		Z1		Z2		Z3	
Fish Larvae	**EG**	**TL (min–max)**	**Total (%)**	**D**	**R**	**D**	**R**	**D**	**R**	**D**	**R**	**D**	**R**	**D**	**R**
Engraulidae															
Engraulidae sp.	MD	1.4–4.0	1.52			2									
Anchoa filifera (Fowler, 1915)	MD	4.5–6.3	1.34		1		2								
Anchoa hepsetus (Linnaeus, 1758)	MD	4.5–11.2	0.14						1						
Anchoa januaria (Steindachner, 1879)	MD	3.0–5.7	4.16	3		4									
Lycengraulis grossidens (Spix & Agassiz, 1829)	MD	3.0	0.04							1					
Clupeidae															
Clupeidae sp.	MD	2.2–3.5	0.70			1				1					
Harengula clupeola (Cuvier, 1829)	MD	3.1–5.4	1.35	4	2	2				1					1
Lile piquitinga (Schreiner & Miranda Ribeiro, 1903)	MD	2.2–5.5	23.11	4	6	38	4		2	3		2	1	2	4
Opisthonema oglinum (Lesueur, 1818)	MD	2.8	0.01									1			
Sardinella brasiliensis (Steindachner, 1879)	MD	2.6–5.5	2.90	1	1	2		2		4			1		1
Mugilidae															
Mugil sp.	MD	1.5–2.8	2.37	1		2							2		31
Atherinopsidae															
Atherinella brasiliensis (Quoy & Gaimard, 1825)	ES	1.9–10.4	12.10	5	11	6	13	1	48	3	9	1	25	4	8
Hemiramphidae															
Hyporhamphus unifasciatus (Ranzani, 1841)	MD	5.3–29.2	1.91			1		1	1		1		2		2
Syngnathidae															
Hippocampus reidi Ginsburg, 1933	ES	5.2	0.02											1	
Cosmocampus elucens (Poey, 1868)	ES	4.5–7.0	0.50				4			1	1				1
Serranidae															
Cephalopholis cruentata (Lacepède, 1802)	MD	1.5–3.4	0.57	3		4	1		3					2	3

➡

TABLE 3 | (Continued)

Family/Taxa				Tubarão						Casqueira					
				Z1		Z2		Z3		Z1		Z2		Z3	
Carangidae															
Carangidae sp.	MD	1.7	1.00									1			
Caranx latus Agassiz, 1831	MD	1.3–10.7	16.2		5		13			2			1		
Oligoplites sp.	MD	1.7–1.8	3.97											5	
Selene vomer (Linnaeus, 1758)	MD	1.6	0.02												1
Oligoplites palometa (Cuvier, 1832)	MD	1.2–11.1	4.89				3	1	1				1		1
Oligoplites saurus (Bloch & Schneider, 1801)	MD	1.3–11.6	10.21	3	3	5	8	2	5		5	1	2	4	10
Gerreidae															
Eucinostomus argenteus Baird & Girard, 1855	MD	11.2–12.8	0.01						2						
Sparidae															
Archosargus rhomboidalis (Linnaeus, 1758)	MD	5.3	0.01									1			
Gobiidae															
Ctenogobius boleosoma (Jordan & Gilbert, 1882)	ES	2.0	0.02				1								
Ephippidae															
Chaetodipterus faber (Broussonet, 1782)	MD	7.6	0.02				1								
Achiridae															
Achirus lineatus (Linnaeus, 1758)	ES	1.6–4.5	0.02						1						
Tetraodontidae															
Colomesus psittacus (Bloch & Schneider, 1801)	ES	1.4–2.1	0.17	2						1					
Sphoeroides greeleyi Gilbert, 1900	MD	1.3–1.6	0.01	2											
Sphoeroides testudineus (Linnaeus, 1758)	ES	1.3–2.2	5.43		1	2	2					1			1
Fish Eggs															
Clupeidae			32.43	226	216	92	55	5	7	14	193	1	123	1	81
Engraulidae			61.33	358	6	559	2	301	2	23	181	1	43		38
Achiridae			2.65	1	1	3	44	2			32		6	2	2
Mugilidae			1.73	12	13	11	2	3			5		8	2	3
Carangidae			1.86	11	10	16	3	2	1	3	15	1	9	3	8

Environmental influences on ichthyoplankton. The relationship between ichthyoplankton and environmental variables in both estuaries was analyzed with multiple regression analysis (DistLM). The marginal test indicated that rainfall was the key environmental factor affecting ichthyoplankton assemblages in both estuaries (Tab. 4). The results are depicted in distance-based redundancy analyses biplots and showed a temporal abundance pattern (Fig. 3).

In the case of the samples from the Tubarão estuary, the first two axes of the dbRDA plot of fish larvae explained 59.7% of the total variation (Fig. 3A). The marginal test resulting from the linear model based on distance (DistLM) indicated that fish larvae in the Tubarão estuary have a significant relationship with water temperature, depth

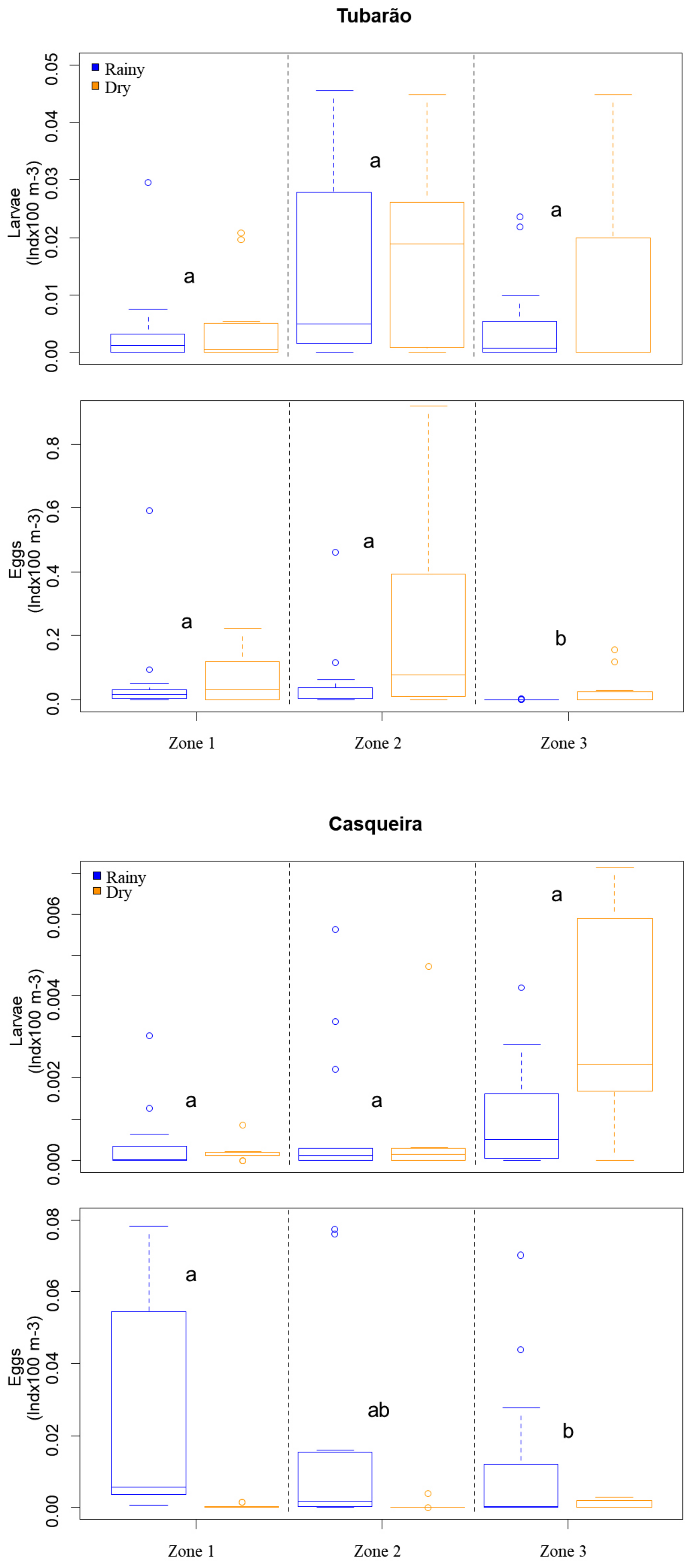

FIGURE 2 | Box Plots of larvae (Ind * 100^{-3}) and egg (Ind * 100^{-3}) densities in three zones of each of estuaries (Tubarão and Casqueira rivers) during their dry and rainy periods. Different letters indicate significant differences (P < 0.05).

and rainfall (Tab. 4). When the factors were considered alone, rainfall explained 4.98%, depth explained 2.87% and water temperature explained 2.49% of the variation in the model. For fish eggs, the two axes of the dbRDA explained 88.25% of the observed variability (Fig. 3A); marginal tests resulting from DISTLM analysis showed that fish eggs presented significant relationships with rainfall (23%), salinity (5.54%) and transparency (5.49%) (Tab. 4).

The analysis of fish larvae in the Casqueira estuary by dbRDA explained 48.8% of the total variation (Fig. 3B). According to the DistLM marginal tests, only rainfall showed a significant relationship with the model and explained the highest proportion of variation (4.31%). On the other hand, the first two axes of the fitted model ordination explained 72.32% of the fitted variation of the structure of the fish eggs in the Casqueira Estuary (Fig. 3B). Marginal tests resulting from DISTLM analysis showed that fish eggs had significant relationships with rainfall (6.10%), channel width (4.90%) and water temperature (3.24%) (Tab. 4).

Larval development. Larvae in different developmental stages were present in different proportions between areas and estuaries. In the Tubarão estuary, vitelline larval and flexion larvae were most abundant in Z1 and Z2 in the dry period, while post-flexion larvae accounted for 60% of the total number of fish larvae collected in Z3 in the same period. Flexion and post-flexion larvae dominated in both estuaries during the rainy period. In the Casqueira estuary, it was possible to observe some substitution of developmental stages between periods, where species in the vitelline larval and flexion stages, present in both estuaries in the dry season, were replaced by a larger number of individuals in the flexion and post-flexion stages in the rainy season (Fig. 4).

The proportions of the development stages also changed between species. In the Tubarão estuary, *L. piquitinga*, a marine-dependent guild representative, was the most representative species for the overall percentage of the vitelline larval stage, while *A. brasiliensis*, representative of the solely-estuarine guild, was the species with the most larvae in the post-flexion stage in both estuaries (Fig. 5).

TABLE 4 | DistLM marginal test showing the influence of environmental variables on the estuarine ichthyoplankton (Tubarão and Casqueira river estuaries, Semiarid Northeastern Brazilian coast). P-values in bold are significant. Prop. = Proportion (%).

	Tubarão						Casqueira					
	Eggs			Larvae			Eggs			Larvae		
Variables	Pseudo-F	P	Prop. (%)	Pseudo-F	P	Prop. (%)	Pseudo-F	P	Prop. (%)	Pseudo-F	P	Prop. (%)
Mouth Distance (m)	0.58	0.71	0.76	0.97	0.46	1.43	1.13	0.33	1.89	1.04	0.37	2.27
Channel Width (m)	0.61	0.69	0.79	0.91	0.53	1.34	3.04	**0.01**	4.90	1.58	0.11	3.39
Water temperature (°C)	1.54	0.18	1.98	1.72	0.05	2.50	1.98	0.08	3.24	0.73	0.70	1.60
Transparency (m)	4.42	**0.00**	5.50	1.37	0.15	2.00	1.00	0.42	1.66	1.46	0.14	3.15
Depth (m)	1.08	0.36	1.40	1.98	**0.02**	2.87	1.02	0.40	1.70	1.00	0.42	2.18
Salinity	4.46	**0.00**	5.54	1.10	0.34	1.61	2.06	0.07	3.37	1.39	0.16	2.99
Chlorophyll a (µg/l)	1.28	0.26	1.66	1.16	0.28	1.70	1.88	0.10	3.08	0.86	0.54	1.88
Rainfall (mm)	22.77	**0.00**	23.06	3.52	**0.00**	4.99	3.83	**0.00**	6.10	2.02	**0.04**	4.31

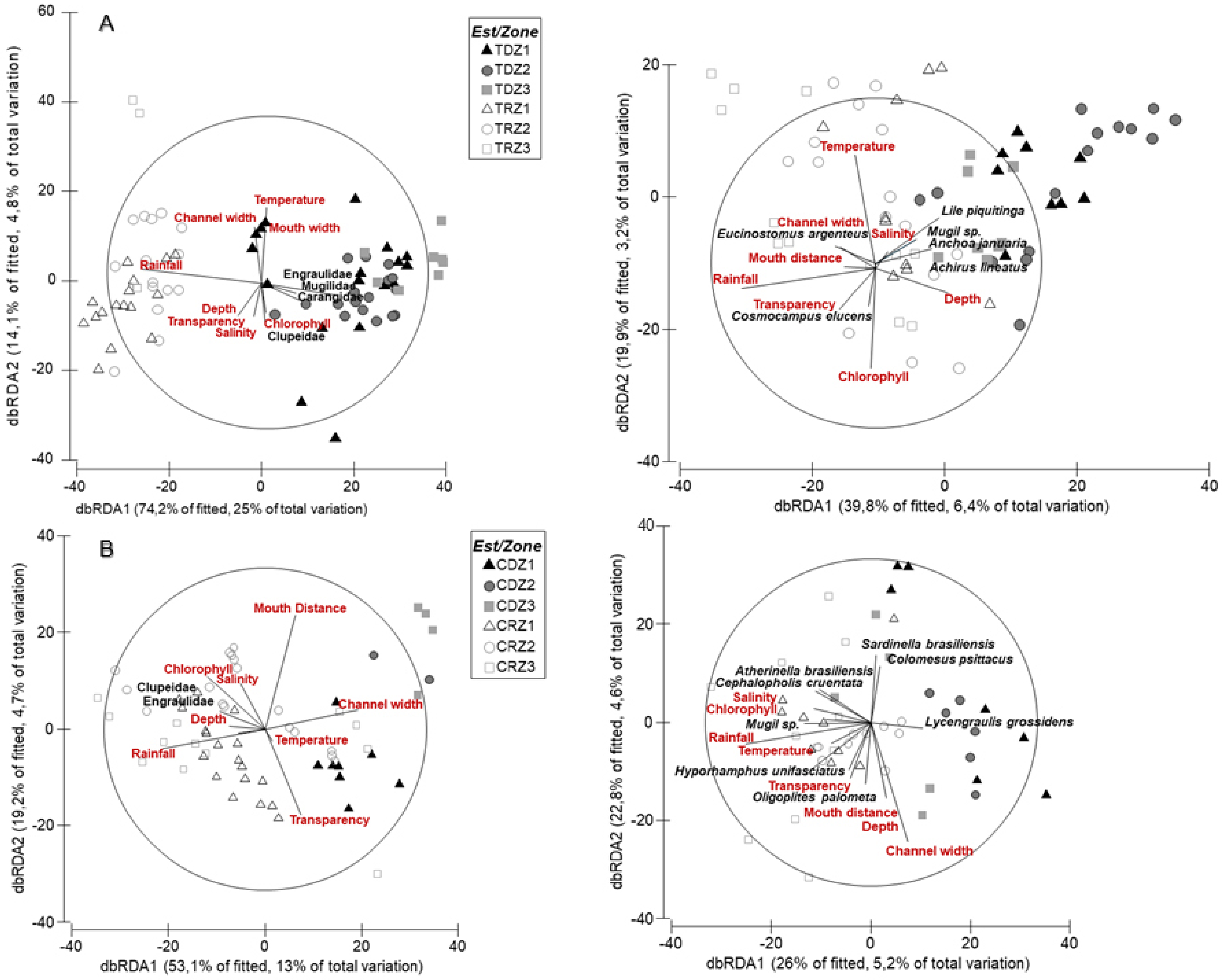

FIGURE 3 | Distance-based redundancy analysis (dbRDA) showing distribution of eggs and larvae by influence of environmental parameters on **A.** Tubarão (T) and **B.** Casqueira river estuaries (C) during seasons (D = dry and R = rainy) and zones (Z1, Z2, Z3).

In the Casqueira River estuary, there was a pattern of replacement of developmental stages similar to that found in the Tubarão River estuary, where the highest percentages of larvae in the dry period are in the vitelline larval and pre-flexion stages, and they are replaced by larvae in the flexion and post-flexion stages in the rainy season. In this estuary, representatives of the Clupeidae family contributed the most to the highest percentage of vitelline larval in the dry season and were replaced by *O. saurus*, a species that dominated the vitelline larval stage in the rainy season. In turn, *A. brasiliensis* was the most representative species for the most developed stages (flexion and post-flexion), especially in the rainy season (Fig. 6). This leads to the observation that, in this environment, the earlier stages of development are mostly represented by marine estuarine-dependent species, while more the developed stages are represented by species belonging to the solely-estuarine guild.

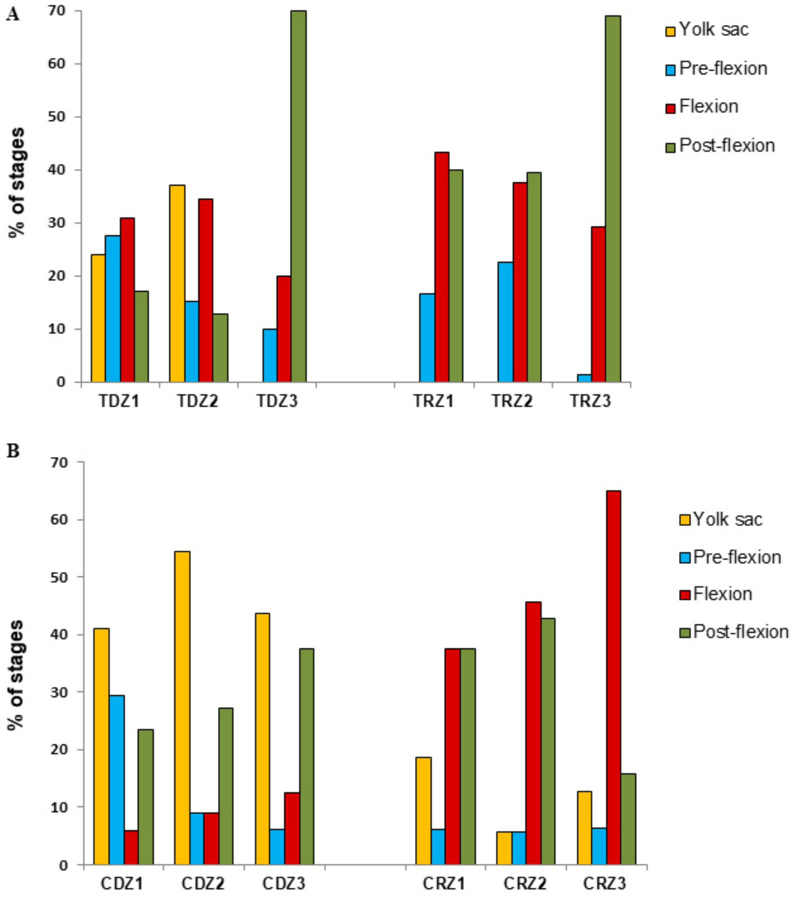

FIGURE 4 | **A.** Percentage of larval stages of ichthyoplankton in each of zones of Tubarão River estuary (Z1: Lower, Z2: Middle, Z3: Upper) in their periods of dry (TD) and rainy (TR); **B.** Percentage of ichthyoplankton larval stages in each of Casqueira River estuary zones (Z1: Lower, Z2: Middle, Z3: Upper) during their dry (CD) and rainy (CR) periods.

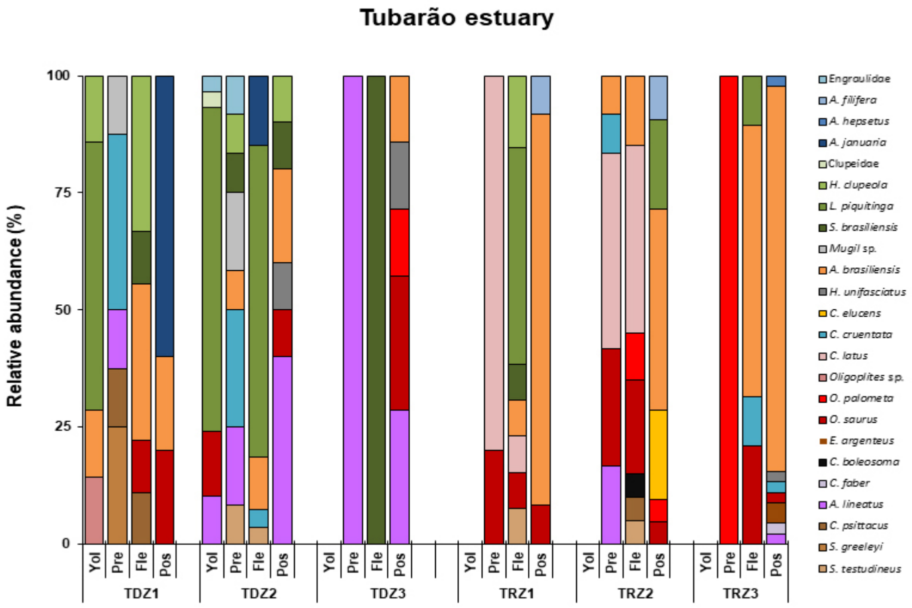

FIGURE 5 | Percentage contribution of species in Tubarão River estuary (Z1: Lower, Z2: Middle, Z3: Upper) in their periods of dry (TD) and rainy (TR). Yol = Vitelline larval; Pre = Pre-flexion; Fle = Flexion; Pos = Post-flexion.

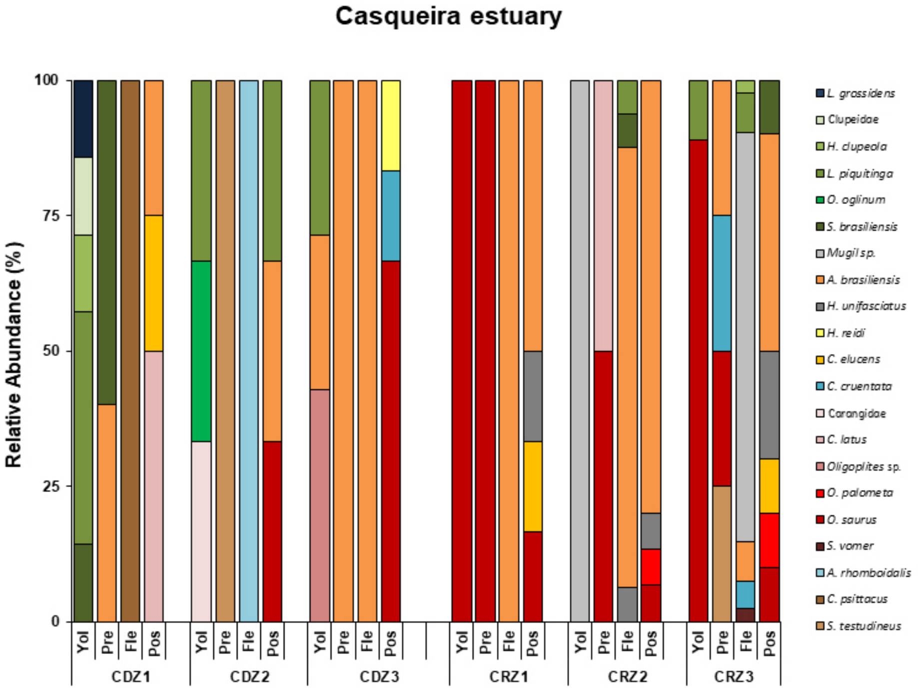

FIGURE 6 | Percentage contribution of species in Casqueira River estuary (Z1: Lower, Z2: Middle, Z3: Upper) zones in their periods of dry (CD) and rainy (CR). Yol = Vitelline larval; Pre = Preflexion; Fle = Flexion; Pos = Postflexion.

DISCUSSION

In both estuaries, the highest salinities change gradually from lower to upper zone creating a complex environmental gradient, such that regulate the ichthyoplankton structure. Although it is not well known to ichthyoplankton abundance with variations linked to landscape characteristics, in our study spatial variations of larval fish stages were also related with channel width and distance of estuary mouth. Thus, a significant increase in abundance of earlier stages of development of fishes was recorded from the lower to the upper zone of these estuaries and may be related to spatial gradient, as has been reported for others estuaries by Barletta-Bergan *et al.* (2005), Costalago *et al.* (2018), and Ooi, Chong (2011). This was evident when a greater abundance was registered near the mouth zone, which decreased noticeably towards the upper zone of estuaries.

The results of our study show that the abundance and composition of estuarine early life stages of marine fishes in both estuaries were represented by a larger number of marine estuarine-dependent species, suggesting continuous inputs of larvae and eggs in these systems. The increased density of larvae of the Carangidae and Clupeidae families in our results, which are typically estuarine-dependent species, supports this hypothesis. In agreement, Costalago *et al.* (2018) concluded that the importance of estuaries as fish nurseries may result from the availability of a wide range of habitats including seagrass meadows and mangrove forests, and higher water temperatures. Indeed, many of these larvae benefit from the hypersaline estuaries on the semiarid coast of Brazil, probably as a response to higher habitat quality, whose characteristics are favorable for their development and to maximize their fitness. For example, Sales *et al.* (2018) registered the presence of structured habitats along the salinity gradient in the Tubarão estuary, such as mangroves or seagrass beds, which necessarily supported this premise because provide abundant food resources and refuge against predators. This confirms the importance of these shallow habitats as nursery habitats for the early life history of marine coastal fishes (Lima *et al*., 2018; Sales *et al*., 2018; Silva *et al*., 2018).

A similar conclusion may be drawn for species belonging to the solely estuarine guild (ES), indicating that these species developed adaptations and specialized their physiological systems for the hypersaline environment (euryhalinity – broad halotolerance and halohabitat distribution) (Ooi, Chong, 2011). Certain members of this group, such as *A. brasiliensis* and *A. lineatus*, are typically found in various estuaries along with the Brazilian coast (positive estuaries) (Barletta-Bergan *et al*., 2002; Katsuragawa *et al*., 2011; Oliveira, Pessanha, 2014), but exhibited a similar trend in these hypersaline environments (Sales *et al*., 2018).

In tropical regions, the inter-seasonal variability of environmental factors influences the larval fish distribution and abundance in estuaries (Pritchett, Pyron, 2012; Eick, Thiel, 2014; Solari *et al*., 2015). Rainfall is often identified as an important factor in determining estuarine ichthyoplankton structure (Kantoussan *et al*., 2012). Our results are in accordance with this hypothesis. Rainfall directly influences the reproduction of species and consequently the recruitment of ichthyoplankton in tropical estuaries (Barletta-Bergan *et al*., 2005). Strong rainfall-related patterns were also found with regard to abundance in this semi-arid environment despite the low rainfall (2.5–60 mm) in the region. This statement is supported by the results of the dbRDA. The main seasonal changes in the ichthyoplankton structure were due to variations in density of *L. piquitinga*, *A. lineatus*, *A. brasiliensis*, and *C. latus*, which probably reflects recruitment success in these systems.

Similarly, the fluctuations that the larvae life stages tended to be correlated with changes in rainfall. Hence, abundant and numerically dominated larvae in flexion and post-flexion stages probably reflect the different times of recruitment of different species and could be associated with the changes in rainfall regimes. In the current study, the largest occurrences of *C. cruentata*, *C. latus*, *O. palometa*, and *O. saurus* in flexion stage coincided with the rainy season and seemed to confirm the greater occurrence of these species in the studied area. In addition, the presence of larvae can be indicative of recent adult spawning in the area as well as the transport and retention of eggs and larvae in estuaries (Katsuragawa, Matsuura, 1992). Representatives of the Carangidae family are thought to spawn in the neritic zone of the tropical northeastern Brazilian coast, but their larvae return to nursery grounds located in shallow waters (Souza, Junior, 2019). The most representative Carangid larvae were more abundant during the rainy period along the Brazilian coastal shelf area (Campos *et al*., 2010). Most of the groups found to reproduce in coastal areas near estuaries were Carangidae and Serranidae, which were also found in our study. Other studies conducted in tropical estuaries highlight the importance of these environments as places of dispersal and growth and consequently their importance for maintaining populations and fish stocks through recruitment processes (Lima, Barletta, 2016; Silva *et al*., 2018). These results, therefore, reinforce the importance of these hypersaline environments as nursery areas for fishes, especially for adults who live in the estuary and have coastal-marine origins.

In addition, based on the high numbers of Engraulidae and Clupeidae eggs in our study it would be easy to conclude recent spawning activity near the coast or in the estuaries. Most Clupeiformes (encompassing the families Clupeidae and Engraulidae) exhibit a long spawning period throughout the year and are therefore able to maintain their populations in coastal marine ecosystems (Trindade-Santos, Freire, 2015; Lopes *et al*., 2018). Teixeira *et al.* (2014), in their work highlighting the commercial importance of Atlantic thread herring (*Opisthonema oglinum* (Lesueur, 1818)) in northeastern Brazil, suggested that the spawning of this group in coastal waters occurs mainly in the dry season. In the case of representatives of the Engraulidae family, Soares *et al.* (2009) and Araújo *et al.* (2008) showed that August to April was the main spawning period of representatives of this family. The transport of Engraulidae and Clupeidae eggs from the marine environment into the studied estuaries is presumably related to the environmental dynamics of the region. The mesotidal semi-diurnal tidal regime and the strong influence of wind on the physical and hydrodynamic characteristics of circulation in these estuaries affect the recruitment process (Vital, 2008).

Although not directly demonstrated here, it seems likely that salinity either directly or indirectly affects the distribution of ichthyoplankton in both estuaries, because our results indicate that the decrease in abundance is associated with the higher salinities in the upper zone (Zone 3). Salinity has a strong effect on larval development and survival since it is correlated with the osmoregulatory balance, influencing stress and mortality rates when larvae are subjected to a saline gradient (Schmitt, Osenberg, 1995). During this phase of the life cycle, many larvae do not yet have fully developed gills or kidneys, which are considered important osmoregulatory and adaptive organs in fish. The larvae are therefore more vulnerable to more saline environments, as the amount of energy required to maintain osmoregulatory balance is greater (Sampaio, Bianchini, 2002; Oliveira, Pessanha, 2014).

Our modelling also suggests the possibility that fish larvae and eggs were significantly affected by changes in physical variables and interactions with geomorphological characteristics. The multivariate analyses revealed greater larvae and egg abundances in estuaries with higher mean channel width and depth. Notably, these characteristics have previously been identified as predictors of richness and density in estuaries because they are indicative of different strategies that guarantee egg and larvae retention in these environments (Lima *et al*., 2015; Rosa *et al*., 2016). Numerous field and modeling studies also showed that physical processes alone were insufficient to explain or predict observed spatial distribution patterns (Xavier *et al*., 2012; Pasquaud *et al*., 2015; Vasconcelos *et al*., 2015). Sloterdijk *et al.* (2017) indicated that the variability in the composition in hypersaline estuaries in Senegal was also driven by different combinations of environmental variables, giving rise to intra- and inter-estuary differences, an idea that corroborates the variations found in this study. In the case of channel width, Sales *et al.* (2018) suggested that a high abundance of fish larvae was related to an important feature of the coastal ecosystem: a permanent opening in the lower zone of the estuary, which allows the recruitment of fish larvae, mainly marine species, which spawn on the continental shelf. Other studies have also indicated a higher density of eggs and larvae in deeper areas of estuaries, as in the case of the subtropical estuary of Bahia Blanca (Uruguay) (Hoffmeyer *et al*., 2009), and in the estuarine part of Bahia de Todos Santos (Brazil), located in a tropical area (Katsuragawa *et al*., 2011).

For the Casqueira estuary, the dbRDA ordination diagram indicated a wide dispersion of samples from the upper zone compared to those from other zones, resulting from the greater abundance of larvae recorded at this site. In this case, the channel width predictor variable presented the lowest correlations with samples of this zone, according to the results of the DISTLM marginal test. The upper area of the Casqueira estuary is heterogeneous due to the mangrove roots in an area where the channel becomes narrower, which favors the retention of larvae in these environments. This supports the hypothesis that mangroves act as nurseries for species, associated with the direct relationship between the number of different habitats and food resources to be explored by larvae. It is important to highlight that the Casqueira estuary has transparent waters that expose larvae to a higher predation rate, and in the more structured environments in the upper part of the estuary, these areas would be considered predator refuge areas. Santos *et al.* (2017) also reported this behavior in ichthyoplankton in Saint Mark's Bay (MA), where larvae used the innermost part of the estuary due to the greater protection provided by the less turbid waters in that ecosystem. Thus, it is noted that the particularities of each environment are also important parameters to consider when assessing patterns of composition and abundance (Pasquaud *et al*., 2015; Vasconcelos *et al*., 2015).

The highest densities of *Eucinostomus argenteus* Baird & Girard, 1855, *L. piquitinga*, and *A. januaria* larvae were recorded in the middle and upper zones of the Tubarão estuary. These findings were likely influenced by the low depth and high water temperature reported in these zones, which acted as an environmental filter. These conditions influenced the density of these larvae in the area (especially those at the vitelline larval stage), which were not present in the upper zone of this estuary. The daily development and mortality rates of fish larvae generally increase with increasing temperatures (Cassemiro, Diniz-Filho, 2010). Changes in environmental conditions influence ecological filtering by altering the behavior, metabolism and distribution of eggs and larvae (Schmitt, Osenberg, 1995). For example, a study on the development of *Lates calcarifer* (Bloch, 1790) indicated that temperatures higher than 26 °C influenced the development and increased the mortality rate of their larvae (Thépot, Jerry, 2015). Furthermore, Sales *et al.* (2018) correlated the high abundance of juvenile fishes with the lowest depth in the Tubarão estuary.

Our results showed the importance of annual rainfall and its seasonality for the occurrence of ichthyoplankton species in hypersaline environments, and the influence of low rainfall was often correlated with temperature and other environmental factors such as transparency and depth. These results showed the high sensitivity of ichthyoplankton to environmental variations, which demonstrates their potential as a tool for assessing the effects of climate change and anthropic pressures, especially in semiarid regions. Recently, Costalago *et al.* (2018) evaluated the effects of several droughts on ichthyoplankton and their recruitment success. They found that during a drought period of approximately two years, fish larvae become significantly more abundant than they were before the drought occurred. Moreover, the presence of the early life stages of typically marine species in this environment suggests that the hypersaline environments provide important nursery areas and play an essential role for coastal fish species. The hypersaline environments of the semiarid northeastern Brazilian coast may support the success of fish recruitment processes and contribute to the adult stocks of economically valuable fish species.

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Not applicable.

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The authors declare no competing interests.

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