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Ichthyoplankton distribution set by different environments shapes in a coastal freshwater lagoon

Distribuição do ictioplâncton determinada por diferentes ambientes em uma lagoa costeira de água doce

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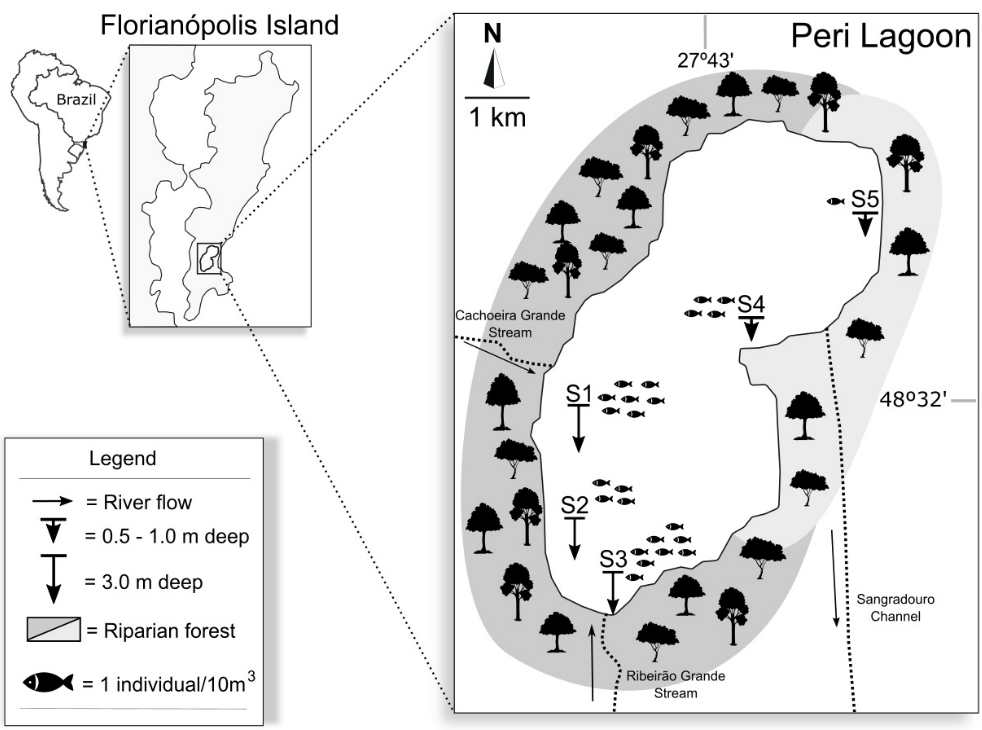
Abstract: Aim: This study aimed to evaluate the spatial and temporal distribution of ichthyoplankton in the Peri Lagoon, a coastal freshwater lagoon in Brazil. **Methods:** Ichthyoplankton samples were collected every two months from June 2008 to April 2010 with 500 µm conical-cylindrical planktonic nets at five sampling stations. **Results:** In total, 181 fish eggs and 1,315 larvae, representing estuarine and freshwater species, were captured. The most representative species were *Awaous tajasica*, *Ctenogobius* sp1, and *Platanichthys platana*. Significant differences were found in temporal egg distribution and larval spatiotemporal distribution (Kruskal-Wallis test, $p < 0.05$). Eggs were predominantly captured during the autumn, winter, and spring Neotropical seasons. Geospatial analysis demonstrated spatial segregation in the distribution of larval assemblages, with higher abundances in areas adjacent to riparian forests, following stream mouths, and deeper areas with rocky substrates. **Conclusions:** Proximity to streams and areas surrounded by dense forests is crucial for the spawning and development of fish species in the Peri Lagoon. The findings of this study provide valuable insights into the conservation of the ichthyofauna in this unique environment.

Keywords: fish; reproduction; Peri Lagoon; freshwater environment; abiotic factors.

Resumo: Objetivo: Este estudo teve como objetivo avaliar a distribuição espacial e temporal do ictioplâncton na lagoa do Peri, uma lagoa costeira de água doce no Brasil. **Métodos:** O ictioplâncton foi coletado bimestralmente de junho de 2008 a abril de 2010 com redes cônico-cilíndricas planctônicas de 500 µm em cinco estações de amostragem. **Resultados:** Neste estudo, foram capturados 181 ovos e 1.316 larvas de peixes de espécies estuarinas e de água doce. As espécies mais representativas foram *Awaous tajasica*, *Ctenogobius* sp1 e *Platanichthys platana*. O teste de Kruskal-Wallis (H) indicou que existem diferenças significativas na distribuição temporal dos ovos e na distribuição espaço-temporal das larvas (p<0,05). Em geral, os ovos foram capturados durante as estações de outono, inverno e primavera na Região Neotropical. A relevância do fator geoespacial mostrou segregação espacial na assembleia de larvas. As larvas foram capturadas em ambientes cercados por mata ciliar, próximo à foz de córregos, em áreas mais profundas com fundo rochoso. **Conclusões:** Regiões próximas a córregos e cercadas por florestas densas parecem ser essenciais para a desova e desenvolvimento de espécies de peixes na lagoa do Peri. Este estudo pode orientar importantes diretrizes ambientais para a preservação da ictiofauna desse ambiente intocado e particular.

Palavras-chave: peixes; reprodução; Lagoa do Peri; ambiente de água doce; fatores abióticos.

Graphical Abstract



1. Introduction

Coastal lagoons are an important part of estuarine complexes, and are essential for supporting the life cycles of marine, estuarine, and anadromous fish species (Potter & Hyndes, 1999; Rosa et al., 2016). These ecosystems are relevant for fish recruitment because of their unique characteristics, including high productivity, abundant food resources, refuge from predators, and optimal temperature conditions for the growth and development of larval and juvenile fish (Bruno et al., 2013; Machado et al., 2011). The physical-chemical parameters of coastal lagoons can exhibit gradients depending on the geographical position, hydrological balance, sea connection (Machado et al., 2021), and other factors, including geospatial variables such as land use practices, depth, riparian or underwater vegetation, presence of streams, and biotope diversity, which can all significantly affect the aquatic biota within them.

Most studies addressing the dynamics of ichthyoplankton have focused on mangroves, bays, continental shelves, and rivers, while limited attention has been paid to coastal lagoons (Castro et al., 2005). Studies of coastal lagoons have predominantly focused on juvenile and adult fish populations, whereas studies examining the early ontogenetic stages of fish remain relatively scarce (Bruno et al., 2014, 2018; Ferreira et al., 2017; Lopes et al., 2018; Pérez-Ruzafa et al., 2004).

Understanding the main environmental components affecting the structure and distribution of ichthyoplankton communities remains challenging (Pérez-Ruzafa et al., 2004; Rodriguez, 2019). Understanding the spatiotemporal variations in ichthyoplankton, and the physicochemical parameters and geospatial variables affecting them in habitats such as coastal lagoons, are essential for assessing the potential impacts of environmental changes and human perturbations on fish assemblages, and managing critical habitats for the conservation of biodiversity (Franco et al., 2019).

Studies conducted on the continental waters of Brazil have revealed spatiotemporal patterns in the abundance, distribution, and structure of ichthyoplankton. These patterns are influenced by various physical factors, including rainfall (Barletta-Bergan et al., 2002), water temperature (McKenna Junior et al., 2008; Mulbert & Weiss, 1991; Pepin & Helbig, 2012), salinity (Franco et al., 2019), pH (Chagas & Suzuki, 2005), as well as geospatial factors such as depth, sandy or rocky substrate characteristics, and riparian vegetation. These parameters indirectly impact the survival of ichthyoplankton by altering, among other things, food availability, water transparency, refuge availability, thermal suitability, and metabolic processes.

Among the coastal lagoons in Brazil, Peri Lagoon is the largest freshwater body by surface area on Santa Catarina Island (Santos et al., 1989). Limited environmental studies have been conducted on this lagoon since the 1970s, resulting in significant gaps in our understanding of its functions (Teive et al., 2008). Regarding the ichthyofauna, only a few studies have focused on adult animals, and even fewer have investigated the distribution of fish eggs and larvae in this lagoon (Ferreira et al., 2017; Lopes et al., 2018).

Considering the studies conducted by Sanvicente-Añorve et al. (2002), Avedaño-Ibarra et al. (2004), and Macedo-Soares et al. (2009) on other coastal lagoons, we hypothesized that the distribution of fish eggs and larvae in the Peri Lagoon would exhibit spatial and temporal variability. This variability would likely be influenced by physicochemical factors, particularly water temperature during the fish reproductive period, as well as geospatial variables such as depth, forest cover, and proximity to streams, which collectively create a mosaic of conditions. The present study had the following objectives: 1) to identify the taxonomic composition of fish larvae, 2) to determine the spatiotemporal distribution of the ichthyoplankton, and 3) to elucidate the relationship between physicochemical and geospatial variables and ichthyoplankton capture.

2. Material and Methods

2.1. Study area

Peri Lagoon is located in the southern parts of Santa Catarina Island (Florianópolis City, Santa Catarina State, Brazil). It is located between coordinates 27°41’28” – 27°45’38”S; 48°31’11”-48°33’38”W. The lagoon covers an area of 5.07 km^2, with a maximum depth of approximately 11 m and an average depth of 4 m (Peralta-Maraver et al., 2017). Owing to its elevation of 3 m above sea level, tidal effects do not directly influence Peri Lagoon. Atlantic rainforest surrounds the lagoon area (Hennemann & Petrucio, 2011). The water column in the lagoon is determined by rainfall in the watershed (Teive et al., 2008) and the drainage of two main streams, Cachoeira Grande and Ribeirão Grande (Peralta-Maraver et al., 2017). The lagoon flows towards the sea through a small stream, the Sangradouro Channel, extending for 3.7 km (Elmahdy et al., 2016). The salinity of the water in the lagoon is 0 ‰, as the influence of oceanic waters is limited to the mouth of the Sangradouro channel and does not reach the main body of the lagoon.

2.2. Data collecting and processing

Sampling was conducted every two months from June 2008 to April 2010 at five sampling stations, each with distinct characteristics. A preliminary assessment was conducted before the sampling period to select sampling stations with varying attributes, including depth, vegetation cover, and distance from the main inlets.

Sampling stations S1, S2, and S3 were characterized by their proximity to the Atlantic Forest, with a gravel substrate at the bottom, close to streams that flow into the lagoon, and greater depths (3.0 meters). Sampling stations S4 and S5 were distinguished by their sandy bottoms, lower organic matter concentrations, and shallow water (0.5 – 1.0 meter) inhabited by aquatic weeds (*Scirpus californicus*) (Figure 1).

Planktonic eggs and larvae were sampled every 24 h on two consecutive days at night after 21:00 (SISBIO Permanent license for collecting animal biological material # 17240-1). Two cylindrical conical plankton nets (500 μm mesh) with a mouth area of 0.11 m^2 were equipped with mechanical flowmeters (General Oceanics 2030R). A low-speed boat dragged the sampling nets to the surface of the water for 10 min.

The captured ichthyoplankton were fixed in a 4.0% formaldehyde solution buffered with calcium

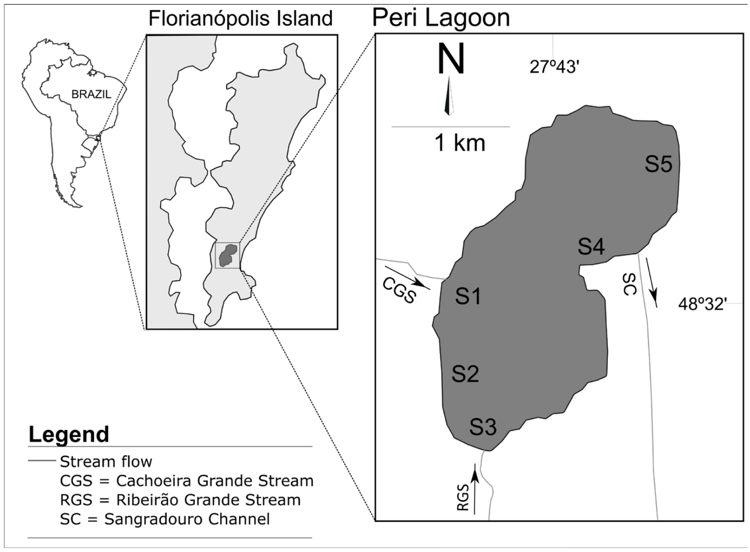


Figure 1. Study area and stations sampled between June 2008 and April 2010 in Peri Lagoon (Santa Catarina state, Brazil).

carbonate. In the laboratory, the fish eggs and larvae were separated from the debris and other organisms, and quantified. Following specialized literature, larvae were identified to the lowest possible taxonomic level (Nakatani et al., 2001; Richards, 2005). The accepted species names were cross-referenced using FishBase (Froese & Pauly, 2022) and Eschmeyer's catalog of fishes (Fricke et al., 2022). The abundance of larvae and eggs was standardized to a volume of 10 m^3 of filtered water, according to Tanaka (1973) and modified by Nakatani et al. (2001).

We characterized the habitat conditions at each sampling station by measuring limnological, land cover, and spatial and geomorphological variables. The following limnological variables were recorded during each sampling event: pH, electrical conductivity (uS.cm^{-1}), dissolved oxygen concentration (mg.l^{-1}), and water temperature (^{o}C). These measurements were performed on a water surface using a multiparameter device (WTW 350I). The water clarity (cm) was assessed using a Secchi disk. All limnological variables were measured prior to ichthyoplankton collection. The precipitation data (mm) were obtained from the Agricultural Research and Rural Extension Company of Santa Catarina (EPAGRI). In addition, the following geomorphological descriptors were recorded for each sampling station: depth, distance from the nearest inlet, and riparian vegetation cover. The distance of each inlet `from the nearest sampling station was determined using georeferenced satellite images from Google Earth Pro (Google, Menlo Park, California, USA). Finally, the percentage of the riparian vegetation at each site was determined. For this calculation, an area of 0.25 km^2 (0.5 km long and 0.5 km wide) was considered along the margin of each sampling station. The Fragstats package (v. 4.0) was used to perform this analysis.

2.3. Statistical analysis

To assess the spatiotemporal variations in the eggs and larvae of the most abundant species between sites and months, we employed the non-parametric Kruskal-Wallis test (H). When significant, Dunn's test was used for *post-hoc* analysis. The decision to use non-parametric tests was based on the data's departure from normality (as determined by the Shapiro-Wilk test) and the violation of homoscedasticity assumptions (as indicated by the Levene test). These tests were chosen instead of parametric Analysis of Variance (ANOVA).

We employed variation partitioning to examine the relative contributions of the environmental, temporal, and spatial variables. This method allows for the calculation of pure and shared components of variation from different sets of explanatory variables (Anderson & Cribble, 1998). We used three sets of variables for this analysis: a) limnological variables: water temperature, dissolved oxygen concentration, pH, electrical conductivity, water transparency, and precipitation; b) temporal variables: February, April, June, August, October, and December, including six binary variables, and a sampling year variable for year one (June 2008 – April 2009) and year two (June 2009 – April 2010), incorporated as two binary variables; and c) geospatial variables: water depth, riparian forest cover, and distance from the nearest inlet (Table 1).

Analysis was conducted using a two-step approach. First, Canonical Correspondence Analyses (CCA) were performed to examine the relationship between the species/genera and each set of explanatory variables (limnological, temporal, and geospatial), and to select the primary variables. The Monte Carlo procedure (999 permutations) was used to test the significance of each variable, and the forward method was applied to reduce multicollinearity in the limnological and geospatial datasets. Second, all the significant variables selected in the CCA analysis were combined to run a Partial Canonical Correspondence Analysis (pCCA) to investigate the correlation between the ichthyoplankton assemblage structure and the main variables selected (Borcard et al., 1992). This approach is valuable for reducing possible predictors, simplifying the investigation, and restricting the analyses of the primary factors of environmental variation. The ratio between the sum of all canonical eigenvalues and the total inertia describes the percentage of total variation explained (TVE).

To depict the spatiotemporal variation in the ichthyoplankton structure, we conducted a Non-metric Multidimensional Scaling Analysis (nMDS) to ordinate samples based on their species abundance and composition.

A Multiple Response Permutation Procedure (MRPP) was used to verify the consistency, significance, and homogeneity among the groups (sampling stations and months). Statistical significance was implied at $p < 0.05$.

3. Results

3.1. Taxonomic groups

We captured 181 eggs and 1.315 larvae from 240 samples throughout the study. The larval assemblage consisted of estuarine and freshwater taxa from four orders, five families, four species, and three species that could only be identified to the genus level. Among these, the most encountered species, based on their relative numerical frequency, were *Awaous tajasica* (Lichtenstein, 1822) (32.2%), *Platanichthys platana* (Regan, 1917) (30.6%), and *Ctenogobius* sp1 (25.2%). These species were found across all sampling stations and months, except *A. tajasica*, which was not collected in August 2009. A small proportion (1.7%) of the total fish larvae were damaged and could not be identified to the species level (Table 2).

3.2. Spatiotemporal distribution

We only found significant differences in the temporal distribution of eggs (Kruskall-Wallis $H_{11} = 111.1$, $p < 0.05$). August 2008 exhibited a significantly higher density of eggs than the other months ($p < 0.05$). Eggs were captured in August 2008, October 2008, 2009, and April 2009, whereas no eggs were captured in the remaining months (Figure 2A).

Larvae were captured at all sampling stations, and their distributions were significantly different ($H_4 = 18.5$, $p < 0.05$). Sampling stations S1, S2, and S3 had significantly higher larval numbers than stations S4 and S5 ($p < 0.05$; Figure 2B). Temporally, larvae were captured in all months, and their distribution exhibited significant differences (H=62.2, DF=11, $p < 0.05$). August 2008 and October 2009 had a higher density of larvae than the other months (Figure 2C).

Temporal variation was significantly different for *A. tajasica* (H = 49.0, DF=11, $p < 0.05$). February 2009, 2010, and April and October 2010 showed significant differences compared to the other months, and larvae of *A. tajasica* were absent only in August 2009 ($p < 0.05$; Figure 3A).

Significant differences between the months were also observed for *Ctenogobius* sp1 larvae (H = 53.5, DF = 11, $p < 0.05$). June and August 2008 and April, June, and October 2009 had significantly higher numbers than the other months ($p < 0.05$). *Ctenogobius* sp1 was captured in all months (Figure 3B).

The Kruskal-Wallis test for *P. platana* larvae indicated significant differences in both spatial (H = 13.5, DF = 4, $p < 0.05$) and temporal (H = 42.9, DF = 11, $p < 0.05$) distributions. S1, S4, and S5 differed significantly from S2 and S3 ($p < 0.05$). Temporally, December 2008, 2009, and June and August 2009 had significantly higher numbers compared to the other months

Table 1. Geospatial variables for each sampling station from June 2008 to April 2010 in Peri Lagoon (Santa Catarina state, Brazil).

Sampling station	Depth (m)	Forest cover (%)	Distance affluent (m)
S1	3.0	100	180
S2	3.0	98	350
S3	3.0	94	100
S4	0.5 -1.0	79	1,400
S5	0.5 -1.0	68	2,500

Table 2. Relative numerical frequency (NF %) of taxonomic groups and average monthly and spatial density (individuals.10m^{-3}) of fish larvae from June 2008 to April 2010 in Peri Lagoon (Santa Catarina state, Brazil). Bold values indicate taxa with NF > 25.0%. Total: Sum of average spatial density of fish larvae. Jun: June; Aug: August; Oct: October; Dec: December; Feb: February; Apr: April.

Taxonomic group	NF %	Months												Sampling stations					
		2008				2009						2010		S1	S2	S3	S4	S5	Total
		Jun	Aug	Oct	Dec	Feb	Apr	Jun	Aug	Oct	Dec	Feb	Apr						
ATHERINIFORMES																			
Atherinopsidae																			
Odontesthes argentinensis (Valenciennes, 1835)	0.7	0.2	0.7					0.1						0.01	0.5	0.3		0.1	**0.9**
CHARACIFORMES																			
Characidae																			
Astyanax spp.	5.3	0.1		1.3	0.3			0.1		6.1		2.1		1.7	1.8	3.7	1.4	1.3	**9.9**
CLUPEIFORMES																			
Clupeidae																			
Platanichthys platana (Regan, 1917)	**30.6**	7.5	19.3	14.0	1.7	2.6	3.5	1.0	0.6	3.9	0.8	12.6	23.57	30.4	14.5	34.0	9.6	2.7	**91.2**
Engraulidae																			
Lycengraulis grossidens (Spix & Agassiz, 1829)	3.2	0.6	4.3	0.7			0.1							0.7	2.4	0.5	1.5	0.6	**5.7**
PERCIFORMES																			
Gobiidae																			
Awaous tajasica (Lichtenstein, 1822)	**32.2**	7.2	3.8	6.7	4.9	9.1	9.3	2.2		12.6	12.1	8.7	7.05	18.7	11.1	30.9	12.5	10.6	**83.8**
Ctenogobius sp1	**25.2**	14.5	11.9	1.9	0.7	1.8	5.1	2.8	0.2	5.6	2.9	0.9	0.36	16.8	9.6	12.0	7.2	2.8	**48.4**
Ctenogobius sp2	0.9	1.1	0.2			0.2								0.4		0.8	0.1	0.1	**1.4**
Unidentified	1.7		0.2			0.2	1.2			1.2			12.46	1.4	0.6	0.4	11.5	1.2	**15.1**
Total														**70.3**	**40.5**	**82.6**	**43.8**	**19.4**	**256.6**

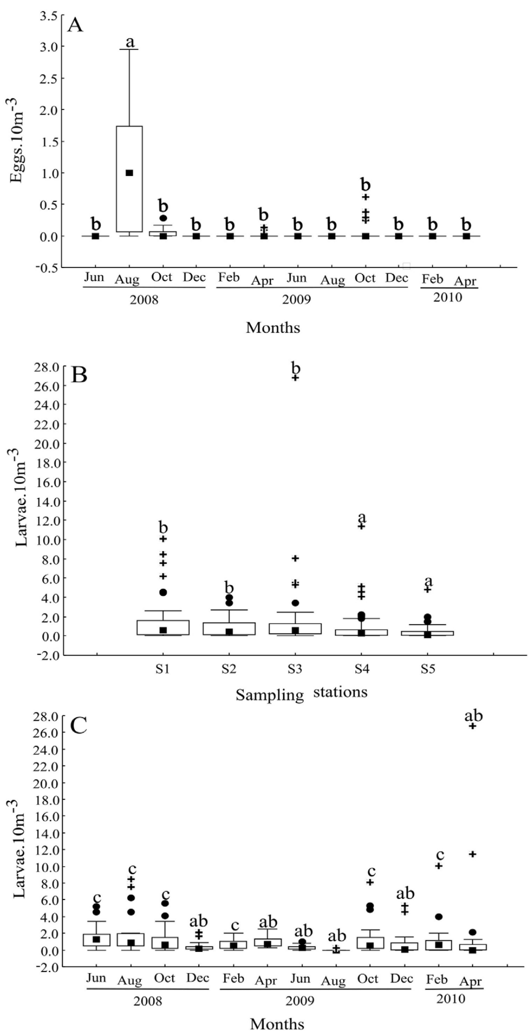


Figure 2. The monthly density of eggs (A), larval density in sampling stations (B), and monthly larval density (C) from June 2008 to April 2010 in the Peri Lagoon (Santa Catarina state, Brazil). Black squares: median; Hollow squares: 25–50%; Lines: non-outlier ranges; Black circles: outliers; Asterisks: extreme values. Jun: June; Aug: August; Oct: October; Dec: December; Feb: February; Apr: April.

($p < 0.05$). *Platanichthys platana* were captured at all sampling stations and during all months (Figures 3C and 3D).

Water temperature exhibited seasonal variations, with higher temperatures ranging from 25.1 ± 0.6 to 29.7 ± 0.4 °C during summer (December and February) and lower temperatures ranging from 18.1 ± 0.2 to 21.1 ± 1.3 °C in winter, June, and August. Dissolved oxygen concentrations showed considerable variation, with the lowest concentration recorded in October 2008 (3.8 ± 0.3 mg L^{-1}) and the highest in August 2010 (10.0 ± 0.1 mg L^{-1}). Precipitation exhibited the highest monthly variation: June 2009 was the month with the lowest precipitation (42.3 ± 4.3 mm), and April of the same year experienced the highest rainfall (307.0 ± 29.9 mm). Warmer months are generally associated with higher precipitation, whereas colder months are drier. The other parameters also showed noticeable variations (Table 3).

CCA identified four limnological variables (water temperature, precipitation, pH, and dissolved oxygen concentration) and all geospatial variables (depth, stream distance, and riparian forest) as significant factors. Temporal variables were also considered. The pCCA analysis on these sets explained 35.4% (TVE) of the total variation in the ichthyoplankton abundance (total inertia = 2.57). Geospatial variables explained the highest proportion of the total variation at 32.3% (TVE), followed by temporal variables explained at 21.4%, and limnological variables at 14.2% (Table 4). Notably, geospatial variables explained the most significant fraction of the TVE, considering either non-overlapping components or components shared with other variable sets (co-variables).

The nMDS analysis reinforced the importance of geospatial factors, showing segregation of the larval assemblage from stations S4 and S5 from the others. The MRPP analysis also confirmed this (T = -1.94, $p < 0.05$; Table 5). At stations S1, S2, and S3, higher abundances of *P. platana* and *Ctenogobius* sp1 were evidenced. This analysis also revealed a slight temporal segregation in larval composition during the summer months (December and February), which was not confirmed by the MRPP (T = -0.97, $p > 0.05$) (Figure 4).

4. Discussion

Spatiotemporal differences were observed in ichthyoplankton abundance in the Peri Lagoon, which were associated with physicochemical and geospatial factors. Temporally, August 2008 exhibited the highest egg density, whereas August 2008 and October 2009 had the highest larval densities. Spatially, sites near streams, characterized by greater depth and vegetation cover, showed higher larval abundance. The species encountered in this study were predominantly small and medium-sized, with certain dominant species, such as *P. platana*, *A. tajasica*, and *Ctenogobius* sp1, displaying spatiotemporal variations in their distribution. The investigated variables, including water temperature, precipitation, pH, dissolved oxygen concentration, geospatial factors, depth, stream distance, and riparian forest were identified

Table 3. Mean (± standard deviation), minimum and maximum values (in parentheses) of environmental variables obtained from June 2008 to April 2010 in Peri Lagoon (Santa Catarina state, Brazil). Jun: June; Aug: August; Oct: October; Dec: December; Feb: February; Apr: April.

Sampling Months	Water Temperature (°C)	pH	Dissolved Oxygen (mg.L^{-1})	Electrical Conductivity (µS.cm $^{-1}$)	Water Transparency (cm)	Precipitation (mm)
Jun/08	18.7±0.4 (18.1 - 19.0)	5.8±0.1 (5.7 - 5.9)	7.4±1.1 (5.5 - 8.0)	74.3±1.8 (71.0 - 75.2)	124.0±5.5 (120.0 - 130.0)	42.3±4.1 (0.0 - 15.7)
Aug/08	21.1±1.3 (19.2 - 22.0)	6.9±0.4 (6.5 - 7.5)	9.1±0.4 (8.5 - 9.4)	69.8±1.2 (68.6 - 71.2)	120.0±14.1 (110.0 - 140.0)	66.4±4.2 (0.0 - 16.1)
Oct/08	21.2±1.0 (20.1 - 22.3)	7.6±0.4 (7.3 - 8.4)	3.8±0.3 (3.3 - 4.2)	76.9±0.1 (76.8 - 77.0)	110.0±0.0 (110.0 - 110.0)	274.0±12.1 (0.0 - 45.9)
Dec/08	25.1±0.6 (24.4 - 26.0)	6.6±0.3 (6.2 - 7.1)	7.4±0.2 (7.1 - 7.6)	69.2±0.2 (69.0 - 69.5)	92.0±20.5 (60.0 - 110.0)	212.4±21.7 (0.0 - 119.1)
Feb/09	27.8±1.0 (25.7 - 28.4)	7.1±0.2 (7.0 - 7.5)	7.7±0.4 (6.9 - 8.2)	69.5±1.3 (68.6 - 72.2)	101.7±13.3 (80.0 - 110.0)	118.5±11.6 (0.0 - 59.3)
Apr/09	24.5±2.0 (21.5 - 25.7)	7.2±0.3 (6.9 - 7.6)	7.7±1.0 (6.2 - 8.3)	71.6±0.6 (71.0 - 72.1)	108.0±9.8 (100.0 - 120.0)	307.0±29.9 (0.0 - 148.4)
Jun/09	18.1±0.2 (17.8 - 18.4)	7.2±0.5 (6.5 - 7.7)	8.8±1.1 (6.9 - 9.5)	70.7±0.2 (70.6 - 71.0)	116.0±32.9 (80.0 - 150.0)	42.3±4.3 (0.0 - 20.7)
Aug/09	19.0±0.4 (18.8 - 19.6)	6.7±0.2 (6.5 - 6.9)	10.0±0.1 (9.9 - 10.1)	61.4±0.3 (61.0 - 61.7)	96.0±5.5 (90.0 - 100.0)	143.2±10.7 (0.0 - 50.8)
Oct/09	19.9±0.1 (19.7 - 20.0)	8.0±0.2 (7.6 - 8.2)	9.4±0.3 (9.0 - 9.6)	62.3±0.2 (62.1 - 62.7)	112.0±4.5 (110.0 - 120.0)	130.2±8.0 (0.0 - 28.1)
Dec/09	26.1±0.5 (25.7 - 26.9)	7.6±0.4 (7.2 - 8.2)	8.0±0.4 (7.6 - 8.6)	75.7±0.7 (75.1 - 76.8)	114.0±8.9 (110.0 - 130.0)	177.1±11.1 (0.0 - 45.0)
Feb/10	29.7±0.4 (29.2 - 30.2)	7.0±0.2 (6.8 - 7.2)	8.2±0.4 (7.9 - 8.8)	66.1±0.1 (66.0 - 66.2)	106.0±10.8 (95.0 - 120.0)	148.7±8.5 (0.0 - 30.8)
Apr/10	23.0±0.6 (22.4 - 23.9)	7.0±0.1 (6.8 - 7.1)	6.8±0.2 (6.5 - 7.0)	64.8±1.3 (63.8 - 66.3)	122.0±8.4 (110.0 - 130.0)	190.1±12.1 (0.0 - 56.1)

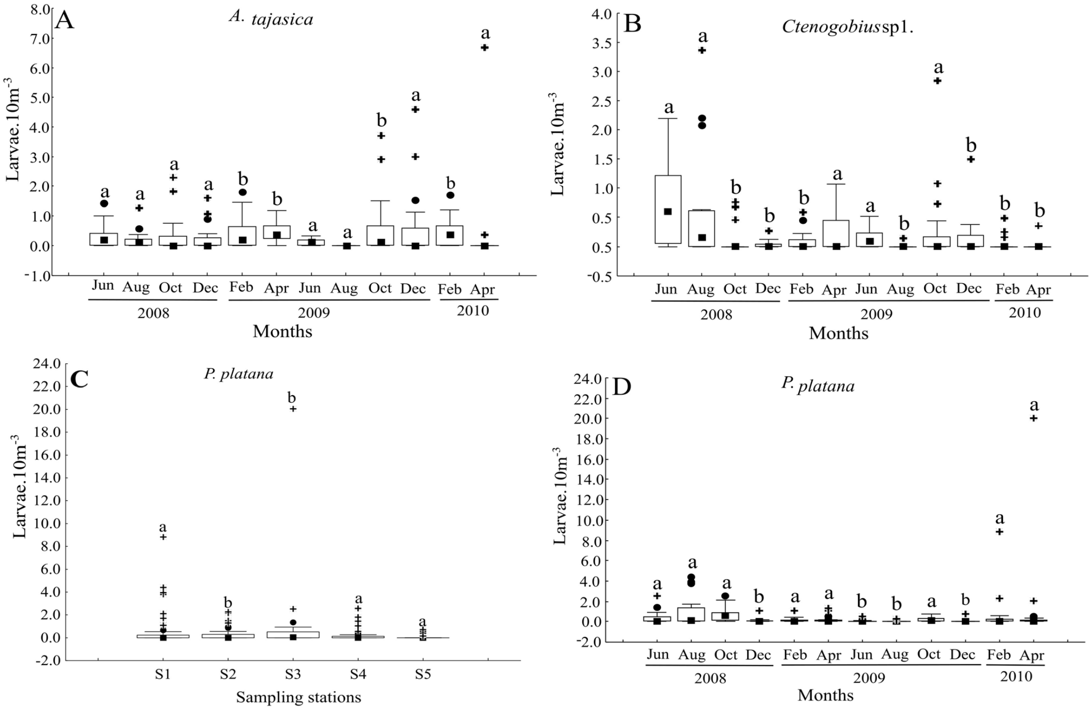


Figure 3. Spatial and temporal larval density of *Awaous tajasica* (A), *Ctenogobius* sp1 (B), and *Platanichthys platana* (C and D) captured from June 2008 to April 2010 in the Peri Lagoon (Santa Catarina state, Brazil). Black squares: median; Hollow squares: 25–50%; Lines: non-outlier ranges; Black circles: outliers; Asterisks: extreme values. Jun: June; Aug: August; Oct: October; Dec: December; Feb: February; Apr: April.

Table 4. Total variation explained (TVE) by each set of explanatory variables. Their corresponding non-overlapping components of variation were obtained with a partial canonical correspondence analysis (pCCA) from June 2008 to April 2010 in Peri Lagoon (Santa Catarina state, Brazil).

	Variables	Co-variables	TVE (%)
Explanatory variables	L		14.2
	T		21.4
	GS		32.3
Non-overlapping components	**L**	**T*GS**	**8.3**
	T	**L*GS**	**11.6**
	GS	**T*L**	**22.1**
	L*T	**GS**	**2.5**
	L*GS	**T**	**3.5**
	T*GS	**L**	**4.1**
	L*T*GS		**0.6**

L: Limnological; T: Temporal; GS: Geospatial; TVE: percentage of total variation explained by each component.

Table 5. A Multiple Response Permutation Procedure analysis (MRPP) applied to compare sampling stations regarding ichthyoplankton assemblage composition from June 2008 to April 2010 in Peri Lagoon (Santa Catarina state, Brazil).

Sampling stations	S2	S3	S4	S5
S1	0.55	1.17	***-1.81***	***-2.84***
S2		-0.43	-0.28	***-2.59***
S3			***-1.96***	***-3.73***
S4				-0.02

Italic bold: significant *t*-values ($p < 0.05$).

as influential factors shaping the distribution patterns of ichthyoplankton in the lagoon.

Coastal lagoons serve as transitional zones between land and ocean, harboring unique faunal components that originate from continental and marine ecosystems (Petry et al., 2016). This characteristic was also observed in the Peri Lagoon, where fish species commonly found in estuaries and freshwater environments were identified.

The capture of fish eggs and larvae in the Peri Lagoon was significantly lower than that in other lagoons in southern Brazil (Macedo-Soares et al., 2009). This reduced density of eggs and larvae may be attributed to the reproductive strategy of the captured species or to the fact that some species living in the lagoon do not use it as a site for reproduction and offspring development.

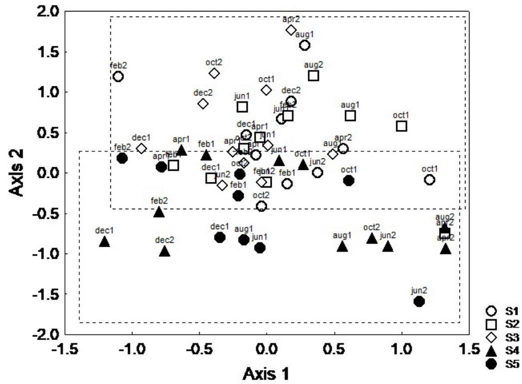


Figure 4. Non-metric Multidimensional Scaling (nMDS) applied to ordinate samples according to variations in composition and abundance of fish larvae sampled from June 2008 to April 2010 in Peri Lagoon (Santa Catarina state, Brazil). Rectangles depict groups confirmed by a Multiple Response Permutation Procedure. Year 1: first-year months (June 2008 – April 2009), Year 2 (June 2009 – April 2010): second-year months, feb: February, apr: April, jun: June, aug: August, and oct: October.

Among the most captured species in the larval stage, the Gobiidae family produces a limited number of adhesive eggs that become attached to substrates such as rocks and vegetation in continental waters, and some species still protect the eggs. After hatching, the larvae have a planktonic phase (Bone & Moore, 2008; Keith & Lord, 2012; Menezes & Figueiredo, 1985). In this study, Gobiidae larvae were observed throughout the study period. Members of this family can reproduce continuously or only once a year (McDowall, 2007). However, information about some Gobiidae species is fragmented, and little is known about their reproductive biology and the development of their early life stages, especially in lagoons (Yamasaki et al., 2011).

Most Clupeiformes (Clupeidae and Engraulidae) exhibit extended spawning periods throughout the year (Lopes et al., 2018; Trindade-Santos & Freire, 2015). They lay pelagic eggs and have short planktonic life cycles (Able & Fahay, 1998; Araújo et al., 2008). For some species, the initial development can occur within 24 h (Able & Fahay, 1998; Araújo et al., 2008; Kraus & Bonecker, 1994). These families, mainly Clupeidae, were well represented in the ichthyoplankton captured in Peri Lagoon. Thus, it is evident that despite a different abundance pattern of eggs and larvae from other coastal lagoons, the Peri Lagoon is a favorable environment for the reproduction and development of some species of fish.

Gobiidae, the family with the highest frequency of larval occurrence (58.3%), were consistently captured throughout the sampling period. This diverse family encompasses freshwater, estuarine, and marine species, most of which inhabit benthic habitats (Heemstra & Smith, 1995). In fish assemblages, the Gobiidae family often dominates or significantly contributes to species richness, and is found in temperate and subtropical estuaries and lagoons worldwide (Franco et al., 2006; Joyeux et al., 2004).

Sampling stations S1 and S3, located near stream mouths, riparian forests, and deep areas, exhibited the highest larval density. The proximity to dense vegetation and well-preserved streams contributes to higher nutrient concentration, promoting the growth of plankton and periphyton organisms that serve as food for the larvae (McKenna Junior et al., 2008). Freshwater inputs from streams transport sediments and nutrients, enhance productivity, and play a significant role as drivers of ecological processes in coastal lagoons (Rodrigues-Filho et al., 2023).

The gravel bottom at three of the stations provides shelter for the larvae and offers protection against predators. Gobiidae species are commonly found at the mouth of lotic rivers and close to various substrates, such as stones, sand, clay, and leaves (Avedaño-Ibarra et al., 2004). This explains the large number of larvae observed at S1 and S3, as these stations provide suitable conditions for Gobiidae reproduction. The reproductive success of Gobiidae is influenced by the increased phosphorus load that enters lakes from neighboring lands and streams (Mooij et al., 2005). In contrast, stations S4 and S5 were located in more open areas characterized by shallow environments with limited refuge for larvae and the absence of nearby streams.

Reproductive events in subtropical environments are typically associated with spring and summer (Munro et al., 1990) because of longer daylight hours and higher temperatures. However, the present study revealed the presence of ichthyoplankton throughout the year, with a notable abundance during spring and autumn. This unusual pattern and the reduced temporal variation in the Peri Lagoon could be attributed to species adapting to a wide range of water temperatures during their reproductive cycles. Such species can sustain their reproductive and larval development under contrasting environmental conditions.

The spawning patterns of many Gobiidae and Clupeidae species vary across seasons, depending on the region and the environmental factors influencing them (Avedaño-Ibarra et al., 2004; Macedo-Soares et al., 2009). The highest egg density was recorded in August 2008, despite the lower water temperature. Interestingly, the water temperature during this month was similar to that during the warmer months. This suggests that the water temperature had a reduced influence on the distribution of ichthyoplankton from these prominent families, indicating their capability to reproduce throughout the year.

Precipitation can modify various chemical factors in water, including the dissolved oxygen concentration and pH. This process involves the transportation of ions and sediments from the surrounding soil into the water body, leading to changes in its pH (Cobelo-García et al., 2012). Additionally, the presence of sediments in the water can reduce the dissolved oxygen concentration. Consequently, fluctuations in these factors directly affect the presence or absence of photosynthesizing organisms and zooplankton, which serve as food sources for fish larvae (Montes-Hugo & Alvarez-Borrego, 2003).

The influence of temporal variables on the distribution of ichthyoplankton from the dominant families was reduced, indicating their ability to reproduce throughout the year. Limnological, temporal, and geospatial processes influence the structures of fish communities in coastal lagoon systems. The effects of these factors on the larval distribution and community composition vary, depending on the intrinsic characteristics of the lagoon. Considering the dispersion and competition capacity of the species, Leibold et al. (2004) identified four types of metacommunity models: "dynamic patch," "species sorting," "mass effects," and "neutral" paradigms. These theoretical models provide crucial information for understanding the dynamics of fish communities and their early stages within a given environment. The management and conservation of lagoon ecosystems depend significantly on knowledge of the processes that affect species coexistence at various scales (Mouillot, 2007; Sanvicente-Añorve et al., 2011).

The results obtained from the MRPP, CCA, and NMDS analysis indicate that the structure of the ichthyoplankton community in Peri Lagoon is associated with the "mass effects" paradigm. The local larval patches exhibited heterogeneity, characterized by discrete and diffuse boundaries influenced by various environmental factors, such as depth, riparian vegetation, and distance from streams. Interestingly, our study revealed that geospatial factors played a more significant role in differentiating the ichthyoplanktonic communities between stations S1, S2, and S3 than between stations S4 and S5. The greater relevance of geospatial factors was unexpected, because the temporal element generally functions as a master modulator in subtropical regions (Barletta-Bergan et al., 2002; Macedo-Soares et al., 2009; Mulbert & Weiss, 1991).

The Peri Lagoon exhibits distinct ichthyoplankton assemblages characterized by a predominance of estuarine species, despite its freshwater nature and the absence of direct influence from ocean waters. Our study identified three species, *P. platana*, *A. tajasica*, and *Ctenogobius* sp1 that utilized the lagoon as a spawning site. A combination of physicochemical, geospatial, and intrinsic factors, such as life cycle strategies, egg types, and larval behaviors, influence the abundance of these species in the ichthyoplankton community.

Notably, areas close to streams and surrounded by dense forests have emerged as crucial habitats for the reproduction and development of certain fish species within the Peri Lagoon. Physicochemical factors did not strongly influence the spatiotemporal distribution of ichthyoplankton in Peri Lagoon, as observed in other Neotropical fish species. Our findings provide valuable insights into preservation efforts aimed at maintaining the recruitment of fish species to this unique ecosystem. By prioritizing the conservation of these specific areas and their associated environmental features, we can contribute to the long-term sustainability of Peri Lagoon and its fish community.

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