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Fishes and Rivers of the State of Rio de Janeiro, Southeastern Brazil: Biogeographic and Diversity Patterns in a Historically Well-Sampled Territory

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Abstract: The fish fauna of Rio de Janeiro has been extensively studied, resulting in a comprehensive database of species collected over more than three centuries. This study aimed to identify fish species, their locations, and compile scattered information to aid in climate action and freshwater conservation prioritization and an evaluation of the sampling effort to date, as well as to identify patterns of diversity and distribution of freshwater ichthyofauna, delineate biogeographic units, and explore similarity relationships between areas. Analyzing data from nearly 25 ichthyological collections and literature on original species descriptions revealed 346 fish species: 172 freshwaters native, 22 allochthonous, and 152 marine species. The checklist includes updated species names. The sampling effort in Rio de Janeiro is high, especially in coastal lowlands. The findings indicate that inventory work is still needed in certain areas. Five bioregions of freshwater ichthyofauna were identified, along with six major areas of higher species richness. This biogeographic assessment underscores the diverse and distinctive freshwater fish fauna in the basins of Rio de Janeiro, with well-defined biogeographic units.

Keywords: distribution; endemism; ichthyofauna; sampling effort; streams

1. Introduction

The state of Rio de Janeiro possesses unique characteristics of the Atlantic Forest Biome, comprising a diverse array of ecological niches shaped by proximity to the coast, varied relief, soil types, and rainfall regimes. These factors have driven the evolution of a rich biotic complex, encompassing both forest and aquatic systems. In the mountainous areas, the Rio Paraíba do Sul stands out to the west in its middle courses, embedded in the Serra da Mantiqueira, and lower course towards the coast. To the east, smaller coastal rivers descend the slopes of the Serra do Mar. The coastal region is distinguished by sandbanks, dunes, mangroves, swampy forests, ponds, and swamps. In the central and southern portions of Rio de Janeiro, bays occupy the coastal lowlands, notably Guanabara Bay, Sepetiba Bay, and Ilha Grande Bay. The remaining rivers and streams regulate water flow, ensure soil fertility, control the climate, and protect escarpments and mountain slopes. In the northern region, lake systems dominate the landscape, with many lagoons such as Maricá, Saquarema, Araruama, and Feia.

Recent knowledge about rivers and fish in the southeastern Atlantic Forest territory is extensive [1,2], yet there remain fewer contributions that evaluate the complete set of species for specific areas within the Atlantic Forest [3–5]. A comprehensive understanding of the species composition across

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the heterogeneous regional landscapes is still lacking. Thus, updating and disseminating knowledge about this crucial biodiversity set is a priority.

Collections as repositories stimulate curiosity about species diversity, leading to the pursuit of answers to new questions. The fish fauna of Rio de Janeiro has been extensively studied [6–14], resulting in the creation of a robust database of species in museums and university collections over more than three centuries. However, there is a gap of comprehensive information. Investigating the fish species inhabiting each region, consolidating scattered information, and making it easily accessible is now more indispensable than ever, particularly for disseminating and valuing freshwater ecosystems in the face of rapid climate change. This study highlights the rivers of Rio de Janeiro, identifies the respective basins in a territorial context, and evaluates the distribution patterns of their fish species.

2. Materials and Methods

Hydrographic region 08 of Brazil corresponds to an area adapted from the Ottobasins division by Pfafstetter [15,16]. This territorial division, named Southeastern Atlantic, comprises river basins flowing into the Atlantic Ocean. It is bordered to the north by the hydrographic basin of the Rio São Mateus in Espírito Santo state and to the south by the hydrographic basin of the Rio Ribeira do Iguape in Paraná state. The hydrographic region is bordered to the west by the hydrographic regions of the São Francisco and Paraná [17]. Within hydrographic region 08, each river basin is recognized by a number, with number 1 being the northernmost river, the Rio São Mateus. Accordingly, each river basin in Rio de Janeiro is identified by a number between 20 and 38, in parentheses, as detailed below.

2.1. Study Area

The Rio de Janeiro state is separated into nine hydrographic areas – a political division towards governance of its territory [18], as follows: RH-1- Ilha Grande Bay drainage; RH-2- Rio Guandu and transposition with Paraíba do Sul (08.22e); RH-3- Middle stretch of Rio Paraiba do Sul basin (08.22d); RH-4- Rio Piabanha and tributaries at Paraíba do Sul basin (08.22c); RH-5- Guanabara bay drainage; RH-6- Lake region and Rio São João; RH-7- Rio Dois Rios and tributaries at Paraíba do Sul basin (08.22b); RH-8- Rio Macaé and Rio das Ostras; RH-9- Lower Rio Paraíba do Sul and Itabapoana (08.22a) (Figure 1).

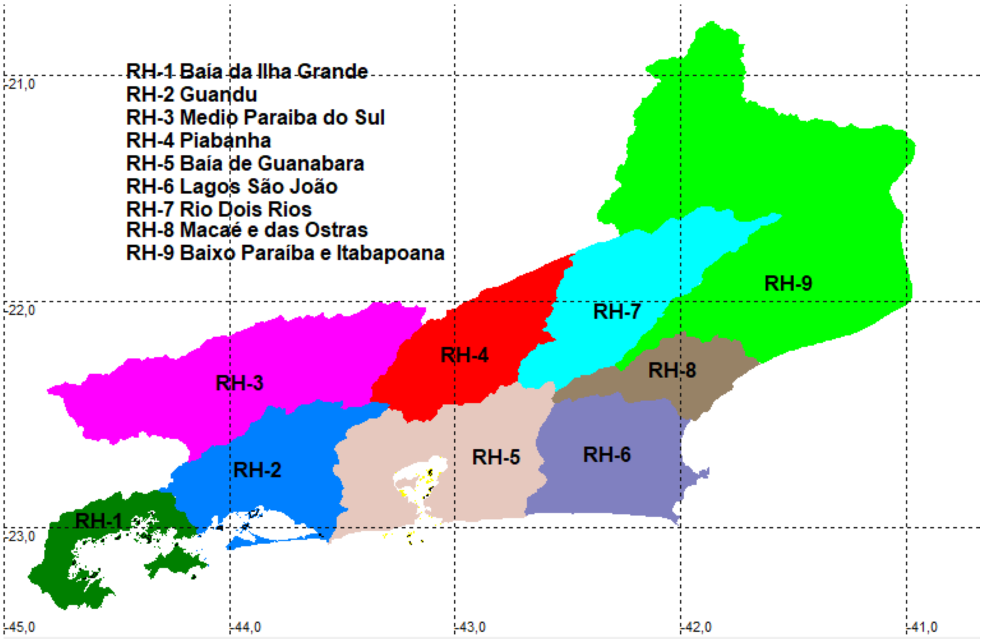

Figure 1. The nine hydrographic regions along Rio de Janeiro. RH-1- Ilha Grande Bay drainage; RH-2- Rio Guandu and transposition with Paraíba do Sul (08.22e); RH-3- Middle stretch of Rio Paraiba do Sul basin (08.22d); RH-4- Rio Piabanha and tributaries at Paraíba do Sul basin (08.22c); RH-5-

Guanabara bay drainage; RH-6- Lake region and Rio São João; RH-7- Rio Dois Rios and tributaries at Paraíba do Sul basin (08.22b); RH-8- Rio Macaé and Rio das Ostras; RH-9- Lower Rio Paraíba do Sul and Itabapoana (08.22a).

The river basins along the Rio de Janeiro territory were divided into 24 groups (Figure 2). Among those areas five belongs to the Rio Paraíba Sul basin, as stated above (RH-9, RH-7, RH-4, RH-3 and RH-2). Additionally 19 are coastal basins and microbasins: Itabapoana Basin (08.20- Figure 2- A), São Francisco de Itabapoana Watersheds (08.21- Figure 2- B), Lagoa Feia Watersheds (08.23- Figure 2- H), Jurubatiba Watersheds (08.24- Figure 2-I), Macaé River Basin (08.25- Figure 2-J), Rio das Ostras Watersheds (08.26- Figure 2-K), São João River Basin (08.27- Figure 2-L), Una River Basin and Búzios Watersheds (08.28- Figure 2-M), Araruama Lagoon Watersheds (08.29- Figure 2-N), Saquarema Watersheds (08.30- Figure 2-O), Maricá Watersheds (08.31- Figure 2-P), Niterói Watersheds (08.32 Figure 2-Q), Guanabara Bay Watersheds (08.33 Figure 2-R), Rio de Janeiro Watersheds (08.34- Figure 2-S), Sepetiba Watersheds (08.35 Figure 2-T), Mangaratiba Watersheds (08.36 Figure 2-U), Angra dos Reis Watersheds (08.37- Figure 2-V), Paraty Watersheds (08.38- Figure 2-W) and Cairuçu Watersheds (08.39- Figure 2-X).

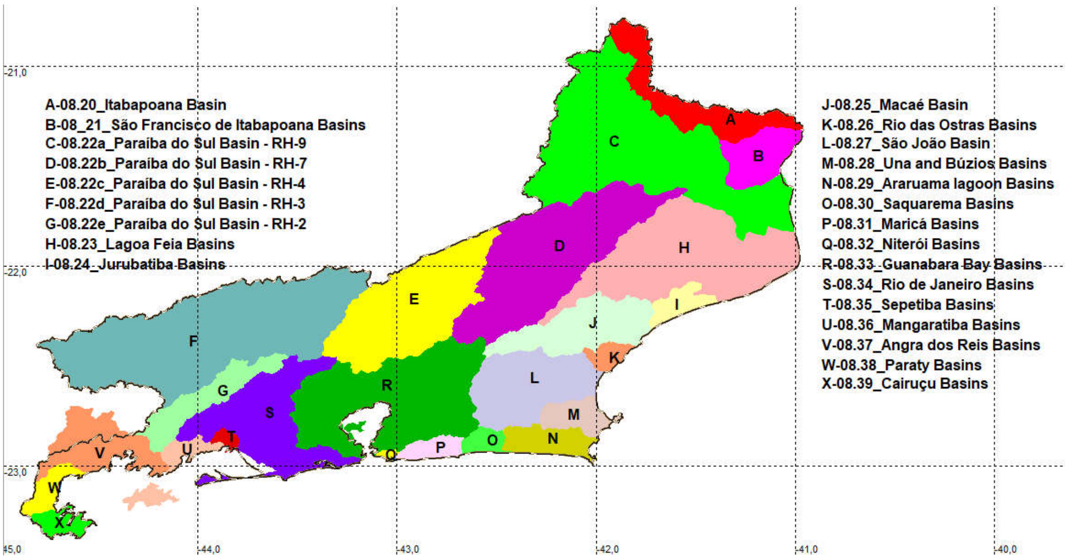

Figure 2. The twenty-nine river basin divisions along Rio de Janeiro. Coastal drainages: Itabapoana Basin (08.20- Figure 2- A), São Francisco de Itabapoana Watersheds (08.21- Figure 2- B)- , Lagoa Feia Watersheds (08.23- Figure 2- H), Jurubatiba Watersheds (08.24- Figure 2- I), Macaé River Basin (08.25- Figure 2- J), Rio das Ostras Watersheds (08.26- Figure 2- K), São João River Basin (08.27- Figure 2- L), Una River Basin and Búzios Watersheds (08.28- Figure 2- M), Araruama Lagoon Watersheds (08.29- Figure 2- N), Saquarema Watersheds (08.30- Figure 2- O), Maricá Watersheds (08.31), Niterói Watersheds (08.32), Guanabara Bay Watersheds (08.33), Rio de Janeiro Watersheds (08.34), Sepetiba Watersheds (08.35), Mangaratiba Watersheds (08.36), Angra dos Reis Watersheds (08.37), Paraty Watersheds (08.38) and Cairuçu Watersheds (08.39). Rio Paraíba do Sul sections (08.22a to 08.22e).

2.2. Species Data

Available records in fish collections from the Rio de Janeiro were consulted and had the identification confirmed. Each of the sampling points at the area had coordinates estimated from the locations indicated in the records. Initially, a curatorial survey of data was carried out in the fish collections of the Museu Nacional (MNRJ) and fish collection at the Museu de Biologia Mello Leitão (MBML). In the same way, records available in the database – SpeciesLink – Centro de Referência em Informação Ambiental [Reference Center for Environmental Information – CRIA] were consulted, and additionally the literature of species descriptions through which the data available in the collections of the AMNH, CAS (including CAS-SU), DZSJRP, FMNH, INPA, MCP, MCZ, MNRJ, MTD, MZFS, MZUEL, MZUSP, NPM, NRM, UF, UFRGS, UFRN, UFRJ, UFMT, UMMZ, UMZC, UNT, USNM and ZUEC. were inventoried (Supplementary file- Table S1). These institutional acronyms follow [19]. The records in collections were geo referred and plotted on a map of the Rio de Janeiro state. A total of 13,327 lots collected on the continent were inventoried (Supplementary file- Table S2).

The taxonomic classification of fishes follows [20]. Taxonomic problems are commented under section results.

2.3. Geographic Data

In georeferencing, for correspondence of the coordinates of each point, the values reported in the respective database were first used. When a small discrepancy was found between the reported value and the reported location, this value was adjusted according to the indication of the location. In cases when there was a large discrepancy between the indicated coordinates and the location, or when these coordinates were not available, the coordinates were estimated considering the available location information.

The hydrographic maps were adapted for use in the TrackMaker software [21], starting with version 1:25,000 made available by Instituto Brasileiro de Geografia e Estatística (IBGE) [22]. In the suggested location, information was used according to the names assigned to the rivers in this version, complemented by the names available in the IBGE topographic maps of 1:50,000. Municipality areas were calculated based on IBGE data [23].

2.4. Sampling Coverage Assessment

To evaluate the quality of sampling in the state, the index of total lots (il) per 100 km² and the index of sampling points (ip) per 100 km² were calculated. These indices were calculated for each municipality, hydrographic region, and group of basins, and these results were compared with the index for the entire state [24]. The sampling quality was considered average when found in the range of about 30%, poor when significantly below 30%, and good when above 30% (for both ilq and ipq). We evaluated the quality of sampling for the nine hydrographic regions, for the twenty-nine river basin divisions and additionally by municipality.

2.5. Biogeographic and Diversity Patterns

We applied the constancy index [25], used to determine which species are constant on a time scale: $C = n/N * 100$, where n = number of collection points where the species were captured and N = total number of collection points. Based on the results obtained, each species was classified as: constant, when $C > 50\%$; accessory, when C varies between 25% and 50%; and accidental when $C < 25\%$.

To assess differences in the fish fauna present in each hydrographic region of the study area the diversity indices absolute richness, Shannon diversity, equitability, and dominance were calculated, using species abundance data for each region [26]. Additionally, we traced diversity profiles, using the Rényi series, to compare the diversity among hydrographic regions. In the Rényi series, the minimum value of α results in an index that is equal to species richness (equability is not considered), and very high values of α assess only equability and disregard species richness [27]. In other words, we can only say that one river basin region is more diverse than another if the curves do not intersect. These analyses were performed using the PAST software [28].

Since determining the total number of species in an area is virtually impossible, especially in regions with high species richness, estimators are useful for extrapolating the observed richness and attempting to estimate the total richness through an incomplete sample of a biological community [29]. Consequently, we employed diversity estimators to assess the completeness of the species sampling for the hydrographic regions: the Chao 1 index, a simple estimator of the absolute number of species in a community. It is based on the number of rare species within a sample [30,31]; the iChao index estimator, which brought greater precision to the evaluation of the results [32]; and the AC estimator, Abundance-based Coverage Estimator [33]. This method works with the abundance of rare species (i.e. low abundance) [33,34]. However, unlike the previous estimator, this method allows the

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researcher to determine the limits for which a species is considered rare. In general, species with an abundance of between 1 and 10 individuals are considered rare. The estimated richness may vary as the abundance threshold is raised or lowered, and unfortunately there are no defined biological criteria for choosing the best range. Lastly, we adopted the Squares index, a richness estimator [35], designed to be more accurate than Chao-1 when abundance distributions are uniform.

We exclusively considered records of native freshwater species for the following spatial assessments. A bioregionalization analysis was performed using the Infomap Bioregions 2 algorithm [36], to subdivide the state of Rio de Janeiro into smaller biogeographical units. This algorithm uses species distribution data, even in cases of inconsistent sampling efforts. It employs an adaptive resolution method that generates a bipartite network of species and grids, followed by a clustering analysis to create bioregions based on the presence of specific taxa. The following parameters were employed: cell size ranging from 1/4° to 1° and cell capacity ranging from 5 to 1000 samples, 500 trials. The remaining settings followed the program defaults. We performed a cluster analysis using the binary matrix resulting from the bioregionalization algorithm to verify the similarity in faunal compositions between the bioregions generated by the UPGMA algorithm, Jaccard's similarity coefficient, in the PAST software [28].

A species richness interpolation analysis was performed to map diversity patterns using the spline interpolation method, which smooths out potential sampling gaps by creating a continuous surface of data values, in the BioDinamica model [37] of the Dinamica-EGO software [38]. The following parameters were used: raster grid size = 0.03, smoothing factor = 10, minimum of one sample per hexagon, using a delimitation mask of the Rio de Janeiro state.

3. Results

3.1. Rio de Janeiro According to the Collections - Diversity in Numbers

Lots sampled. The records of 16,299 lots from the collections were analyzed. Of these, 13,327 lots (81.77%) were sampled in continental waters of the Rio de Janeiro state. In addition, 2,890 (17.73%) were in the oceanic area and 82 (0.50%) could not be evaluated in its respective municipality. Of the lots sampled in inland waters, 985 (7.4%) are of marine origin, 498 (3.7%) are allochthonous freshwater, 11,724 (88.0%) are native to freshwater and 120 (0.9%) were not identified at the species level (Table 1).

Table 1. Lots sampled in the state of Rio de Janeiro.

	Ocean	Continental	Not identified	%
Marine origin	2,890	985	-----	7.39%
Allochthonous freshwater	-----	498	-----	3.74%
Native freshwater	-----	11,724	-----	87.97%
Not identified at the species level	-----	120	-----	0.90%
Not identified at the locality level	-----	-----	82	
Total	2,890	13,327	82	16,299
%	17.73%	81.77%	0.50%	

From a geographical point of view, from the records in continental waters, it was possible to georeference 13,327 lots (81.74%), leaving 86 lots (0.53%) for which it was only possible to identify them at the state level.

Sampling index. The average sampling index based on lots of freshwater fish recorded for the state of Rio de Janeiro was 30.5 lots per 100 km². The average index of sampling points on the continent was 3.7 sampling points per 100 km².

Regarding the hydrographic regions (Table 2), three were considered poorly sampled: RH-3 (Middle Paraíba do Sul) with il = 12.1 and ip = 1.9; RH-7 (Rio Dois Rios) with il = 15.8 and ip = 1.6, and

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RH-9 (lower Paraíba do Sul and Itabapoana) with il = 12.8 and ip = 1.4. Four regions appear with a good number of lots and sampling points, and two are within the state average (Table 2, Figure 3).

Table 2. Quality of sampling per hydrographic region.

Code	Hydrographic region	Area (km²)	Lots	Points	il	ilq	ip	ipq
RH-1	Baía da Ilha Grande	1,919.1	1,150	140	59.9	Good	7.3	Good
RH-2	Guandu	4,087.8	1,789	234	43.8	Good	5.7	Good
RH-3	Middle Paraíba do Sul	7,114.1	860	133	12.1	Poor	1.9	Poor
RH-4	Piabanha	3,831.4	816	121	21.3	Average	3.2	Average
RH-5	Baía de Guanabara	696.0	3,190	428	458.3	Good	61.5	Good
RH-6	Lagos São João	4,030.2	1,353	143	33.6	Average	3.5	Average
RH-7	Rio Dois Rios	4,940.9	780	81	15.8	Poor	1.6	Poor
RH-8	Macaé and das Ostras	2,226.9	1,474	133	66.2	Good	6.0	Good
RH-9	Lower Paraíba do Sul and Itabapoana	14,904.0	1,915	210	12.8	Poor	1.4	Poor
	Rio de Janeiro State	43,750	13,327	1.623	30.5		3.7	

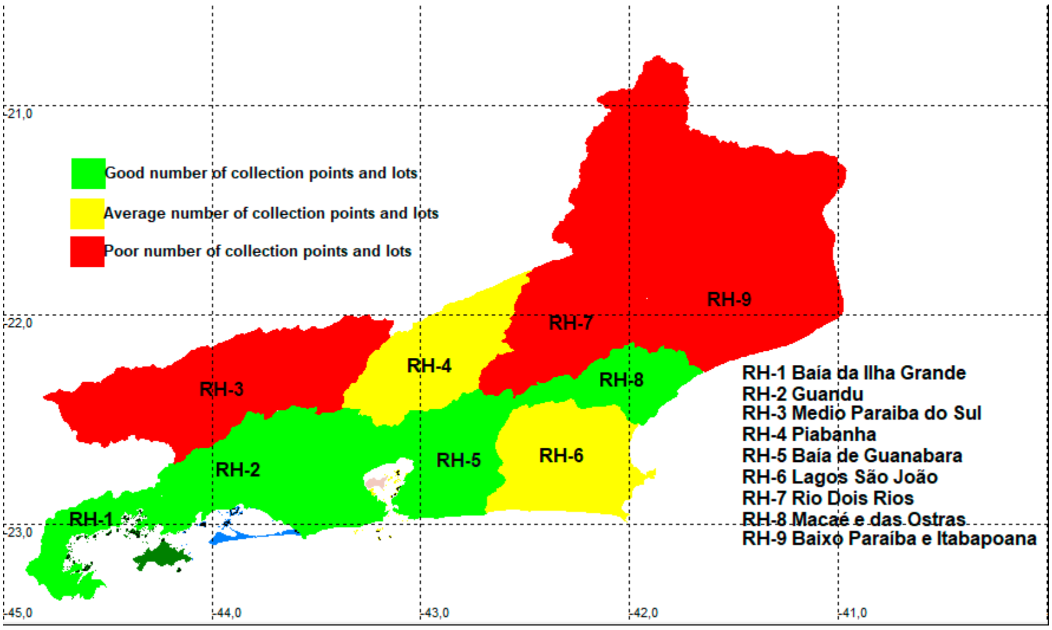

Figure 3. Quality of sampling per hydrographic regions RH1 to RH-9. Green = good quality of both indices; yellow = average quality of both indices; red = poor quality of both indices.

Twenty-four municipalities (Table A1) appear with a good number of lots, 14 are within the state average and 54 appear with a poor number of lots. Regarding sampling points, there are 25 with a good number of points, 15 are within the state average and 52 have a poor number of sites (Figure 4). Eight municipalities (Armação dos Búzios, Arraial do Cabo, Belford Roxo, Macuco, Miracema, Porciúncula, São João de Meriti and Varre Sai) do not have records deposited in ichthyological collections for freshwater species, and the first two have only records of marine species.

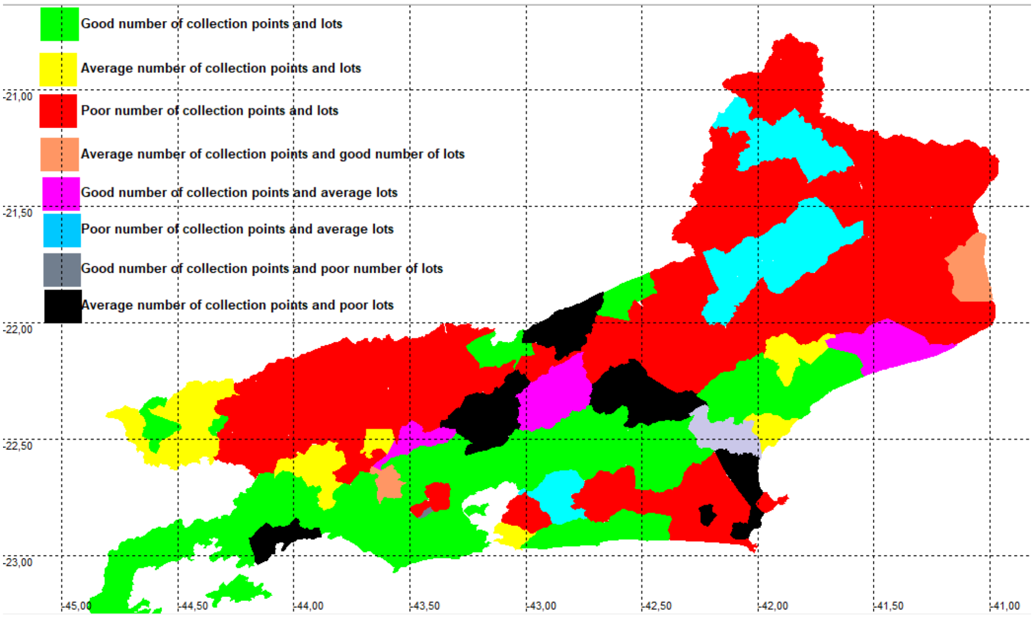

Figure 4. Quality of sampling per municipality. Green = good quality of both indices; yellow = average quality of both indices; red = poor quality of both indices; orange = average number of collection points, good number of lots; pink = good number of collection points, average number of lots; blue = poor number of collection points, average number of lots; gray = good number of collection points, poor number of lots; black = average number of collection points, poor number of lots.

In the evaluation of the basin groups (Table 3), in relation to the number of lots, 12 have a good number of lots, four are within the state average and eight have a poor number of lots. Regarding the sampling points, 11 have a good number of sites, five are within an average number and eight have a poor quality of sampling points.

Table 3. Sample quality per basin groups.

Code	Basin groups	Area (km²)	Lots	Points	Il	Ilq	Ip	Ipq
08.20	Itabapoana	1,523.4	122	19	8.0	Poor	1.2	Poor
08.21	São Francisco do Itabapoana	971.3	38	6	3.9	Poor	0.6	Poor
08.22a	Rio Paraíba do Sul - RH-9	6,321.4	1012	63	16.0	Poor	1.0	Poor
08.22b	Rio Paraíba do Sul - RH-7	4,468.6	780	81	17.5	Poor	1.8	Poor
08.22c	Rio Paraíba do Sul - RH-4	3,469.0	816	121	23.5	Average	3.5	Average
08.22d	Rio Paraíba do Sul - RH-3	6,430.8	860	133	13.4	Poor	2.1	Poor
08.22e	Rio Paraíba do Sul - RH-2	1,014.1	611	68	60.3	Good	6.7	Good
08.23	Lagoa Feia	4,310.8	512	93	11.9	Poor	2.2	Poor
08.24	Jurubatiba	410.1	707	62	172.4	Good	15.1	Good
08.25	Rio Macaé	1,706.4	894	92	52.4	Good	5.4	Good

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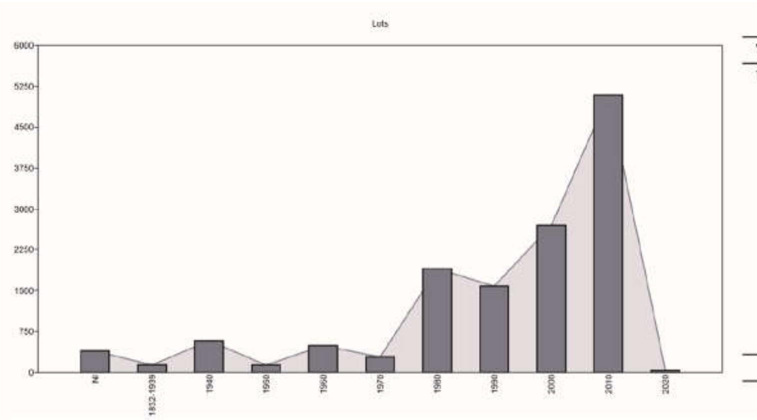
08.26	Rio das Ostras	249.4	104	8	41.7	Good	3.2	Average
08.27	Rio São João	2,155.6	1052	86	48.8	Good	4.0	Average
08.28	Rio Una and Búzios	541.7	11	4	2.0	Poor	0.7	Poor
08.29	Lagoa de Araruama	677.5	67	16	9.9	Poor	2.4	Poor
08.30	Saquarema	265.2	210	35	79.2	Good	13.2	Good
08.31	Maricá	349.5	167	33	47.8	Good	9.4	Good
08.32	Niterói	51.5	23	6	44.7	Good	11.7	Good
08.33	Baía de Guanabara	4,073.8	2412	269	59.2	Good	6.6	Good
08.34	Rio de Janeiro	2,636.3	1673	269	63.5	Good	10.2	Good
08.35	Sepetiba	107.0	39	7	36.4	Average	6.5	Good
08.36	Mangaratiba	289.8	67	12	23.1	Average	4.1	Average
08.37	Angra dos Reis	1,028.2	557	59	54.2	Average	5.7	Average
08.38	Paraty	376.9	301	48	79.9	Good	12.7	Good
08.38	Cairuçu	322.2	292	33	90.6	Good	10.2	Good
	Rio de Janeiro State	43,750	13,327	1,623	30.5		3.7	

Temporal variation. The growth of the records deposited in ichthyological collections after the year 2000 was 50% greater than all previous years (Figure 5). The earliest records are from 1832. From 1980 onwards, the collections had a significantly higher growth than in the entire previous period, continuously increasing since the year 2000.



Time period	Lots	%
Uninformed	395	2.96
1832-1939	140	1.05
1940-1949	581	4.36
1950-1959	138	1.04
1960-1969	493	3.70
1970-1979	285	2.14
1980-1989	1898	14.24
1990-1999	1580	11.86
2000-2009	2691	20.19
2010-2019	5092	38.21
2020-2021	34	0.26
	13327	

Figure 5. Temporal variation in the cataloging of fish records in museum collections.

3.1.1. Taxonomic Diversity

Entire set of records. Considering the entire set of records (Supplementary file- Table S3), 346 species were documented for the state of Rio de Janeiro (27 orders, 80 families and 207 genera), of which 172 are native freshwater species, 22 are allochthonous freshwater species and 152 are marine

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(Table 4). The orders Siluriformes (93 spp., 26.9% of the total) and Characiformes (50 spp., 14.5%) have the highest species richness, followed by Acanthuriformes and Cyprinodontidormes (33 spp. each, 9.5%). The most representative families of the total (Figure 5B) were Loricariidae (35 spp., 10.1%), Trichomycteridae (30 spp., 8.7%), Characidae (25 spp., 7.2%) and Rivulidae (21 spp., 6.1%).

Table 4. Number of fish species sampled in inland waters in the state of Rio de Janeiro.

Environment/Origin	S	%
Native freshwater	172	49.28%
Allochthonous freshwater	22	6.30%
Marine origin	152	43.55%
Not identified at the species level	3	0.86%
Total	349	

Native freshwater records. Regarding native freshwater species (Figure 6, Table 5, Table A2) (eight orders, 26 families, 31 subfamilies and 82 genera), the orders Siluriformes and Characiformes were the most representative, with 86 (54.7% of the total freshwater species) and 40 (29.1%) species, respectively, followed by Cyprinodontiformes (32 species., 19.2%). The most representative freshwater families are Loricariidae (36 species, 20.9%), Trichomycteridae (30 species, 17.4%), Characidae (25 species, 14.5%) and Rivulidae (21 spp., 12.2%). The most representative native freshwater fish genera were *Trichomycterus* (21 species), *Characidium*, and *Deuterodon* (7 species).

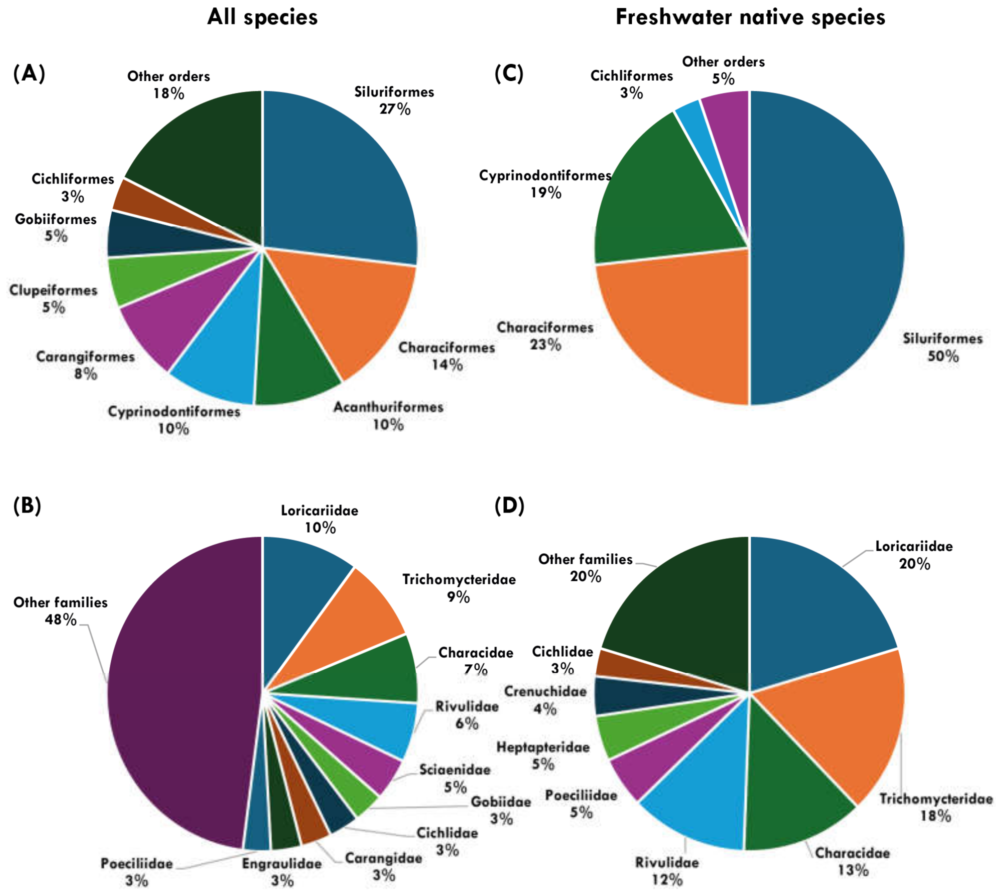

Figure 6. Taxonomic representativeness of fish orders and families for all species (A, B) and freshwater native species (C, D) within the territory of Rio de Janeiro.

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Table 5. Inventory of native freshwater species recorded for Rio de Janeiro state.

Order	Family	Subfamily	Suggested species	Author
Gymnotiformes	Sternopygidae		*Eigenmannia virescens*	(Valenciennes, 1836)
	Gymnotidae	Gymnotinae	*Gymnotus carapo*	Linnaeus, 1758
			Gymnotus pantherinus	(Steindachner, 1908)
	Hypopomidae		*Brachyhypopomus janeiroensis*	(Costa & Campos-da-Paz, 1992)
Characiformes	Crenuchidae	Characidiinae	*Characidium alipioi*	Travassos, 1955
			Characidium grajahuense	Travassos, 1944
			Characidium interruptum	Pellegrin, 1909
			Characidium japuhybense	Travassos, 1949
			Characidium lauroi	Travassos, 1949
			Characidium litorale	Leitão & Buckup, 2014
			Characidium vidali	Travassos, 1967
	Erythrinidae		*Hoplerythrinus unitaeniatus*	(Spix & Agassiz, 1829)
			Hoplias malabaricus	(Bloch, 1794)
	Anostomidae		*Hypomasticus copelandii*	(Steindachner, 1875)
			Hypomasticus mormyrops	(Steindachner, 1875)
			Hypomasticus thayeri	(Borodin, 1929)
			Megaleporinus conirostris	(Steindachner, 1875)
	Curimatidae		*Cyphocharax gilbert*	(Quoy & Gaimard, 1824)
	Prochilodontidae		*Prochilodus lineatus*	(Valenciennes, 1837)
			Prochilodus vimboides	Kner, 1859
	Bryconidae	Bryconinae	*Brycon insignis*	Steindachner, 1877
			Brycon opalinus	(Cuvier, 1819)
	Characidae	Stethaprioninae	*Astyanax keronolepis*	Silva, Malabarba & Malabarba, 2019
			Astyanax lacustris	(Lütken, 1875)
			Deuterodon giton	(Eigenmann, 1908)
			Deuterodon hastatus	(Myers, 1928)
			Deuterodon heterostomus	(Eigenmann, 1911)
			Deuterodon intermedius	(Eigenmann, 1908)
			Deuterodon janeiroensis	(Eigenmann, 1908)
			Deuterodon luetkenii	(Boulenger, 1887)
			Deuterodon taeniatus	(Jenyns, 1842)
			Hollandichthys multifasciatus	(Eigenmann & Norris, 1900)
			Hyphessobrycon bifasciatus	Ellis, 1911
			Hyphessobrycon boulengeri	(Eigenmann, 1907)
			Hyphessobrycon flammeus	Myers, 1924
			Oligosarcus hepsetus	(Cuvier, 1829)
			Psalidodon parahybae	(Eigenmann, 1908)
		Spintherobolinae	*Spintherobolus broccae*	Myers, 1925
		Stevardiinae	*Bryconamericus microcephalus*	(Miranda Ribeiro, 1908)

			Bryconamericus ornaticeps	Bizerril & Perez-Neto, 1995
			Bryconamericus tenuis	Bizerril & Auraujo, 1992
			Knodus moenkhausii	(Eigenmann & Kennedy, 1903)
			Mimagoniates microlepis	(Steindachner, 1877)
			Piabina argentea	Reinhardt, 1867
Siluriformes	Trichomycteridae	Trichogeninae	*Trichogenes longipinnis*	Britski & Ortega, 1983
		Trichomycterinae	*Trichomycterus albinotatus*	Costa, 1992
			Ituglanis parahybae	(Eigenmann, 1918)
			Trichomycterus auroguttatus	Costa, 1992
			Trichomycterus caipora	Lima, Lazzarotto & Costa, 2008
			Trichomycterus claudiae	Barbosa & Costa, 2010
			Trichomycterus florensis	(Miranda-Ribeiro, 1943)
			Trichomycterus fuliginosus	Barbosa & Costa, 2010
			Trichomycterus giganteus	Lima & Costa, 2004
			Trichomycterus goeldii	Boulenger, 1896
			Trichomycterus itatiayae	Miranda Ribeiro, 1906
			Trichomycterus jacupiranga	Wosiacki & Oyakawa, 2005
			Trichomycterus largoperculatus	Costa & Katz, 2022
			Trichomycterus macrophthalmus	Barbosa & Costa, 2012
			Trichomycterus mariamole	Barbosa & Costa, 2010
			Trichomycterus mirissumba	Costa, 1992
			Trichomycterus nigricans	Valenciennes, 1832
			Trichomycterus nigroauratus	Barbosa & Costa, 2008
			Trichomycterus paquequerense	(Miranda Ribeiro, 1943)
			Trichomycterus potschi	Barbosa & Costa, 2003
			Trichomycterus puriventris	Barbosa & Costa, 2012
			Trichomycterus travassosi	(Miranda Ribeiro, 1949
			Trichomycterus vitalbrazili	Vilardo, Katz & Costa, 2020

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	Microcambevinae	*Listrura costai*	Villa-Verde, Lazzarotto & Lima, 2012
		Listrura nematopteryx	de Pinna, 1988
		Listrura tetraradiata	Landim & Costa, 2002
		Microcambeva barbata	Costa & Bockmann, 1994
		Microcambeva bendego	Medeiros, Moreira, de Pinna & Lima, 2020
	Stegophilinae	*Homodiaetus banguela*	Koch, 2002
		Homodiaetus passarellii	(Miranda Ribeiro, 1944
Callichthyidae	Callichthyinae	*Callichthys callichthys*	(Linnaeus, 1758)
		Hoplosternum littorale	(Hancock, 1828)
	Corydoradinae	*Corydoras nattereri*	Steindachner, 1876
		Scleromystax barbatus	(Quoy & Gaimard, 1824)
		Scleromystax prionotos	(Nijssen & Isbrücker, 1980)
Loricariidae	Delturinae	*Delturus parahybae*	Eigenmann & Eigenmann, 1889
		Hemipsilichthys gobio	(Lütken, 1874)
		Hemipsilichthys nimius	Pereira, Reis, Souza & Lazzarotto, 2003
		Hemipsilichthys papillatus	Pereira, Oliveira & Oyakawa, 2000
	Rhinelepinae	*Pogonopoma parahybae*	(Steindachner, 1877)
	Loricariinae	*Harttia carvalhoi*	Miranda Ribeiro, 1939
		Harttia loricariformis	Steindachner, 1877
		Loricariichthys castaneus	(Castelnau, 1855)
		Rineloricaria nigricauda	(Regan, 1904)
		Rineloricaria nudipectoris	Mejia, Ferrar & Buckup, 2023
		Rineloricaria steindachneri	(Regan, 1904)
		Rineloricaria zawadzki	Silva, Costa & Oliveira, 2022
	Hypoptopomatinae	*Hisonotus notatus*	Eigenmann & Eigenmann, 1889
		Hisonotus thayeri	Martins & Langeani, 2016
		Kronichthys heylandi	(Boulenger, 1900)
		Neoplecostomus microps	(Steindachner, 1877)
		Neoplecostomus paraty	Cherobim, Lazzarotto & Langeani, 2016
		Neoplecostomus variipictus	Bizerril, 1995
		Otocinclus affinis	Steindachner, 1877

			Otothyris lophophanes	(Eigenmann & Eigenmann, 1889)
			Pareiorhaphis garbei	(Ihering, 1911)
			Pareiorhina brachyrhyncha	Chamon, Aranda & Buckup, 2005
			Pareiorhina rudolphi	(Miranda Ribeiro, 1911)
			Parotocinclus bidentatus	Gauger & Buckup, 2005
			Parotocinclus fluminense	Roxo, Melo, Silva & Oliveira, 2017
			Parotocinclus maculicauda	(Steindachner, 1877)
			Parotocinclus muriaensis	Gauger & Buckup, 2005
			Pseudotothyris janeirensis	Britski & Garavello, 1984
			Schizolecis guentheri	(Miranda Ribeiro, 1918)
		Hypostominae	*Ancistrus multispinis*	(Regan, 1912)
			Hypostomus affinis	(Steindachner, 1877)
			Hypostomus auroguttatus	Kner, 1854
			Hypostomus luetkeni	(Steindachner, 1877)
			Hypostomus punctatus	Valenciennes, 1840
			Hypostomus vermicularis	(Eigenmann & Eigenmann, 1888)
	Auchenipteridae	Centromochlinae	*Glanidium melanopterum*	Miranda Ribeiro, 1918
		Auchenipterinae	*Trachelyopterus striatulus*	(Steindachner, 1877)
	Heptapteridae	Rhamdiinae	*Pimelodella lateristriga*	(Lichtenstein, 1823)
			Rhamdia quelen	(Quoy & Gaimard, 1824)
		Heptapterinae	*Acentronichthys leptos*	Eigenmann & Eigenmann, 1889
			Imparfinis minutus	(Lütken, 1874)
			Imparfinis piperatus	Eigenmann & Norris, 1900
			Rhamdioglanis frenatus	Ihering, 1907
			Rhamdioglanis transfasciatus	Miranda Ribeiro, 1908
			Taunayia bifasciata	(Eigenmann & Norris, 1900)
	Pimelodidae		*Pimelodus maculatus*	Lacepède, 1803
			Steindachneridion parahybae	(Steindachner, 1877)
	Pseudopimelodidae		*Microglanis nigripinnis*	Bizerril & Perez-Neto, 1992
			Microglanis parahybae	(Steindachner, 1880)
			Microglanis pleriqueater	Mattos, Ottoni & Barbosa, 2013
	Ariidae	Ariinae	*Paragenidens grandoculis*	(Steindachner, 1877)
Gobiiformes	Eleotridae	Eleotrinae	*Dormitator maculatus*	(Bloch, 1792)
			Eleotris pisonis	(Gmelin, 1789)

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	Oxudercidae	Gobionellinae	*Awaous tajasica*	(Lichtenstein, 1822)
Synbranchiformes	Synbranchidae		*Synbranchus marmoratus*	Bloch, 1795
Cyprinodontiformes	Rivulidae	Rivulinae	*Atlantirivulus guanabarensis*	Costa, 2014
			Atlantirivulus janeiroensis	(Costa, 1991)
			Atlantirivulus jurubatibensis	(Costa, 2008)
			Atlantirivulus lazzarotoi	(Costa, 2007)
			Atlantirivulus maricensis	Costa, 2014
			Atlantirivulus simplicis	(Costa, 2004)
		Kryptolebiatinae	*Kryptolebias brasiliensis*	(Valenciennes, 1821)
			Kryptolebias caudomarginatus	(Seegers, 1984)
			Kryptolebias gracilis	Costa, 2007
			Kryptolebias ocellatus	(Hensel, 1868)
		Cynolebiinae	*Leptolebias marmoratus*	(Ladiges, 1934)
			Leptopanchax citrinipinnis	(Costa, Lacerda & Tanizaki, 1988)
			Leptopanchax opalescens	(Myers, 1942)
			Leptopanchax sanguineus	Costa, 2019
			Leptopanchax splendens	(Myers, 1942)
			Nematolebias papilliferus	Costa, 2002
			Nematolebias whitei	(Myers, 1942)
			Notholebias cruzi	(Costa, 1988)
			Notholebias fractifasciatus	(Costa, 1988)
			Notholebias minimus	(Myers, 1942)
			Ophthalmolebias constanciae	(Myers, 1942)
	Poeciliidae	Poeciliinae	*Phalloceros anisophallos*	Lucinda, 2008
			Phalloceros enneaktinos	Lucinda, 2008
			Phalloceros harpagos	Lucinda, 2008
			Phalloceros leptokeras	Lucinda, 2008
			Phalloceros tupinamba	Lucinda, 2008
			Phalloptychus januarius	(Hensel, 1868)
			Phallotorynus fasciolatus	Henn, 1916
			Poecilia reticulata	Peters, 1859
			Poecilia vivipara	Bloch & Schneider, 1801
	Anablepidae	Anablepinae	*Jenynsia darwini*	Amorim, 2018
			Jenynsia lineata	(Jenyns, 1842)
Cichliformes	Cichlidae	Cichlinae	*Australoheros ipatinguensis*	Ottoni & Costa, 200
			Australoheros oblongus	(Castelnau 1855)
			Crenicichla lacustris	(Castelnau, 1855)
			Crenicichla lepidota	Heckel, 1840
			Geophagus brasiliensis	(Quoy & Gaimard, 1824)
Acanthuriformes		Sciaenidae	*Pachyurus adspersus*	Steindachner, 1879

Constancy index. A total of 1,680 sampling points with different coordinates were identified in the state of Rio de Janeiro. No species was classified as constant and only *Geophagus brasiliensis*

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appeared as an accessory species, having been recorded in 497 points (29.58%). The others were all accidental, such as *Poecilia vivipara* with 268 sites (16.95%) and *Phalloceros harpagos* with 267 (15.89%). It is noticeably that 72 species were collected in one sampling point only.

Considering only the native freshwater fishes, 1,553 sampling points with georrefered coordinates were identified. In this scenario of native species, again only *Geophagus brasiliensis* again appeared as an accessory species. The others were classified as accidental.

Non-parametric estimation and diversity indices. All species richness estimators indicate that the species catalogued for the hydrographic regions RH-1, RH-2 and RH-6 are within the expected range (Table 6). The greatest variation between the species catalogued for a region and the estimated species is in RH-9, which estimates the possibility of an increase of up to 28.0% (ACE) in the species richness indicated by the records, and in RH-4 with up to 25.7% (iChao-1).

The highest species richness was in the Guandu hydrographic region (RH-2), with 97 species, followed by the Baía de Guanabara hydrographic region (RH-5), with 89 species. The lowest richness was in the Baía da Ilha Grande hydrographic region (RH-1) with 40 species, the Médio Rio Paraíba do Sul hydrographic region (RH-3) and the Macaé e das Ostras hydrographic region (RH-8), both with 67 species. The Shannon index indicates to a greater diversity of RH-5 (H = 3.528), followed by the Rio Dois Rios hydrographic region (RH-7) (H = 3.516), and the Lagos São João hydrographic region (RH-6) (H = 3.366). The lowest diversity was identified at the Baixo Paraíba do Sul e Itabapoana hydrographic region (RH-9) (H = 2.513). The dominance index was higher in RH-9 (D = 0.1549), RH-8 (D = 0.1214), and the Piabanha hydrographic region (RH-4) (D = 0.1038). In contrast, the equitability index indicates that RH-9, RH-8 and RH-4 are the less even communities, and RH-7 the most even one.

Table 6. Parametric and non-parametric diversity estimation indices per hydrographic region in the state of Rio de Janeiro.

	RH-1	**RH-2**	**RH-3**	**RH-4**	**RH-5**	**RH-6**	**RH-7**	**RH-8**	**RH-9**
Taxa_S	40	97	67	69	89	80	74	67	81
Individuals	20058	24736	4581	9256	29430	11829	4243	27928	40232
Dominance_D	0.1032	0.0915	0.05703	0.1038	0.04186	0.06386	0.04392	0.1214	0.1549
Shannon_H	2.7	3.176	3.284	2.858	3.528	3.366	3.516	2.595	2.513
Equitability_J	0.732	0.6944	0.7811	0.675	0.786	0.7682	0.8169	0.6172	0.5719
Chao-1	40	97.17	74	78.33	90.5	80.17	75.5	70	102
iChao-1	40	97.17	78.57	86.75	93.5	80.4	77.07	76.5	103.7
ACE	40	97.3	73.45	74.2	90.16	81.2	75.69	68.96	85.34
Squares	40	97.09	70.66	75.65	89.38	80.26	74.71	68.94	88.59
Variation of species richness for the non-parametric estimation indices									
	RH-1	**RH-2**	**RH-3**	**RH-4**	**RH-5**	**RH-6**	**RH-7**	**RH-8**	**RH-9**
Chao-1	0.00%	0.18%	10.45%	13.52%	1.69%	0.21%	2.03%	4.48%	25.93%
iChao-1	0.00%	0.18%	17.27%	25.72%	5.06%	0.50%	4.15%	14.18%	28.02%
ACE	0.00%	0.31%	9.63%	7.54%	1.30%	1.50%	2.28%	2.93%	5.36%
Squares	0.00%	0.09%	5.46%	9.64%	0.43%	0.32%	0.96%	2.90%	9.37%

The Guandu region (RH-2) was the one with the highest richness of native freshwater species with 97 species, followed by the Baía de Guanabara (RH-5) with 89 species, Baixo Paraíba do Sul e Itabapoana (RH-9) with 81 species, and Lagos São João (RH-6) with 80 species, a result consonant with the special interpolation of species richness. The Baía da Ilha Grande region (RH-1), on the other hand, presented the lowest richness, with only 40 species. The highest values of the Shannon diversity index were reached in hydrographic regions RH-2, RH-3, RH-5, RH-6, RH-7, areas also identified as hotspots of ichthyofaunistic biodiversity in Rio de Janeiro (see Figure 9).

The diversity profiles of the hydrographic regions using the Rényi series indicate that the diversity of the Baía da Ilha Grande region (RH-5) is lesser than the diversity of the Guandu region

(RH-2) only when considering indices more dependent on species richness, but their diversities are very close when using the indices more dependent on equability (Figure 7a).

Despite the great difference between the richness of the hydrographic regions from the extremes south and north of Rio de Janeiro, Baía da Ilha Grande (RH-1, 40 spp.) and lower Paraíba do Sul and Itabapoana (RH-9, 81 spp.), the graph with the diversity curves (Figure 7b) indicates that it is not possible to define which region has the greatest diversity.

The diversity profile of the hydrographic regions that include only the tributaries of the Rio Paraíba do Sul (Middle Paraíba do Sul, RH-3; Piabanha, RH-4; Rio Dois Rios, RH-7) (Figure 7c) show a greater diversity in a lower part of Rio Paraíba do Sul (RH-7), while in the highest parts (RH-3, RH4) the crossing of the curves suggests that these diversities are not comparable and will alternate depending on the index that is considered.

The hydrographic region Baía de Guanabara (RH-5) is more diverse than the hydrographic region Lagos São João (RH-6), which in turn is more diverse than the hydrographic region Macaé and das Ostras (RH-8, Figure 7d).

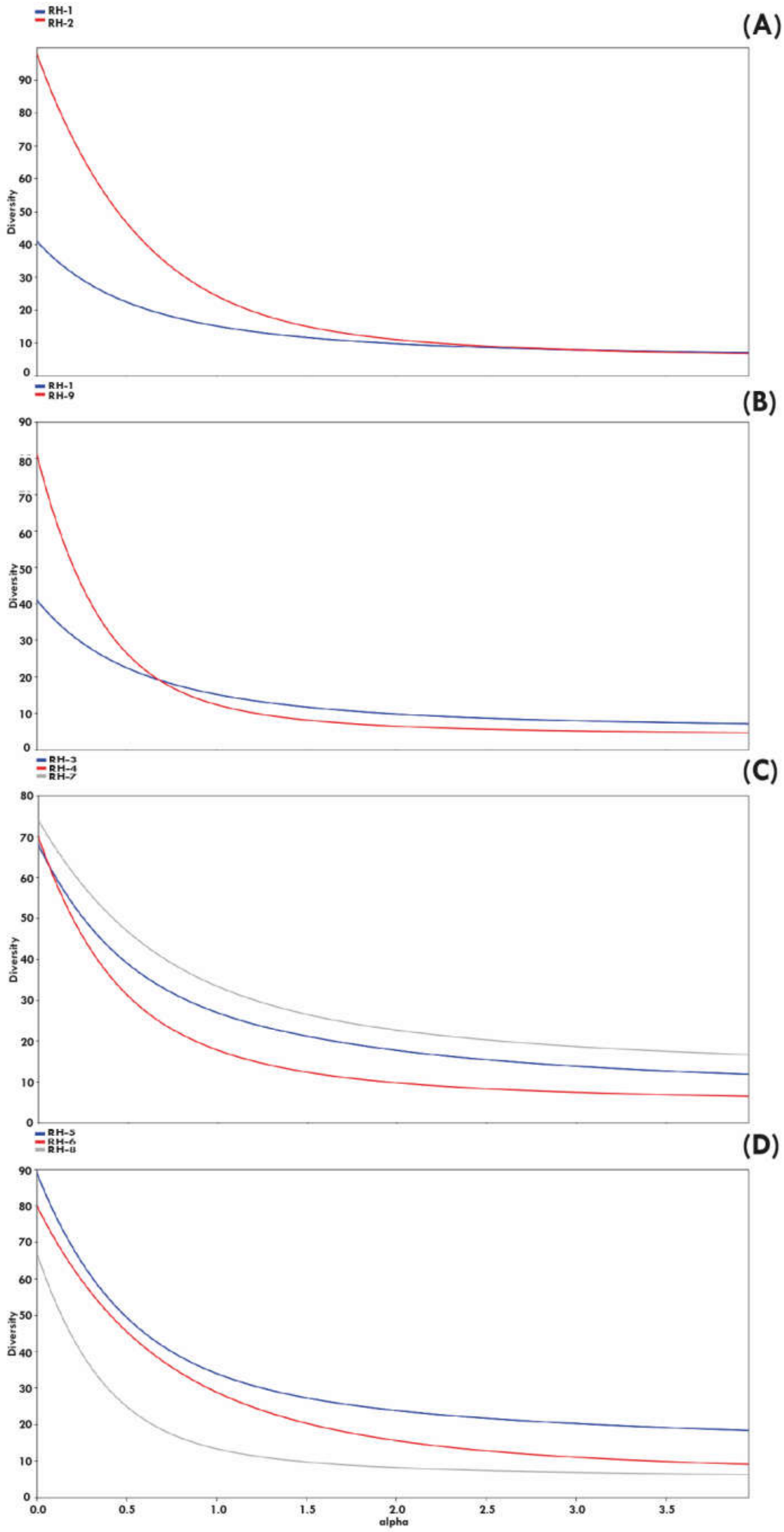

Figure 7. Diversity profile using the Rényi series representing the fish fauna documented in the museum collections for the hydrographic regions of Rio de Janeiro. A. Diversity profile between RH-

1 and RH-2. B. Profile between RH-1 and RH-9. C. Profile between RH-3, RH-4 and RH-7. D. Profile between RH-5, RH-6 and RH-8.

Although Rio de Janeiro is a widely collected territory within the Atlantic Forest, this sampling is not equal. The quality indices of the sampled lots are good for an area varying between 20% and 32% of the state (according to the division per municipalities, basins or hydrographic regions), between 11% and 18% of the state area presented average sampling quality, and between 55% and 60% of the state presented poor sampling. These results suggest that there are still under-sampled areas in the territory that may be the target of future studies and inventories.

3.2. Spatial Patterns of Distribution

Five bioregions have been delineated based on patterns of distribution of the freshwater fish fauna (Figure 8A). These areas are herein referred to as Lower Rio Paraíba do Sul bioregion, Guanabara-Guandu bioregion, Middle Rio Paraíba do Sul bioregion, Costa Verde bioregion and Lagos bioregion.

1. **Lower Rio Paraíba do Sul bioregion**: The largest area in terms of territorial extension, this biogeographic unit is composed mainly of the lower Rio Paraíba do Sul basin and its tributaries, such as the Rio Muriaé, Rio Dois Rios and Rio Pomba, as well as independent basins such as the Rio Itabapoana (the geographical divide with the state of Espírito Santo), Rio Macaé and Rio São João, and coastal lagoon systems such as the Lagoa Feia. Species that delimit this bioregion include *Listrura tetraradiata*, *Microglanis pleriqueate*r, and *Trichomycterus puriventris*, present in most of the drainages that compose this area. The bioregion has 114 species, of which 26 (22.8%) occur only in this area (e.g., *Atlantirivulus janeiroensis*, *A. jurubatibensis*, *Bryconamericus tenuis*, *Characidium litorale*, *Delturus parahybae*, *Homodiaetus banguela*, *Ituglanis parahybae*, *Trichomycterus caipora*, *T. fuliginosus* and *T. vitalbrazili*). Covering a large part of the basins of the state of Rio de Janeiro, many of the species present in these basins are common to several other drainages of the Atlantic Forest, such as fish species within the genera *Deuterodon*, *Hypostomus* and *Trichomycterus*.
2. **Guanabara-Guandu bioregion**: It consists mainly of the basins that drain the Baía de Guanabara and Baía de Sepetiba, such as the Rio Caceribu, Rio Guapimirim, Rio Macacu, Rio Roncador, Rio Suruí, Rio Guandu and the Jacarepaguá lagoon system. Species that delimit this bioregion include *Kryptolebias caudomarginatus*, *Listrura nematopteryx*, and *Notholebias minimus*. Presents 99 species, 17 of them (17.2%) occurring only in this area (e.g., *Atlantirivulus guanabarensis*, *Australoheros macacuensis*, *Characidium grajahuense*, *Homodiaetus passarelli*, *Kryptolebias brasiliensis*, *Leptopanchax opalescens*, *L. sanguineus*, *L. splenden*s, *Microglanis nigripinnis*, *Trichomycterus giganteus*, and *T. potschi*).
3. **Middle Rio Paraíba do Sul bioregion**: Formed by tributaries of the middle course of the Rio Paraíba do Sul, such as the Rio Piraí, Rio Paquequer, Rio Preto, Rio Piabanha, and the Rio Paraíba do Sul. This bioregion is supported by the presence of species such as *Parotocinclus bidentatus*, *Trichomycterus nigroauratus*, and *Trichomycterus florensis*. The area presents 81 species, of which 11 (13.6%) occur only in this bioregion, especially species of the genus *Trichomycterus*, such as *T. itatiayae*, *T. macrophthalmus*, *T. mariamole*, and *T. mirissumba*.
4. **Costa Verde bioregion**: This biogeographic unit consists of small basins that flow into the Baía da Ilha Grande, as the drainages of the Rio Mambucaba, Rio Perequê-Açu, Rio Taquari and Rio Parati-Mirim. Supported by the presence of species such as *Characidium japuhybense*, *Hemipsilichthys nimius*, and *Neoplecostomus paraty*. The bioregion presents 40 species, of which nine (22.5%) occur only in this area (e.g., *Atlantirivulus lazzarotoi*, *A. simplicis*, *Listrura costai*, and *Phalloceros enneaktinos*).
5. **Lagos bioregion**: The smallest of the delimited areas, this bioregion consists of small drainages and lagoon systems that are part of the Região dos Lagos area, in the coast of Rio de Janeiro. It includes the drainages of the Rio Ubatiba, Rio Mato Grosso, coastal wetlands and lagoons of Maricá and Saquarema. The region is supported by the presence of species of rivulids such as *Atlantirivulus maricensis*, *Leptopanchax citrinipinnis*, *Nematolebias papilliferus*, and *Notholebias fractifasciatus*. It has 36 species, of which four (11.1%) only occur in that area.

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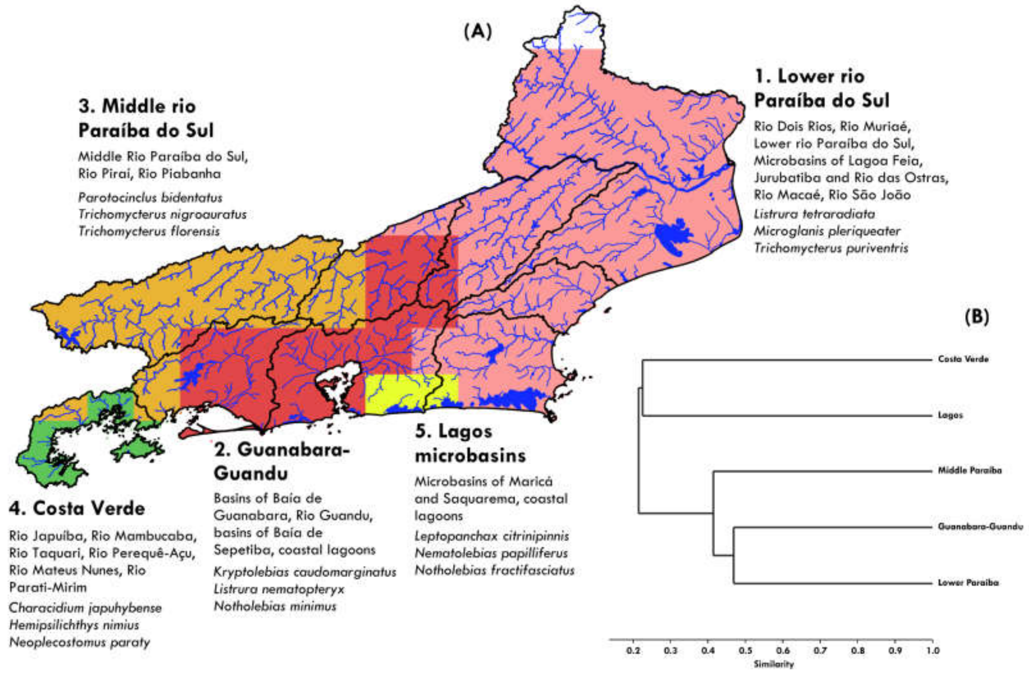

Figure 8. Bioregions of the freshwater icthyofauna within the territory of Rio de Janeiro (A) and Jaccard similarity among these areas (B).

The cluster analysis (cophenetic correlation: 0.93) indicates that the Lower Paraíba do Sul and the Guanabara-Guandu bioregions have approximately 47% of ichthyofaunistic similarity, and both present about 40% of congruence with the Middle Paraíba do Sul region (Figure 8B). The Costa Verde and Lagos bioregions present greater dissimilarity with hydrographic networks of the state, showing less than 20% of global similarity.

The interpolation of species richness shows six areas with the highest density of species in hydrographic regions of the state of Rio de Janeiro (Figure 9): (1) the middle Rio Paraíba do Sul, on the border with the state of São Paulo, in the vicinity of the Funil Reservoir, in the region of Itatiaia (RH-3); (2) the lower Rio Paraíba do Sul, in the region of the mouth of the Rio Dois Rios (RH-7); (3) the upper course of the Rio São João and Rio Macaé (RH-6 and RH-8); (4) several basins that flow into Baía de Guanabara (RH-5); (5) the Rio Guandu basin and adjacent basins (RH-2); and (6) Costa Verde basins (RH-1). In general, the region with the highest intensity of this index is specifically the sub-basin of the Rio Macacu and the Rio Guapimirim, followed by the upper Rio São João. In contrast, the regions with the lowest species richness were a stretch of the Middle Rio Paraíba do Sul, in the Rio das Flores basin; the upper course of the Rio Carangola and Rio Muriaé, in the Lower Rio Paraíba do Sul; and the region surrounding the lagoon system of Araruama and Cabo Frio.

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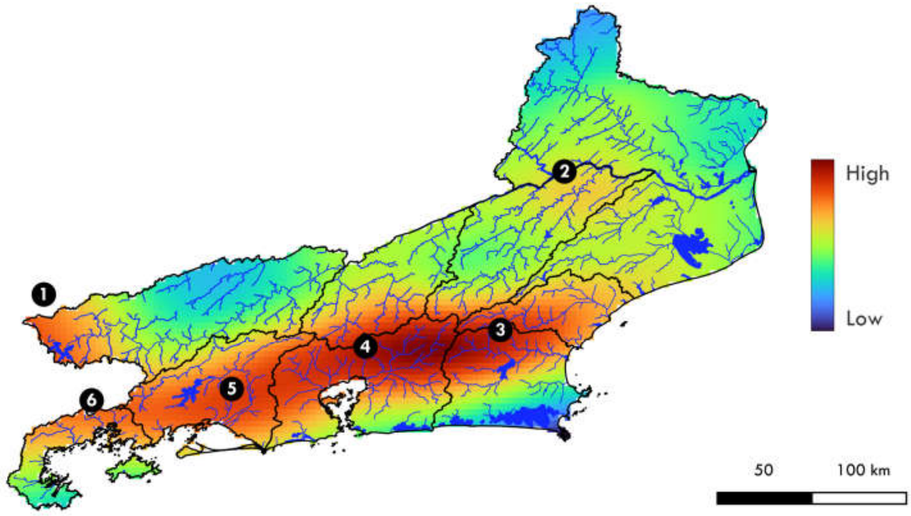

Figure 9. Interpolation of species richness within the state of Rio de Janeiro. The most relevant areas are highlighted with numbers 1-6.

4. Discussion

The perception that the rivers of the Atlantic Forest in Rio de Janeiro comprise sets of distinct areas of endemism for fish has been previously detailed by authors who have worked with the biome as a whole [39,40]. Subsequently, [41], in a global analysis of freshwater ecoregions, recognized three distinct ecoregions that include, in part, the territory of Rio de Janeiro: 329, Paraíba do Sul; 330, Ribeira de Iguape, and 352, Fluminense (see figure 1 in [41]). The division of Rio de Janeiro in bioregions of ichthyofaunal endemism recognized here roughly match the findings of [41]. The bioregions Lower Rio Paraíba do Sul and Middle Rio Paraíba do Sul partially adjusts to the ecoregion 329. The bioregion Costa Verde corresponds to part of the Ribeira do Iguape ecoregion. Additionally, the bioregions Guanabara-Guandu and Lagos almost corroborate the delineation of the Fluminense ecoregion [41].

The particularities of the relief and the configuration of the hydrographic basins in the Atlantic Forest biome in the territory of Rio de Janeiro include the Paraíba valley—depressed tectonic valley corridors along faults [42]—with rivers flowing between Serra do Mar and Serra da Mantiqueira Mountain ranges. Although the Rio Paraíba do Sul is the largest river system partially crossing the Rio de Janeiro territory, it was not recognized as the most diversified area for freshwater fishes. Possible reasons for this include the presence of numerous coastal drainages flowing from the Serra do Mar, as well as extensive areas of coastal lowlands with bays and lagoon systems. These diverse environments support a significant diversity of species. The mountainous nature with vertical escarpments and difficult access, that contributed to keep the mountain barrier impassable during the initial centuries of colonization [43], was also the feature that functioned as a geographical divide, isolating the Rio Paraíba do Sul from the coastal rivers. In the set of coastal lowlands, it is worth highlighting the special interest and diversity of freshwater species on the small river drainages at the Baía de Guanabara region. To mention its origin in a simplified way, Baía de Guanabara was geologically configured in the Cenozoic as a result of a tectonic depression, in a phenomenon known as block tipping, later filled by sediments derived from the erosion of adjacent mountain ranges, and in the Quaternary period drowned by the marine transgression that generated water mass of the bay [44]. Since the uplift of the mountains, the bay has been receiving sediments derived from the numerous rivers that drain into its interior. By its formation, the bay area holds a variety of living environments for freshwater forms, in different relief extracts. Additionally, the Sepetiba and Paraty bays were formed in a similar manner [42].

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In the set of coastal lowlands, it is worth highlighting the special interest and diversity of freshwater species on the small river drainages at the Costa Verde bioregion. Despite corresponding to a small area of territory, the Costa Verde has a high endemism of species, with a unique set of stream fishes [14]. Being mostly fish of the first order, that is, intolerant of survival in brackish or salty waters, the process of isolation, dispersion and occupation of these species in the numerous small coastal streams has always been intriguing. The coastal drainages of the Costa Verde have particularities not observed in other areas, such as rivers flowing abruptly towards the coast, some of which are even devoid of coastal plain areas. Such topographic configuration of these small basins that flow from the mountains towards the sea has important implications for the aquatic biota, considering that isolated basins present similar fish fauna [45]. The coastal basins of the Atlantic Forest where the Serra do Mar is very close to the coast, such as those in the Costa Verde area, were influenced by climate change that caused oscillations in sea level during the Pleistocene. These transgressions and marine regressions generated isolation and connection between rivers [46]. The past connections among these coastal basins are hypothetized by [47] based on molecular evidence and paleodrainage reconstruction.

The orders Siluriformes and Characiformes were predominant in number of species, repeating a pattern commonly found in drainages of the Neotropical region and the Atlantic Forest biome [40,48], followed by Cyprinodontiformes. The predominance of these three orders is the result of characteristics that facilitate the occupation of species in different habitats and the great heterogeneity of environments available in the drainages of the state. This result is in line with several regional studies for Rio de Janeiro basins (e.g., [8,10–14,39,49].

Some species considered here have complex taxonomy, with phylogenies that need to be solved and probable species complexes, but we consider them as single taxa for analytic and inventory purposes. *Rhamdia quelen* has recently been redescribed and its distribution is now restricted to coastal basins from Rio de Janeiro south to the Rio Tubarão basin, in the state of Santa Catarina [50]. [51] describe seven subspecies of *Gymnotus carapo* for South American basins and suggest that the species appears to be absent from the coastal drainages of Northeastern and Southeastern Brazil, despite several records tentatively identified as *G. carapo*, *G.* aff. *carapo* or *G.* cf. *carapo* for these regions in museum collections and databases. *Hoplias malabaricus* and *Synbranchus marmoratus* most likely represent species complexes that require revision [52–55].

The greatest species richness in RH-2 (97 spp.) is associated with the fact that this hydrographic region encompassing coastal hydrographic systems is connected to the Rio Paraíba do Sul though links with the Rio Guandu system, which supplies water to the city of Rio de Janeiro. In contrast, the lowest species richness in RH-1 (40 spp.) is related to the geographic characteristics of this region, where the Serra do Mar is very close to the coast. The habitats are either characterized by steep rapids or estuarine plains.

5. Conclusions

This is the first time an evaluation of freshwater fishes in the Rio de Janeiro territory is accomplished with a geographical accuracy of data. We hope our results contribute for future research in the area and for conservation management measures of this complex and diverse territory. The distribution patterns of the fish species in the area corroborate previous studies of the Atlantic Forest and indicate that the recognized bioregions are in accordance with previous established biogeographic units.

The more sampled and diversified freshwater area —the vicinities of the Baía de Guanabara— may be due to the variety of environments in an area where rivers come from a slope mountainous area, the Serra dos Órgãos, with fast-flowing, clear water rivers and pebbles substrate, as well as swamps, slow flowing creeks and transitional environments such as mangroves in the coastal areas. Additionally, the proximity to the metropolitan area of Rio de Janeiro and its research centers historically facilitated the access. The less sampled regions in Rio de Janeiro corresponds to the middle reaches of Rio Paraíba do Sul at Rio das Flores, and also at its lower section, at traditional areas of coffee crops and nowadays mostly deforested, with river siltation and pollution.

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Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: Ichthyological collections with inventoried records from the state of Rio de Janeiro; Table S2: Records of fish species from the state of Rio de Janeiro listed for this study; Table S3: Inventory of all species recorded for the state of Rio de Janeiro.

Author Contributions: All authors designed the study; RFMP built the dataset and checked species distribution ranges. LMSS, FVG performed data curation and taxonomic validation. Biogeographical analysis was performed by FVG. Statistical analysis was performed by RFMP and FVG. All authors wrote the manuscript.

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Data Availability Statement: Data is available in Supplementary Material Table S2.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Quality of sampling per municipality.

Municipality	Area (km²)	Lots	Points	Il	Ilq	Ip	Ipq
Angra dos Reis	813.21	541	56	66.5	Good	6.9	Good
Aperibé	94.54	2	2	2.1	Poor	2.1	Poor
Araruama	638.15	34	4	5.3	Poor	0.6	Poor
Areal	110.72	1	1	0.9	Poor	0.9	Poor
Armação dos Búzios	70.98	0	0	0.0	Poor	0.0	Poor
Arraial do Cabo	152.11	0	0	0.0	Poor	0.0	Poor
Barra do Piraí	584.61	41	8	7.0	Poor	1.4	Poor
Barra Mansa	547.13	40	7	7.3	Poor	1.3	Poor
Belford Roxo	78.99	0	0	0.0	Poor	0.0	Poor
Bom Jardim	382.43	19	5	5.0	Poor	1.3	Poor
Bom Jesus do Itabapoana	596.66	32	8	5.4	Poor	1.3	Poor
Cabo Frio	413.58	65	14	15.7	Poor	3.4	Average
Cachoeiras de Macacu	954.75	927	83	97.1	Good	8.7	Good
Cambuci	558.28	6	2	1.1	Poor	0.4	Poor
Campos dos Goytacazes	4 032.49	608	75	15.1	Poor	1.9	Poor
Cantagalo	747.21	48	6	6.4	Poor	0.8	Poor
Carapebus	304.89	293	20	96.1	Good	6.6	Good
Cardoso Moreira	522.60	24	3	4.6	Poor	0.6	Poor
Carmo	305.75	252	23	82.4	Good	7.5	Good
Casimiro de Abreu	462.92	343	32	74.1	Good	6.9	Good
Comendador Levy Gasparian	108.64	1	1	0.9	Poor	0.9	Poor
Conceição de Macabu	338.26	114	15	33.7	Average	4.4	Average
Cordeiro	113.05	8	1	7.1	Poor	0.9	Poor
Duas Barras	379.62	3	1	0.8	Poor	0.3	Poor
Duque de Caxias	467.32	233	38	49.9	Good	8.1	Good
Engenheiro Paulo de Frontin	139.38	31	4	22.2	Average	2.9	Average
Guapimirim	358.44	317	28	88.4	Good	7.8	Good

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Iguaba Grande	50.98	7	2	13.7	Poor	3.9	Average
Itaboraí	429.96	127	10	29.5	Average	2.3	Poor
Itaguaí	282.61	167	16	59.1	Good	5.7	Good
Italva	291.19	18	2	6.2	Poor	0.7	Poor
Itaocara	433.18	118	8	27.2	Average	1.8	Poor
Itaperuna	1 106.69	319	16	28.8	Average	1.4	Poor
Itatiaia	241.04	230	38	95.4	Good	15.8	Good
Japeri	81.70	59	3	72.2	Good	3.7	Average
Laje do Muriaé	253.53	7	1	2.8	Poor	0.4	Poor
Macaé	1 216.99	886	82	72.8	Good	6.7	Good
Macuco	78.36	0	0	0.0	Poor	0.0	Poor
Magé	390.78	308	44	78.8	Good	11.3	Good
Mangaratiba	367.82	67	12	18.2	Poor	3.3	Average
Maricá	361.57	174	35	48.1	Good	9.7	Good
Mendes	95.32	15	2	15.7	Poor	2.1	Poor
Mesquita	41.17	1	1	2.4	Poor	2.4	Poor
Miguel Pereira	287.93	98	16	34.0	Average	5.6	Good
Miracema	303.27	0	0	0.0	Poor	0.0	Poor
Natividade	387.07	7	1	1.8	Poor	0.3	Poor
Nilópolis	19.39	1	1	5.2	Poor	5.2	Good
Niterói	133.76	35	8	26.2	Average	6.0	Average
Nova Friburgo	935.43	182	32	19.5	Poor	3.4	Average
Nova Iguaçu	520.58	479	58	92.0	Good	11.1	Good
Paracambi	190.95	24	3	12.6	Poor	1.6	Poor
Paraíba do Sul	571.12	15	4	2.6	Poor	0.7	Poor
Paraty	924.30	609	84	65.9	Good	9.1	Good
Paty do Alferes	314.34	8	2	2.5	Poor	0.6	Poor
Petrópolis	791.14	143	25	18.1	Poor	3.2	Average
Pinheiral	82.25	2	1	2.4	Poor	1.2	Poor
Piraí	490.26	120	17	24.5	Average	3.5	Average
Porciúncula	291.85	0	0	0.0	Poor	0.0	Poor
Porto Real	50.89	41	4	80.6	Good	7.9	Good
Quatis	284.83	51	8	17.9	Poor	2.8	Poor
Queimados	75.93	33	2	43.5	Good	2.6	Average
Quissamã	719.64	267	38	37.1	Average	5.3	Good
Resende	1 099.34	283	42	25.7	Average	3.8	Average
Rio Bonito	459.46	32	5	7.0	Poor	1.1	Poor
Rio Claro	846.80	719	74	84.9	Good	8.7	Good
Rio das Flores	478.78	10	2	2.1	Poor	0.4	Poor
Rio das Ostras	228.04	81	7	35.5	Average	3.1	Average
Rio de Janeiro	1 200.33	932	182	77.6	Good	15.2	Good
Santa Maria Madalena	810.96	84	19	10.4	Poor	2.3	Poor
Santo Antônio de Pádua	603.63	47	3	7.8	Poor	0.5	Poor
São Fidélis	1 034.83	308	16	29.8	Average	1.5	Poor
São Francisco de Itabapoana	1 118.04	212	18	19.0	Poor	1.6	Poor
São Gonçalo	248.16	2	1	0.8	Poor	0.4	Poor
São João da Barra	452.40	228	13	50.4	Good	2.9	Average
São João de Meriti	35.22	0	0	0.0	Poor	0.0	Poor
São José de Ubá	249.69	29	3	11.6	Poor	1.2	Poor

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São José do Vale do Rio Preto	220.18	12	5	5.5	Poor	2.3	Poor
São Pedro da Aldeia	332.49	22	6	6.6	Poor	1.8	Poor
São Sebastião do Alto	397.21	108	9	27.2	Average	2.3	Poor
Sapucaia	540.67	98	14	18.1	Poor	2.6	Average
Saquarema	352.13	207	34	58.8	Good	9.7	Good
Seropédica	265.19	129	27	48.6	Good	10.2	Good
Silva Jardim	937.76	681	51	72.6	Good	5.4	Good
Sumidouro	413.41	18	3	4.4	Poor	0.7	Poor
Tanguá	143.01	8	2	5.6	Poor	1.4	Poor
Teresópolis	773.34	229	42	29.6	Average	5.4	Good
Trajano de Moraes	591.15	28	5	4.7	Poor	0.8	Poor
Três Rios	322.84	170	16	52.7	Good	5.0	Good
Valença	1 300.77	6	4	0.5	Poor	0.3	Poor
Varre-Sai	201.94	0	0	0.0	Poor	0.0	Poor
Vassouras	536.07	29	3	5.4	Poor	0.6	Poor
Volta Redonda	182.11	14	4	7.7	Poor	2.2	Poor
Rio de Janeiro State	43 750	13 327	1 623	30.5		3.7	

Table A2. Abundance of freshwater native fish species per hydrographic region.

	RH-1	RH-2	RH-3	RH-4	RH-5	RH-6	RH-7	RH-8	RH-9
Acentronichthys leptos	109	20	0	0	171	17	36	5	7
Ancistrus multispinis	145	119	0	0	501	31	0	5	0
Astyanax keronolepis	1091	97	0	0	551	0	0	0	0
Astyanax lacustris	2	511	81	72	115	184	173	1950	1582
Atlantirivulus janeiroensis	0	0	0	0	0	11	0	0	0
Atlantirivulus jurubatibensis	0	0	0	0	0	0	0	0	51
Atlantirivulus guanabarensis	0	0	0	0	73	0	0	0	0
Atlantirivulus lazzarotoi	17	0	0	0	0	0	0	0	0
Atlantirivulus maricensis	0	0	0	0	1	0	0	0	0
Atlantirivulus simplicis	43	0	0	0	0	0	0	0	0
Australoheros ipatinguensis	0	6	112	99	0	23	32	0	257
Australoheros oblongus	0	18	4	0	89	49	0	126	47
Awaous tajasica	115	5	0	3	81	17	35	113	23
Brachyhypopomus janeiroensis	0	0	0	1	1	82	12	11	49
Brycon insignis	0	0	1	0	0	10	0	7	26
Brycon opalinus	0	30	20	8	0	0	14	0	1
Bryconamericus microcephalus	919	0	0	0	0	0	0	0	0
Bryconamericus ornaticeps	0	287	0	0	1900	0	0	0	0
Bryconamericus tenuis	0	0	0	20	0	128	88	287	40
Callichthys callichthys	0	47	12	3	198	19	11	56	165
Characidium alipioi	0	0	0	21	0	119	45	18	58
Characidium grajahuense	0	140	0	0	321	0	0	0	0
Characidium interruptum	0	14	0	0	249	236	0	38	152
Characidium japuhybense	869	0	0	0	0	0	0	0	0
Characidium lauroi	0	660	135	411	0	0	30	0	0

Characidium litorale	0	0	0	0	0	588	0	172	33
Characidium vidali	0	146	0	124	931	0	10	342	0
Corydoras nattereri	0	63	4	97	314	86	2	7	87
Crenicichla lacustris	0	19	36	7	0	43	60	71	597
Crenicichla lepidota	0	47	0	0	83	2	0	0	0
Cyphocharax gilbert	0	467	1	6	43	344	13	740	381
Delturus parahybae	0	0	0	0	0	0	0	0	1
Deuterodon giton	0	141	154	312	0	2217	243	677	1954
Deuterodon hastatus	193	269	0	32	2620	0	0	0	0
Deuterodon heterostomus	0	4	42	0	2	50	0	1	1
Deuterodon intermedius	179	2574	463	187	0	0	151	0	35
Deuterodon janeiroensis	0	5745	0	7	1384	512	17	0	0
Deuterodon luetkenii	0	0	0	0	35	98	6	6284	1450
Deuterodon taeniatus	0	26	9	70	6	982	346	3072	865
Dormitator maculatus	11	13	0	0	8	1	0	3	80
Eigenmannia virescens	0	0	7	17	7	42	125	14	17
Eleotris pisonis	31	9	0	0	28	26	5	26	23
Geophagus brasiliensis	4092	983	241	346	1809	200	364	875	1114
Glanidium melanopterum	0	14	26	9	0	2	25	3	11
Gymnotus carapo	0	90	37	52	51	44	11	13	23
Gymnotus pantherinus	38	10	0	0	61	47	5	41	5
Harttia carvalhoi	0	88	11	24	0	0	0	0	23
Harttia loricariformis	0	32	13	52	0	0	55	0	7
Hemipsilichthys gobio	0	9	0	10	1	0	8	0	0
Hemipsilichthys nimius	145	0	0	0	0	0	0	0	0
Hemipsilichthys papillatus	0	7	1	0	0	0	0	0	0
Hisonotus notatus	0	205	4	3	689	24	31	0	113
Hisonotus thayeri	0	0	0	0	0	557	92	92	107
Hollandichthys multifasciatus	334	11	0	0	0	0	0	0	0
Homodiaetus banguela	0	0	0	0	0	9	0	0	0
Homodiaetus passarellii	0	2	0	0	48	0	0	0	0
Hoplerythrinus unitaeniatus	0	2	1	0	17	10	0	10	121
Hoplias malabaricus	14	45	13	20	104	83	6	142	163
Hoplosternum littorale	0	96	23	8	38	1	4	2	31
Hyphessobrycon bifasciatus	0	154	8	58	1070	192	11	5063	2894
Hyphessobrycon boulengeri	0	33	0	0	245	15	0	311	496
Hyphessobrycon flammeus	0	48	0	1	35	12	0	0	4
Hypomasticus copelandii	0	10	2	13	13	13	19	19	132
Hypomasticus mormyrops	0	10	14	7	0	0	17	1	3
Hypomasticus thayeri	0	0	0	3	0	0	0	0	21
Hypostomus affinis	0	0	3	0	5	98	1	65	0
Hypostomus auroguttatus	0	0	2	2	0	0	2	0	0
Hypostomus luetkeni	0	34	20	155	0	0	168	0	87
Hypostomus punctatus	0	95	0	0	244	2	0	0	0
Hypostomus vermicularis	0	0	52	4	0	0	2	0	4
Imparfinis minutus	0	61	59	4	0	0	6	0	7
Imparfinis piperatus	0	4	4	0	4	0	0	0	0

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Ituglanis parahybae	0	0	0	0	0	10	0	0	3
Jenynsia darwini	0	0	0	0	7	8	0	160	1516
Jenynsia lineata	0	0	0	0	318	65	0	0	0
Knodus moenkhausii	0	0	0	267	0	0	10	0	29
Kronichthys heylandi	664	167	0	1	151	4	0	0	0
Kryptolebias brasiliensis	0	54	0	0	164	16	0	0	0
Kryptolebias caudomarginatus	0	166	0	0	56	0	0	0	0
Kryptolebias gracilis	0	0	0	0	0	28	0	11	0
Kryptolebias ocellatus	0	86	1	0	0	2	0	0	0
Leptolebias marmoratus	0	0	0	0	10	0	0	0	0
Leptopanchax citrinipinnis					184	0	0	0	0
Leptopanchax opalescens	0	7	0	0	55	0	0	0	0
Leptopanchax sanguineus	0	0	0	0	15	0	0	0	0
Leptopanchax splendens	0	0	0	0	50	0	0	0	0
Listrura costai	15	0	0	0	0	0	0	0	0
Listrura nematopteryx	0	0	0	0	156	0	0	0	0
Listrura tetraradiata	0	0	0	0	0	100	0	0	1
Loricariichthys castaneus	0	89	15	1	19	317	19	1	122
Megaleporinus conirostris	0	3	0	4	0	0	23	0	37
Microcambeva barbata	0	0	0	0	0	71	0	4	0
Microcambeva bendego	0	0	0	0	7	0	0	0	0
Microglanis nigripinnis	0	0	0	0	21	0	0	0	0
Microglanis parahybae	0	31	0	0	0	0	44	0	61
Microglanis pleriqueater	0	0	0	0	0	55	0	10	0
Mimagoniates microlepis	808	255	0	637	1328	501	0	30	33
Nematolebias papilliferus	0	0	0	0	28	0	0	0	0
Nematolebias whitei	0	0	0	0	17	291	0	9	0
Neoplecostomus microps	0	825	225	135	82	0	118	219	1
Neoplecostomus paraty	163	0	0	0	0	0	0	0	0
Neoplecostomus variipictus	0	0	0	55	0	0	80	0	0
Notholebias cruzi	0	0	0	0	29	32	0	0	0
Notholebias fractifasciatus	0	0	0	0	20	2	0	0	0
Notholebias minimus	0	181	0	0	8	0	0	0	0
Oligosarcus hepsetus	10	346	94	80	64	24	92	154	249
Ophthalmolebias constanciae	0	0	0	0	0	47	0	65	0
Otocinclus affinis	0	6	1	14	26	3	1	1	13
Otothyris lophophanes	2	24	4	3	45	135	3	69	41
Pachyurus adspersus	0	3	9	1	0	0	7	0	29
Paragenidens grandoculis	0	0	0	0	0	0	0	0	1
Pareiorhaphis garbei	0	0	0	0	232	13	22	54	0
Pareiorhina brachyrhyncha	0	0	160	0	0	0	0	0	0
Pareiorhina rudolphi	77	553	672	0	0	0	0	0	0
Parotocinclus bidentatus	0	0	22	1	0	0	0	0	0
Parotocinclus fluminense	0	0	0	0	0	515	0	0	0
Parotocinclus maculicauda	0	390	0	0	940	36	4	179	0
Parotocinclus muriaensis	0	0	0	0	0	0	0	0	12

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Phalloceros anisophallos	3391	1144	0	0	101	0	0	0	0
Phalloceros enneaktinos	701	0	0	0	0	0	0	0	0
Phalloceros harpagos	468	3200	276	1295	773	887	247	3306	1148
Phalloceros leptokeras	946	57	121	2216	1419	56	0	0	0
Phalloceros tupinamba	0	200	0	0	0	0	0	0	0
Phalloptychus januarius	0	33	0	0	1076	133	0	0	11100
Phallotorynus fasciolatus	0	0	0	0	0	0	0	0	47
Piabina argentea	0	0	0	0	0	0	10	0	0
Pimelodella lateristriga	101	58	2	25	224	201	81	167	236
Pimelodus maculatus	0	11	57	11	0	0	8	0	13
Poecilia vivipara	120	378	3	58	2278	298	130	1660	10094
Pogonopoma parahybae	0	0	3	1	0	0	18	0	0
Prochilodus lineatus	0	2	4	0	0	0	13	6	233
Prochilodus vimboides	0	0	0	1	0	0	0	11	170
Psalidodon parahybae	0	138	179	105	82	192	401	9	1395
Pseudotothyris janeirensis	0	147	0	0	29	9	0	29	18
Rhamdia quelen	43	138	24	29	188	26	24	53	55
Rhamdioglanis frenatus	55	72	0	0	48	0	3	0	0
Rhamdioglanis transfasciatus	0	1	0	0	63	108	1	131	0
Rineloricaria nigricauda	0	553	309	381	0	0	4	0	4
Rineloricaria nudipectoris	0	22	0	263	1249	62	0	145	0
Rineloricaria steindachneri	0	3	0	0	0	0	107	0	23
Rineloricaria zawadzki	40	227	14	0	95	0	0	0	0
Schizolecis guentheri	2592	622	0	20	1394	123	42	513	0
Scleromystax barbatus	431	147	0	134	732	144	37	51	7
Scleromystax prionotos	0	0	0	0	0	0	0	11	7
Spintherobolus broccae	0	10	0	0	158	39	0	17	0
Steindachneridion parahybae	0	0	11	4	0	0	1	0	0
Synbranchus marmoratus	3	7	11	2	56	11	4	10	7
Taunayia bifasciata	2	0	1	0	0	0	0	0	0
Trachelyopterus striatulus	0	0	0	0	5	0	7	0	0
Trichogenes longipinnis	627	0	0	0	0	0	0	0	0
Trachelyopterus striatulus	0	31	1	4	0	23	0	71	78
Trichomycterus albinotatus	0	0	94	0	0	0	0	0	0
Trichomycterus auroguttatus	0	11	142	0	0	0	0	0	0
Trichomycterus caipora	0	0	0	0	0	0	0	110	97
Trichomycterus claudiae	0	83	0	0	0	0	0	0	0
Trichomycterus florensis	0	0	16	16	0	0	0	0	0
Trichomycterus fuliginosus	0	0	0	0	0	0	58	0	0
Trichomycterus goeldii	0	0	0	179	0	0	27	0	0
Trichomycterus giganteus	0	201	0	0	153	0	0	0	0
Trichomycterus itatiayae	0	0	197	0	0	0	0	0	0
Trichomycterus jacupiranga	452	30	0	0	77	0	0	0	0

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Trichomycterus largoperculatus	0	0	0	33	0	0	28	0	1
Trichomycterus macrophthalmus	0	142	0	0	0	0	0	0	0
Trichomycterus mariamole	0	13	82	0	0	0	0	0	0
Trichomycterus mirissumba	0	0	90	0	0	0	0	0	0
Trichomycterus nigricans	0	0	0	0	972	16	0	0	0
Trichomycterus nigroauratus	0	215	24	0	0	0	0	0	0
Trichomycterus paquequerense	0	0	0	1012	80	0	0	0	0
Trichomycterus potschi	0	134	102	0	0	0	0	0	0
Trichomycterus puriventris	0	0	0	0	0	0	228	0	3
Trichomycterus vitalbrazili	0	0	0	0	0	0	60	0	0

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