AQUATIC HABITAT ECOLOGY & CONSERVATION: CONTINENTAL AND MARINE ECOSYSTEMS CONNECTIVITY

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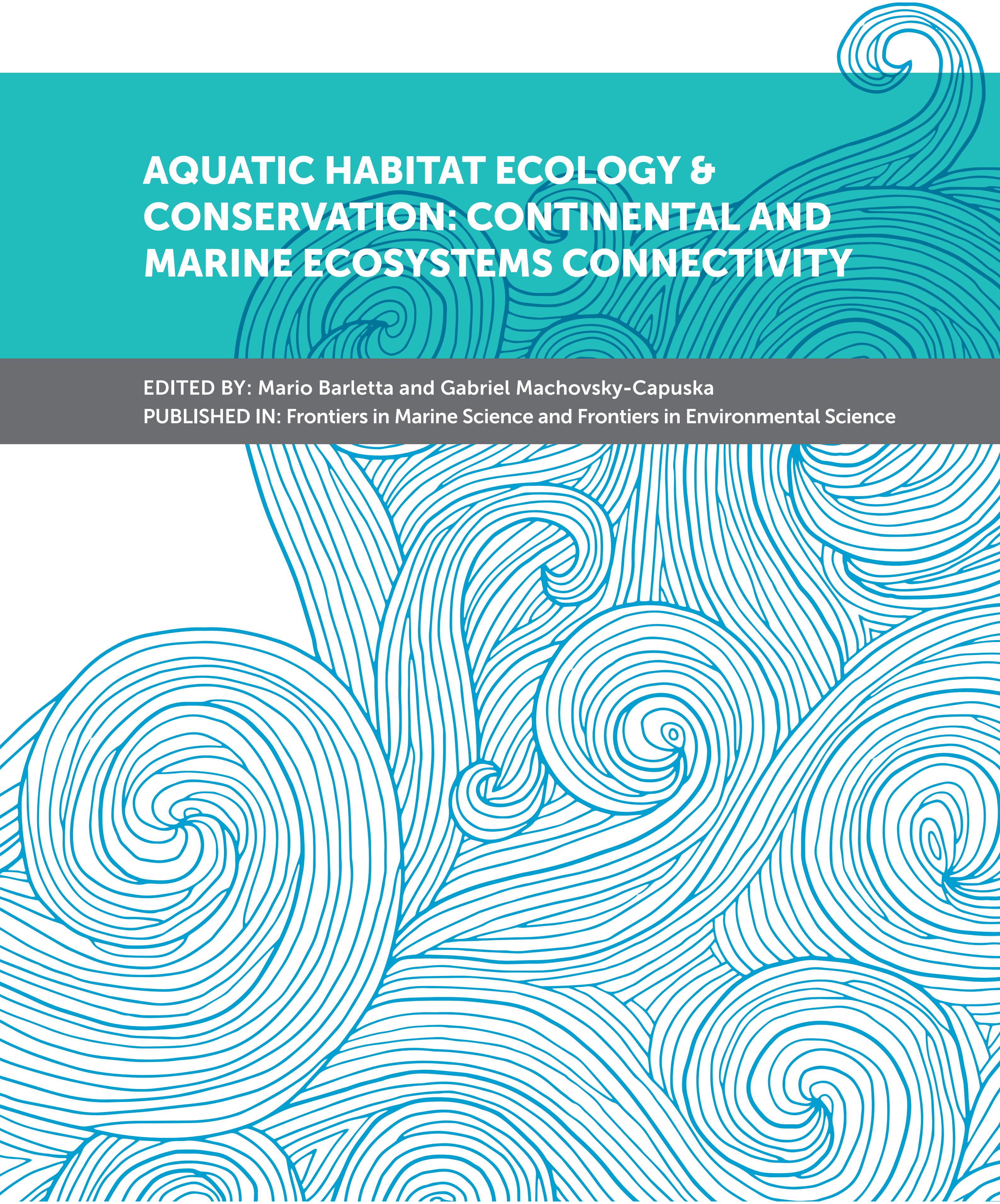

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AQUATIC HABITAT ECOLOGY & CONSERVATION: CONTINENTAL AND MARINE ECOSYSTEMS CONNECTIVITY

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The 'Aquatic Habitat Conservation in South America' Symposium occurred during the XXI Brazilian Society of Ichthyology Meeting. The proceedings were published as a special issue in the Journal of Fish Biology (vol. 89, Number 1, June 2016). In this special issue, authors provided an analytical overview of problems faced by the conservation of fishes and aquatic habitats of South America. Habitat loss emerged as the greatest concern for all South American aquatic ecosystems, with a long list of causes related to unsustainable development models.

Based on this finding, we would like to extend this topic to other continents, different climates, fauna and flora around the world. Our goal is to provide a comprehensive and multidisciplinary overview of variables that influence flora and fauna distributions and shape their ecological interactions within aquatic ecosystems

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Table of Contents

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Spongivory by Fishes on Southwestern Atlantic Coral Reefs: No Evidence of Top-Down Control on Sponge Assemblages

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Predator-prey dynamics can affect assemblage structure and ecosystem processes representing a central theory in ecology. In coral reef ecosystems, recent evidences have suggested that sponge assemblages in regions with high diversity, like the Caribbean, are controlled by reef fishes (i.e., top-down control); however, this has been poorly studied in low diversity coral reefs. This study investigated the influence of fish predators on sponge assemblage structure in South Atlantic coral reefs, systems with high endemism and relatively low hermatypic coral diversity. We investigates (i) whether sponge cover is negatively correlated to spongivorous fish density, (ii) potential spongivory effects on competitive interactions between sponges and hermatypic corals, and (iii) foraging preferences of spongivorous fishes. Benthic cover and spongivorous fish density were assessed by photo sampling and visual census, respectively. We did not observe a negative correlation of the total density of spongivorous fish with total sponge cover. However, a significant negative correlation between density of fish species *Pomacanthus arcuatus* and cover of sponge species *Scopalina ruetzleri* was found. Spongivorous fish consumed preferentially the sponges *Desmapsamma anchorata*, *Niphates erecta, Aplysina cauliformis,* and *S. ruetzleri,* the first two species considered palatable and the second two with chemically defense mechanism. An increase to angelfish density was not related with the number of coral-sponge encounters. Thus, the effects of spongivorous fishes on sponges cover and competitive interactions with hermatypic corals is weaker in Southwestern Atlantic than previously reported in Caribbean coral reefs. We discuss how local human impacts (e.g., fishing and nutrients input) can influence the observed patterns.

Keywords: predation, angelfishes, porifera, sponge-coral interaction, top-down control, Todos os Santos Bay, reef ecology

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INTRODUCTION

Predation is an important ecological process that impacts energy and matter flows in food chains. Food web dynamics has been proposed as one of the most important theories in ecology (Fretwell, 1987) and as the main regulatory mechanism of biological assemblage structure at local levels (Paine, 1966).

In marine systems, it is well-known that predator-prey interactions can affect the structure of biological assemblages and ecosystem functions (Hixon, 1991; Bellwood et al., 2004b). Furthermore, predation may reduce competitive exclusion by decreasing abundances of superior competitors (Paine, 1966; Hay, 1991). Competition for space is often an important regulator process in marine hard bottoms, as coral and rocky reefs, and influences patterns of abundance and diversity of biological assemblages (Connell et al., 2004; Chadwick and Morrow, 2011).

Within reef environments, generally sponges are better competitors for space than corals (Aerts, 1998; Pawlik, 2011), mostly due to their defense strategies (Wulff, 2006), as secondary metabolites, and overgrow ability (Aerts, 1998; Meurer et al., 2010). Sponges can negatively affect the recruitment and growth of hermatypic corals, as well as other important coral reefs processes (e.g., substrate construction) (Chadwick and Morrow, 2011). The effects of sponge competition on corals can be indirectly reduced by fish predation on sponges (i.e., fish spongivory) which may reduce competitive encounters between both taxa (Hill, 1998; Loh et al., 2015). Since Paine's work (Paine, 1966), it is widely accepted that the indirect effects of predation can have an influence on community structure, identifying and examining these effects is an important task in understanding community dynamics (Menge, 1995).

Sponges are frequently diverse and abundant in coral reef benthic communities, thus being a good model to evaluate predator-prey interactions (Dunlap and Pawlik, 1996; Ruzicka and Gleason, 2009). Sponges are key to ecosystem functioning because they are highly efficient filters, removing microbes and organic matter from water, transferring nutrient from pelagic to benthic habitats (Bell and Barnes, 2000; Wulff, 2001; de Goeij et al., 2013). Sponges contribute to complex balance between calcium carbonate loss or accretion, essential in the dynamics of coral reef growth (Wulff Buss and Buss, 1979; Wulff, 2001; Bell, 2008) and are an important food source for many marine organisms, especially for fishes (Randall and Hartman, 1968; Wulff, 1994).

Spongivory is mainly performed by angelfishes (Pomacanthidae family) of genera *Pomacanthus* and *Holacanthus* (Randall and Hartman, 1968; Carballo and Camacho, 2010), which are the most common and conspicuous sponge-feeding reef fishes around the world (e.g., Bellwood et al., 2004a). Different approaches have been used to investigate the potential effect of predation by reef fishes, for instance by using stomach content analysis (Randall and Hartman, 1968; Andréa et al., 2007; Reis et al., 2013) and fish feeding activity observations (Longo and Floeter, 2012; Pratchett et al., 2014). Although there is information about fish predation pressure on sponge assemblages (Pawlik et al., 2018), little is known about the spongivorous fish foraging behavior. Foraging activity is an essential aspect of habitat use by fishes and a predominant daily activity.

Evidences in high diversity coral reefs, such as Caribbean reefs, showed that top-down regulation by fish play a decisive role on growth of different sponge species, consequently affecting benthic assemblages (Dunlap and Pawlik, 1996; Pawlik, 1997, 1998; Pawlik et al., 2013, 2018). Brazilian coral reefs have peculiar features as relatively low coral diversity, high sedimentation rates and elevated turbidity due to abundant river flow into shore. These conditions have been considered marginal for coral optimal growth, so these reefs are known as marginal coral reefs (Leão et al., 2003; Suggett et al., 2012; Loiola et al., 2013). A small number of studies have conducted spongivorous fish stomach content analysis in rock (Andréa et al., 2007; Batista et al., 2012) or coral reefs (Reis et al., 2013) in Brazil and spongivorous feeding behavior was not previously investigated.

Here, we evaluate whether spongivory performed by angelfishes can influence the sponge assemblage structure and indirectly influence competitive encounter number between sponges and hermatypic corals (i.e., each contact found between different colonies, or encounter closer than 5 cm) in marginal coral reefs. To achieve this, we tested whether (1) sponge cover would be negatively related to angelfish density, (2) whether competitive encounter number between sponges and hermatypic corals would be negatively related to angelfish density and (3) sponge preferences by angelfishes during foraging activities. With (1) we investigated if top-down control would directly be acting, with (2) we considered a potential indirect effect of top-down control and with (3) we explored potential specific relationships between spongivorous fish and sponges.

MATERIALS AND METHODS

Study Area

The study was conducted at Todos os Santos Bay (TSB), located in eastern coast of Brazil (**Figure 1**), a region with high endemism of coral species in the South Atlantic Ocean (Leão et al., 2003) and considered priority for conservation (Vila-Nova et al., 2014; Cruz et al., 2015). Coral reefs in TSB are located both in entrance (the outer reefs, occupying an area of 17.7 km^2) and in its interior (the inner reefs, 13 km^2) (**Figure 1**). The sponge assemblage are specially well-developed in inner reefs where are subject to several types of human interference (e.g., nutrient input, fishing) (Cruz et al., 2009). These interferences can contribute to changes in sponge assemblages by reducing of fish predators and increasing nutrients through discharge of domestic and industrial effluents. These reefs, at depths of ∼2–13 m, consists of reef patches 20–60 m in length surrounded by fine sediments. Ten reef sites haphazardly selected in TSB (**Supplementary Table 1**), were sampled between January and March 2016 (**Figure 1**).

Benthic and Angelfishes Assemblages Surveys

We characterized sponge and coral assemblages using photo-quadrats (0.25 × 0.25 m). Two SCUBA divers haphazardly took 100 high resolution digital images (CANON G12 model, 3,648 × 2,736 pixels) on each of the 10 reef sites using a PVC frame at 40 cm distance from the substrate. Photo-quadrats (e.g., **Supplementary Figure 1**) were taken around 2 m of each other, resulting to a total sampled area of 6.25 m^2 for each reef site. Benthic cover (%) were estimated through 20 randomly distributed points per photo-quadrat using Coral Counting Point with Excel Extensions Software (CPCe) (Kohler and Gill, 2006). These quadrats (n = 100) were used to sample the

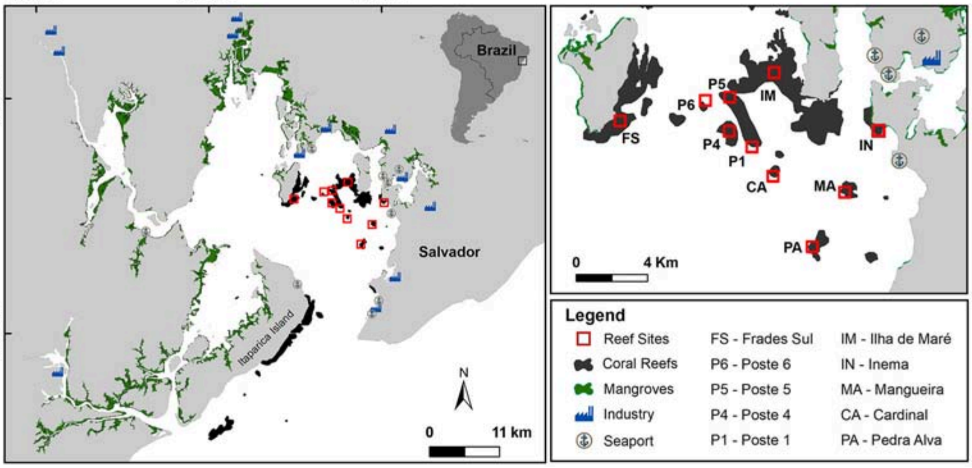

FIGURE 1 | Map of coral reefs sampled in Todos os Santos Bay.

sponge assemblage and other benthic invertebrates at each site. Identification of sponges and benthic groups was performed *in situ* for each photo-quadrat. Whenever identification in the field was not possible, the specimen was collected, fixed in 80% ethanol and identified in the laboratory following available literature (Hajdu et al., 2011). The number of sponge-coral encounter (i.e., all sponges in contact with scleractinian corals and calcified hydroids colonies) was quantified in the photographs. We considered a natural encounter when one sponge was in contact with, or closer than 5 cm to, a coral colony (Chadwick and Morrow, 2011). Encounters were quantified in the entire area of each photo-quadrat and photos of each reef were pooled for analyses.

Densities of angelfish species *Pomacanthus arcuatus, P. paru,* and *Holacanthus ciliaris* were estimated by trained divers along ten 20 × 2 m transects (400 m² per reef site) following fish monitoring protocol of the Atlantic and Gulf Rapid Reef Assessment (AGRRA) (Kramer and Lang, 2003).

Fish Foraging Activity

Focal animal method was used to measure angelfishes foraging activity (i.e., feeding rates and food preferences) (Bonaldo et al., 2006; Pereira et al., 2016). For each focal animal, angelfish specimen was followed and observed during 2 min intervals by SCUBA divers at 3 m distant from the fish, during this time we counted number of bites identifying sponge species. All occurrences were recorded on clipboards.

To avoid observation of the same specimens, each observation was conducted at least 5 m distant (Nunes et al., 2013). A total of 36 specimens of *P. arcuatus*, 12 *P. paru,* and 11 *H. ciliaris* were observed across all the reef sites, excepting Ilha de Maré where visibility was lower than 3 m. All observations were conducted between 09:00 and 15:00 h. We sampled spongivorous fish behavior in similar conditions of temperature and luminosity.

Data Analysis

To evaluate the relationship between angelfish density and (i) sponge cover and (ii) number of sponge-coral encounters, Spearman correlation coefficients were calculated with 95% confidence intervals and $\alpha = 0.05$. For (i) we used means of angelfish density and means of sponge percentage cover on each reef and, for (ii) we used polled data (from all photo-quadrats of each reef) to test whether encounter would be negatively related to mean angelfish density and also used reefs as replicates. To evaluate the species-specific relationship of each angelfish species (three species, *Pomacanthus paru*, *P. arcuatus,* and *Holacantus ciliares*) mean density and their interactions with 8 sponge species mean cover (five sponge species selected by fishes observed in focal animal method and three most abundant found in the benthic data survey), multiple regressions using the stepwise model selection method were conducted with an α of 0.01, using each reef as a replicate. These analyses were performed using the R software (R Core Team, 2013): the packages *pspearman* and *My.stepwise* were used for Spearman correlation and stepwise multiple regression (Savicky, 2015; Hu, 2017), respectively.

The Ivlev's electivity index was used to verify angelfish preference or rejection by sponges that were bitten during foraging activity (focal animal). The electivity index was calculated, with pooled data from all reefs, as $E_i = (r_i - n_i)/(r_i + n_i)$ where E_i is the value of electivity for the sponge species i; r_i is the percentage of bites on the sponge i and ni is the sponge cover i across all locations. The electivity index varies from -1 to $+1$, where values near -1 indicate low preference or rejection while values near $+1$ indicate high preference for a particular sponge (Krebs, 1989). To generate a 95% confidence interval around the observed E_i, we used non-parametric bootstrapping procedures, in which fish samples were pooled for each reef and used as sample units (10,000 randomizations). The confidence limits were determined using the percentile method (Manly, 1997).

We used permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) to explore potential differences of fish and sponge assemblages between reef sites, based on the untransformed data with Bray-Curtis dissimilarities, using 9,999 random permutations. A pair-wise test was used to analyze which reef differs from each other. To visualize the spatial structure of both assemblages we used nonmetric multidimensional scaling (nMDS). These analyses were performed using the software PRIMER 6 (Clarke and Warwick, 2001).

RESULTS

Benthic and Angelfish Assemblages

Overall sponge cover were 9.96 ± 0.76% (mean for all sites ± standard error), while hermatypic corals were 11.30 ± 2.25%, zoanthids 12.76 ± 6.34%, and turf algae 38.15 ± 3.93%. The Ilha de Maré reef site had the highest sponge cover 15.13 ± 0.51%, whereas Poste 1 had the lowest 7.3 ± 0.16% (**Figure 2**).

The top five most abundant sponge species were *Desmapsamma anchorata* (3.8 ± 0.79%), *Neopetrosia* sp. (0.84 ± 0.22%), *Clathria venosa* (0.83 ± 0.16%), *Aplysina cauliformis* (0.78 ± 0.1%) and *Ircinia strobilina* (0.67 ± 0.24%) (**Supplementary Figure 2A**; **Supplementary Table 2**). The angelfish density was 2.96 ± 0.24 (fishes mean for all sites/40 m^2 ± standard error). The highest angelfish density were observed at Inema (3.9 ± 4.82), Poste 4 (3.7 ± 2.0) and Frades Sul (3.7 ± 2.16) while Cardinal were the lowest (1.5 ± 1.2) (**Supplementary Figure 2B**). The most abundant species was *P. arcuatus* (1.92 ± 2.9) followed by *H. ciliaris* (6.0 ± 1.89) and *P. paru* (4.4 ± 1.39) (**Supplementary Figure 2B**).

Overall, in assemblage level, there was no significant relationship between angelfish density and sponge cover (**Figure 3A**). However, the species-specific relationship among *P. arcuatus* density and *S. ruetzleri* cover was significant (**Figure 3B**). PERMANOVA showed significant differences in the structure of sponge ($p < 0.001$) and angelfish assemblages ($p < 0.001$) between sites (**Supplementary Tables 3–5**; **Supplementary Figure 3**) showing a lot of spatial variability in the abundance of both groups along Todos os Santos Bay.

Foraging Activity

P. arcuatus had the highest bites rates (10.1 bites mean per 2 min ± 2.2, $n = 36$), followed by *H. ciliaris* (4.66 ± 2.19, $n = 12$) and *P. paru* (1.55 ± 0.69, $n = 11$). The electivity index showed that all three angelfish species selected *D. anchorata* during foraging activities (**Figure 4**). *S. ruetzleri* was selected by both *P. arcuatus* and *H. ciliaris*. In addition, *P. arcuatus* also selected other two sponge species *Niphates erecta* and *A. cauliformis*.

Sponge-Coral Encounters

A total of 109 sponge-coral encounters were observed. The average sponge-coral encounters TSB was 12.6 ± 1.6 and the top three most abundant sponge species had the higher number of encounters with corals were *D. anchorata* (29%, $n = 32$), *A. cauliformis* (15%, $n = 16$) and *C. venosa* (12%, $n = 13$). The most frequent coral species encountered with sponges was *Montastraea cavernosa* (**Supplementary Table 6**). There was no significant relationship between sponge-coral encounters and angelfish density ($\rho = 0.05$; $p = 0.8$; **Figure 5**).

DISCUSSION

Top-down or bottom-up control of sponge assemblages in coral reefs is an important contemporary discussion (e.g., Pawlik et al., 2018). An evidence for top-down control in TSB reefs would be if sponge cover in sites with higher angelfish density were smaller than in sites with low angelfish (spongivorous) densities. Concomitantly, there would be more competition between hermatypic corals and sponges in sites with smaller densities of angelfish. The results did not indicate a general negative relationship between abundances of angelfish and sponges and there was no significant relationship between coral-sponge encounters and angelfishes density. However, a significant species-specific negative relationship between *P. arcuatus* density and *S. ruetzleri* cover was observed. Additionally, both angelfish *P. arcuatus* and *H. ciliaris* selected *S. ruetzleri* during feeding activities. Thus, our results do not suggest a general top-down control of sponge assemblages but potential important species-specific relationships.

In Caribbean reefs sponge assemblages have been found to be primarily controlled by predatory reef fishes (Pawlik et al., 2013) and by hawksbill turtles (Pawlik et al., 2018). The biodiversity and abundance of spongivorous fishes and sponges in Caribbean

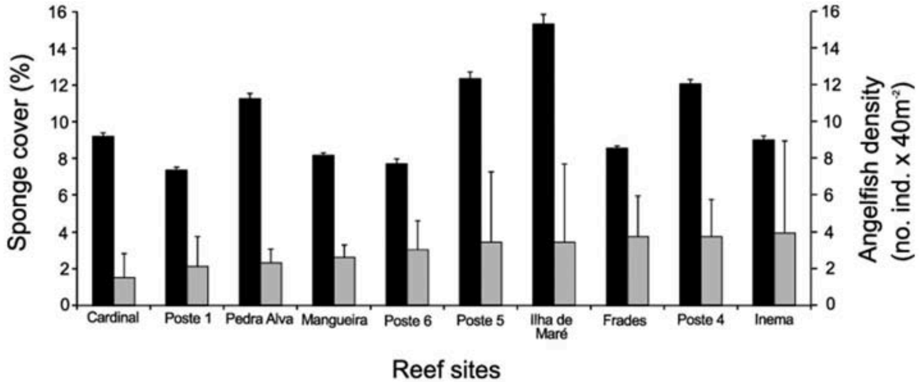

FIGURE 2 | Mean (+s.e.) sponge cover (black bars) and mean angelfish density (gray bars) of 10 reef sites in Todos os Santos Bay.

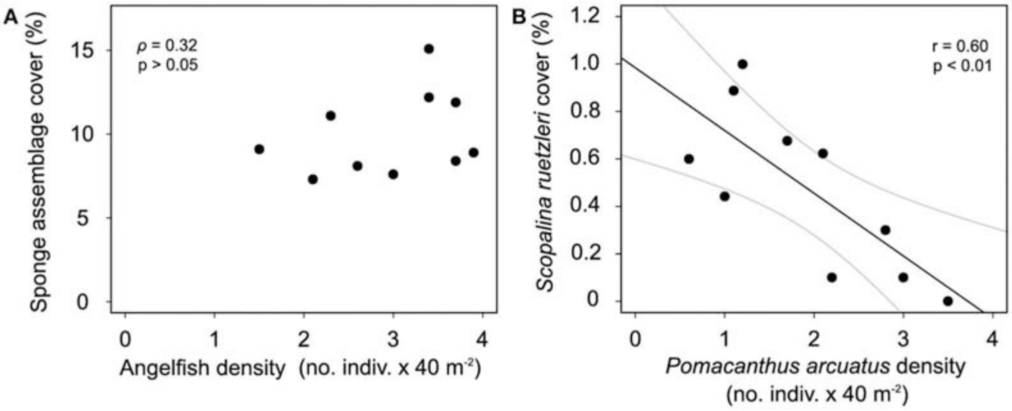

FIGURE 3 | (A) Relation between mean percentage of sponge cover and mean angelfish density ($\rho = 0.32$, $p > 0.05$) on each reef and **(B)** relation between *Scopalina ruetzleri* and *Pomacanthus arcuatus* on each reef with best fit-line showing negative correlation (*S. ruetzleri* cover = 1.02–0.28 *P. arcuatus* density). Gray lines indicate 95% confidence intervals.

reefs are considerably higher than in Southwestern Atlantic reefs (Roberts et al., 2002; van Soest et al., 2012). High predator species number and abundance could explain regional differences in ecosystem processes (Hooper et al., 2005; Floeter et al., 2008). For instance, biodiversity strongly influences ecosystem processes by altering pathways of energy and material flows due to functions performed by different groups of organisms at different systems (Hooper et al., 2005).

Local stressors such as sedimentation, nutrient inputs and overfishing also may contribute to reduce top-down effects decreasing fish predator density or favoring growing of certain sponges (Hughes, 1994; Roberts, 1995; Fabricius, 2005; Bell et al., 2015). High natural sedimentation rates intensified by human activities, can affect benthic sessile groups like sponges (Bell et al., 2015) and hermatypic corals (Fabricius, 2005). Nevertheless, some sponges can tolerate it, and in some cases thrive in turbid environments (Cerrano et al., 2007; de Voogd, 2012; Schönberg, 2015). The most abundant sponge species in TSB, *D. anchorata*, presented two important characteristics. First, it is able to incorporate free sediment particles that may give structural reinforcement to their body (Hajdu et al., 2011; Schönberg, 2016). Second, it can establish interactions with several organisms, mainly growing over other organisms with erect growth such the octocoral *Carijoa riisei* (Calcinai et al., 2004) and the branching coral *Millepora alcicornis* (McLean and Yoshioka, 2008). In fact, we observed contact between *D. anchorata* and *M. alcicornis* and *M. cavernosa* in the present study, potentially allowing *D. anchorata* to avoid sediment accumulation (McLean and Yoshioka, 2008; Schönberg, 2016). Sediment-incorporation by the sponge can also reduce the necessity of spicule formation (i.e., spiculogenesis) saving energy that can be allocated to other biological demands such as growth, reproduction and competition (Schönberg, 2016). In addition, *D. achorata* morphology can also occur as a branching form, avoiding sediment accumulation, with relatively high growth rates, that may accelerate the recovery of predation and competition damages (Wulff, 2006). These adaptations to high sediment conditions (e.g., branching morphology, fast growth rates and rapid regeneration) can explain the increased cover of *D. anchorata* in TSB reefs. The hypothesis of superior competitive abilities due to tolerance of natural and/or anthropogenic sedimentation can also be important to explain higher abundance of other sponge species. However, manipulative experiments are necessary to understand the role of competition in shaping sponge assemblages in TSB.

The relative high sponge cover found in TSB may be associated with availability of particulate food as picoplankton (Lesser, 2006; Lesser and Slattery, 2013) and dissolved organic carbon (DOC), both important resources used by sponges (de Goeij et al., 2013; Poppell et al., 2014; Pawlik et al., 2015, 2018). Local aspects of TSB such as natural and anthropic nutrient inputs and picoplankton availability may favor or control sponge assemblages. However, studies that suggested bottom-up control on sponge assemblages do not analyzed DOC as available resource (Lesser, 2006; Lesser and Slattery, 2013), not helping to sustain the argument (see review in Pawlik et al., 2015). Thus, in order to investigate what regulates sponge assemblages, futures studies must also evaluate nutritional aspects. From our results, considering the current status of TSB (e.g., anthropogenic impacts), the bottom-up control appears to have major influence on sponge assemblages in the area.

We observed a large variability in the structure of sponges and angelfishes between reefs. Unlikely these spatial differences are only caused by natural variables. But, we believe that these patterns are strongly influenced by multiple human activities (e.g., fishing, sedimentation, effluents) which also change in space and influence reef environmental quality in this bay (e.g., Cruz et al., 2014). For instance, several coral reefs in TSB have historically undergone anthropic impacts such as contamination by organic and inorganic pollution from domestic influxes and industrial effluents (e.g., Souza Santos et al., 2000; Barros et al., 2012; Hatje and Barros, 2012). High levels of nutrients can increase cover and abundance

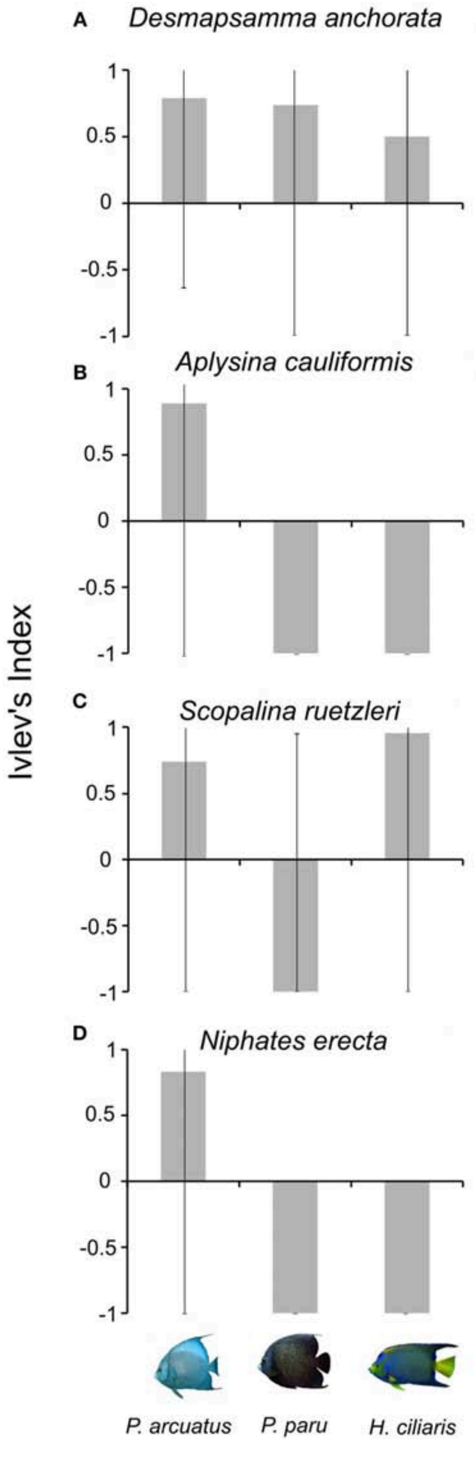

FIGURE 4 | Ivlev's electivity index results of the spongivourous fish *Pomacanthus arcuatus*, *Pomacanthus paru*, and *Holacanthus ciliaris* for sponges (**A**–*Desmapsamma anchorata*, **B**–*Aplysina cauliformes*, **C**–*Scopalina ruetzleri*, **D**–*Niphates erecta*) bitten by at least one spongivourous fish. Lines indicate 95% confidence intervals.

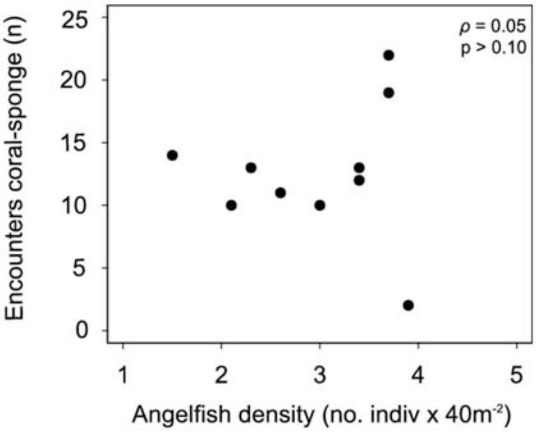

FIGURE 5 | Relationship between total number of sponge-coral encounters and mean angelfish (spongivorous) density ($\rho = 0.05$; $p = 0.8$).

of some sponge species (Zea et al., 1994), although it has been shown as a factor that reduces sponge species diversity (Muricy, 1989). *C. venosa*, frequently found in TSB, can increase its abundance in sites with large organic contamination while *S. ruetzleri*, with relatively lower abundances in TSB, was suggested as sensible to organic pollution (Alcolado and Herrera, 1987).

A possible evidence that top-down control was operating in TSB was that *S. ruetzleri* had negative relationship with *P. arcuatus* abundance, showing a specific top-down control. Surprisingly, our results of electivity index showed that *S. ruetzleri*, previously considered chemically defended (Chanas and Pawlik, 1996), was selected by both *P. arcuatus* and *H. ciliaris*. The sponge *D. anchorata* was selected by all spongivorous fish, probably due to intense use (i.e., high bite rates) and high availability on coral reefs studied, being easily find by fish.

Marine fishes have been affected by many anthropogenic stressors such as overfishing and pollution (Pauly et al., 2002; Pereira et al., 2014) which can cause a decline on species richness and abundance (e.g., McKinley and Johnston, 2010). Overfishing is generally regarded as the major human activity impacting fish assemblages. In Brazil, several studies suggested that a large number of edible and ornamental fish, have been exploited, leaving significant changes in structure of fish assemblages (Costa et al., 2003; Gasparini et al., 2005; Floeter et al., 2006). For instance, angelfishes (*Pomacanthus* and *Holacanthus* genus) are often target of ornamental fishing in Brazil (Gasparini et al., 2005) and there are regulations for exploitation (Sampaio and Nottingham, 2008), however, the enforcement of such laws are usually not efficient.

Overfishing on Caribbean coral reefs increases the incidence of sponge-coral interactions, especially with sponges overgrowing corals (Loh et al., 2015), but we did not find a significant correlation between the number of encounters of sponge-coral and spongivorous fish density. Generally, *D. anchorata* was frequently observed in contact with corals (especially with *M. cavernosa)* in TSB. This sponge showed highest relative frequency of contact with corals also in

Caribbean coral reefs, frequently overgrowing corals (Aerts and Van Soest, 1997).

The depletion of consumer fishes by overfishing may indirectly result in elevate prey abundance modifying the ecosystem structure and function according to trophic cascade theory (Pinnegar et al., 2000; Dulvy et al., 2004). Therefore, the top-down control of spongivory on sponge assemblages could also be weak on coral reefs at other Southwestern Atlantic reef sites. In TSB, coral reefs are under intense ornamental fishing and trade (Sampaio, 2006) and combined with organic matter influxes and other factors can result in dominances of non-reef build groups, as sponges (McClanahan et al., 2002; Maliao et al., 2008; Cruz et al., 2014). Furthermore, there is an urgent need to carefully evaluate regulations of fishing and implementation of management plans for TSB, as in many parts of the world.

The interactions between fishes and sponges and indirect effects on hermatypic corals could be a suitable model to evaluate coral reef integrity and functioning. We believe that the inclusion of fish-sponge-coral interactions to coral reef monitoring protocols will bring important insights of coral reef functioning and will allow the detection of annual or decadal changes. Nevertheless, ongoing coral reef monitoring programs are essential but will be of little use if the data are not available to support management actions and support investigations of different reef processes.

ETHICS STATEMENT

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

AUTHOR CONTRIBUTIONS

FL, RM, and JN hypotheses building, sample design, sampling, data analyses, writing. FB hypotheses building, sample design, data analyses, writing, financial support, supervision.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00256/full#supplementary-material

Supplementary Figure 1 | Examples of photo quadrats taken on different reefs of Todos os Santos Bay. Superior left: Frades Sul (*Aplysina fistularis*); Inferior left: Cardinal *Ectyoplasia ferox*); Superior right: Mangueira (*Desmapsamma anchorata)*; Inferior right: Pedra Alva (*Neopetrosia sp.*).

Supplementary Figure 2 | (A) Mean (+s.e.) of the five most abundant sponge species at each reef and **(B)** mean (+s.e.) density of the three spongivorous fish at each reef.

Supplementary Figure 3 | nMDS showing similarities between reefs based on **(A)** sponge assemblages (% cover) and **(B)** spongivorous fish assemblages (densities).

Supplementary Table 1 | Sampling sites coordinates and depth range. The fieldwork was conducted between January and March of 2016.

Supplementary Table 2 | Mean percentage cover of the different taxa sampled by photo-quadrats in ten reefs of Todos os Santos Bay (MA, Mangueiras; IM, Ilha de Maré; P1, Poste 1; CA, Cardinal; IN, Inema; P4, Poste 4; P5, Poste 5; P6, Poste 6; PA, Pedra Alva; FS, Frades Sul).

Supplementary Table 3 | Summary of PERMANOVA for sponge and fish assemblages based on Bray-Curtis dissimilarity with $\alpha = 0.05$.

Supplementary Table 4 | Par-wise testing for differences among reefs with sponge assemblages, based on Bray–Curtis dissimilarity with $\alpha = 0.05$.

Supplementary Table 5 | Par-wise testing for differences among reefs with angelfish assemblages, based on Bray–Curtis dissimilarity with $\alpha = 0.05$.

Supplementary Table 6 | Number of interactions among sponge species and hermatypic coral species.

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Interannual and Seasonal Variations in Estuarine Water Quality

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Anthropic processes degrade quality of estuarine environments, resulting in a worrying form of water pollution. The objective of the study was to describe and discuss interannual and seasonal changes of water quality based on indicators monitored in Goiana River estuary, as well as identifying the main drivers of such changes. We considered three estuarine areas or habitats (upper estuary, middle estuary and lower estuary), and two seasons (dry and rainy) for anchoring sample design. The information collected for surface and bottom water include water temperature (°C), salinity, dissolved oxygen (mg L^{-1}), saturation (%) and Secchi depth (cm) ($n = 864$). The monthly total rainfall (mm) was compiled from public database. Multivariate analyses highlight inter dependency among these parameters. Water quality was reduced in dry periods (including episodes of hypoxia), but generally increased toward the mouth of estuary. Rainfall is the most important factor in the renewal and maintenance waters of small tropical estuaries. Regions most sensitive to climate change where water resources are depleted and/or compromised should pay even more attention to upcoming changes in rainfall (seasonal) and climatic patterns in addition to better water management practices.

Keywords: physico-chemical parameters, sample design, tropical estuaries, aquatic habitat conservation, hypoxia

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INTRODUCTION

Water is an indispensable natural resource for human survival and essential for the development of most our activities (World Health Organization, 2011, 2014). Its abundance on Earth's surface gave rise to the thought that it would be an inexhaustible resource, not being initially considered as deserving of conscious use, or reason to avoid the significant shift of the demand/availability ratio to an unfavourable condition (Brooks et al., 2006; Haynes et al., 2007).

Many communities emerged close to where water could be easily obtained to ensure food and maintenance of the population. Estuaries are examples of environments that provide the necessary means for the development of human communities (World Health Organization, 2014) and indeed support large populations. These ecosystems are in a transitional range between the fluvial and marine environments, influenced by the maritime amplitude, which causes a marked variation of its environmental parameters, such as nutrients and salinity (Kennish, 1991, 1998). They also have the capacity to shelter numerous species, from the juvenile forms to adult phases, which use the environment for feeding, breeding or protection from predators; in addition to resident species, that spend their entire life cycle in estuaries, many of these resources reach high economic and social values (Kennish, 1991, 1998; Barletta and Dantas, 2016).

Water quality loss in estuaries are, therefore, one of the worst forms of water pollution (Karydis and Kitsiou, 2013). The main causes of decline in quality of the estuarine aquatic bodies are related to water subtraction and releases of agricultural, domestic and industrial effluents (Alexakis, 2011; Brockmeyer and Spitzy, 2011), altering the physical, chemical and biological properties of water (Kitsiou and Karydis, 2011; Karydis and Kitsiou, 2013), and consequently dropping the concentrations of dissolved oxygen (Yin et al., 2004; Mudge et al., 2007; Breitburg et al., 2009).

Dissolved oxygen in marine and coastal waters can directly influence environmental health (Mudge et al., 2007; Breitburg et al., 2009). Episodes of low concentrations of dissolved oxygen in the water are considered cases of hypoxia (Breitburg et al., 2009; Zhang et al., 2010). These events have been recorded and studied in literature, mainly due to the occurrence of effluent and organic matter flows into coastal waters (Attrill and Power, 2000; Tett et al., 2003; Yin et al., 2004; Roselli et al., 2013). Reduced oxygen in waters affects the ecology of diverse populations of organisms (growth, distribution, recruitment, reproduction, and survival) and the state of local pollution (Mudge et al., 2007; Breitburg et al., 2009). The reduction of dissolved oxygen is a strong indicator of poor water quality and needs to be monitored and treated.

The assessment of water quality parameters is a tool for maintaining the best possible water conditions across entire basins, including estuaries and adjacent coastal waters (Kitsiou and Karydis, 2011; Karydis and Kitsiou, 2013). Consistent information on water quality and its patterns of change is the key to better manage and use these resources rationally (World Health Organization, 1996; Karydis and Kitsiou, 2013). Being capable of accommodate changes (episodic or permanent) to managerial plans require a solid knowledge about the drives of water quality and natural resources availability at different timescales.

The objective of the present study was to describe and discuss the interannual and seasonal changes of water quality based on indicators monitored in the Goiana River estuary, as well as identifying the main drivers of such changes and the main hypothesis is the estuary of the Goiana River presents seasonal and interannual changes in water quality in its different habitats.

METHODS

Study Area

The main activities developed along the Goiana River basin are sugarcane agro-industry, industrial activities and urban occupation. Effluents are discharged directly into the water, causing damages to the full extent of the basin, in addition to water use for public supply and irrigation (Garlipp et al., 2010; CPRH-Agência Estadual de Meio Ambiente e Recursos Hídricos., 2015; Costa et al., 2017). There are two gauges which measure river flow upstream (Brazilian Water Agency gauges #39080000 and #39084000). Year-round average flow at these tow gauges are 11.0 and 8.8 $m^3\ s^{-1}$ (∼90% catchment area), but it can vary from 3.5 $m^3\ s^{-1}$ (dry season) to 60 $m^3\ s^{-1}$ (rainy season) (Arruda-Santos et al., 2018).

The Goiana River estuary (7° 30′S – 34° 47′W) (**Figure 1**) is a tropical shallow estuary that supports important ecological processes (Barletta and Costa, 2009; Dantas et al., 2010; Silva et al., 2013) and is under legal protection as an extractive reserve aimed at traditional fishers populations. There, the impact of greater significance is caused by sugarcane crops, prawn farming and lime extraction, which are connected directly to degradation of the mangrove flooded forest (Barletta and Costa, 2009; Garlipp et al., 2010; CPRH-Agência Estadual de Meio Ambiente e Recursos Hídricos., 2015). Despite recent trends in economic diversification, the area remains strongly linked to primary activities.

According to Kjerfve (1990), the main axis of an estuary can be sectioned into large compartments or areas—upper, middle, and lower—considering its morphology and salinity, since riverine environments down to adjacent coastal areas. Each section of the main channel is an habitat (Barletta et al., 2005; Lima et al., 2014), with different biogeochemical behaviour, plant and animal communities, giving rise to an ecological gradient (Attrill and Rundle, 2002; Barletta and Dantas, 2016). Composed of a combination of rivers, streams, ponds, tidal channels, islands, wetlands and flooded mangrove forests, this estuary accommodates a diverse aquatic fauna (fish, molluscs, crustaceans) (Barletta and Costa, 2009; Dantas et al., 2010; Lima et al., 2014) with high conservation, social and economic importance. The main channel has a total length of ∼25 km (Barletta and Costa, 2009; Dantas et al., 2010; Costa et al., 2017). The upper estuary varied in depth from 1.2 to 11.6 m, middle estuary ranged from 1.2 to 10.1 m and the lower estuary had a depth variation of 1.0 to 9.1 m.

Data Acquisition

The sampling strategy adopted in this study was successfully used by several authors (Barletta et al., 2005, 2008; Dantas et al., 2010; Lima et al., 2014), attesting for the robustness of sample design. The strategy was implemented from 2006 to 2009 in this estuary. Based on previous literatures (Lima et al., 2014) and a previous sampling that covered the whole extent of the main estuarine channel, were recognized three areas (upper, middle and lower estuary) and two seasons (dry and rainy). The months chosen for this study were those at end of each seasons, when the environment presents clearer responses to the environmental stressors (**Figure 2A**). During the pilot sampling, water temperature, salinity, dissolved oxygen, Secchi depth and water depth were probed to define the limits of each area.

The data for the present study was collected for surface and bottom waters (6 samples/area, in the central area of the main channel; once a month; during 3 months in each season). So, each month has 18 replicas per area, per month per year; $n = 864$. Measurements include water temperature (°C), salinity, dissolved oxygen (mg L^{-1}) and oxygen saturation (%) (measured with a WTW LF 197, Wissenschaftlich Technische Werkstätten with a 20 m cable) and Secchi depth (cm). Monthly total rainfall (mm) was compiled from public database (www.apac.gov.pe.br), collected from a weather station located 10 km south of the city of Goiana.

Statistical Analysis

Data collected were processed into an orthogonal matrix for analysis ($n = 864$). Cochran's test was used to check the homogeneity of variances.

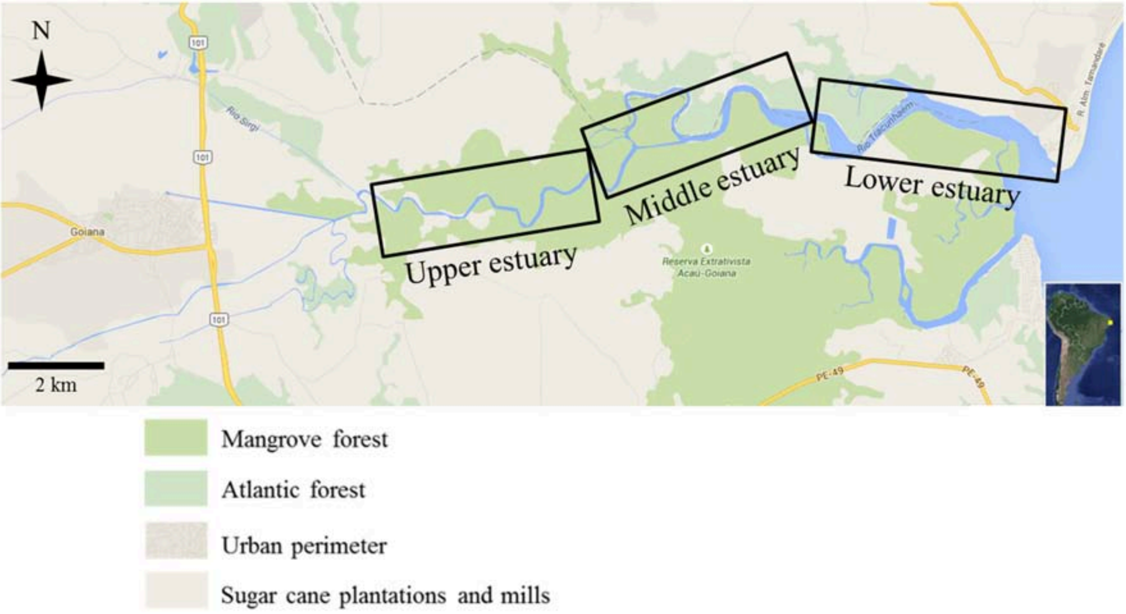

FIGURE 1 | Location of Goiana River estuary, showing upper estuary, middle estuary, and lower estuary along the main channel. Source: Google maps, adapted.

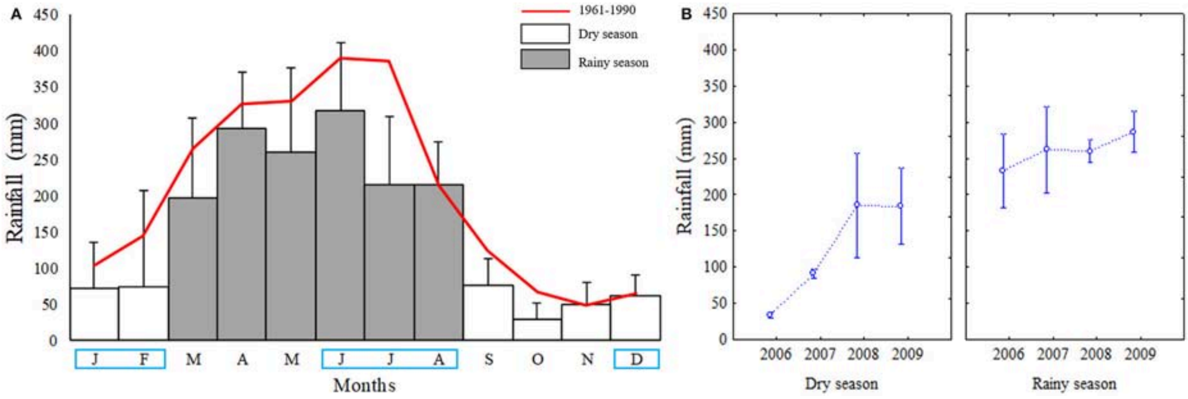

FIGURE 2 | (A) Most recent climatic rainfall average 1961–1990 (red line) and at Goiana River estuary in periods 2006–2009 (bars) (highlighted months in blue) were those used in this study; **(B)** Average seasonal rainfall of years studied (2006–2009).

The original data were Box–Cox transformed to ensure it conformed to a normal distribution.

The analysis of variance (factorial ANOVA with a 5% level of significance) were carried out. This was used to determine whether significant differences in categorical predictors (factors) occurred in years (2006, 2007, 2008, and 2009), areas (upper, middle and lower estuary) and seasons (dry and rainy) and depth in water column (surface and bottom). The variables (water temperature, salinity, dissolved oxygen and oxygen saturation) were first studied and analysed separately for their individual behaviours (see **Supplementary Material**) and detect possible differences between surface and bottom waters. With the ANOVA results, it was possible to observe that there were no differences and therefore, depth was not further considered. Samples from surface and bottom waters were treated as replica, increasing the sample number from six to twelve (see above section Data acquisition).

Subsequently, a multivariate analysis of variance (MANOVA) analysis was performed, excluding the depth factor. A *posteriori* Bonferroni's test was used to determine which means were significantly different at the 5% level of significance.

Clusters were determined based on similarity matrix using the method of complete linkage with Euclidean distance and a principal components analysis was made using a 95% confidence interval, for all variables studied. A multivariate analysis highlights the inter dependency among water physico-chemical parameters. For these analyses, observations were homogenized in averages ($n = 24$), due to large number of samples ($n = 864$), allowing for better observation and interpretation of results. Averages were made between samplings of same spatiotemporal condition (year, area and season—replica).

RESULTS

MANOVA showed that salinity, temperature, dissolved oxygen, saturation and Secchi depth differ significantly between seasons, areas and years. The interactions year vs. season vs. area also significantly differ for these variables ($F = 3.4$, $p = 0.0000$) (**Table 1**). Such interactions suggest that the physico-chemical parameters are affected by the years, the seasonality and the main channel area.

Monthly total rainfall in the studied period, ranged from 20.2 to 364.0 mm. In the dry season, averages were between 33.9 ± 8.5 mm and 184.1 ± 106.0 mm, while in the rainy season range was 233.4 ± 102.3 mm to 286.6 ± 57.2 mm (**Figures 2A,B**). Among dry seasons, 2006 presented the lowest rainfall (33.9 ± 8.5 mm). Dry seasons of 2008 (185.2 ± 144.5) and 2009 (184.1 ± 106.0), presented very similar behaviour regarding the rainy seasons of all years studied (and in comparison, with the climatic average 1961–1990). Rainy seasons presented a very similar pattern in all the studied years, varying less than dry seasons during the study period in respect to total monthly rainfall.

Water temperature varied from 25.3 to 31.4°C, presenting values with small variation between years and areas, and higher in dry season (**Figure 3**). Variations were less prominent in rainy season. Upper and middle areas showed no differences but were different from lower area. Year 2009 was different from the others. The seasons were also different (**Table 1**).

Salinity varied from 0 to 36.9, with 121 of the 432 sampled values being equal to zero, especially in areas upper and middle during rainy season. Areas and seasons were different (**Table 1**; **Figure 4**).

TABLE 1 | Summary of the MANOVA ($F = 3.4$; $gf = 859$) and Bonferroni's test results for water temperature, salinity, Secchi depth, dissolved oxygen, and oxygen saturation for year - 2006 (06), 2007 (07), 2008 (08), 2009 (09) for estuarine area - upper (U), middle (M), lower (L) - for season - dry (D), rainy (R).

	Source of variance			
Parameters	**Year (1)**	**Area (2)**	**Season (3)**	**Mean interactions**
Water temperature	** 06 07 08 **09**	** U M **L**	** D **R**	** 1 × 2 × 3
Salinity	** 07 *08* *06* **09**	** U *M* **L**	** D **R**	** 1 × 2 × 3
Dissolved oxygen	** 06 07 08 **09**	** U M **L**	** D **R**	** 1 × 2 × 3
Oxygen saturation	** 06 07 08 **09**	** U M **L**	NS	** 1 × 2 × 3
Secchi depth	** 06 *07* 08 **09**	** U *M* **L**	** D **R**	** 1 × 2 × 3

*NS, non-significant differences ($p > 0.05$); *$p < 0.05$; **$p < 0.01$; differences among year, area and season were determined by Bonferroni's test ($p < 0.05$) post-hoc comparisons.*

Dissolved oxygen varied from 1.4 to 10.4 mg L^{-1} in the period, with the highest averages concentrated in lower estuarine portion (**Figure 5**). **Figure 5** shows an histogram with the normal distribution of number of observations of dissolved oxygen values obtained ($n = 864$). It is observed a wide range, from 0 to 11 mg L^{-1}, but with a high number of observations between 4 and 6 mg L^{-1}. For this parameter, 4.2% of the values were between 0 and 2.0 mg L^{-1} (critical); 42.8% between 2.1 and 5.0 mg L^{-1} (acceptable) and; 53.0% of the values were >5mg L^{-1} (safe) (Conselho Nacional de Meio Ambiente, 2005) (**Figure 5**). The seasons were different, and so were the lower area and year 2009 (**Table 1**).

Oxygen saturation showed values between 17 and 123.7% and followed the trend presented by dissolved oxygen (**Figure 6**). There were no significant differences between seasons (**Table 1**).

Secchi depth varied from 12 to 276 cm, showing large variations between the years in the dry seasons, while in rainy seasons measurements, once again showed less variability (**Figure 7**). All factors (year, area, and season) were significantly different for this variable (**Table 1**).

In the cluster analysis (**Figure 8**), observations were grouped into 2 major groups, I e II. Group I was subdivided into 2 subgroups. Subgroup IA, was subdivided in IA1 comprised samples from 2008 in dry season in lower area and IA2, were samples in dry season in upper and middle areas in 2008 and 2009 and lower area in 2009. Subgroup IB, was subdivided in IB1, samples taken in 2009, in three areas, during rainy season and IB2, comprised samples from 2006, 2007, and 2008 in three areas during the rainy season. Group II presented two subgroups: IIA, which comprised samples from 2006 and 2007, lower area in dry season. In subgroup IIB were samples from years 2006 and 2007, in upper and middle areas, during dry season.

Interpreting the principal components analysis, 76.73% (PC1 and PC2) of the variation of data are satisfactorily explained, revealing inter-relations among variables. According to Clarke and Warwick (2001), a PCA must explain 70% or more initial variations in a data set. If so, it is a reasonable interpretation of the phenomenon, or global structure of interactions. In this case, PC1 explained 44.70% of the total variance, was formed mainly by the variables temperature, salinity, rainfall and seasons of the year (**Table 2**), while PC2 represented 32.03%, formed mainly by the dissolved oxygen and its saturation (**Table 2**). The weights plot (**Figure 9A**) show the distribution of variables and the scores plot (**Figure 9B**) the distribution of replica.

DISCUSSION

Water temperature was strongly marked by seasonality. The difference between years was small, but the difference between seasons was highlighted. The estuary is located in a tropical area (Barletta and Costa, 2009; Costa et al., 2017), which favoured high water temperatures throughout the year. This factor can affect the dissolution of gases as oxygen in the water, decreasing their availability for biological and chemical processes (Yin et al., 2004;

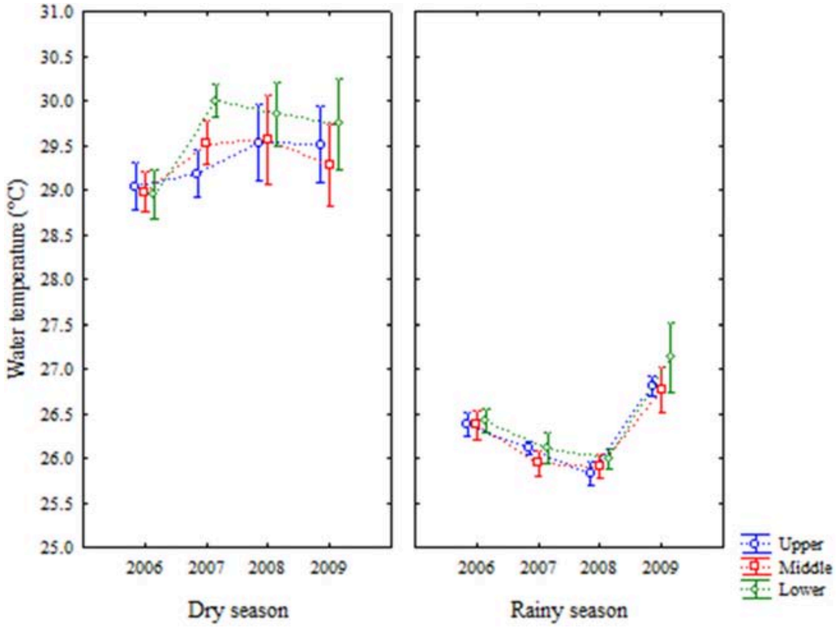

FIGURE 3 | Average (±standard deviation) of temporal (interannual and seasonal) variations of water temperature at the Goiana River estuary from 2006 to 2009.

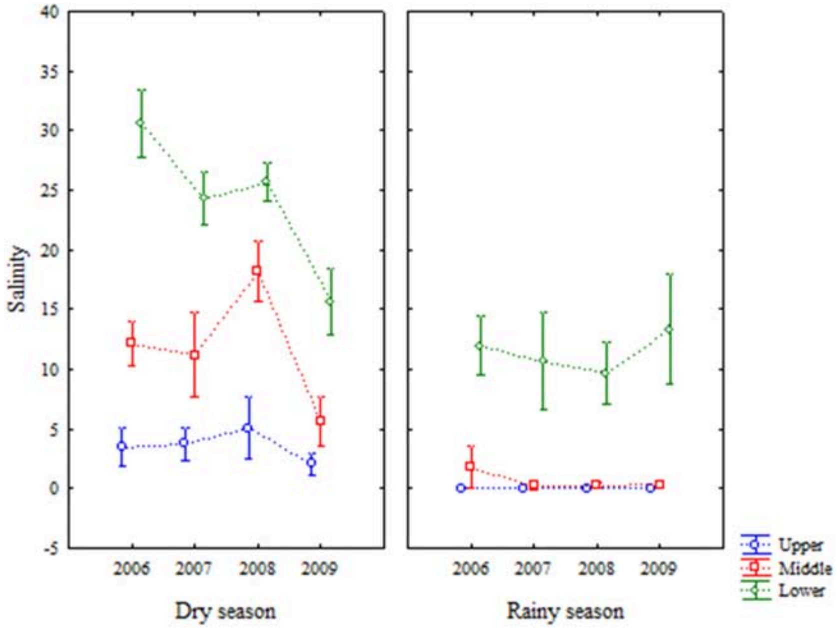

FIGURE 4 | Average (±standard deviation) of temporal (interannual and seasonal) variations of salinity at the Goiana River estuary from 2006 to 2009.

Harrison and Whitfield, 2006; Kong and Ye, 2014; Wu et al., 2016).Salinity variations defined the estuarine gradient (Attrill and Rundle, 2002; Barletta and Dantas, 2016). In 2006, the dry season was very severe (33.9 ± 8.5 mm), decreasing freshwater entering the estuary and significantly increasing salinity locally, with the greatest marine influence on the estuary of all years, similarly to other reports in the literature (Yin et al., 2004).

Water temperature and salinity are important abiotic variables, which together play a fundamental role in the distribution of aquatic biota, with the determination of ecoclines (Attrill and Rundle, 2002; Yin et al., 2004; Harrison and Whitfield, 2006; Nejrup and Pedersen, 2008; Barletta and Dantas, 2016; Dolbeth et al., 2016). Sudden and/or large changes in these parameters may compromise environmental quality over

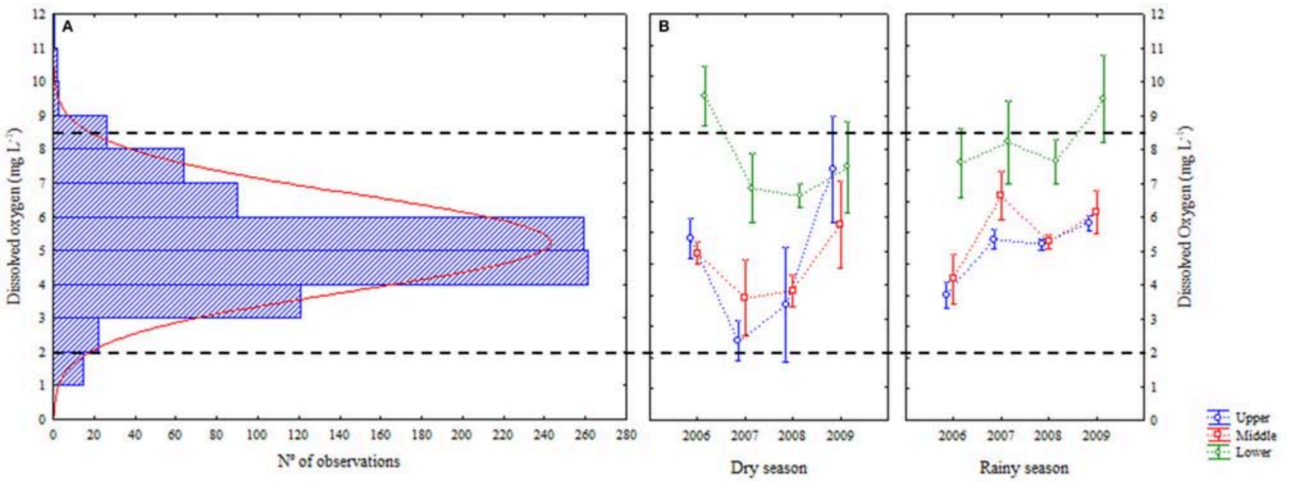

FIGURE 5 | (A) Histogram of observations ($n = 432$) for dissolved oxygen, following the normal distribution; **(B)** Average (±standard deviation) of temporal (interannual and seasonal) variations of dissolved oxygen at the Goiana River estuary from 2006 to 2009. Colour scale shows the levels of water quality according to this parameter.

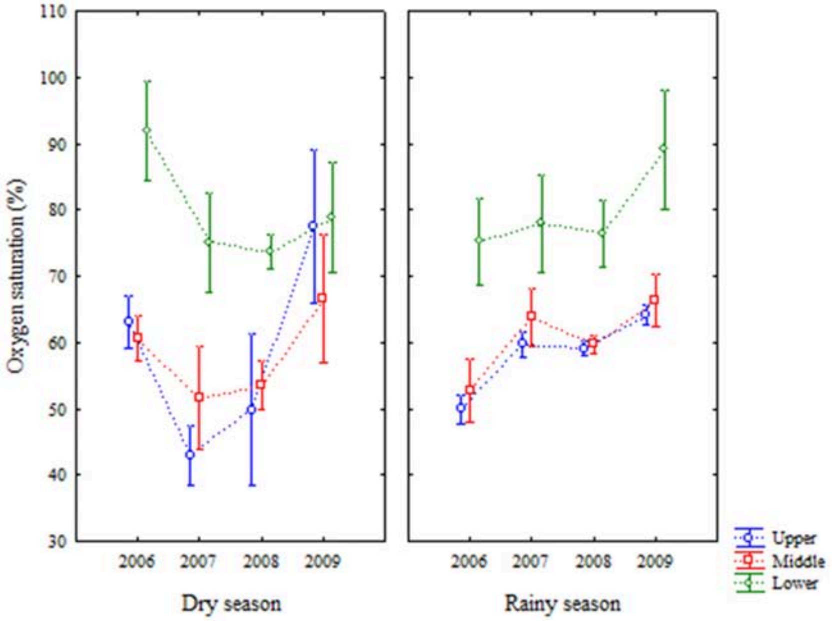

FIGURE 6 | Average (±standard deviation) of temporal (interannual and seasonal) variations of oxygen saturation at the Goiana River estuary from 2006 to 2009.

time, as may change the composition and distribution of biota (Lucena-Moya and Duggan, 2017; Paul and Calliari, 2017), alteration of areas of high ecological importance considered nurseries (Barletta et al., 2005; Blaber, 2013), increase the effect of organic pollution on estuaries as well as the distribution of plastics and microplastics (Possatto et al., 2011; Ivar do Sul and Costa, 2013; Ivar do Sul et al., 2014; Lima et al., 2014), dilution of effluents (Govindasmy and Chandrasekaran, 1992; Uriarte and Villate, 2004; Whitehead et al., 2009; Telesh and Khlebovich, 2010), and absorption and accumulation of pollutants by biota (Tett et al., 2003; Roselli et al., 2013; Zhou et al., 2017).

Dissolved oxygen and oxygen saturation showed similar behaviours, although the water temperature also influenced oxygen saturation indexes. Temperature variation was small, being predominant the interdependence between the dissolved oxygen and its saturation (Nezlin et al., 2009; Shah and Pant, 2012). The oxygen contents were higher in the lower area of the estuary, where there is a greater influence of marine waters, more oxygenated (Tett et al., 2003; Yin et al., 2004; Mudge et al., 2007;

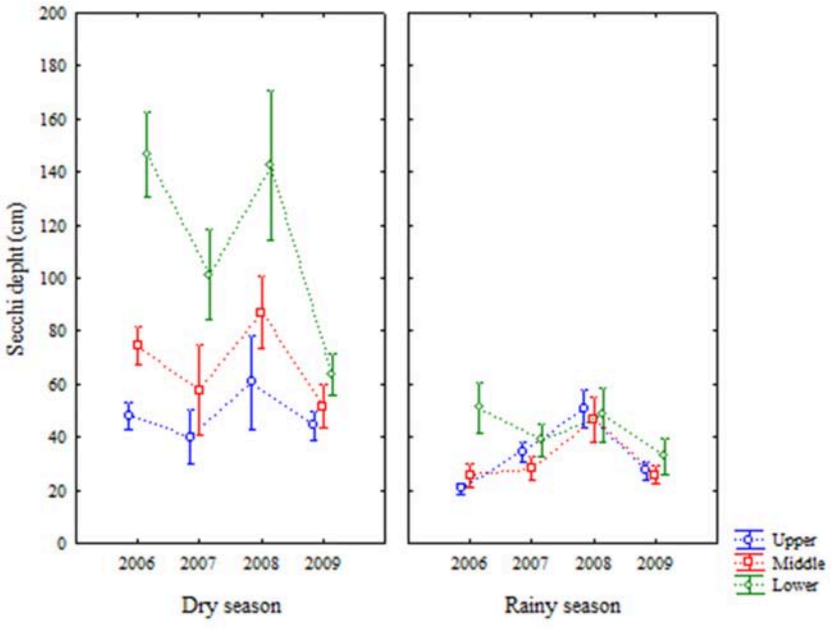

FIGURE 7 | Average (±standard deviation) of temporal (interannual and seasonal) variations of Secchi depth at the Goiana River estuary from 2006 to 2009.

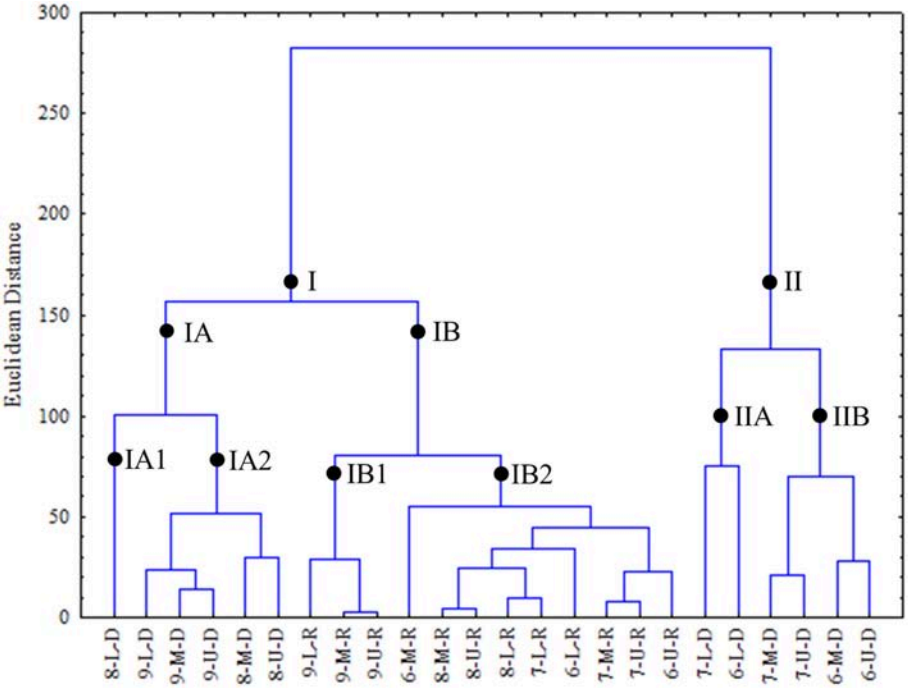

FIGURE 8 | Cluster of interannual seasonal averages of water quality parameters and rainfall at the Goiana River estuary through Euclidean distance. Legend for samples: first numeral represents the year (6 - 2006, 7 - 2007, 8 - 2008, 9 - 2009); second letter represents estuarine area (U, upper; M, middle; L, lower) and third letter represents season (D, dry; R, rainy).

Zhang et al., 2010). Year 2009 presented an atypical character related to oxygen concentrations, due to the dry season of this year having similar precipitation indices of the rainy season of that year. Other works report an increase of oxygen related to the occurrence of increased rainfall (Delpla et al., 2011; Li et al., 2015). Rainfall events occurring mainly in tropical areas are important for water renewal and dilution of possible effluents, thus improving its quality (Delpla et al., 2011; Corbari et al., 2016; Delpla and Rodriguez, 2016). There was homogenization of the oxygen distributed, making the values measured for this parameter similar in all estuarine areas. The levels of dissolved oxygen recommended for aquatic conservation are above 4–5 mg L^{-1} (Conselho Nacional de Meio Ambiente, 2005; Breitburg et al., 2009; Osode and Okoh, 2009), being occasionally lower, resulting from anthropic interference.

Secchi depth presented higher values in dry season, when the water column is more stable, lower resuspension of particles, as well as lower flow sediment and particulate matter carried by runoff. In the rainy season as well as in dry season of 2009, lower values are observed, due to the greater volume of rains, increasing the turbidity, and being able to shift primary production (Schlacher and Wooldridge, 1996; Kronvang et al., 2005; Devlin et al., 2008). The variation of solar radiation is probably not a determining factor because the estuary is located in a tropical area (Qasim et al., 1968; Kronvang et al., 2005).

TABLE 2 | Eigenvalues used in the construction of PCA.

	Eigenvalues	
Variables	**Factor 1**	**Factor 2**
Water temperature	*0.744*	−0.523
Salinity	*0.934*	0.177
Dissolved oxygen	0.399	*0.860*
Oxygen saturation	0.526	*0.788*
Secchi depth	−0.680	0.600
Rainfall	*0.892*	−0.047
Year	−0.095	0.291
Area	0.593	0.646
Season	*−0.736*	0.595

The values in italics are the most important in the formation of the principal axis.

Episodic Hypoxia

Regional legislation (Conselho Nacional de Meio Ambiente, 2005) establishes for estuarine environments, that hypoxia conditions are those in which the dissolved oxygen levels are <3 mg L^{-1}. This study used as basis the international literature, which adopt more conservative levels, being considered <2 mg L^{-1} the limit for hypoxia (Attrill and Power, 2000; Tett et al., 2003; Mudge et al., 2007; Breitburg et al., 2009; Zhang et al., 2010; Roselli et al., 2013).

Hypoxia in coastal waters can be of natural and/or anthropogenic origin and is defined by levels of dissolved oxygen <2 mg L^{-1} and $<30\%$ of oxygen saturation (Mudge et al., 2007; Breitburg et al., 2009; Zhang et al., 2010). In this study, there were some episodes of hypoxia (15 in 864 observations), mainly during the dry season, in the upper and middle areas of the estuary (**Figure 5**). In these moments, river flow and the renewal of waters was severely affected by lack of rainfall both along the basin and locally (Attrill and Power, 2000; Yin et al., 2004; Dai et al., 2006) Concentrations of dissolved oxygen in surface waters are regulated by the balance between production, consumption (respiration and other chemical reactions) and exchange with the atmosphere (Wannamaker and Rice, 2000; Uriarte and Villate, 2004). The decrease in renewal caused the consumption of available oxygen in water to almost its entirety. Also, less flow results in limited turbulence and consequently less diffusion from the atmosphere. Hypoxia is a typical consequence of continued

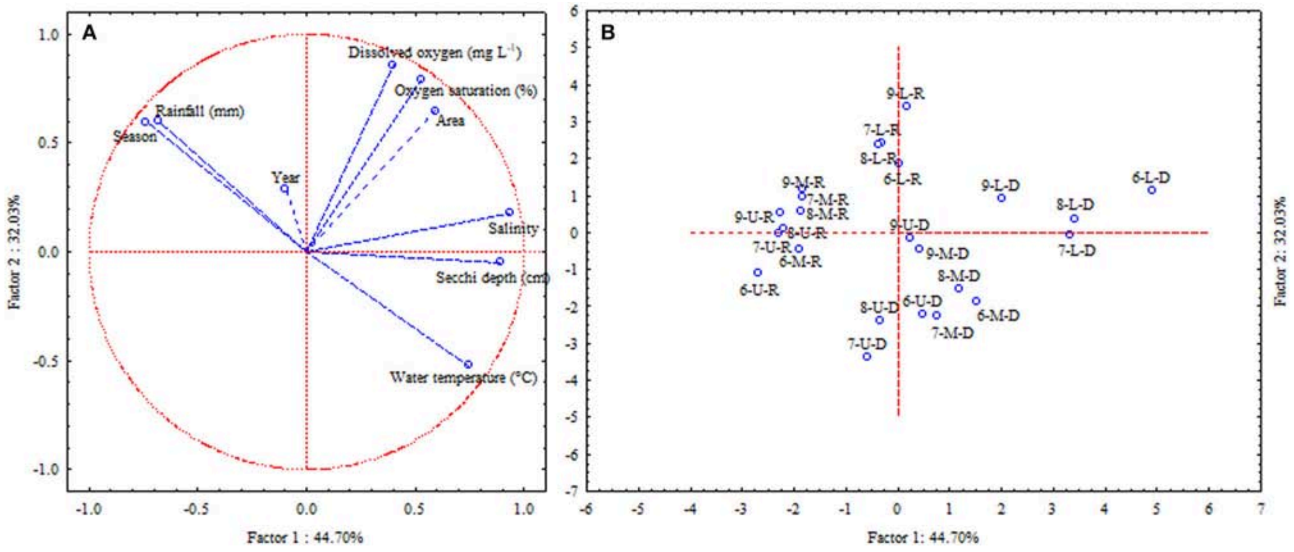

FIGURE 9 | (A) Weight graph (PCA) showing the contribution of environmental variables to the water quality patterns at the Goiana River estuary from 2006 to 2009. **(B)** Score graph (PCA) showing the contribution of environmental variables to the water quality patterns at the Goiana River estuary from 2006 to 2009. Legend for samples: first numeral represents the year (6 - 2006, 7 - 2007, 8 - 2008, 9 - 2009); second letter represents estuarine area (U, upper; M, middle; L, lower) and third letter represents season (D, dry; R, rainy).

decline in water quality (Wannamaker and Rice, 2000; Schmidt et al., 2016; Qian et al., 2018). It may result in habitat degradation and habitat loss (Wannamaker and Rice, 2000; Tett et al., 2003; Mudge et al., 2007; Gelesh et al., 2016). In the world, a number of hypoxia cases have already been reported in scientific literature. Shallow and warm waters from tropical estuaries are particularly vulnerable (Attrill and Power, 2000; Wannamaker and Rice, 2000; Yin et al., 2004; Dai et al., 2006; Bianchi et al., 2010; Bourgault and Cyr, 2015; Costa and Barletta, 2016; Jeppesen et al., 2016; Schmidt et al., 2016).Hypoxic conditions will, eventually, be responsible for decrease in biological abundance and diversity (Uriarte and Villate, 2004; Ram et al., 2014; Jeppesen et al., 2016), altered growth and mortality rates of juvenile fish (Wannamaker and Rice, 2000; Ram et al., 2014), altered behaviour, feeding and other habits change (Zhang et al., 2010; Weinke and Biddanda, 2018), methane production (Gelesh et al., 2016). The phenomenon is, in addition, aggravated by acidification (Miller et al., 2016) and global warming (Zhang et al., 2010). All these changes concur for permanent environmental changes and, finally, resilience rupture at an ecosystem scale.

The samples analysed in the present work were taken from the main channel of the estuary, where water is expected to have the best possible chances of renewal and oxygen diffusion/production. In effect, most of the observations for dissolved oxygen were in a range considered safe for the environment (**Figure 5**). There is a higher than average chance that hypoxia is already installed at smaller tidal creeks and less turbulent reaches of the drainage system that composes the estuary (Ramos et al., 2011). If, the frequency, range and duration of such hypoxia episodes increase in the Goiana River estuary in the future, there will be cause of concern for the conservation of water resources and should therefore be closely monitored.

Variables Interdependence

The change in water quality resulting from the change in the amount of rainfall was noticed thanks to the interannual sampling carried out. Carefully planned sampling is also an important tool for the detection of cyclic phenomena, which are detected only at larger temporal scales (Karydis and Kitsiou, 2013), and a less intense but similar sample design is suggested for the water quality assessment of this estuary in order to detect long-term permanent changes due to anthropic interference.

Basin-wide to local rainfall volumes are the main factors determining the quantity and quality of estuarine waters (Karydis and Kitsiou, 2013; Corbari et al., 2016). Although it temporarily reduces sunlight penetration into the water column, limiting primary production (Qasim et al., 1968; Kronvang et al., 2005; Cloern et al., 2014), freshwater inputs promoted the increase of available dissolved oxygen, as well as the diffusion, dilution and transportation of effluents and pollutants (Yin et al., 2004; Brooks et al., 2006; Osode and Okoh, 2009; Zhang et al., 2010). In the dry seasons, the water quality drop is also observed, mainly due to lack of water renewal promoted by the rain (Attrill and Power, 2000; Dai et al., 2006).

Dissolved oxygen was the most important variable related to water quality in this study, highlighted in its important contribution to the formation of the PC2 axis (**Figure 9**; **Table 2**). Several authors have developed studies in the area, which have not demonstrated that oxygen could a limiting factor for organisms' distribution. This might result from the still existing conservation status of the system or, due to the sampling in the main channel. For the demersal fish assemblages, salinity and temperature appears as the main limiting factors (Barletta et al., 2005; Dantas et al., 2010; Ramos et al., 2016).

Managerial and Conservation Implications

Water scarcity is a critical problem around the world. In Northeast South America there are few large river basins, so the numerous small estuaries along the coast are the most important source of water for the most diverse uses (World Health Organization, 1996). Rainfall is the most important factor in the renewal and maintenance of these waters (Schlacher and Wooldridge, 1996), causing considerable improvement in their quality (Karydis and Kitsiou, 2013; Corbari et al., 2016), however, of a temporary nature.

The important relationship dependence of the Goiana River estuary with rainfall to the renewal of its water resources was also observed in other estuaries. Mérigot et al. (2016) observed the same for four estuarine complexes in Brazil and Harrison (2004), in South Africa, in another 109 studied estuaries. The maintenance of these waters is crucial for the continuity of the provision of ecological services (Karydis and Kitsiou, 2013; Corbari et al., 2016).

Climatic events, such as above-average precipitation years (2008 and 2009), contribute in principle to improving environmental conditions (Bouvy et al., 1999; Jackson et al., 2001; Nijssen et al., 2001). However, changes in rainfall and freshwater discharge patterns from basins can increase freshwater flows, change the flow rate and increase sedimentary loads with potential to alter the morphology of the environments, as well as altering natural biogeochemical cycles, thus impacting habitats (Tett et al., 2003; Yin et al., 2004; Whitehead et al., 2009; Roselli et al., 2013). Since such changes are driven by deforestation of the basin soil and estuarine margins, consequences are permanent, although partially reversible if the vegetation is minimally restored.

The Goiana River estuary is under numerous human interferences. Like many other tropical estuaries, it is highly impacted by sugarcane plantations (Brockmeyer and Spitzy, 2011; Thorburn et al., 2011; Davis et al., 2013; de Melo Gurgel et al., 2016; Valera et al., 2016).

Tropical soils present low levels of organic matter, causing difficulties for their maintenance for the cultivation of sugarcane. Large quantities of fertilizers which are carried toward the estuarine channel by the rainfall is necessary for the yield of crops (Alexakis, 2011; Brockmeyer and Spitzy, 2011; Humbert, 2013), causing the consumption of the available dissolved oxygen in the water. The projected trend of change influenced by anthropogenic actions in global climate includes several events: water heating (change in chemical kinetics of reactions in the estuary, stratification of the water column, hypoxia); rising sea levels; reduction of water pH (acidification); loss/replacement of habitats (species migration, invasion of exotic species) and the expansion of the tropics (Attrill and Power, 2000;

Mudge et al., 2007; Zhang et al., 2010; Statham, 2012; Madsen et al., 2014). The importance of environments such as tropical estuaries will be even more prominent in the near future, demanding a considerable understanding of the functioning of these ecosystems. In addition the demand for water resources tends to increase and surface water quality will become a priority (World Health Organization, 2014).

FINAL REMARKS

Our work assessed the water quality conditions at the main channel of Goiana River estuary from 2006 to 2009. The sample design used allowed for the detection of interannual changes in water quality due mainly from variations in rainfall patterns. It also corroborated previous ecological studies by confirming that the aquatic habitats of the main channel offer conditions to the maintenance of biological resources most of the time.

Water quality in study area remains overall reasonable, despite hypoxia events. These events should be seen as a warning sign of the sensitivity and vulnerability of this and other similar environments to human interferences (e.g., domestic effluents discharge, sugarcane irrigation, fertilization and milling effluents).

As a way to maintain environmental quality, measures to mitigate impacts on the aquatic habitats start with basin-wide mitigation actions and include the estuarine region. Soil use and occupation, as well as water uses (restoration of riparian vegetation, soil recovery, and effluents treatment before disposal) must be improved. Measures such as these are essential for the maintenance of ecosystem services offered by the estuary. There is uncertainty about the likely impacts on water quality due to changes in regional rainfall patterns—especially due to deforestation and increasing demands on water resources. Projects for new water supplies, urban drainage and water treatment systems will have to account for the effects of local climate change.

Rainfall is an important factor in promoting seasonal discharges and maintaining ecosystem health in regions with resources-limited watersheds, especially those where flow control is in place. Dry season is a critical period, where due to tropical temperatures and low water renewal, water quality can be severely reduced. As suggested by our results, regions that are most sensitive to environmental and socioeconomic changes and overuse of their water resources should pay more attention to changes in seasonal and climatic rainfall patterns, for they will condition water availability in the near future.

AUTHOR CONTRIBUTIONS

CC analyzed data and prepared the manuscript; MC secured funds, participated in field work and assisted in the preparation of the manuscript; DD participated in fieldwork and in early data processing and analysis; MB secured funds, designed the experiment, conduced fieldwork, analyzed data and assisted in the preparation of the manuscript; all authors have read and contributed to the final version of the text.

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SUPPLEMENTARY MATERIAL

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The Challenges Associated With Connectivity in Ecosystem Processes

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Developing a framework to quantify the transformation, sequestration or connectivity of energy and matter across habitats is one of the most significant challenges faced by ecologists and resource managers today. However, there are significant challenges associated with quantifying the ecosystem processes that connect and interact across habitats. These processes include the movement of nutrients and energy and can have substantial effects on the structure and dynamics of adjacent habitats and ecosystem functioning. Here, we use a connectivity framework developed for populations to inform our understanding of the challenges associated with connectivity in ecosystem processes, and how specific habitats can contribute to overall ecosystem functioning. The landscape patterns and potential connections between habitats in terms of material storage or transformation have important implications for understanding how fragmentation and degradation of habitats in ecosystems will influence broad-scale ecosystem function.

Keywords: connectivity, ecosystem function, ecosystem process, heterogeneity, population

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INTRODUCTION

Connectivity plays a central role in population dynamics in heterogeneous environments (Hanski, 2005). However, there are other dimensions to connectivity that are critical to many ecosystem functions (Polis et al., 1997). These dimensions include how resources are moved, transformed or stored within and between habitats. It was not until 1984 that the term "connectivity" was first defined in relation to environmental science (Merriam, 1984). Today the term encompasses a variety of fluxes in nature; population connectivity typically refers to the exchange of genes, propagules, larvae, sub-adult, and adult organisms, whereas aspects of ecosystem process-based connectivity include fluxes and sinks in energy, nutrients, and the propagation of disturbance effects. Frameworks that articulate replicable and pragmatic metrics of connectivity are vital as the interaction between processes and landscape features is increasingly recognised as an integral aspect of resource management plans (Calabrese and Fagan, 2004). Here we assess the suitability of the frameworks provided by population connectivity to identify the challenges and possible solutions associated with the patterns and connections between habitats via processes, and thus how ecosystems function and how their functionality changes with changes to habitats and connections between habitats.

To understand ecosystems connectivity, we require a currency with which to track energy and matter through the system, not only in terms of simple mass balance, but in terms of how processes interact. We define ecosystem functioning as the aspects of an ecosystem that influence their operation and provision of ecosystem services. Ecosystem functioning includes ecosystem processes (e.g., nutrient cycling, mineralisation), and properties of the ecosystem (e.g., resource use, standing biomass; Loreau et al., 2001). We define ecosystem services as the benefits people obtain from ecosystems, recognising that they are context-dependent and highly sensitive to income, technology, gender, culture, and geographical location (Millenium Ecosystem Assessment, 2005). The structure of patches and patch mosaics influences connections between populations and processes in different ways and at different spatial scales (Boström et al., 2011). Ecological interactions that occur within patches and among different types of patches are also critically important in supporting primary and secondary production, trophic transfer, biodiversity, and protection (Loreau et al., 2003). A habitat refers to an area with particular contributions to ecosystem processes. Habitats can be defined by physical and biological features (ecosystem engineers), and the level of variability within these habitat features can also be a defining characteristic (Diaz et al., 2004).

Extrapolating and generalising spatial relationships between ecological patterns and processes across scales remains a challenge and is a crucial aspect of managing and responding to an inevitably changing environment (Boström et al., 2011). Human activities, as well as an increasingly variable climate, have affected the capacity of ecosystems to maintain their function (Smit et al., 2000). Fragmentation, degradation and loss of habitats alter all the components of ecosystem service provision through changes in the matrix within which ecosystem processes are transferred between habitats within an ecosystem. To manage these systems, we therefore need to understand how changes in environmental and human drivers impact both habitat fragmentation and degradation, and their associated faunal and floral communities, to determine impacts on exchanges of fluxes and materials that are essential to maintaining ecosystem function (Braeckman et al., 2014; Mitchell et al., 2015).

THE EXISTING—POPULATION CONNECTIVITY FRAMEWORKS

Population connectivity frameworks have the potential to be used to develop new insights into process-based connectivity and ecosystem function. Dispersal mechanisms are important in determining species distributions across habitat patches, and seascape genetics have shown that a variety of forces impact connectivity at distinct spatio-temporal scales. GIS data and genomic scale sequencing illuminate differences between demographic, functional and neutral genetic connectivity (Selkoe et al., 2016). The scale of the landscape and connectivity of patches of organisms varies between species, between different life stages within species, and with differing environmental settings. Recent advances in landscape genetics, mechanistic dispersal modelling and ecological network analysis has shown that studies of the dispersal of both propagules and pollen by biotic or abiotic vectors must include the production of seeds and pollen at the source patch as well as the successful establishment of new individuals at the recipient patch (Auffret et al., 2017). Many organisms utilise wind, water and animal transport as long-distance dispersal mechanisms (Muñoz et al., 2004). In marine systems there is the potential for a high level of population connectivity as a result of pelagic/planktonic larval dispersal (Cowen et al., 2007). Larvae of marine organisms are not simply passively dispersed by water current, but can control their depth and thus direction, and these capabilities can increase with body size (Cowen and Sponaugle, 2009). Non-planktonic larval dispersal is also common, particularly in soft-sediment systems, with crawling and brooded larvae dispersing only short distances from the site of initial release (Grantham et al., 2003). Macroalgae population connectivity measures have shown that ignoring fluctuations in fecundity may overestimate connectivity, highlighting the need to include the fecundity, dispersal, recruitment, and survival of target species (Castorani et al., 2017). Post-settlement dispersal occurs in many taxa, via the bedload and in the water column (Pilditch et al., 2015). Adult movement is used by species in all taxon groups, with dispersal and connectivity dependent on mobility (Brückmann et al., 2010).

Population connectivity frameworks describe connectivity patterns of landscapes, allowing inferences about how changes in landscape patterns (i.e., presence, quantity, quality, and configuration of habitat types) influence the exchange of individuals of different life stages, and the possible feedbacks between scale of dispersal and persistence of a population. Individual life histories interact with landscape patterns to determine the scale of the landscape experienced by an organism, and how changes in landscape features and patterns influence population persistence. In a dynamic landscape, habitat patches have a finite lifetime and the linkage or connectivity between specific habitats may decrease with time, reducing habitat continuity and increasing fragmentation. The disappearance of patches increases the rate of local extinction, while a reduced amount of linked habitat decreases the rate of colonisation and thereby makes metapopulation persistence more difficult (Hanski, 1999). Knowledge of habitat heterogeneity is therefore an important management tool for maintenance of biodiversity (Hewitt et al., 2004).

Habitats can be defined by their heterogeneity, rather than the homogenous domination by individual species or sediment type. Heterogeneity refers to any variation in a habitat that is related to the relative abundance of any structural components (Bell et al., 1991). Habitat structure may be so intertwined with other components of the environment that documentation of its unique effect upon the organism(s) of interest is difficult (Bell et al., 1991). Both metapopulation and meta-community studies highlight the importance of connectivity in terms of the movement of structure formers and the implications of these movements for system heterogeneity (e.g., Loreau and Mouquet, 1999). We can utilise these concepts to inform our understanding of how specific habitats contribute to ecosystem function in terms of functional performance, the degree to which they sequester or release energy or matter that affect the supply and flow of ecosystem services, and how this changes with landscape fragmentation and degradation.

THE CHALLENGES IN PROCESS CONNECTIVITY

Many ecosystems are defined by multiple processes occurring over multiple temporal and spatial scales, with processes varying between habitats and their associated biotic community. This complexity requires a framework to enable us to determine ecosystem functioning, particularly with respect to addressing impacts of future changes. Loreau et al. (2003) expanded the concept of meta-community dynamics to include the movement of propagules, migrants, nutrients and energy under the framework of meta-ecosystems. However, it is difficult to practically assess ecosystem connectivity for ecosystem processing (see **Table 1**). The use of multiple drivers is important as the interactions among processes, communities and habitats are complex; a single factor alone cannot adequately describe a system in terms of multiple functions and ecosystem services. Once the source-sink nature of particular habitats has been empirically characterised in terms of connectivity of key processes or functions, empirical data reflecting multiple ecosystem processes can be combined to investigate how different habitats are connected (e.g., **Figure 1**).

There have been few empirical tests of process connectivity in a meta-ecosystem framework (see Loreau and Holt, 2004; Gravel et al., 2010a,b; Massol et al., 2011; Menge et al., 2015), and further developments are needed to be able to use this framework to understand heterogeneous ecosystems. Previous research into ecosystem process connectivity has focussed on tracking material and energy through an ecosystem, similar to early larval movement studies. Following particulate matter is more difficult than following larvae (though this is not easy!), as it is often much smaller (e.g., mud grains), and often cannot be tracked using modern techniques such as DNA fingerprinting (e.g., Almany et al., 2017). Instead techniques include, for example, the use of turbidity plumes and aerial images to ground-truth particle or particulate dispersion models. Inferring connectivity patterns with particulate tracers has had some success, but there are assumptions made with these methods, particularly as they are often based on limited empirical measurements that are unlikely to incorporate the range of typical diurnal, seasonal, climate, and storm-related variability that influences dispersal trajectories. Advances have been made in model frameworks for tracking larvae, which have led to advances in particle and sediment tracking models, but it is crucial that these models are validating using empirical data to confirm that they realistically predict how particulate matter will behave, and to generalise across hydrodynamic scenarios.

The composition of the faunal and floral communities in a meta-ecosystem framework also influences the flux of materials and energy. Species dominance in a community can directly influence a particular process (e.g., nutrient efflux, sediment stability), for example, through movement or feeding activity that is tightly coupled to the interactions within a community based on individual species' functional traits (Kristensen et al., 2014). This coupling is important for understanding changes in ecosystem functioning, as ecosystems experience change due to anthropogenic impacts which often directly influence community composition. Ecosystems collectively determine the biogeochemical processes that regulate the Earth's system as a whole, so biological communities have the potential to buffer or exacerbate global change (Cardinale et al., 2006; Davies et al., 2012). Furthermore, ecosystem process studies should incorporate multiple functional traits, rather than just one aspect such as size, as the largest species do not always have the greatest impact on ecosystem functioning (Solan et al., 2004). The results of human pressures on a community are not random; instead the sequence of species losses depends on the functional traits of the organisms and the mechanisms associated with how specific stressors affect species. Localised extinction rates will continue to accelerate into the next century (Snelgrove et al., 2014), so for the environment to be sustainably managed we need to be able to predict the potential impacts of large-scale environmental changes and the ecosystem consequences of altered biodiversity in order to effectively direct management and policy.

Through material and energy exchanges, ecosystem changes at a local scale can influence adjacent areas, and these effects can be extrapolated to regional and global scales (Arndt et al., 2013). Thus, habitat maps at scales that allow for interpretation of source-sink dynamics and quantification of ecosystem function are essential building blocks for meta-ecosystem models. However, resources are unlikely to be sufficient to empirically monitor each habitat at the temporal and spatial scales required to inform a meta-ecosystem framework. Rather, extrapolations of habitats using models to assess ecosystem predictors across space have become important. In heterogeneous systems, habitats are likely to differ in the degree to which they sequester and/or transform materials, or enhance transport rates, linking to the concepts of source/sink dynamics, whereby habitat patches serve as either sources or sinks in terms of the production of propagules. The general definition of the source and sink concept was developed to transcend disciplines and is based on net flows between the components of a system. This concept is context-dependent, but a source is a subsystem that is a net exporter of the entity of interest (living or non-living), and a sink is a net importer of these entities (Loreau et al., 2013). Population and process-based dynamics may not correspond in space, and patches may serve as sinks in terms of population dispersal (i.e., a retention zone for larval settlement), but as sources of processes (i.e., hotspots of primary production and nutrient cycling). Variability in spatial structure both within and between habitats is therefore an important functional component of a landscape, influencing not only population and community dynamics, but also the nature and efficiency of ecosystem processes (Legendre, 1993).

Subsidies represent the movement from a resource-rich location to a poorer location, and thus relate clearly to the concepts of source-sink dynamics in meta-population dynamics (Loreau and Holt, 2004). When a new subsidy is introduced into a system, the organisms and processes that rely on the subsidised resource increase as the ecosystem processes and community structure respond to the available resources (Polis et al., 1997). Spatial subsidies can be episodic but result in a legacy in the sink system, such as in the case of whale-falls or deposition of plant debris to the food-limited deep-sea floor, yielding pulses of

TABLE 1 | Summary of the challenges, considerations and potential solutions for process-based connectivity studies, with corresponding examples.

Challenges	Considerations	Solutions	Examples	
Dominant organisms and their behaviours have disproportionate influences on ecosystem processes	- Infaunal organisms may dominate ecosystem function, but are difficult to quantify	- Develop new techniques to recognise and quantify behaviour of key organisms, including infauna and cryptic species with disproportionate influences on ecosystem processes	Woodin et al., 2010	- Describe the major players in bioadvection and its impacts on ecosystem functioning
			Needham et al., 2011	- Habitat-specific functional role of crabs showed highly complex organism-sediment interactions
			Duffy et al., 2015	- Site variation found to be a better predictor of grazer and algal biomass in eelgrass beds than global environmental gradients
			Murray et al., 2017	- Environmental stress caused species to alter their rate and mode of activity, and thus their influence on ecosystem functioning
Dominant community types within a habitat, particularly the large organisms, can greatly influence the ecosystem processes	- Biological and ecological habitat definitions are important, and habitat classifications should not be solely based on physical attributes	- Catalogue the role of key species in defining the source-sink attributes of habitats and how these attributes vary with abundance of key organisms	Thrush et al., 2006	- Loss of large deposit-feeders from the sediment caused shifts in biogeochemical processes and production
			Norkko et al., 2013	- Large, deep-burrowing bivalves the best predictor of ecosystem functioning
			Smyth et al., 2013a	- Oyster-mediated denitrification shifted microcosms from a source to a sink of nitrogen
Entities can transform from one state to another, to the extent that they leave the environment completely (e.g., into the atmosphere)	- Ecosystem and habitat boundaries are often diffuse and poorly defined - Multiple similar habitats are often assumed to be homogenous	- Define sources and sinks that include material transformations and the potential for different scales of transport associated with transformation (gas, solute, particle)	Eyre et al., 2011	- Functional contribution determined of major benthic habitats in an ecosystem to the flow of energy and nutrients
			Eyre and Maher, 2011	- Constructed maps of ecosystem processes and habitat classes and determined functional value of impacts
Changing the scale can alter or lose patterns, or new ones can emerge	- Habitats need to be defined at a range of scales	- Real-world experiments at a range of scales	Thrush et al., 1997	- Synopsis of cross-disciplinary workshop for informing management on the challenges of extrapolation from small-scale studies
			Hewitt et al., 2004	- Used large-scale acoustic data in combination with small-scale ecology to inform management
			Barnes et al., 2016	- Measured drivers of spatial variation in ecosystem functioning at the landscape scale over spatial and environmental gradients
Monitoring and modelling long-distance dispersal can be difficult	- Passive and active transport occur at different scales - Energy and matter can be transformed both via biogeochemical pathways or in food webs	- Develop ecosystem assays to define source and sink habitats - Develop surrogates for dispersal (connectivity maps; habitat landscape maps)	Lundquist et al., 2004	- Used a combined hydrodynamic and particle tracking model to predict how limited dispersal of dominant organisms influences estuarine communities

(Continued)

TABLE 1 | Continued

Challenges	Considerations	Solutions	Examples	
			Pilditch et al., 2015	- Present the importance of understanding post-settlement dispersal processes on the seafloor for management
Interactions of processes with organisms need to be considered	- Mechanistic understanding of interactions between ecosystem components	- Empirically test hypotheses concerning interactions and their effects on source-sink dynamics	Laliberté and Tylianakis, 2012	- Shifts in grassland plant functional composition and diversity caused by grazing intensity and soil resource availability
Spatial scales involved can be extensive (i.e., global)	- Upscaling and combining habitats may lead to loss of detail	- Incorporate heterogeneity of habitats when scaling up estimations	Lohrer et al., 2015	- Found coherence in results from small and large scale manipulations of key consumers effects on net primary production
Process connectivity requires detailed information on habitat patch structure, including information on adjacent and nearby patches	- Habitats are often defined at scales unrelated to process connectivity	- Develop new techniques to map habitats in ways that relate to ecosystem function and source-sink dynamics	Smyth et al., 2013b	- Estimated whole watershed nitrogen load by measuring individual habitats within the ecosystem
			Lavorel et al., 2017	- Synthesis on linkages between ecosystem service mapping and ecosystem functioning
			Thrush et al., 2017	- Manipulated sediment pore water nitrogen demonstrated functional patchiness across a sandflat landscape
Estimates of environmental change are needed to assess large- or long-scale processes, such as climate change	- Current estimates are scarce and restricted to regions of human interest	- Ensure long-term monitoring of environmental change, and develop metrics that incorporate large- and long-scale processes	Craine et al., 2015	- Synthesis of soil nitrogen measures across climate gradients
			Hawkins et al., 2017	- Illustrate the need for long-term studies when identifying climate change impacts and present recommendations for adaptive management

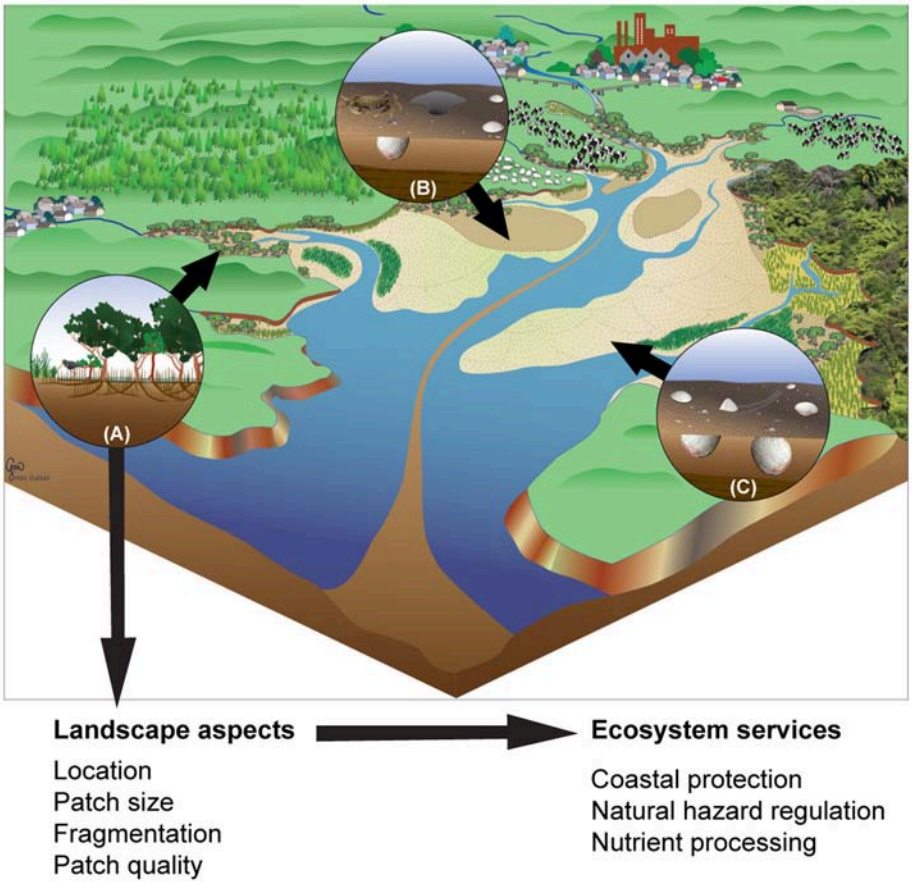

FIGURE 1 | Estuarine habitats that vary in their role in sequestering or exporting materials. Fine sediments are sequestered in mangroves **(A)**, sediment erosion rates are increased by crab burrows in sandy sediments **(B)**, and the rate of organic matter transformation and the remineralisation of nutrients are enhanced by the activities of infaunal bivalves **(C)**. These processes serve to connect habitats by moving material between habitats within the estuary and the surrounding areas. Examples of the connectivity factors and ecosystem services are shown, highlighting not only the performance of specific habitats but also how the arrangement of the habitats within the estuary may influence the effective functioning and service delivery at the scale of the estuary.

labile organic matter and energy (Lundsten et al., 2010). These linkages help to define the nature of ecosystem functions and the level of functional performance at multiple spatial scales and, when supporting humans in the ecosystem, provide ecosystem services. However, whilst these allochthonous subsidies show the unidirectional flows between habitats, understanding the full extent of the multidirectional fluxes requires integration of more complex interactions between ecology and landscape elements.

In the most general sense, connectivity represents the flux of energy or matter, dissolved or particulate, and the changes that can occur as these components move through, or are stored or transformed in habitats. For example, dissolved nutrients can turn into particulate plant matter and then be remineralised due to the behaviour of organisms or via biogeochemical reactions that occur in either the sediment or the water column. At the habitat scale a patch may be a source or a sink of a specific magnitude, but patches are additionally coupled by the multi-directional flow of propagules, energy and matter, each in turn influencing ecosystem functionality. Extrapolating to the landscape scale; fragmentation and degradation of habitats results in non-linear decreases in patch connectivity and collapse of process linkages that contribute to ecosystem function (Debinski and Holt, 2000). This spatial heterogeneity produced as a result of local disturbance events also influences the structure and function of benthic communities, and thus determines the recovery potential of both ecosystem structure and function (Thrush and Dayton, 2002).

CONCLUSIONS

Whilst methods for measuring population connectivity continue to advance, substantial challenges remain in elucidating generalisations about process-based connectivity at the scale of ecological habitats. The complexity of the processes involved, as well as the need to quantify ecosystem function on multiple temporal and spatial scales, provide numerous areas for future research (**Table 1**). However, the methods developed in population connectivity research can serve as a useful building block for further development of process connectivity. The "meta-ecosystem concept" provides one conceptual framework to inform our understanding of ecosystem connectivity in the form of energy and matter (Loreau et al., 2003). However, the meta-ecosystem concept has been difficult to empirically operationalise. A simpler source-sink approach can be extrapolated across multiple processes and habitat patches, providing a more tractable framework to allow for empirical validation of theoretical concepts. The performance of the system can be altered along multiple dimensions reflecting both different processes and functions, and interactions with dominant community types that populate each habitat (Loreau and Holt, 2004). When impacts of system disturbances are considered, the hotspots of functionality across multiple processes can shift, and the system may become less effective at supporting ecosystem function (Thrush et al., 2017).

Natural ecosystems are moulded by ecological and environmental processes, which make them inherently complex on multiple temporal and spatial scales. We are only just beginning to realise the importance of how these processes interrelate with local species interactions to control the structure and function of meta-ecosystems (Gravel et al., 2010a). Increased spatial subsidies, due to regional climatic or anthropogenic factors, have been shown to affect the health and structure of interconnected ecosystems (Spiecker et al., 2016). The impact of source-sink dynamics associated with ecosystem functions such as nutrient cycling and sediment transport differ depending on the context, the associated habitats, and the entity in question, all of which must be accounted for when using the source-sink concept. There is clearly a need to understand how habitat structure changes may affect the functioning of an ecosystem, in association with anthropogenic impacts. This will lead to understanding of the implications at a system scale, encompassing change both within and across habitats.

The effectiveness of reserves and the optimal spatial management of meta-ecosystems is important for resource managers to consider how to balance the multitude of ecosystem services in light of the increasing threats these systems face. Developing a fundamental understanding of the patterns and connections that exist between habitats via processes will lead to key insights into how ecosystems function and how changes in function are linked to changes in habitats and habitat connectivity. Filling this gap in our knowledge is crucial as it will allow for better mapping of ecosystem services, better understanding of the functional implications of habitat loss and fragmentation, and how breaking these connections impacts on ecosystem functionality.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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The Coherence of the European Union Marine Natura 2000 Network for Wide-Ranging Charismatic Species: A Mediterranean Case Study

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The Natura 2000 (N2k) network is an important site-based protection tool for the protection of biodiversity in Europe. However, for highly mobile and adaptable marine species, such a tool might not be the most effective way to achieve conservation objectives, unless this includes a broader consideration of the direct threats to these species throughout their range. Considering that the N2k network requires that a "*significant proportion*" of 60% of the population be under protection, this creates a challenge for the conservation of these wide-ranging species. This paper reviews the efficacy of the N2k network as it is presently implemented within the Adriatic Sea for the conservation of two highly mobile marine species—the common bottlenose dolphin and the loggerhead turtle. In particular, it considers the appropriateness of the current Sites of Community Importance (SCIs) in the region and the relevance of the existing marine N2k network for the conservation of these species. It provides new insights on the approach used to evaluate SCI designations highlighting important weaknesses in the system, including threat identification after SCI designation, and the relevance of SCI size in relation to management commitments. Data from two basin-wide aerial surveys were used to define areas of relative high density of these species, in comparison to other areas in the basin. Given the ambitious 60% conservation target of the N2k network, analysis shows that site-based protection tools are unlikely to be sufficient to protect a "significant proportion" of either species, unless very large areas are designated as SCIs. However, given that the main threats known to affect these species in this region (i.e., fishery bycatch and seismic surveys) are present throughout the basin, these large SCIs would still have limited conservation success without implementing other wide-scale mitigation measures. For these two species, the Member States and the European

Union authorities should give higher priority to the implementation of another pillar of the Habitats Directive, mitigating accidental catches in fishing gear and other human-induced mortalities. This should take into consideration the full effects of these mortalities on the populations of these two species through regular transboundary monitoring programs.

Keywords: marine protected areas, Natura 2000, aerial surveys, cetaceans, marine turtles, *Tursiops truncatus*, *Caretta caretta*

INTRODUCTION

The Natura 2000 (N2k) network of the European Union (EU) consists of Special Areas of Conservation (SACs) designated under the Habitats Directive (Council directive 92/43/EEC, HD) and Special Protection Areas (SPAs) under the Birds Directive (Council directive 79/409/EEC, BD). The overall conservation objective of the network is to "*. . . maintain or restore, at favorable conservation status, natural habitats and species of wild fauna and flora of Community interest*" (Article 2, HD). Given the working definition of "*favorable conservation status*," this means protecting at least 60% the populations (Anonymous, 1997). The N2k is one of the World's most extensive networks of protected areas, which currently includes over 27,500 terrestrial and marine sites, covering almost 19% of the territorial waters of EU member states but <4% of their EEZs (Agnesi et al., 2017).

When evaluating the need for the designation of marine N2k sites for species listed in Annex II of the HD and identifying Sites of Community Importance (SCI), which are the first step for SACs designation, national administrations must follow the framework laid out in Article 4 and Annex III. Stage 1, must take into account the overarching objective to set up "*a coherent European ecological network of special areas of conservation*" that will enable "*the species' habitats concerned to be maintained or* [. . .] *restored at a favorable conservation status in their natural range*" (HD Article 3).

Thus, the only two key factors that need to be considered to achieve this objective are the species and its habitat. Once an SCI has been adopted and published in the Union list by the European Commission, it becomes part of the N2k network and the relevant Member State (MS) shall designate it as a SAC "*within 6 years at most*." It is only at this point that aspects related to threats become important, as priorities for designation of a SCI into a SAC are formally established "*in the light of the threats of degradation or destruction to which those sites are exposed*" (HD Article 4.4).

The bottlenose dolphin (*Tursiops truncatus*) and the loggerhead turtle (*Caretta caretta*) are wide-ranging aquatic species listed in Annexes II and IV of the HD. The loggerhead turtle is also a priority species, with known nesting and feeding areas within the Mediterranean region (Casale and Margaritoulis, 2010). According to Article 1(k) of the HD, sites selected for wide ranging species, "*shall correspond to the places within the*[ir] *natural range*" with "*the physical or biological factors essential to their life and reproduction*." Additionally, Article 4.1 of the HD requires that for aquatic species, such sites can "*be proposed only where there is a clearly identifiable area* [emphasis added]" encompassing those factors.

The EU authorities encourage MSs to coordinate through the existing Regional Seas programs when working with other MSs and third countries (EC, 2005). Within the Mediterranean Sea the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean (Barcelona, 1976; amended in 1995), particularly the Protocol Concerning Specially Protected Areas and Biological Diversity in the Mediterranean (SPA Protocol; Barcelona, 1995). The Barcelona Convention also lists the bottlenose dolphin and loggerhead turtle as threatened species requiring parties to adopt cooperative measures for their conservation. It has also adopted the criteria for ecologically or biologically significant areas (EBSAs) of the Convention on Biological Diversity several of which include the waters of the Adriatic Sea (decisions COP-09-DEC-20 and COP-12-DEC-22; Fortuna C. et al., 2014).

The Adriatic Sea, although representing only 5% of the surface area of the Mediterranean Sea, includes the largest continental shelf in the region, which makes it ecologically important for these two species. From the policy perspective the Adriatic Sea has been identified of particular importance for coordination the of MSs and third countries as it has been identified as a sub-region of the Marine Spatial Planning DirectiveEU Marine Strategy Framework Directive (MSFD; 2008/56/EC). The MSFD promotes a wider ecosystem-based approach to marine management identifying that Good Environmental Status cannot be achieved within national borders but only in a wider, regional context (van Hoof et al., 2014). In addition, the macro-regional EU Strategy for the Adriatic and Ionian Region (EUSAIR) was launched in 2014 by the European Commission to coordinate the future of the region, including an environmental quality pillar, which focuses on the marine environment and transnational terrestrial habitats and biodiversity (EC, 2014).

At present, there are 77 fully or partially marine N2k sites (either SCI or SAC) within the Adriatic Sea, at different stages of designation (http://natura2000.eea.europa.eu/; data extracted from N2k Standard Data Forms, downloaded in May 2018) of which 29 list either one or both of these species (see **Table 1**). Currently, Croatia does not list the loggerhead turtle for any existing site, and Slovenia does not list either species for any existing site.

Given the transboundary nature of these species, the four criteria from the Habitats Directive used to assess the relative importance of sites for species in Annex II, were applied at the level of the Adriatic Sea rather than the usual national scale, as the national scale would be meaningless. The N2k criteria are: (1) "*Size and density of the population of the species present on the site in relation to the populations present within a national territory*" (B.a); (2) "*Degree of conservation of the features of*

TABLE 1 | Adriatic Sea Natura 2000 sites listing the bottlenose dolphin and the loggerhead turtle.

Site name and code	Area	Bottlenose dolphin		Loggerhead turtle	
		Abundance	**Population**	**Abundance**	**Population**
ITALY					
Special areas of conservation: *N = 8; Total area = 103.8 km^2 (Bottlenose dolphin 34.7 km^2; Loggerhead turtle: 103.8 km^2)*					
Aree Carsiche della Venezia Giulia [Kartstic areas of Venezia Giulia], IT3340006	2.4 km^2	Common	$2\% \geq p > 0\%$	Present	Insignificant
Carso Triestino e Goriziano [Triestian & Goritian karst], IT3340006	1.9 km^2	Common	$2\% \geq p > 0\%$	Present	Insignificant
Valle Cavanata e Banco Mula di Muggia [Cavanata basin and Muggia bank], IT3330006	6.1 km^2	Present	insignificant	Present	Insignificant
Cavana di Monfalcone, IT3330007	0.2 km^2	–	–	Present	Insignificant
Foce dell'Isonzo—Isola della Cona [Isonzo delta—Cona Island], IT3330005	11.7 km^2	Rare	$2\% \geq p > 0\%$	Present	$2\% \geq p > 0\%$
Laguna di Marano e Grado [Grado and Marano lagoon], IT3320037	11.5 km^2 +	Rare	$2\% \geq p > 0\%$	Present	$2\% \geq p > 0\%$
Litorale di Porto d'Ascoli [Porto d'Ascoli littoral], IT5340001	1.0 km^2	Present	$2\% \geq p > 0\%$	Present	$2\% \geq p > 0\%$
Litorale Brindisino [Littoral of Brindisi], IT9140002	68.9 km^2	–	–	Present	Insignificant
Sites of community importance: *N = 13; Total area = 216.5 km^2 (Bottlenose dolphin 91.1 km^2; loggeerhead turtle 216.5 km^2)*					
Area marina di Miramare [Miramare Marine Protected Area], IT3340007	0.2 km	Present	$2\% \geq p > 0\%$	Present	$2\% \geq p > 0\%$
Trezze San Pietro e Bardelli, IT3330009	23.8 km^2	Present	$2\% \geq p > 0\%$	Present	$2\% \geq p > 0\%$
Relitti di Posidonia presso Grado [Posidonia relicts in Grado], IT3330008	0.01 km^2	Present	insignificant	Present	$2\% \geq p > 0\%$
Tegnùe di Porto Falconera [Porto Falconera reefs], IT3250048	6.2 km^2	Present	insignificant	Present	Insignificant
Tegnue di Chioggia [Chioggia reefs], IT3250047	26.6 km^2	Present	insignificant	Present	Insignificant
Sacca di Goro, Po di Goro, Valle Dindona, Foce del Po di Volano [Goro embayment, Didona basin, Po Delta of Volano], IT4060005*	29.7 km^2	–	–	V. rare	Insignificant
Bosco di Volano [Volano wood], IT4060007*	1.2 km^2	–	–	Present	Insignificant
Vene di Bellocchio, Sacca di Bellocchio, Foce del Fiume Reno, Pineta di Bellocchio [Vene of Bellocchio, Bellocchio embayment, Reno delta, Bellocchio Pinewood], IT4060003*	3.1 km^2	–	–	Present	Insignificant
Ortazzo, Ortazzino, Foce del Torrente Bevano [Ortazzo, Ortazzino and delta of Bevano creek], IT4070009*	1.8 km^2	–	–	Present	Insignificant
Relitto della piattaforma Paguro [Dismissed Paguro platform], IT4070026	0.7 km^2	Present	insignificant	Present	Insignificant
Torre del Cerrano [Cerrano Tower], IT7120215	33.5 km^2	Very rare	insignificant	V. rare	Insignificant
Torre Guaceto e Macchia S. Giovanni [Guaceto Tower and S. Giovanni bush], IT9140005	75.8 km^2	–	–	Present	Insignificant
Torre Veneri [Veneri Tower], IT9150025	13.9 km^2	–	–	Present	Insignificant
Special Protection Area: *N = 1; Total area = 5.5 km^2*					
Torre Guaceto [Guaceto Tower], IT9140008	5.5 km^2	–	–	Present	$2\% \geq p > 0\%$
Proposed site of community importance: *N* = 1; Total area = 0.4 km^2					
Costa del Piceno—San Nicola a mare [Piceno coast—St Nicholas at sea], IT5340022	0.4 km^2	Present	$2\% \geq p > 0\%$	Present	$2\% \geq p > 0\%$
CROATIA					
Sites of community importance: *N = 6; Total area = 3,638.6 km^2*					
Akvatorij zapadne Istre [western Istrian archipelago], HR5000032	763.0 km^2	Rare	$15\% \geq p > 2\%$,	*NIG*	*NIG*
Cres-Lošinj [Cres-Lošinj archipelago], HR3000161	525.7 km^2	Rare	$15\% \geq p > 2\%$,	*NIG*	*NIG*
[Archipelago of] *J. Molat-Dugi-Kornat-Murter-Pašman-Ugljan-Rivanj-Sestrunj-Molat* [islands], HR3000419	580.5 km^2	Rare	$15\% \geq p > 2\%$,	*NIG*	*NIG*
Nationalni park Kornati [Kornati National Park], HR4000001	165.7 km^2	Common	$2\% \geq p > 0\%$	*NIG*	*NIG*
Viški akvatorij [Vis archipelago], HR3000469	518.8 km^2	*NIG*	$15\% \geq p > 2\%$,	*NIG*	*NIG*
Lastovski i Mljetski kanal [Lastovo and Mljet channel], HR3000426	1085.0 km^2	Rare	$15\% \geq p > 2\%$,	*NIG*	*NIG*

The HD defines population categories: A, 100% ≥ p > 15%; B, 15% ≥ p > 2%; C, 2% ≥ p >0%; D, non-significant population. There are no management obligations if a population is listed as insignificant at a site. Sites marked with an asterisk are also SPAs. NIG: No information given. Data was extracted from Natura 2000 Standard Data Forms (http://natura2000.eea.europa.eu).

the habitat which are important for the species concerned and restoration possibilities" (B.b); (3) "*Degree of isolation of the population present on the site in relation to the natural range of the species*" (B.c); and (4) "*Global assessment of the value of the site for conservation of the species concerned*" (B.d).

The existing Adriatic N2k sites in which bottlenose dolphins and/or loggerhead turtles occur are diverse and reflect the substantially different approaches used by Italy and Croatia for their designation. As shown in **Table 1** (based on N2k Standard Data Forms available from: http://natura2000.eea.europa.eu), Croatian SCIs are much larger (ranging between 166 and 1,085 km^2 and encompassing around 11% of the territorial waters) and were established specifically for the conservation of the bottlenose dolphin. The Italian sites in contrast, were established based on the presence of several habitat types and different species, including the bottlenose dolphin, the loggerhead turtle, and marine and coastal bird species (some are also SPAs). They are much smaller, ranging from 10,000 m^2 to about 70 km^2, and together, they cover about 1% of the Italian territorial waters in the Adriatic Sea. Within these sites, the proportions of the populations of the two species present in respect to national waters were self-assessed as insignificant (in 6 for bottlenose dolphins and 16 for loggerhead turtles), therefore, not requiring any management action, according to the rules of the HD (Anonymous, 1997, 2007).

An essential criterion to consider when designating N2k sites is the degree of isolation of different populations (criterion B.c). The Mediterranean bottlenose dolphin meta-population is highly structured with a clear differentiation between the eastern and the western Mediterranean (Natoli et al., 2005). Recent studies (Gaspari et al., 2013, 2015) have rejected the hypothesis of a single stock within the Adriatic. Genetic evidence suggests the existence of three broad management units within the Adriatic Sea: the north-eastern, the north-western, and central-south Adriatic-Ionian sub-populations (Gaspari et al., 2013, 2015), notwithstanding the importance of local groups identified through photo-identification studies showing strong site fidelity (Bearzi et al., 1997; Fortuna, 2006; Genov et al., 2008; Pleslić et al., 2013). This structure approximates the physiography of the Adriatic (Artegiani et al., 1993).

The loggerhead turtle population structure in the Mediterranean is also complex, with three independent Regional Management Units (RMUs: the Mediterranean, the North West Atlantic and the North East Atlantic; Wallace et al., 2010). The individuals belonging to Mediterranean RMU, which reproduce in the region, are additionally classified into seven independent units (Shamblin et al., 2014). The Adriatic Sea is almost exclusively frequented by individuals of Mediterranean origin, with rookeries from Western Greece and Western Turkey providing the greatest contribution. Loggerhead turtles appear to be "randomly" distributed across the Adriatic Sea regardless of origin, and it is not possible to define an "Adriatic population" (Tolve et al., 2018).

This paper reviews the efficacy of the N2k framework as presently implemented for the conservation of these two wide-ranging transboundary marine species within the Adriatic Sea. In particular the terms of (i) the appropriateness of criteria laid down in Annex III of the HD for identifying potential SCIs in relation to its Article 4; and (ii) the relevance of the existing and potential new marine N2k sites to their conservation. The analysis is based primarily upon data collected on the distribution and abundance of the two species obtained through two basin-wide aerial surveys carried out in the summers of 2010 and 2013.

MATERIALS AND METHODS

Systematic data on the distribution and abundance of cetaceans and sea turtles throughout the Adriatic were collected during two aerial surveys carried out in the summers (31 July—9th September) of 2010 and 2013 (Fortuna C. M. et al., 2014; Holcer et al., 2015).

The survey design (equally spaced parallel transects and equal coverage probability for the three strata) followed standard line-transect distance-sampling methods (Buckland et al., 2004) using the software package Distance 7.0 (http://www.ruwpa.st-and.ac.uk/distance/; Thomas et al., 2009). A twin-engine aircraft (*Partenavia* P-68), equipped with bubble windows to allow visibility directly below the plane, was used (target altitude and ground speed 200 m and 185 km/h, respectively). Experienced researchers were employed for data collection. Data analysis was restricted to sightings and effort in good visibility and Beaufort state ≤ 3.

In addition to the bottlenose dolphin, other small cetacean species sighted included the striped dolphin (*Stenella coeruleoalba*), common dolphin (*Delphinus delphis*), and Risso's dolphin (*Grampus griseus*) (Holcer et al., 2015), which are all easily distinguishable from a plane flying at a height of 100 m. The category "sea turtles" within the Adriatic Sea represents almost exclusively the loggerhead turtle. The green turtle (*Chelonia mydas*), although indistinguishable from the loggerhead turtle from a plane, is primarily found in the southern Adriatic in low densities (about 1–5% of the total sightings; Lazar et al., 2004a; Fortuna et al., 2015).

For the surveys themselves, the study area was subdivided into three strata (north, central and south Adriatic) based upon bathymetry and existing knowledge of cetacean and sea turtle distribution. For this paper, additional sub-strata were also considered (**Figure 1**): (a) territorial waters (12 nautical miles (nm) from coast); (b) "Exclusive Economic Zones (and variations thereof)" and Continental Shelf Margin (CSM; mid-line); and (c) all Croatian N2k sites for bottlenose dolphins combined. The 12 nm and CSM borders were downloaded from EIONET (http://www.eionet.europa.eu/gis/) and while they do not necessarily reflect officially agreed or disputed borders, the difference is negligible in the context of this paper.

A grid of cells with resolution of 100 km^2 was built (10 × 10 km cells, projection ETRS 1989 LAEA; European Environmental Agency Standards), totaling 1,535 grid cells. The cell size was determined in relation to the size of the study area and the overall survey effort (km searched) to minimize empty cells and ensure adequate spatial replication. Data from the two aerial surveys in 2010 and 2013 were pooled and distance

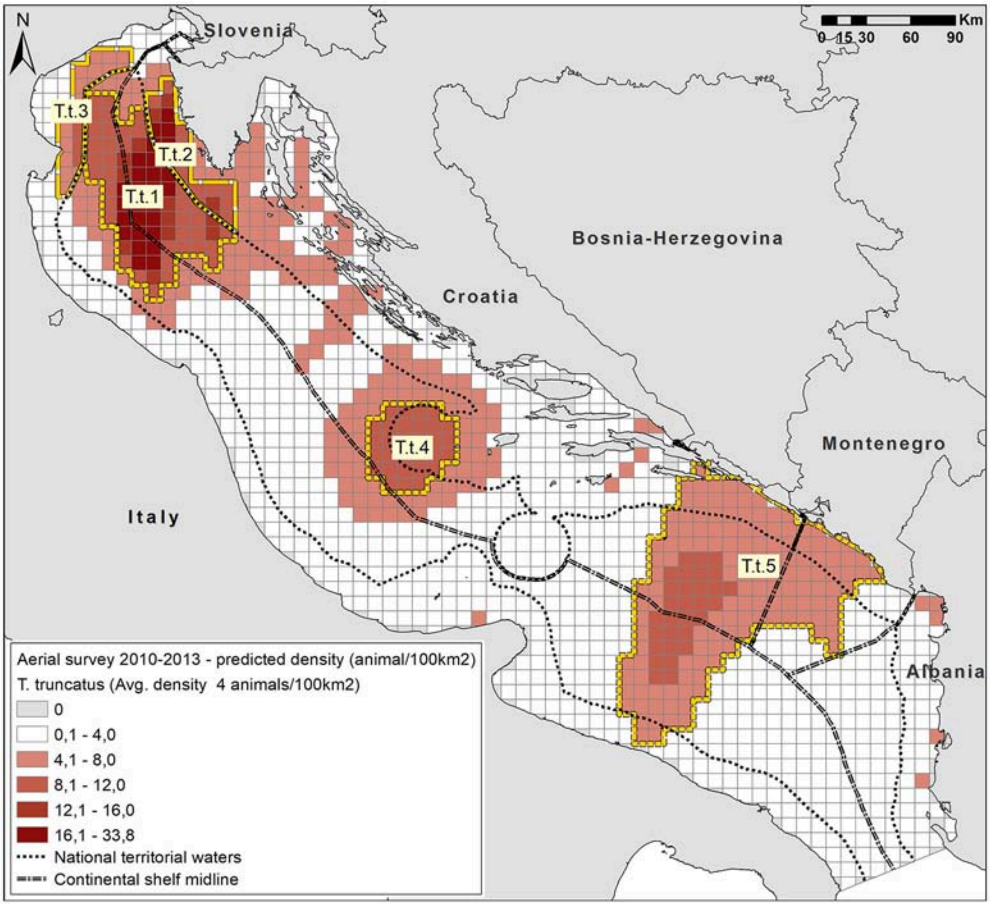

FIGURE 1 | Density Surface predicted distribution of the bottlenose dolphin in the Adriatic Sea based on 2010 and 2013 aerial survey data (darker red scale indicates higher relative density). The scales represent below average (white; L), and then up to twice (L-MD), up to three times (M-HD), up to four times (H-HHD) and greater than four times (MAXD), in shades of dark red. The proposed key areas (**Table 3**) are identified by yellow dotted (within 12 nm), dashed (over 12 nm), and dot-dashed shapes (areas within and over 12 nm).

analyses for estimating abundance (total number of animals) and density (individuals/km^2) was performed using the Distance 7.0 software. Data used were: (i) species identification, (ii) school size (best estimate), (iii) declination angle (to allow calculation of perpendicular distance of the sighting from the track-line), (iv) environmental information (including sea state, turbidity, cloud cover, etc.), (v) effort status and positional/time data. Abundance was estimated applying Density Surface Modeling (DSM) (e.g., Cañadas et al., 2018) and a prediction of abundance was extracted for the whole area and for all the strata created. Given that each grid cell was characterized by a predicted abundance, estimates for jurisdictional waters and all other sub-strata were obtained by filtering these cells according to the stratum to which they belong. Cells that were fully or partially overlapped by two strata were assigned to only one stratum, according to the higher overlap.

Applying estimated abundance after DSM shows the total number of bottlenose dolphins and loggerhead turtles present in a "generalized summer snapshot" for each sub-stratum. These abundance estimates were rounded to the nearest hundred and remain uncorrected for availability bias (i.e., animals that were underwater and not visible) and perception bias (i.e., animals at/or near the surface, but missed by observers). Thus, these estimates are lower than the true abundance and should be seen as only indices of relative abundance rather than absolute per stratum.

To map areas of higher density, we used the average density estimated for the entire Adriatic (2010–2013 pooled dataset) as an example reference value. For each species, densities categories were created as follows: (i) low density (densities below the Adriatic average, LD); (ii) low to medium densities (between the average and twice, L-MD); (iii) medium to high densities (two to three times the average, M-HD); (iv) high to highest (three to four times the average, H-HHD); (v) maximum densities (over four times the average, MAXD). For comparative purposes and to illustrate levels of variation, annual density maps were also prepared.

Using relative densities instead of absolute numbers does not affect the overall results or create biases in strata comparisons. Correction factors for availability and perception bias are simple multipliers that would be added to the uncorrected numbers and thus would have affected the density and abundance in all strata equally. Hence the ratio between strata would stay the same. As data in both surveys were collected by the same crew (constant perception bias), from the same platform (Partenavia P-68), using the same methods, during the same season (no behavioral changes affecting availability bias expected), this should guarantee that perception and availability bias were constant throughout the study.

RESULTS

The density and abundance estimates for the two species in summer are shown in **Table 2**. The estimated summer density distribution of bottlenose dolphins and loggerhead turtles are shown in **Figures 1**, **2**. The results are for the analysis of the combined 2010 and 2013 datasets.

Those sub-strata with a bottlenose dolphin density higher than the Adriatic average (0.042 dolphins/km^2) were the North Adriatic (0.057 dolphins/km^2), Croatian and Montenegrin territorial waters (0.046 and 0.049 dolphins/km^2, respectively), Croatian CSM (0.056 dolphins/km^2) and Croatian SCIs (0.048 dolphins/km^2).

Loggerhead turtle densities were double the Adriatic average (0.203 turtles/km^2) in the North Adriatic (0.405 turtles/km^2) and slightly over the average in the Croatian CSM (0.251 turtles/km^2).

The North Adriatic is the most important stratum for both species (about 47% and 69% of the total Adriatic bottlenose dolphins and loggerhead turtles, respectively; **Table 2**). Territorial waters of EU Member States included about a third of the total numbers of both species whilst about 90% of both species were found in jurisdictional waters of EU Member States (Croatian CSM, plus Italian and Slovenian territorial waters). The Croatian CSM hosted 57% of the Adriatic bottlenose dolphins and 53% of the loggerhead turtles. The Croatian SCIs designated for the bottlenose dolphin included about 12% of the putative sub-populations frequenting Croatian territorial waters, 7% of the North Adriatic sub-population but only around 3% of the total Adriatic population. Italian territorial waters included only 7% of the entire Adriatic bottlenose dolphin population. Given their reduced size, Slovenian waters were confirmed relatively unimportant for both species.

There were an estimated 5,700 bottlenose dolphins (C.I. 4,300–7,600) and 27,000 loggerhead turtles (C.I. 24,000–31,000) in the Adriatic Sea. As noted above these are underestimates as they are not corrected for availability or perception bias.

Density values, Summer patterns for combined years (**Figures 1**, **2**) and annually (**Figures 3**, **4**) helped identifying key areas for bottlenose dolphins and loggerhead turtles (**Tables 3**, **4**). The summer distribution of the bottlenose dolphin (**Figure 3**) was less consistent than that for the loggerhead turtle (**Figure 4**), at least for the 2 years of the survey.

DISCUSSION

Implementing a Policy

N2k network is an important EU tool for site protection and there is evidence that it can work well for many terrestrial species (e.g., Trochet and Schmeller, 2013), provided that appropriate protection measures are put in place and implemented. Nevertheless, for highly mobile generalist marine species, the concept of a network of marine protected areas (MPAs) may not be the most effective conservation approach. This is especially so when threats extend throughout the range of these species and conservation objectives are extremely ambitious (i.e., protection of a "significant proportion").

The effectiveness of spatial conservation measures depends on the combination of factors, such as the ecology of the species and their life cycles, the extent of the area protected, and the quality and level of enforcement of management measures undertaken to reduce the impact of threats on populations (Agardi et al., 2011; Hooker et al., 2011; Di Franco et al., 2018). Recognizing that there are limited resources devoted to conservation of nature, it becomes fundamental to prioritize actions (Wilson et al., 2007; Bottrill et al., 2008). For highly adaptable and generalist species, such as the bottlenose dolphins (Bearzi et al., 2009), it would seem appropriate to prioritize the management of at least those anthropogenic activities that have a measurable impact on their populations (i.e., fisheries and seismic exploration) throughout their entire range instead of focusing solely on MPAs (Wilson et al., 2007).

In the context of the designation of N2k sites, it is a weakness that the distribution of species, in relation to the threats that they face, is considered only after the designation of a SCI. Depending on the distribution of threats, mitigation measures should be implemented on the full range of the population (as required by HD Art. 12). The establishment of only a network of MPAs will probably be inadequate. In addition, variability in annual and seasonal distribution of these species may preclude the establishment of effective "small areas" with fixed boundaries (see **Figure 3** that shows considerable annual variability for the bottlenose dolphin). This also highlights the difficulty of designating areas based upon limited datasets in time and space for such species, which has been the case for most Adriatic SCIs.

The N2k framework also establishes that, within designated SCIs, species whose populations are assessed as "non-significant" (D) do not require management actions. Management measures are only considered for species whose populations are assessed as above 0%, possibly between 2 and 15% of the national population (categories: A: $100\% \geq p > 15\%$, B: $15\% \geq p > 2\%$, C: $2\% \geq p > 0\%$). This creates an apparent loophole (see **Table 1**), where the smaller a site is, the higher the possibility that it will not to be necessary to commit to specific species related management actions once the SCI becomes a SAC, making it only a protection "on paper."

Ecology and Jurisdiction: Different Rules and Scales

Ecological Setting

The available data shows that both species are present year-round in the Adriatic Sea (e.g., Lazar and Tvrtkovic, 1995;

TABLE 2 | Uncorrected (see text) abundance and densities for the bottlenose dolphin and loggerhead turtles in the Adriatic Sea.

Stratum		Bottlenose dolphin			Loggerhead turtle		
		Abundance (N)	**Relative weight**	**Relative density (ind/km^2)**	**Abundance (N)**	**Relative weight**	**Relative density (ind/km^2)**
ADRIATIC		5,700 (CIs = 4,300–7,600)	100%	0.042	27,000 (CIs = 24,000–31,000)	100%	0.203
North		2,600 (CIs = 2,200–2,900)	47%	**0.057**	18,200 (CIs = 17,700–20,000)	69%	**0.405**
Central		1,100 (CIs = 800–1,500)	21%	0.034	1,900 (CIs = 1,600–2,200)	7%	0.057
South		1,800 (CIs = 1,500–2,400)	33%	0.032	6,300 (CIs = 5,000–7,500)	24%	0.114
EU 12 nm	HR	1,500 (CIs = 1,300–1,800)	27%	**0.046**	5,400 (CIs = 5,000–6,100)	21%	0.172
	IT	400 (CIs = 300–2,400)	7%	0.017	2,700 (CIs = 2,300–8,400)	10%	0.117
	SI	na	negligible	na/negligible	na	negligible	na/negligible
Non-EU 12 nm	AL	100 (CIs = 40–200)	2%	0.023	200 (CIs = 100–300)	1%	0.041
	BH	Na	negligible	na/negligible	na	negligible	na/negligible
	MN	100 (CIs = 40–200)	2%	**0.049**	200 (CIs = 100–200)	1%	0.078
EU CSM	HR	3,100 (CIs = 2,800–3,600)	57%	**0.056**	14,000 (CIs = 12,700–14,800)	53%	**0.251**
	IT	1,800 (CIs = 1,500–3,000)	33%	0.030	10,400 (CIs = 9,200–12,500)	39%	0.171
	SI	NA	Negligible	na/negligible	na	negligible	na/negligible
Non-EU CSM	AL	300 (CIs = 100–1,000)	6%	0.031	700 (CIs = 300–1,000)	3%	0.074
	BH	na	negligible	na/negligible	na	negligible	na/negligible
	MN	200 (CIs = 100–300)	4%	0.029	1,200 (CIs = 800–1,400)	5%	0.166
	All HR SCIs	200 (CIs = 100–1,000)	3%	**0.048**	700 (CIs = 600–7,00)	2%	0.185

N, total number of animals; na, not available; HR, Croatia; IT, Italy; SI, Slovenia; AL, Albania; BH, Bosnia Herzegovina; MN, Montenegro.
Numbers are rounded to the closest hundred. The relative weight is the percentage of individuals included in different sub areas in relation to the estimate of the whole Adriatic Sea. Densities marked in bold are those higher than the Adriatic average. Italy does not have an Ecologic Protection Zone in the Adriatic yet. Slovenia and Croatia have a disputed border in the Bay of Piran.

Lazar et al., 2003; Bearzi et al., 2009; Casale et al., 2012). The present data confirm that the north Adriatic, as a whole, is an important area for the conservation of both species, at least in Summer. Using the combined data and taking into account the jurisdictional boundaries, three key areas were identified for the loggerhead turtle in the north Adriatic (Cc. 1–3). These spatially overlap with three high-density areas for bottlenose dolphins (Tt. 1–3; Tab. 2). The boundaries for these key areas should be considered tentative, especially because our reference point (the Adriatic average density for each species) is also temporally variable and does not necessarily capture areas of absolute importance for these species. Identifying an appropriate reference point requires more data (at both local and regional level) and some discretionary choice in relation to the agreed conservation targets. In addition, in the context of defining robust boundaries, considering a summation of the high-density areas by year (see **Figures 3**, **4**), rather than using the combined dataset, may be a better approach.

The summer survey data confirm the north Adriatic as a key neritic habitat for loggerhead turtles. It is in fact the largest such area in the Mediterranean, frequented by turtles hatched in western Greece, Crete and western Turkey (Lazar et al., 2011; Tolve et al., 2018). Given this species' benthic feeding strategy (Lazar et al., 2011) and overwintering behavior (Hochscheid et al., 2005, 2007), the entire northern Adriatic seafloor should be considered a "critical habitat" for the Mediterranean RMU.

The pelagic waters of the southern Adriatic (Cc. 4; **Figure 4**) also seem to be another important, but highly variable (**Figures 3**, **4**), habitat for loggerhead turtles. This is consistent with earlier tagging studies and dispersal models (Casale et al., 2007; Casale and Mariani, 2014). How to manage this highly variable transboundary pelagic habitat is a challenging issue.

The summer survey data confirm the north Adriatic as important bottlenose dolphin habitat, but the annual variation of local distribution can be quite large (**Figure 3**), making determining robust boundaries complex (possible examples are Tt. 1–3). The broad result is in line with the described preference of the species in the Mediterranean for habitats with depths <100 m (Bearzi et al., 2009; Gnone et al., 2011). The data also emphasize the importance of Croatian and Montenegrin territorial waters for this species, in comparison to a lower or negligible importance of Italian and Slovenian territorial waters, respectively (**Tables 2**, **3**).

A higher density area for bottlenose dolphins was found in the central Adriatic in 2013 (Tt. 4, around Jabuka/Pomo island, currently a GFCM Fishery Restricted Area; see Resolution GFCM/41/2017/3)—no such area was identified in 2010. Similarly, high density areas were seen in the southern Adriatic in both 2010 (only on the east) and 2013 (highest in the west). Designating "clearly identifiable areas" is therefore difficult (Tt. 5, based upon an analysis of the combined data does not capture the high density seen in the west in

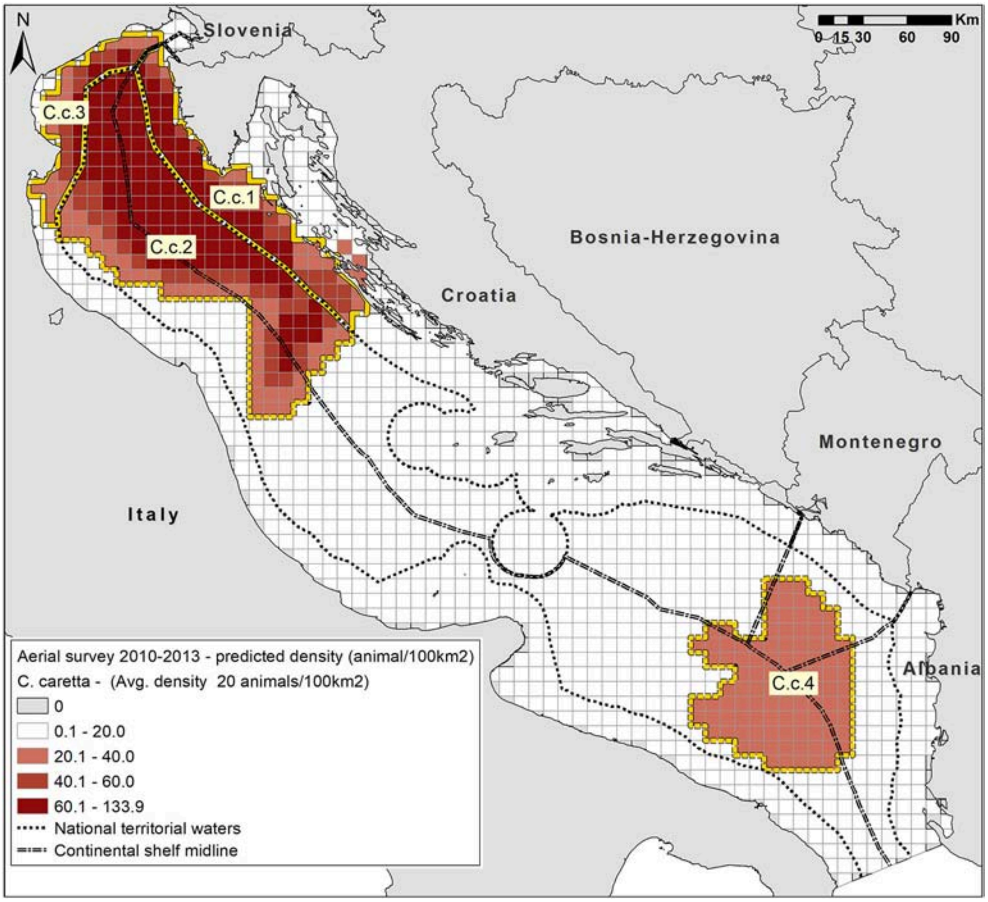

FIGURE 2 | Density Surface predicted distribution of sea turtles (mostly loggerhead turtles) in the Adriatic Sea based on 2010 and 2013 aerial surveys data (darker red scale indicates higher relative density). The scales represent below average (white; L), and then up to twice (L-MD), up to three times (M-HD), up to four times (H-HHD) and greater than four times (MAXD), in shades of dark red. The proposed key areas (**Table 3**) are identified by yellow dotted (within 12 nm), dashed (over 12 nm) and dot-dashed shapes (areas within and over 12 nm).

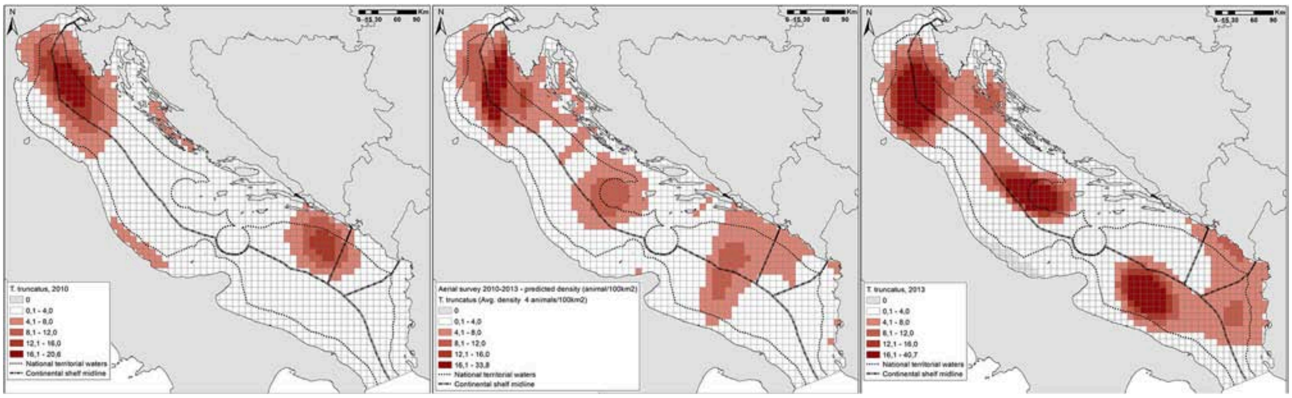

FIGURE 3 | Bottlenose dolphin densities for the data from 2010 (left); 2010–2013 (center), and 2013 (right). The scales represent below average (white), and then up to twice, up to three times, up to four times and greater than four times the average (shades of dark red).

2013). The ecological reasons for these temporally variable higher density areas are poorly understood. They could be related to food resources (especially in the more homogeneous northern Adriatic) and/or influx of specimens of the pelagic ecotype (especially in the south Adriatic; Gaspari et al., 2015).

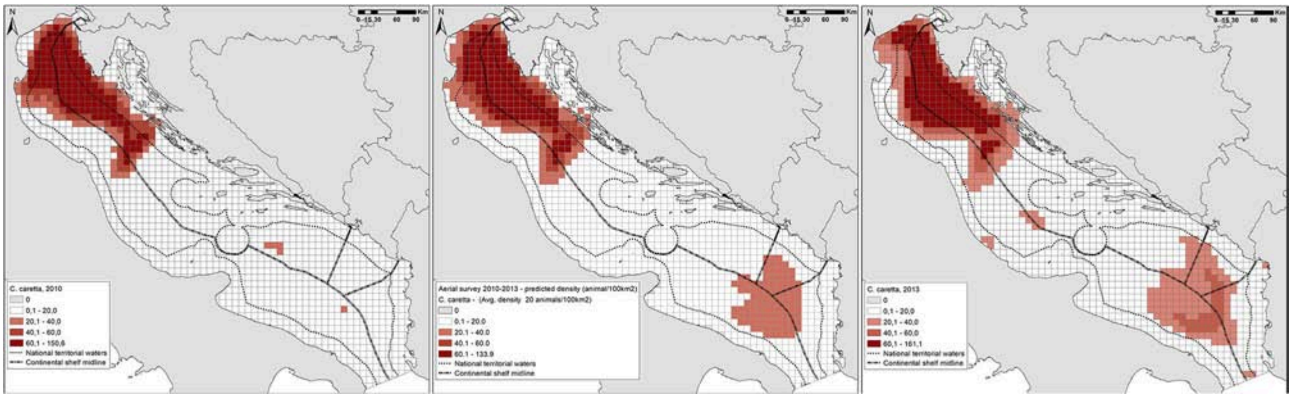

FIGURE 4 | Loggerhead turtle densities for the data from 2010 (left); 2010 + 13 (center), and 2013 (right). The scales represent below average and then twice, three times, and greater than three times average density (shades of dark red).

Jurisdictional Setting

Jurisdictional boundaries are irrelevant for these highly mobile transboundary species. Ideally, key areas should be identified without concern for jurisdiction in the expectation that the concerned countries will collaborate for conservation. However, there are several issues that complicate what appears to be simple in principle. The most obvious, in the context of the N2k framework, is that the animals are found not only within the EU waters, but also outside where the HD is not in force. While there is an obligation for MSs to apply the HD in their jurisdiction, it is not consistently applied. Each MS harmonizes their national law to the HD, which may create problems when applying the directive in a transboundary context. Also, the legal requirement to implement the HD is different in the different jurisdictions of the EU countries. For Italy, in the Adriatic, the HD requirements apply only to territorial waters and the seafloor of the continental shelf, and only for non-living resources, such as benthic habitats of species and sedentary living organisms (Anonymous, 1997, 2007). This is because Italy has not declared an EEZ within the Adriatic Sea. By contrast in 2003, the Croatian government declared an Ecological and Fisheries Protection Zone (EFPZ), extending its jurisdiction and thus also the commitment to implement the HD out to the mid-line with Italy (CSM). In practical terms, the distribution patterns described in this study for both species (**Figures 1–4**) emphasized the importance of offshore areas (particularly, Tt. 1, Tt. 4, Tt. 5, and Cc. 2), i.e., waters lying outside territorial waters and partially outside EU jurisdiction.

HD Article 4.1 states that N2k sites should "be proposed **only** where there is a **clearly identifiable area** representing the physical and biological **factors essential to their life and reproduction** [emphasis added]." However, for wide-ranging and behaviorally flexible species, this is difficult to apply without considerable and robust data that is seldom available and costly to obtain. Difficulties arise in selecting a "clearly identifiable area" unless it is permissible to include (a) a wide area to incorporate temporal and spatial variability and (b) to consider the nature of threats (and their mitigation) at an early stage. This rule has been legitimately used by some Member State to justify the lack of Natura 2000 sites for bottlenose dolphins and loggerhead turtles in their waters, especially when the robust information on "criteria B" (see below) is lacking not only nationally, but at the Mediterranean level. Our data and other studies (e.g., Lazar et al., 2004b; Casale et al., 2007, 2012) suggest that for loggerhead turtles a single site encompassing Cc. 1–3 feeding and wintering grounds could be proposed (**Figure 2**). Concerning the bottlenose dolphin, due to the fact that they do not have specific areas where they feed, mate or reproduce (Bearzi et al., 1997, 1999; Genov et al., 2008; Holcer, 2012; Pleslić et al., 2013; Triossi et al., 2013), the variability of their distribution is greater. Yet, higher density areas (**Figure 1**) and their annual variability (**Figure 3**) consistently suggest that at least the entire northern half of the north Adriatic could be proposed for protection. However, fine-tuning strict boundaries around these higher density areas for both these species it is challenging.

On one hand, the general legal requirements of the HD (and possibility of sanctions in case of non-compliance), may incentivize Member States to establish marine N2k sites in locations where studies have been carried out, rather than actual important habitats, or based on just "expert opinion." This may lack true understanding of the actual distribution of the species, the estimated proportion of the management/population unit that will benefit from such designation and the biological significance of proposed areas (as characterized under criteria B.a-B.d (Annex III of HD).

Important additional complications come from the wording in those four criteria.

(1) "Size and density of the population of the species present on the site in relation to the populations present within a national territory" (B.a). As illustrated in **Table 2**, the relevance of using the baseline of the size and density present "within a national territory" can be rather dubious in terms of biological significance considering the relevant biological population or management unit. In addition (e.g.,

TABLE 3 | Key areas for bottlenose dolphins in the Adriatic Sea based upon the combined 2010 and 2013 datasets (see **Figure 1**).

	Description	Relevance to existing Natura 2000 sites
Tt. 1	North Adriatic offshore waters (includes areas from H-HHD to MAXD)	–
Tt. 2	North-eastern Adriatic (includes areas from H-HHD to MAXD)	Overlapping sites HR5000032, HR3000161 and HR3000419 and adjacent to HR4000001
Tt. 3	North/north-western coastal waters off the Po delta and offshore waters off Veneto and Emilia-Romagna (Italy) (includes areas from L-MD to M-HD)	Overlapping sites IT3250047 and IT3250048, and adjacent to IT3320037; also overlaps or is adjacent to IT4060005, IT4060003, IT4060005, which do not list the bottlenose dolphin
Tt. 4	Pelagic habitat around Jabuka/Pomo island, including waters over 12 nm (includes areas with H-HHD)	Adjacent to site HR3000469
Tt. 5	Southern Adriatic, offshore waters off the of Dubrovnik, Croatia and Montenegro (includes areas with H-HHD)	Adjacent to site HR3000426

TABLE 4 | Proposed key areas for loggerhead turtles in the Adriatic Sea based upon the combined 2010, and 2013 datasets (see **Figure 2**).

	Description	Details
Cc. 1	Coastal waters of the north-eastern Adriatic (Istrian peninsula, Croatian waters and outside the Croatian archipelagos (includes areas from L-MD to MAXD)	Overlapping Natura 2000 site HR5000032 and adjacent to HR3000161, HR3000419 and HR4000001, none of which lists the loggerhead turtle
Cc. 2	Offshore waters off the Istrian peninsula, Croatia, outside the Croatian archipelagos (Cres-Lošinj, Premuda-Molat, Dugi Otok-Kornati) and off the Italian Regions of Veneto and Emilia Romagna (includes areas from H-HHD to MAXD)	–
Cc. 3	Coastal waters of the north and north-western Italian Adriatic (area between the Marano Lagoon, Friuli, and Sacca di Goro, Emilia Romagna) (includes areas from L-MD to MAXD)	Overlapping Natura 2000 site IT4060005, IT4060003, IT4060005 IT3250047, IT3250048, IT3320037 and IT3330008, and adjacent to IT3330005
Cc. 4	Offshore waters in the southern Adriatic (between the Italian Region of Puglia, Montenegro and Albania) (includes areas with L-MD)	

see **Figure 3**), the abundance and density can vary widely from year-to-year.

(2) "Degree of conservation of the features of the habitat which are important for the species concerned and restoration possibilities" (B.b). In many cases, identifying the important "physical and biological features" of the habitat for highly mobile species is difficult (and thus so is the concept of "restoration"). For example, whilst nesting sites of loggerhead turtles are easily identified and site protection designation is an effective conservation tool, only sporadic nesting activity has been recorded in the western Adriatic (Mingozzi et al., 2007) so the overall contribution to conservation of the RMUs of such site(s) may be minimal or even irrelevant. However, applying criterion B.b to their other important habitats—such as a feeding and wintering neritic habitat—is more difficult and is yet to be applied.

(3) "Degree of isolation of the population present on the site in relation to the natural range of the species" (B.c); and (4) "Global assessment of the value of the site for conservation of the species concerned" (B.d). The difficulty with both of these items lies in their use of phrases, such as "natural range of the species" and "global assessment [...] of the species" implying that the species is the suitable baseline. For widespread species, such as the bottlenose dolphin and the loggerhead turtle this would make the Adriatic Sea almost inevitably a "less important" area. This is clearly not an advisable baseline for conservation efforts that should focus on smaller "management units," such as biological or demographically isolated populations or sub-populations.

CONCLUSIONS

This paper does not propose any new protected areas for these species despite highlighting areas of relatively high density within the region. Rather it shows how data and modeling can be used to inform the designation process. In addition, it shows that there are weaknesses within the N2k designation process for marine wide-ranging species and proposes changes to the use of the Habitats Directive with regards to the use of Annex III. Utilizing biological data alone will have limited effect for conservation. Combining socio-economic data and stakeholder use patterns will enable conservation measures to be tailored to the regulatory context (Gissi et al., 2018). This is in line with other EU instruments that apply within this region, such as the Marine Strategy Framework Directive (2008/56/EC) (MSFD), the Marine Spatial Planning Directive (2014/89/EU) (MSP), the Environmental Impact Assessment Directive (2014/52/EU) (EIA), the European Common Fisheries Policy (CFP) and the EU Strategy for the Adriatic Ionian Region (EUSAIR).

Scientific Basis for Natura 2000 Sites

The experience from the Adriatic has shown the value of systematic large-scale aerial survey data for identifying abundance, density and broad-scale distribution of many large marine species, such as cetaceans and turtles (e.g., Pollock et al., 2006; Rowat et al., 2009; Lauriano et al., 2011; Panigada et al., 2011; Fortuna C. M. et al., 2014). However, such surveys can only produce a "snapshot" for time the survey is carried out. There are natural variations in density and distribution, as illustrated by the differences between the summer 2010 and 2013 surveys, which may complicate the definition of conservation goals. There are also often seasonal differences as witnessed in the Mediterranean by Panigada et al. (2011). For these reasons, especially for the species considered in this study but not only, the identification of site-based conservation measures must:

(1) be based upon several (we would suggest at least three) years of good quality broad-scale surveys to capture natural variability;
(2) incorporate effort in different seasons;
(3) take into account any methodological issues (e.g., missing smaller turtles <30 cm in carapace length, Fortuna C. M. et al., 2014) incorporating the uncertainty;
(4) take into account relevant small-scale studies (e.g., photo-identification for bottlenose dolphins, telemetry studies, data on bycatch from independent observers' schemes);
(5) undertake regular surveys after boundaries have been established to validate their suitability; and, in parallel,
(6) be based upon good knowledge of stock structure.

These "golden rules" are all "*sine qua non.*" Applying only some of these rules undermines the final objective of designating effective site-based conservation measures. At present, in the usual marine N2k context, these are not applied consistently nor fully.

Improved Conservation Approaches for These Species

This review has identified a number of features of the N2k process in relation to wide-ranging and/or migratory marine species, such as cetaceans and sea turtles, which require attention:

(1) the scientific basis for any sites must be robust, including identification of management units at supranational level (possibly through one of the exists coordinating bodies, such as the EUSAIR or Barcelona Convention);
(2) the nature of threats should be incorporated from the start of the process (e.g., in identifying potential SCIs and establishing their likely effectiveness at the supranational management unit level);
(3) Member States should collaborate with each other (and with non-EU range states) in developing SCIs and SACs that will actually improve conservation at the supranational management unit level rather than a perceived national level; and
(4) recognition should be given to the fact that to be effective, marine N2k sites may have to be extremely large in comparison to others for species with smaller ranges or well-identifiable critical habitats (e.g., feeding and breeding grounds).

Our study clearly shows that site protection measures alone are unlikely to have a significant conservation effect in protecting a sufficient proportion of the bottlenose dolphins or loggerhead turtles found in the Adriatic waters under EU jurisdiction, unless vast areas are designated as SCIs. Without implementing high priority wide-scale conservation measures to mitigate specific threats to these species, MPAs may in fact provide a sense of false security in terms of meeting their conservation objectives (Agardi et al., 2011).

While small MPAs have a direct conservation role where habitats are static, such as Posidonia beds, reef systems or shipwrecks, they have a limited direct conservation effect on wide ranging species. Conversely, MPAs may have multiple secondary effects on conservation, such as raising public awareness about a species, threat or issue, applying political pressure on decision makers or generally improving behavior and responsibility on the sea, which has previously been considered as open access and therefore the responsibility on none.

The objective of the EU Habitats Directive is improved conservation of species within their natural range; hence, implementing this overarching objective should be seen as primary focus, rather than focusing on only on the implementation of one of the available tools (i.e., site-based protection) in order to appear to be meeting HD legal requirements.

For wide-ranging and migratory species, HD Article 4.1 should be applied rigorously. Member States and European authorities in charge of the protection of these wide-ranging species should engage in cost-benefit analyses of all alternative conservation tools, before selecting a costly site-based solution, such as the designation of N2k sites. They should give the highest priority to the full implementation of Articles 11 and 12—two other HD conservation pillars. Particularly MS should (a) "*undertake surveillance of the conservation status of the natural habitats and species*," (b) "*establish a system to monitor the incidental capture and killing*," and (c) "*take further research or conservation measures as required to ensure that incidental capture and killing does not have a significant negative impact on the species concerned*."

In practice, all suggested actions or refinements to the HD are in line with the principle of creating an assessment framework for species and anthropogenic threats, with priority given to the evaluation and mitigation of incidental captures in fisheries and any other direct or indirect mortality caused by, for example, seismic surveys and ship strikes. This approach is fully in line with other European directives and policies, including the MSFD, MSP Directive, CFP and EIA Directive. It is worth noting that a draft Regulation related to the new EU Common Fisheries Policy on technical measures on the conservation of fishery resources and the protection of marine ecosystems, is currently being discussed (Anonymous, 2016). This proposed Regulation contains new potentially important provisions on gears, fishing techniques and gears' modification (e.g., gear length, mesh size, soaking/towing time, seasonal closures, excluder devices, pingers, etc.) to be used to mitigate the impact of bycatch on sea turtles and cetaceans. These technical measures, if fully developed and implemented by EU MSs, would be key legislative tools and they would have a more promising impact on the protection of these charismatic species than the designation of an area either as SCI or MPA.

While this paper focuses specifically on the HD in relation to other EU legislations, it has implications for the other policies relevant to this region including the Barcelona Convention and the Convention for Biological Diversity (Rio, 1992) which lists three areas within the Adriatic as EBSAs (dec-COP-12-DEC-22).

The regional seas agreement could provide a platform that can be used to improve coordinated conservation of species and habitats at international level (Bastari et al., 2016). However, it is down to the relevant national authorities to focus on streamlining and fully implementing all the relevant management and mitigation tools established under these policies to be applied at supranational level.

AUTHOR CONTRIBUTIONS

CF conceived the manuscript. All authors contributed to the writing and revisions of the manuscript. AC analyzed all data. DH edited all figures. CF, GD, and PM edited the final manuscript.

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Intertidal Biogeographic Subprovinces: Local and Regional Factors Shaping Fish Assemblages

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Intertidal zones shelter a wealth of species and natural resources, provide important ecological services, and sustain several economic activities in coastal communities. However, the tidepool fish species that inhabit the intertidal zone are subject to a wide array of impacts due to the human presence and their accessibility, creating a challenge for the mitigation of habitat loss, in particular in tropical regions where the ecology and distribution of species are poorly known. In this study, we investigated tidepool fish species distribution patterns systematically across *ca*. 4,900 km of tropical Brazilian coastline (00–21° latitude) in order to verify the latitudinal trends and environmental variables influencing tidepool communities. A total of 5,113 fish specimens belonging to 67 taxa were collected at the 19 sites, revealing four distinct biogeographic subprovinces: Amazon Estuary (AE), Northern Mangrove (NM), Northeastern Semiarid (NS), and Tropical Warm (TW). Distance-based linear modeling evidenced in sequence water salinity, tidal range, shape of rocky shore formation, algae cover, distance to subtidal zone, latitude and rainfall as the most important environmental variables to shape biogeographic subprovinces. Fish species such as *Bathygobius soporator*, *Bathygobius geminatus*, *Labrisomus nuchipinnis*, and *Scartella cristata* presented wide distribution, occupying more than one subprovince. The trophic structure of the tidepool fishes also varied among subprovinces, with carnivores being associated with the AE subprovince, omnivores with the NM, and herbivores dominating the NS and TW. These findings reinforce the determining role of local and regional factors in the geographic distribution of fish and, in particular, highlight a new arrangement for the intertidal subprovinces of the tropical Brazilian shoreline, which may provide a valuable tool for the more effective management and conservation of this vulnerable ecosystem at the land-ocean interface.

Keywords: tidepool, rockpool, reef fish, Brazil, endemism, biogeography

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INTRODUCTION

The latitudinal distribution patterns of aquatic and terrestrial organisms have been discussed by ecologists worldwide in an attempt to understand large-scale patterns and predict human-made impacts on wildlife (Mittelbach et al., 2007; Schemske et al., 2009; Wiens, 2015; Chaudhary et al., 2016; Cutter and Gray, 2016; Pecl et al., 2017). The ecological dynamics shaping natural populations are also dependent on processes at a local scale (Vilar et al., 2013; Heffernan et al., 2014; Elahi et al., 2015). This scale is especially important in the case of the intertidal zone, which comprises a harsh, but biologically productive habitat where exposure to sunlight, wave, and tidal processes create a highly dynamic habitat in which conditions fluctuate substantially over time (Raffaelli and Hawkins, 1996; Zander et al., 1999). In this context, biogeographic provinces and subprovinces can be proposed in accordance with the variation in these environmental features and related differences in species composition (see Briggs and Bowen, 2012; Pinheiro et al., 2018). In the beginning of this century some important global studies have addressed the challenge in proposing biogeographic arrangements and successfully contributed on this issue in terrestrial (Olson et al., 2001), freshwater (Abell et al., 2008) and marine realms (Spalding et al., 2007).

Historically, tidepool fishes studies have focused primarily on inventories and small-scale spatial patterns (Bennett and Griffiths, 1984; Nieder, 1993; Mahon and Mahon, 1994; Gibson and Yoshiyama, 1999; Castellanos-Galindo et al., 2005; Griffiths et al., 2006; Macieira and Joyeux, 2011), given that large-scale, biogeographic questions are more difficult to assess due to the variation among studies in sampling procedures, and the absence of a standardized sampling protocol (Prochazka et al., 1999). Since the publication of 'Intertidal fishes' by Horn et al. (1999), latitudinal (biogeographic) patterns of intertidal fishes have only been investigated, on a major spatial scale, by Griffiths (2003) and Harasti et al. (2016), in Australia, and Arakaki et al. (2014), in Japan. Intertidal fish communities may vary in response to latitude (see Harasti et al., 2016), however, local factors (e.g., substrate composition, water temperature, tidepool morphology, and height above sea level) may also have a strong influence on the distribution of fish species (Mahon and Mahon, 1994; Arakaki and Tokeshi, 2011; Macieira and Joyeux, 2011; White et al., 2015), even in a large-scale setting (Arakaki et al., 2014). Even so, the paucity of the data available for this vulnerable environment, which is at risk from both local and global impacts, is a major drawback (Helmuth et al., 2002, 2006; Thompson et al., 2002; Halpern et al., 2008; Vinagre et al., 2016; Andrades et al., 2017, 2018). In general, the large-scale distribution of species can be explained by dispersal capacity and geographic patchiness (Macieira et al., 2015), while community patterns at a local scale are driven strongly by local environmental characteristics, such as substrate type, the morphology of tidepools, and oceanographic features (Gibson and Yoshiyama, 1999; Cox et al., 2011).

As local habitat features can influence communities to the degree that they affect regional arrangements, it is imperative understand the underlying processes that determine these patterns (Ricklefs, 1987; Rivadeneira et al., 2002; Arakaki et al., 2014; Navarrete et al., 2014). The processes include biological interactions, such as herbivory, predation, and competition, as well as the effects of the physical environment (Horn and Ojeda, 1999; Arakaki and Tokeshi, 2011; Arakaki et al., 2014; Ahmadia et al., 2018). Given this, we will also attempt to understand how these regulatory mechanisms influence the organization of communities, in particular in tropical regions, where there is a scarcity of primary data. In the tropical Brazilian seascape, recent studies have investigated large-scale patterns in estuarine and reef fishes distributions, as well as the influence of local and regional factors (Vilar et al., 2013; Pinheiro et al., 2018). These studies have identified a number of local factors that structure fish assemblages on the Brazilian coast, but only Pinheiro et al. (2018) has discussed in detail the role of ecological and evolutionary processes in the fish distribution and proposed a set of biogeographic subprovinces based on the existing configuration of the Brazilian Province (*sensu* Briggs and Bowen, 2012). As intertidal habitats on the tropical Brazilian coastline are used by subtidal marine and estuarine fish species, also as nursery habitats or during their whole life-cycle (Macieira and Joyeux, 2011; Andrades et al., 2018), it is reasonable to expect that the intertidal fish fauna is highly influenced by local factors, resulting in more heterogeneous and complex biogeographic patterns than previously observed in reef fishes (Pinheiro et al., 2018).

We conducted our study in Brazilian tropical coast to verify the spatial shifts in the structure of tidepool fish assemblages in response to intertidal biological, physical, and physicochemical variables at a large-scale, while also considering local-scale variables. In addition, we predicted four subprovinces for tropical Brazilian intertidal coastline that have confirmed under both environmental and biological variables from 19 sites (0°–21° latitude).

MATERIALS AND METHODS

Study Area

The Brazilian coast extends over *ca*. 7,490 km, from 4° N to 34° S (**Figure 1**), with an enormous diversity of climatic, geomorphologic, oceanographic, and ecologic features. As the ecological dynamics of classic rocky shores and flat intertidal reefs are distinct (Mahon and Mahon, 1994; Macieira and Joyeux, 2011; Andrades et al., 2018), the present study surveyed sites between 0°S and 21°S, which encompasses the transition of intertidal flat reefs to rocky shore (slope is present).

The northern coast has a humid tropical climate (Köppen Am type), while the northeast region is divided in two main climates, a tropical coast recording dry summer (semi-arid) (Köppen As type) and another section recording humid tropical type (Köppen Af and Aw types), and subtropical climate dominating southern coast (Köppen Cfa and Cfb types) (Bernardes et al., 2012; Alvares et al., 2013). The Brazilian coast can be divided into four major geological sectors (Bernardes et al., 2012), the Northern Quaternary or Amazon plain (4° N to 3° S), Eastern Tertiary (3° to 20° S), Southeastern Granitic (20° to 29° S), and Southern Quaternary (29° to 34° S). The Brazilian coast is dominated by semi-diurnal tides with the greatest tidal range in

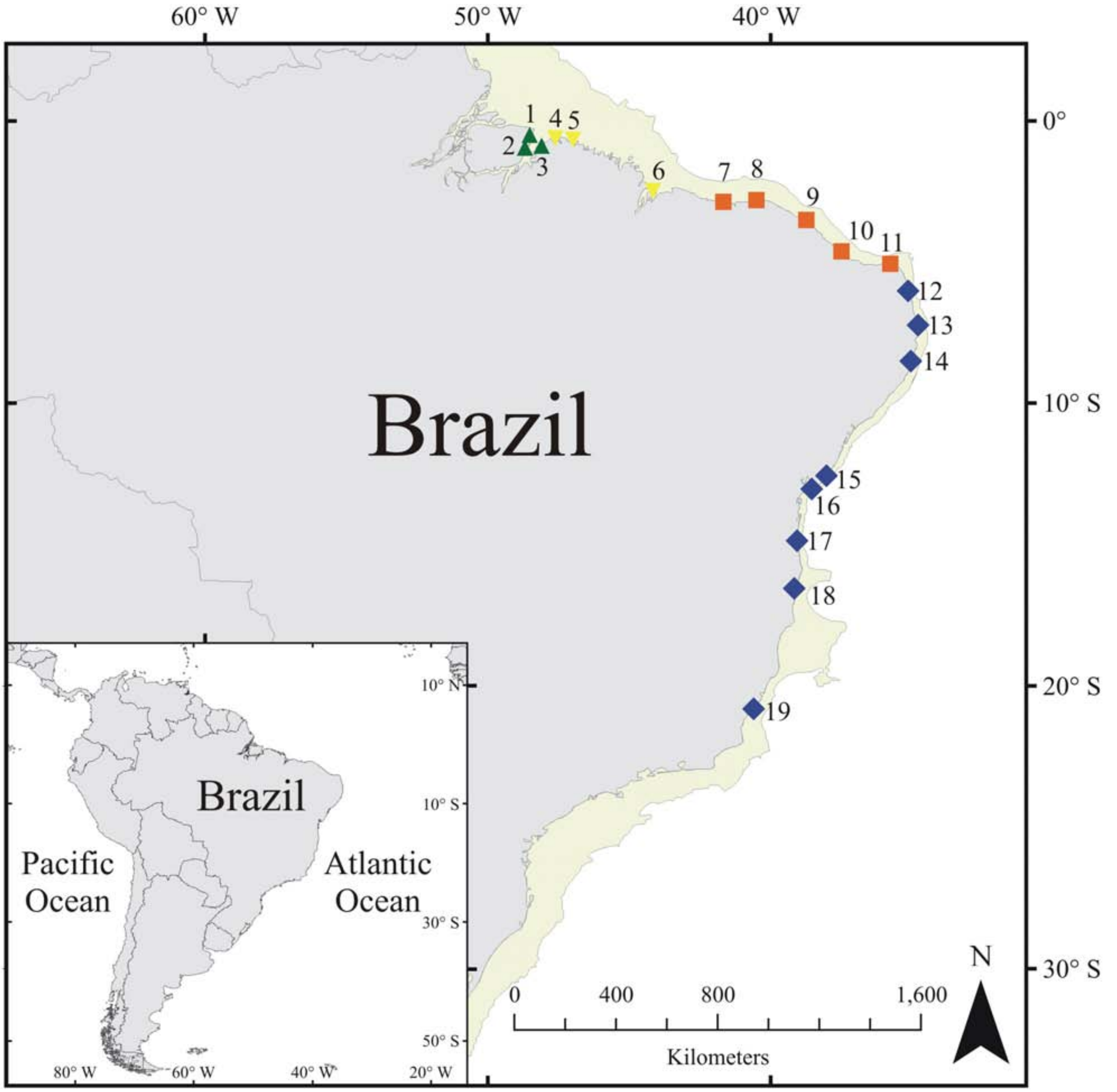

FIGURE 1 | The 19 sites sampled in our study. Each symbol and color denotes one of the four Brazilian intertidal subprovinces identified here; Amazon estuary (AE) = green triangles, Northern mangrove (NM) = yellow inverted triangles, Northeastern semiarid (NS) = orange squares, and Tropical warm (TW) = blue diamonds.

the North region (>4 m), declining southward to less than 1 m (Dominguez, 2009). Three principal surface currents flow across the Brazilian Continental Shelf: the oligotrophic South Equatorial Current off the northeast coast (12–15° S), the North Brazil Current, which meets the Amazon plume off the northern coast, and the southward meandering Brazil Current off the eastern, southeastern, and southern coasts as far as its confluence with the Malvinas current (Peterson and Stramma, 1991; Campos et al., 1996). Based on this set of features, we divided the tropical intertidal Brazilian coast (0–21° S) into four major subprovinces (**Table 1** and **Figure 1**):

(i) *The Amazon estuary (AE) subprovince* (0–1° S) is characterized by a strong riverine influence, with a run-off of *ca.* 180,000 m^3s^{-1} representing 30% of the freshwater discharge into the Atlantic Ocean (Perry et al., 1996; Wisser et al., 2010). Turbid waters with mean annual salinity below 10 and a tidal range of up to 3–4 m. The intertidal areas are dominated by tropical freshwater swamp-forest, mud flats, mangrove forest, saltmarsh, and rock formations (see Machado et al., 2017). Mean water temperature is 26°C throughout the year, and mean annual rainfall is 2,800 mm.

TABLE 1 | Summary of environmental characteristics found in the four subprovinces of the Brazilian coast.

Subprovince	Latitude	Tidal range (m)	Mean annual rainfall (mm)	Mean annual temperature (°C)	Salinity
Amazon estuary (AE)	0 – 1° S	3 – 4	2,800	26	<10
Northern mangrove (NM)	0 – 2° S	4 – 6	2,500	27	15 – 35
Northeastern semiarid (NS)	2 – 5° S	2 – 4	989	27	32 – 42
Tropical warm (TW)	5 – 21° S	1 – 4	1,400	24	35

(ii) *The Northern mangrove (NM) subprovince* (0–2° S) encompasses 23 estuaries and 30 freshwater basins, draining a total area of 330,000 km^2 along a 480-km coastline (Kjerfve et al., 2002). Salinity varies considerably throughout the year, ranging from 15 to 35. Semidiurnal tides range up to 4–6 m, flooding an area of *ca.* 7,600 km^2 of continuous mangrove forests (Souza-Filho, 2005). Mean annual temperature is 27°C and mean annual rainfall is 2,500 mm. This subprovince extends from eastern tip of the mouth of the southern channel of the Amazon estuary to Parnaíba coast (Delta do Parnaíba; 2°43′S), state of Piauí.

(iii) *The Northeastern semiarid (NS) subprovince* (2–5° S) comprises a coastline of 720 km dominated by mobile dune fields propelled by south-easterly and easterly trade winds, which reach speeds of over 15 m/s (Freire et al., 2008). Low riverine input and clear and salty waters (annual salinity range 32–42) are characteristics of this region, in addition to relatively reduced mangrove forest cover along the coastline in comparison with the AE and NM subprovinces. Small coral reefs and rock formations are common. Mean annual temperature is 27°C and mean annual rainfall is 989 mm. This subprovince extends to Rio Grande do Norte state (5°22′ S).

(iv) *The Tropical warm (TW) subprovince* (5–21° S) is a sector of coastline influenced by the Brazil Current, with a moderate continental run-off (Ekau and Knoppers, 1999; Leão and Dominguez, 2000). In this subprovince, tidal range decreases southward to 1–2 m, the coast is fringed by a mosaic-rich landscape, including coral, carbonate and rocky reefs (see Rosa et al., 1997; Macieira and Joyeux, 2011), as well as mangrove-reef ecotones, Atlantic rainforest, seagrass meadows, estuarine mud flats, and sandy beaches can be observed (Leão and Dominguez, 2000; Kjerfve et al., 2002). The mean annual temperature is 24°C and mean annual rainfall is 1,400 mm.

Sampling Design

A total of 19 sites (**Figure 1**), intertidal flat reefs, were sampled along *ca.* 4,900 km of the Brazilian coast. The distance between each site ranged from 10 to 200 km. Field sampling was conducted in a single season (March–June/2012) in order to minimize the effect of seasonal shifts in environmental data among sites. Eight tidepools (N = 152) were randomly chosen at each site to describe its fish assemblage. Sampling was always carried out during diurnal low tides in isolated tidepools (i.e., without connection to either the sea or other tidepools).

Environmental Variables

Water temperature (±0.1°C; mercury thermometer), salinity (±0.1; optical refractometer – Model: Q767), and pH (±1; ColorpHast tape) were recorded during the low tide in each tidepool immediately prior to the sampling procedures. The topography and bathymetry of the tidepools were surveyed using a 20 cm × 20 cm grid for the measurement of the depth, area, and volume of each tidepool. The area and volume were calculated by the kriging method. The type of substrate in each pool was assigned to one of four categories: (i) mud (silty substrate), (ii) sand (grain size < 1 mm), (iii) gravel (grain size ≤ 50 mm), and (iv) rock (solid aggregated substrate > 50mm). The substrate type and algal cover within each pool were estimated using a 50 cm × 50 cm measuring grid, subdivided internally into a 5 cm × 5 cm grid, which was used to estimate relative coverage. The rugosity index was calculated by the ratio of surface to planar area. The distances between the tidepool and the coastal plateau and subtidal areas were calculated with a tape measure, and height was measured as the vertical distance between water surface of the tidepool and sea level. The tidal range at each site was calculated as the difference between the maximum and minimum height of the water, recorded on the sampling day from Brazilian National Oceanographic Database (DHN, 2012). Rainfall data were based on the mean annual rainfall of the preceding 10 years (INMET, 2012) and the latitude was determined by GPS. The area (m^2) and perimeter (m) of the rock formation of each intertidal landscape were calculated using satellite images. Rocky shore was assessed based on the method described by Burrough (1981) and Milne (1988), defined by the Fractal Dimension, or Frac (McGarigal and Marks, 1995): Frac = 2 * ln [(P/4) / ln (A)], where P is the patch perimeter and A is the patch area. Lower Frac values indicate square or more structured shapes, while higher values indicate more irregular shapes. To assess the orientation of the rocky shore formation, the lengths of two axes (orthogonal – D1, and parallel – D2 to the coastline) were measured from image satellites in ArcGis software to determine the L1/L2 ratio. High ratio values indicate that the rocky intertidal shore is more orthogonal to the coast. The intertidal shores sampled in the present study were identified based on the lithological classification, as carbonate, ferruginous sandstone or sandstone. All 25 environmental variables determined in this study are described in **Supplementary Table S1**.

Tidepool Fish Fauna

The tidepool fish fauna was sampled using anesthetic clove oil (see Griffiths, 2000) and the specimens were fixed in 10% formalin solution, after being preserved in 70% alcohol. Density was calculated by the number of individuals per pool volume (m^3). The fish taxa were assigned to one of three major feeding categories: Carn = carnivore; Omni = omnivore; Herb = herbivore, and the degree of residency was classified according to Macieira and Joyeux (2011), Oliveira et al. (2016), complemented by personal observations from the authors.

Data Analysis

Multivariate analyses were performed in PRIMER-E (following Clarke and Gorley, 2006). Firstly, the full dataset containing all 25 environmental variables (**Supplementary Table S1**) was tested for collinearity using a Draftsman plot and Spearman correlation matrix. Where pairs of variables had a correlation coefficient of 0.9 or more, one of the correlated variables was excluded from the analysis (Clarke and Ainsworth, 1993). Two pairs of variables (tidepool area vs. planar area, and perimeter of the rock formation vs. Frac) were highly correlated ($r^2 > 0.9$), so one of each pair (tidepool area and perimeter of the rock formation) was omitted from the analysis, to avoid collinearity. Eight variables required transformation (e.g., log- or fourth root-transformation) to compensate for skew.

All the selected variables were standardized and a Principal Components Analysis (PCA) was used to evaluate their variation among sites and subprovinces. A permutational multivariate analysis was also used to test for differences in tidepool fish composition and environmental characteristics in the different "subprovinces" (4 fixed levels: Amazon estuary, Northern mangrove, Northeastern semiarid and Tropical warm), and "site," nested within "subprovinces" factor, 19 random levels (see PERMANOVA; Anderson et al., 2008). Statistical significance was tested using 9,999 permutations of the residuals in a reduced model (according to Freedman and Lane, 1983) and the Type III (partial) sums of squares (see Anderson et al., 2008). In these analyses, the PERMANOVA was run on a Bray-Curtis similarity matrix, calculated from the fourth-root transformed biological data and a Euclidean similarity matrix for the environmental data (see Anderson, 2001; McArdle and Anderson, 2001). When the results were significant, post-hoc pair-wise contrasts were performed to establish where the differences in assemblage structure and environmental variables were found. In addition to the PERMANOVA, we conducted a Permutational Analysis of Multivariate Dispersions (PERMDISP) on the same Bray–Curtis matrix to test for differences in the multivariate dispersions of the "subprovinces" and "sites."

The Similarity Percentages – species contributions (SIMPER; Clarke and Warwick, 2001) procedure was applied to reveal which fish species contributed most to the multivariate community patterns within the "subprovinces." A constrained ordination technique, the Canonical Analysis of Principal Coordinates (CAP; Anderson and Robinson, 2003; Anderson and Willis, 2012), was performed to test the null hypothesis, given that no differences were found in the species composition among the "subprovinces" established *a priori*. A Spearman correlation of over 0.7 was used as an arbitrary limit for the display of the potential correlations between fish densities by feeding category and the canonical axes.

A Permutational Distance-based Linear Modeling (PERMDISP; Anderson, 2001; McArdle and Anderson, 2001) was used to test the relationship between fish assemblages and environmental variables. This procedure consists of a multivariate multiple regression method in which the ordination axes from a resemblance matrix of the response dataset (species composition) are regressed on a matrix of explanatory variables (the 23 environmental variables). A stepwise DISTLM routine was also run with 9,999 permutations selected using the Bayesian Information Criterion, BIC (Kuha, 2004). A distance-based redundancy analysis (dbRDA) was used as a constrained ordination technique to visualize the results of the DISTLM (Anderson et al., 2008).

RESULTS

Environmental Variables

The PCA revealed a clear segregation of the four proposed intertidal subprovinces (**Figure 2**). Five of the components of the environmental data modeled approximately 61% of the total variation. The first principal component (PC1) explained 21.8% of the total variation, and clearly separated the equatorial (AE and NM) from the tropical (NS and TW) subprovinces, based on salinity, rainfall, and the environmental features of the tidepools. Except for rainfall and rock coverage, the environmental data were negatively correlated with PC2, explaining 13.8% of the total variation. Similarly, the PERMANOVA indicated significant differences among sites ($p = 0.0001$) and subprovinces ($p = 0.0001$; **Supplementary Table S2**), where "site" was the main effect, explaining 37.2% of the variability in the data, followed by "subprovince," which explained 30.6%.

Tidepool Fish Fauna

A total of 5,113 fish, representing 67 taxa belonging to 27 families was sampled from the 152 tidepools studied (**Supplementary Table S3**). No fish were recorded in three tidepools. *Scartella cristata* was the most abundant species, accounting for 33.5% of all the individuals collected (1,309 ind.), followed by *Bathygobius soporator*, with 21.4% (899 ind.), and *Bathygobius geminatus* with 9.3% (388 ind.). The most representative families were Blenniidae (38.8%) and Gobiidae (14.7%), and only three families (Blenniidae, Gobiidae, and Batrachoididae) were recorded in all subprovinces (**Supplementary Table S4**). Species richness increased gradually from the AE to the TW subprovince, although a larger number of local endemics and exclusive species were recorded in the AE in comparison with the other subprovinces (**Supplementary Table S5**). Four species (*B. soporator*, *B. geminatus*, *Labrisomus nuchipinnis*, and *S. cristata)* were broadly distributed in the intertidal zone of the Brazilian coast, occurring in 17, 11 and 10 (both *L. nuchipinnis* and *S. cristata*) sites, respectively. By contrast, 28 taxa were restricted

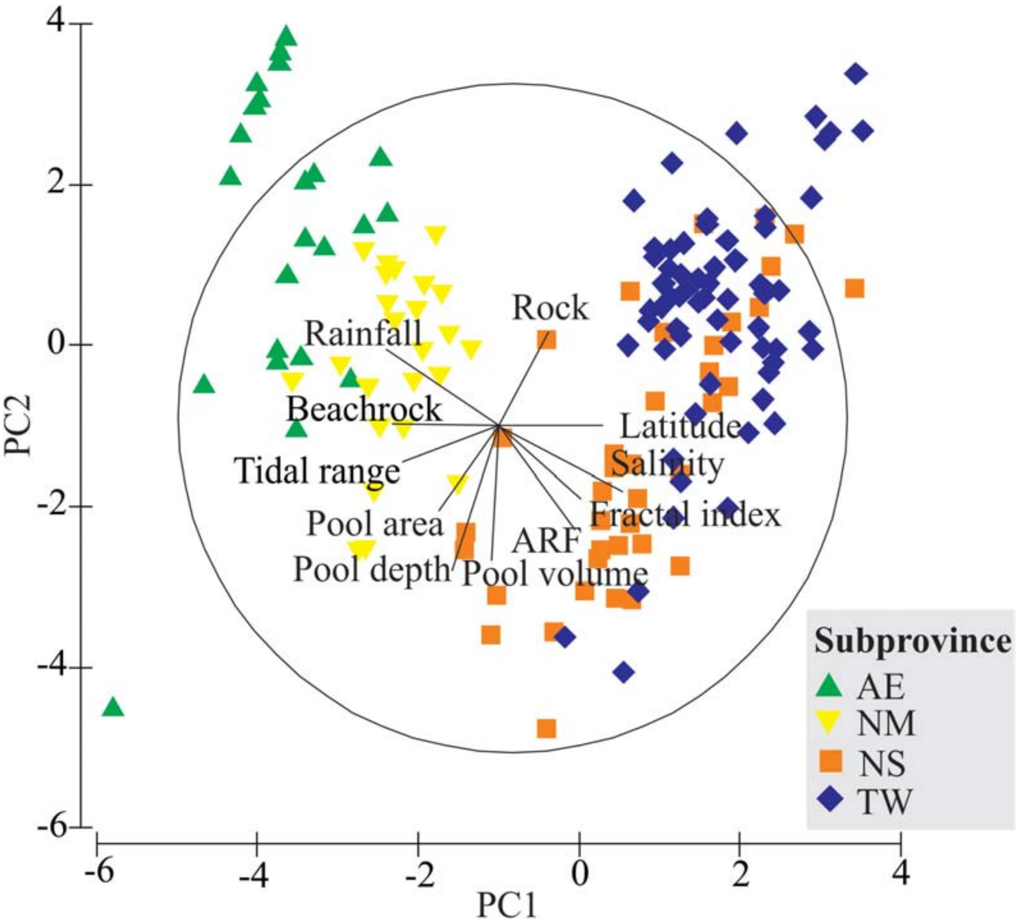

FIGURE 2 | Principal Components Analysis (PCA) ordination constructed from the environmental data (**Supplementary Tables S1, S2**) of 149 tidepools sampled at 19 sites along the Brazilian coast. Only the variables with the highest loadings, positive or negative, are shown. The length and direction of the vectors represent the strength and direction of the relationship. The samples with no fish data ($N = 3$) were omitted from the analysis. Subprovinces: AE, Amazon estuary; NM, Northern mangrove; NS, Northeastern semiarid; TW, Tropical warm.

to a single site. Two species were endemic to subprovince AE (*Gobiosoma* sp. and *Eleotris* sp.), and one to NS (*Paraclinus* sp.).

The PERMANOVA explained 32.5% of the variation at the local scale ("site") and 22.5% at the regional scale ("subprovince"), demonstrating the strong influence of local-scale factors shaping fish assemblages along the tropical Brazilian coast (p-values < 0.001; **Supplementary Table S6**). The PERMDISP analysis also revealed that the dispersion of the fish assemblages in tidepools varied significantly ($F = 4.3169$, $p = 0.0003$) across sites. The results of the SIMPER analysis indicated that *B. soporator* is typical of all four subprovinces, contributing most to similarity with the AE (94.79%). The most representative fish species in NM subprovince were *Gobiesox barbatulus*, *Omobranchus punctatus*, *Barbulifer enigmaticus*, *Bathygobius soporator*, *Mugil curema*, *Genyatremus luteus*, and *Thalassophryne nattereri*, whereas *Scartella cristata*, *B. soporator*, *Abudefduf saxatilis*, *Lutjanus alexandrei*, and *Bathygobius geminatus* were typical of the NS province. The TW subprovince was characterized by *B. geminatus*, *S. cristata, Labrisomus nuchipinnis*, *B. soporator*, *Stegastes fuscus*, and *Ctenogobius boleosoma* (**Figure 3**). Mean dissimilarity between subprovinces was 88.1, ranging from 81.8 for AE *vs.* NS to 96.2 for NM *vs.* TW.

The Canonical Analysis of Principal coordinates (CAP; **Figure 4**) revealed a clear spatial trophic structure, with the fish taxa grouped in the four subprovinces ($\delta^2{}_1 = 0.80$, $p = 0.0001$). Overall, the leave-one-out allocation success was 82.5% (i.e., misclassification error of only 17.5%) for the "subprovince" factor. The CAP axis scores indicated higher herbivore densities associated with the TW and NS. Omnivorous fish were correlated with the NM and carnivores with the AE (**Table 2**).

Habitat Variables Driving Fish Assemblage Structure

Distance based Linear Model (DistLM) identified water salinity explaining the largest proportion (11.3%) of the variation in the fish assemblages. Similarly, 20 of the other 23 predictive environmental variables tested were also significant ($p < 0.05$) in the marginal tests, with the only non-significant results

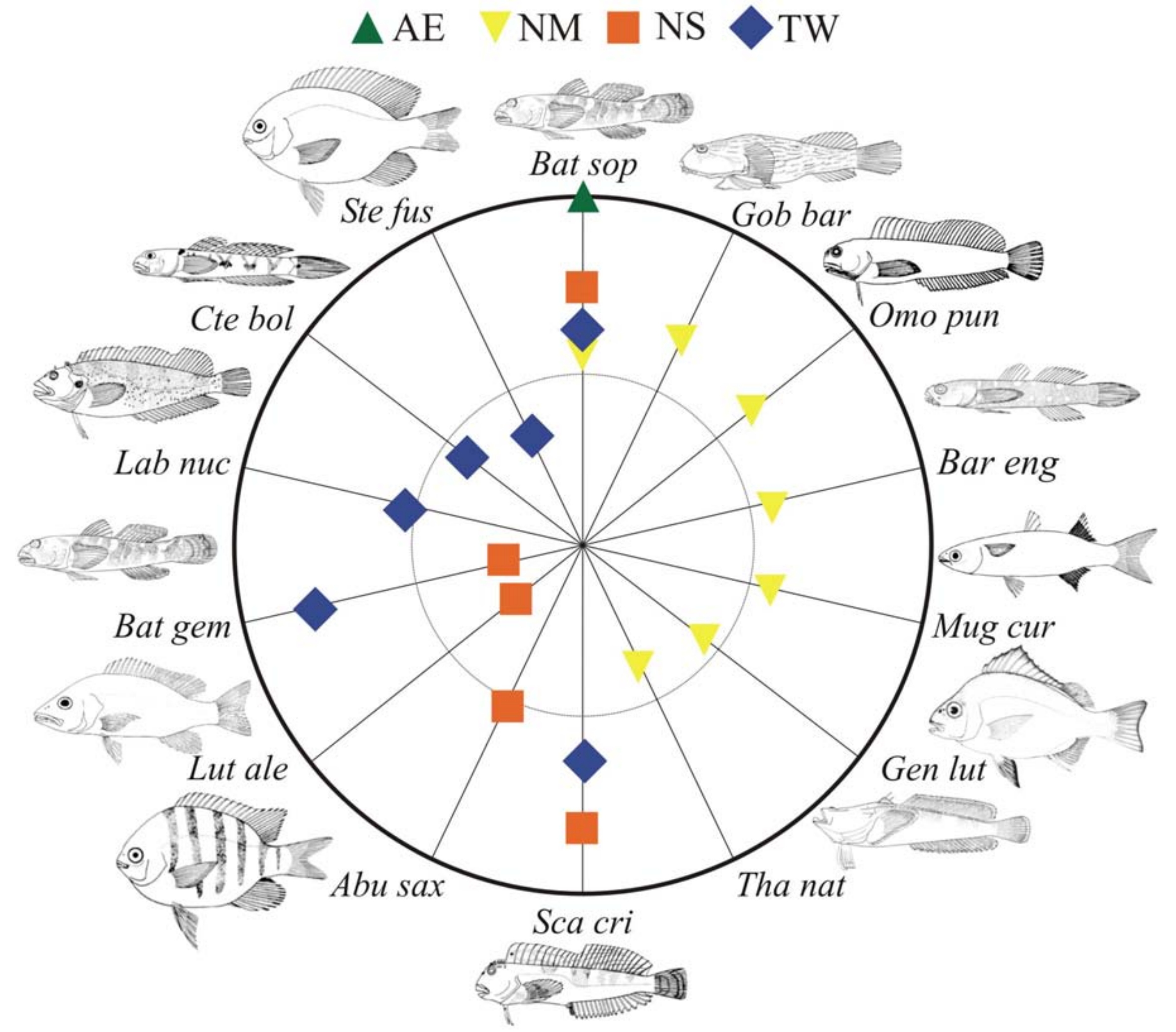

FIGURE 3 | Percentage contributions (log scale; 0 – center, 10 – inner circle and 100 – outer circle) of the most important fish species to the typical "subprovinces," based on the SIMPER analysis. Subprovinces: AE, Amazon estuary; NM, Northern mangrove; NS, Northeastern semiarid; TW, Tropical warm. *Bat sop*, *Bathygobius soporator*; *Gob bar*, *Gobiesox barbatulus*; *Omo pun*, *Omobranchus punctatus*; *Bar eng*, *Barbulifer enigmaticus*; *Mug cur*, *Mugil curema*; *Gen lut*, *Genyatremus luteus*; *Tha nat*, *Thalassophryne nattereri*; *Sca cri*, *Scartella cristata*; *Abu sax*, *Abudefduf saxatilis*; *Lut ale*, *Lutjanus alexandrei*; *Bat gem*, *Bathygobius geminatus*; *Lab nuc*, *Labrisomus nuchipinnis*; *Cte bol*, *Ctenogobius boleosoma*; *Ste fus*, *Stegastes fuscus*.

being recorded for rugosity, temperature, and percentage sand cover (**Supplementary Table S7**). The optimal model solution consisted of the combination of seven environmental variables: salinity, tidal range, the shape of the rocky shore formation (SRF), percentage algal cover, distance to the subtidal area (DSA), latitude, and rainfall (**Supplementary Table S7** and **Figure 5**). The results plotted in the RDA ordination indicated the segregation of AE and NM from the TW and NS samples (**Figure 5**). The most important variables contributing to the first axis of the dbRDA plot, explaining 44.4% of the fitted variation, were related to the DSA, salinity, rainfall, algal cover, and SRF. On the second axis, which explained 19.4% of the fitted variation, tidal range and latitude were the principal environmental variables.

DISCUSSION

The Brazilian coast is part of a single marine biogeographic region, the Brazilian Province (Briggs, 1974; Floeter et al., 2008; Briggs and Bowen, 2012; Pinheiro et al., 2018), although this province presents a number of local environmental, ecological, and evolutionary features, which characterize distinct biogeographic subprovinces (Pinheiro et al., 2018). In the specific case of reef fishes, Pinheiro et al. (2018) proposed two tropical coastal subprovinces, the north and north-east Brazil subprovince, and the east and south-east Brazil subprovince, although this division does not coincide exactly with our proposal of four coastal subprovinces, in the case of intertidal fishes. Clearly, despite the taxonomic and ecological proximity between fishes from intertidal reef environments (tidepools)

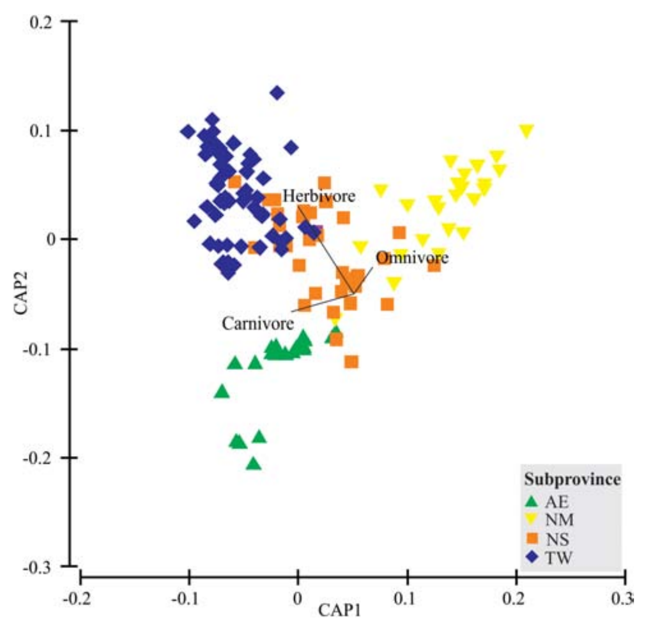

FIGURE 4 | Plot of the canonical analysis of principal coordinates (CAP) generated from the Bray-Curtis similarity matrix of species composition using "subprovince" as the predictor factor. Vector overlay denotes feeding categories with a Spearman rank correlation of above 0.7. Subprovinces: AE, Amazon estuary; NM, Northern mangrove; NS, Northeastern semiarid; TW, Tropical warm.

and subtidal reefs, the subprovinces proposed for these two groups are related to the specific evolutionary, geological, oceanographic, and ecological processes that are characteristic of each ecosystem. This implies that distinct management and conservation strategies are necessary for the two groups of fishes.

The four coastal subprovinces proposed here added more precision on the previously known three coastal ecoregions (Amazonia, Northeastern Brazil and Eastern Brazil), which were inserted into two provinces (North Brazil Shelf and Tropical Southwestern Atlantic) defined by Spalding et al. (2007) and on the two regions (North-eastern and South-eastern Brazil Areas) resulted from distribution of prosobranch gastropods (Barroso et al., 2016). In addition, our results are partially aligned with the tropical marine geomorphological sectors proposed by Leão and Dominguez (2000), although our study also included equatorial latitudes (0°–2°). Given this, present study provides a more definitive proposal for the delimitation of the subprovinces of the tropical Brazilian coast, based on biological (tidepool fish diversity) and environmental data (23 in total) of the intertidal seascape. We further discuss below how the environmental and biological data support the proposed subprovinces from the perspective of the tropical Brazilian intertidal fishes.

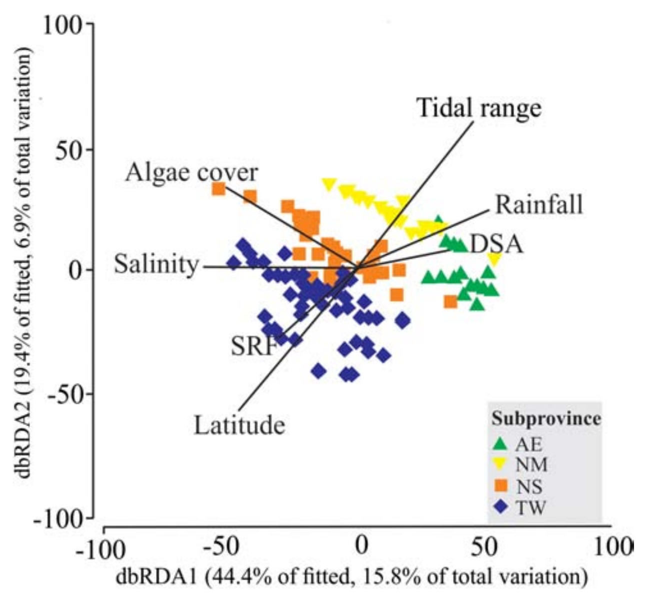

FIGURE 5 | Biplot of the results of the redundancy analysis of the biological and environmental data from 149 tidepools sampled at 19 sites in the four Brazilian coastal subprovinces. Samples with no fish data ($N = 3$) were omitted from this analysis. SRF, Shape of Rocky shore Formation; DSA, Distance to Subtidal Area. Subprovinces: AE, Amazon estuary; NM, Northern mangrove; NS, Northeastern semiarid; TW, Tropical warm.

Environmental Variables Influencing Intertidal Fish Distribution

Subprovinces evidenced here clearly shape intertidal fish communities. The main drivers acting on the spatial distribution of the fish were low salinity and high tidal ranges in the northernmost subprovinces (AE and NM), and high algal cover

TABLE 2 | Results of the Canonical Analysis of Principal coordinates (CAP), which examines the effect of the "subprovince" factor on the tidepool fish assemblages.

Subprovince	Classified as:				Allocation success (%)	*m*	δ^2	*P*
	AE	NM	NS	TW				
Amazon estuary (AE)	23	0	0	0	100	16.78	0.78	0.0001
Northern mangrove (NM)	3	19	2	0	79.16			
Northeastern semiarid (NS)	3	4	29	3	74.36			
Tropical warm (TW)	1	0	9	53	84.13			
					Total = 83.22			

Leave-one-out allocation of the observations of the groups to the Amazon estuary (AE), Northern mangrove (NM), Northeastern semiarid (NS), and Tropical warm (TW). Allocation success (%), percentage of samples correct allocated to each subprovince. δ^2*, squared canonical correlation.*

(NS and TW) and latitude (TW) toward the south. While the substrate has been identified as an important variable structuring intertidal fish communities (Arakaki et al., 2014), local-scale factors (the mouth of the Amazon, mangroves, and low-salinity estuarine waters) were the main factors defining the coastal subprovinces (e.g., AE and NM). However, regional-scale latitudinal trends were also key factors determining the configuration of the Tropical West subprovince. Local and regional drivers also act synergistically to shape subprovinces in intertidal and subtidal reefs worldwide (Rivadeneira et al., 2002; Floeter et al., 2008; Travers et al., 2010; Arakaki et al., 2014).

The spatial segregation of the geomorphological and oceanographic characteristics observed in the present study, together with the positive correlations between physical tidepool features (e.g., salinity, DSA, algal cover) and community variables further support the subprovinces proposed here. In this case, the established Brazilian Province (Briggs and Bowen, 2012; Pinheiro et al., 2018) can be divided into at least four distinct coastal subprovinces, based on the tropical intertidal seascapes. No strong correlations were found between physical tidepool features (e.g., pool volume and rugosity) and community variables, however, although a number of other studies have identified the area and volume of tidepools among the principal factors that determine fish density and diversity (Prochazka and Griffiths, 1992; Mahon and Mahon, 1994; Prochazka et al., 1999; Meager et al., 2005). The analytical approach we adopted allowed us to incorporate local and regional variables in a step-wise procedure, which indicated that species distributions and its composition may be the result of responses to the predominant environmental gradient. This contrasts with local-scale studies, which point to factors such as competition, foraging, and predator avoidance strategies, as principal drivers of fish assemblage structuring, which is the typical perspective in other marine environments (Martino and Able, 2003). In particular, intertidal reefs in the low latitude subprovinces (AE and NM) represent relatively harsh environments for marine fish, given their high rainfall and reduced salinity, emphasizing the influence of estuarine features (see Crabtree and Dean, 1982). In northern Brazil, the influence of the Amazon and other estuaries on coastal ecosystems is fundamental to the distribution and organization of marine species (Barletta et al., 2003; Rocha, 2003; Giarrizzo et al., 2010). For example, many of the intertidal ecotones of these two subprovinces are located within estuaries (Giarrizzo and Krumme, 2008; Oliveira et al., 2016), which not only determines the presence of a specific intertidal fish community, but also provides habitats for relatively large populations in comparison with the subprovinces located at higher latitudes (see **Supplementary Table S3**). Crabtree and Dean (1982) also found that estuarine tidepools harbor high fish densities. However, the stability of the environmental variables in the NS and TW subprovinces is demonstrated by the closer grouping of their samples in PCA ordination in comparison with the AE and NM, highlighting the heterogeneity of the intertidal habitats in these subprovinces, which also likely affects population density. In fact, Oliveira et al. (2016) observed three distinct intertidal habitats (rocky shore, mangrove, and salt marsh) within one coastal bay in the AE subprovince.

In general, the paucity of consistent significant effects of the local and structural environmental variables on the abundance and distribution of intertidal fishes is surprising given the apparent prevalence and importance micro-habitat arrangements in other habitats, terrestrial or marine (Pickett and White, 1985; Hector and Bagchi, 2007). However, the approach adopted in the present study provides alternative insights through a broader analysis of the factors regulating the biogeographical processes that mold intertidal reef fish communities, that is, the large-scale environmental factors that influence the distribution of fish most intensely. Further research incorporating data on the life cycle of the species that inhabit tidepools (i.e., residents and non-residents) will contribute to a better understanding of the micro- and meso-scale regulatory factors, which will be necessary to determine the exact nature of the processes that determine fish distribution patterns.

Biogeographic Patterns

The plume of the Amazon River forms a natural biogeographic barrier to many marine fish species, limiting the passage between the Caribbean and Brazilian provinces (Gilbert, 1973; Collette and Rützier, 1977; Rocha, 2003; Floeter et al., 2008). However, this barrier is considered to be semi-porous, allowing many marine species to cross when permitted by specific environmental conditions (e.g., Amazon run-off, sedimentation rates) and the ecological traits of the species, e.g., reproductive mode and body size (Joyeux et al., 2001; Rocha, 2003; Floeter et al., 2008; Pinheiro et al., 2018). Highly mobile species of large body size, with pelagic spawning (e.g., the Carangidae and Serranidae), and with capacity to tolerate a diversity of conditions will generally have a much greater chance of crossing the Amazon plume than small-sized species with restrict ranges, demersal spawning, and parental care, e.g., the Gobiidae (Luiz et al., 2012; Pinheiro et al., 2018). In this context, the dispersal capacity of species resident in tidepools is limited by their ecological traits, which include small body size, as well as their reduced swimming mobility, demersal spawning, and cryptic behavior (Barlow, 1999; DeMartini, 1999; Macieira et al., 2015).

In the present study, the AE and NM subprovinces limit the presence of many resident species of both the Caribbean and the NS–TW subprovinces. This spatial pattern is expressed through (i) number of families/species that are permanent residents in the AE–NM *vs.* the NS–TW subprovinces (**Supplementary Tables S3, S4**); (ii) the absence of permanent marine resident species in the AE subprovince (**Supplementary Table S4**), and (iii) the exclusive and endemic species of the AE subprovince (**Supplementary Table S5**). Considering the two adjacent pairs of subprovinces, the AE–NM and NS–TW, only six species – *Barbulifer enigmaticus*, *Bathygobius soporator*, *Ctenogobius boleosoma*, *Gobiesox barbatulus*, *Microdesmus bahianus*, and *Omobranchus punctatus* – occur in both pairs of subprovinces, and as *O. punctuatus* is an invasive species, it does not represent a true biogeographic pattern. Low species richness to the north (i.e., the Amazon Estuary; **Supplementary Table S5**) may be related to the same environmental filters (i.e., the Amazon plume and sedimentation rates, with low salinity and turbid waters) that limit the presence of typical marine species.

The environmental filters of the subprovinces are best exemplified by the distribution of the resident tidepool frillfin gobies, *B. soporator* and *B. geminatus*, which each present distinct habitat requirements and niche. *Bathygobius soporator* was distributed in all subprovinces, but at particularly high mean densities at the AE sites (225.9 individuals per m^3), which is likely related to its preference for tidepools with estuarine features (Macieira and Joyeux, 2011; Oliveira et al., 2016). By contrast, *B. geminatus*, which is distributed between Florida and the TW subprovince, typically inhabits classical marine tidepools (Macieira and Joyeux, 2011; Andrades et al., 2018), and is absent from the AE and NM sites, while increasing in density toward the south. The subprovincial endemism of tidepool fishes in the AE also highlights the local features that act as barriers. Van Tassell et al. (2015) reported two resident species of *Gobiosoma* (denominated here as *Gobiosoma* spp.) endemic to intertidal areas of the Amazon estuary, as we observed in *Eleotris* (Guimarães-Costa et al., 2016), which has two endemic intertidal resident species (currently undescribed) in the AE and NM subprovinces, one of which (from the NM) was not record in the present study. This high degree of endemism may be accounted for by sympatric speciation events, through which the local drivers (e.g., environmental filters) of a subprovince may promote scenarios favorable to speciation at a local-scale (Doebeli and Dieckmann, 2003; Rocha et al., 2005; Bowen et al., 2013).

One other process that should be considered is ephemeral ecological speciation (Cutter and Gray, 2016; Pinheiro et al., 2017), given the observation of one new *Gobiosoma* species closely related to *Gobiosoma alfiei* (Van Tassell et al., 2015), and the other two new, cryptic *Eleotris* species (Guimarães-Costa et al., 2016), which probably evolved in the context of dynamic changes in the characteristics of the Amazon barrier (run-off, sedimentation rates) over geological time (Joyeux et al., 2001; Rocha, 2003). This incipient speciation would be the result of intermittent dispersal and colonization events (Cutter and Gray, 2016; Pinheiro et al., 2017). Pinheiro et al. (2017) concluded that the fusion process between nascent species and source area populations explains why most marine species are not differentiated without strong genetic selection. This further reinforces the role of the Amazon River as a biogeographic barrier for several tidepool species, which may be related to the high degree of endemism recorded in the AE subprovince. A second barrier highlighted by Pinheiro et al. (2018) is the South Equatorial Current bifurcation, where the Brazil Current flows to the south and the North Brazil Current flows to the north-west, between 10 and 14°S (Rodrigues et al., 2007), which may also constrain population movements and dispersal. Although, the São Francisco River run-off cited as possible barrier in this same study, it's not helps to define our intertidal coastal subprovinces.

In general, herbivores are expected to prevail at lower latitudes and carnivores at higher ones in the marine realm, due to the species' physiological constraints and the relative availability of primary resources in the tropical region (Choat, 1991; Ferreira et al., 2004; Floeter et al., 2005). In the present study, however, the observed trophic patterns did not correspond exactly to latitudinal trends, although we did identify local and regional patterns of trophic group distribution, with carnivores (AE) and omnivores (NM) dominating the subprovinces at lower latitudes. This can be at partly accounted for by the turbid waters and high river discharge of this region, which restrict algal development, reducing the availability of resources for herbivores in the AE and NM subprovinces. The carnivore and omnivore trophic structures of assemblages were also influenced strongly by the high densities of *B. soporator* and *O. punctatus* in the AE and NM subprovinces, respectively. The presence of these species and other estuarine-related species, such as *Mugil curema*, *Genyatremus luteus*, and *Thalassophryne nattereri*, further reinforces the role of local-scale factors (e.g., river discharge) in the structuring of tidepool assemblages in these subprovinces. At the nine TW sites, herbivores were the predominant group structuring the intertidal communities, which is expected in shallow reef habitats of tropical regions (Steneck et al., 2017).

Conservation Issues and Conclusion

From a conservation perspective, the subprovince profiles observed in the present study represent an essential step toward the more effective management of Brazilian coastal zones. Overall, the Amazon Estuary subprovince appeared to be the most vulnerable, due to its endemism and environmental particularities. Conservation priority actions in the Amazon coastal region were also suggested by Vilar et al. (2017) for estuarine fishes. Currently, oil drilling and coastal urban development are the principal threats to the marine biota of the Brazilian Province (Buruaem et al., 2012; Moura et al., 2016). Urban development, in particular, not only causes habitat losses, but also favors biological invasions through the discharge of ballast water by international shipping (Carlton, 1996; Wonham et al., 2001), which invariably occurs close to intertidal areas. All the Brazilian subprovinces identified here have already undergone invasions from species such as the sun corals, *Tubastrea* spp. (Creed, 2006), and the muzzled blenny *Omobranchus punctatus* (Lasso-Alcalá et al., 2011), and ongoing invasions, such as that of the lionfish, *Pterois* spp., are even more preoccupying (Luiz et al., 2013). We recorded *O. punctatus* at seven sites. Potential niche overlap and competition with native intertidal species seems to be unavoidable, and will be harmful, given that the ecological traits and habitat requirements of this species are highly similar to those of endemic species of the Brazilian Province, such as *Entomacrodus vomerinus*, *Ophioblennius trinitatis*, and *Gobiosoma alfiei*.

Currently, while Marine Protected Areas contemplate 26% of Brazilian marine territory, less than 2% of these areas include coastal zones and intertidal seascapes. This leaves these coastal zones extremely vulnerable to countless impacts (oil and gas exploration, tourism, mariculture, fisheries, and port activities), which could be minimized through more participative management, firm intention and concerted actions by environmental agencies (Jablonski and Filet, 2008). In this context, we would recommend an integrated approach, involving environmental agencies (at federal, state, and municipal levels), research institutions (universities and research centers), and general society (community leaders and NGOs), for the establishment of priorities for the use and conservation of coastal zones. While it will be impossible to eliminate conflicts altogether, collaborative networks have led the way to effective management and conservation in large-scale territories under multiple jurisdictions (Wyborn and Bixler, 2013).

ETHICS STATEMENT

This study was conducted in accordance with all ethical guidelines and Brazilian legislation, including authorization to collect fishes from Brazilian Environmental Protection Agency (ICMBio; license number 35625). Also, this study was carried out in accordance with the recommendation of Ethics Committee (CEUA; #29/2016).

AUTHOR CONTRIBUTIONS

TG conceived and designed this study. FM and TG collected the data. All authors discussed and analyzed the data. RA, TG, and FM wrote the first draft. All authors revised and contributed to the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00412/full#supplementary-material

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Growing in the Dark Warmth: The Case of Amazonian Fish *Colossoma macropomum*

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Photoperiod is considered an important synchronizer of biological activities and endocrine pathways, including growth. As ectotherms, fish have many physiological functions controlled by the photoperiod. However, the combined effects of photoperiod and temperature should be clarified, particularly for tropical fish living near their upper thermal limit, as is the case of Amazonian fish. The central aim of this study was to evaluate the combined effect of photoperiod and temperature on growth and physiological aspects of tambaqui (*Colossoma macropomum*). Juveniles of tambaqui were distributed in 70 L tank, following a factorial design that included three photoperiods (light 0 h: darkness 24 h; light 12 h: darkness 12 h; and light 18 h: darkness 6 h) associated with three temperatures (26, 29, and 32°C). They were maintained under these conditions for 2 months. Fish reared in the dark at 29 and 32°C showed better performance compared to fish reared under extended light conditions at all temperatures. Among physiological responses, it has been observed that blood parameters tend to be disturbed with increasing temperature and that extended light conditions at low temperatures caused similar effects on the analyzed fish, suggesting blood hemoconcentration. Fish under extended light conditions showed an increase in glucose, cortisol, cholesterol, and total proteins, indicating additional physiological disturbances. In conclusion, our study shows that, unlike marine and temperate fish, *C. macropomum*, a fish species endemic to the Amazon, grows better in warmth dark, showing no significant physiological disturbances, similar to observations described for wild animals of this species. Our results support that changes in fish growth occur in response to environmental conditions. Therefore, fish species from freshwater, estuarine, and marine environments, must be specifically analyzed regarding the combination effects of photoperiod and temperature.

Keywords: amazon, aquaculture, climate change, environmental factors, metabolism, neotropical fish

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INTRODUCTION

Climate change affects fish growth and physiology (Cheung et al., 2013; Campos et al., 2017). In the coming years, warming of water bodies will force fish to migrate to areas previously unsuitable for their survival in response to declining food resources (Perry et al., 2005; Pörtner and Farrell, 2008). As a consequence, a decline in fish growth rates of 14–24% is expected, which will affect fisheries and the respective food industry due to changes in the dynamics of marine, estuarine, and freshwater ecosystems (Cheung et al., 2013).

For many decades, environmental manipulation has been used to improve growth of several species in aquaculture (Nerici et al., 2012; Imsland et al., 2013) and light has been shown to be an important synchronizer of biological fish activities, improving breeding conditions, and growth (Boeuf and Le Bail, 1999; Bromage et al., 2001). Photoperiod is an important *zeitgeber* for fish affecting feeding, behavior, and modulating the responses associated to the stress over seasons (Trippel and Neil, 2003; Imsland et al., 2006). Studies with salmonids and other temperate species have highlighted a positive relationship between prolonged or continuous light and growth, with stimulus of food intake, better feed conversion rate, and nutrient uptake (Taylor et al., 2006). In addition, many studies report an effect of light on the somatotrophic axis, regulating the production of growth hormone, which is responsible for the somatic development in vertebrates (Björnsson, 1997; Handeland et al., 2003; Taylor et al., 2005).

Seasonal changes in photoperiod and temperature are synchronized in natural environments. Fish activity are, in general, highly dependent on temperature (Elliott, 1982). The optimal temperature for growth in freshwater fish can be altered according to changes in the photoperiod (Coutant et al., 1984; Woiwode and Adelman, 1991). However, light also affects marine and temperate species, as showed by Døskeland et al. (2016) for the Atlantic salmon *Salmo salar* L. Some studies have revealed limiting effects of continuous light at higher temperatures for growth, whereas at lower temperatures these effects appear to increase fish development (Solbakken et al., 1994; Imsland et al., 1995, 2017; Lohne et al., 2012). These studies suggest an interactive effect of photoperiod and temperature on fish growth. Nonetheless, as far as we know, there are no evidences if the impact of the variations of these environmental factors can cause losses on the growth of cultivated animals in the Amazon, althought some studies have indicated effects of light or temperature (not in combination) on metabolic indexes (Biswas and Takii, 2016), and hematological parameters (Biswas et al., 2004; Bani et al., 2009) for others species.

Tambaqui, *Colossoma macropomum*, belongs to the Serrasalmidae family and is endemic to the Orinoco and Amazon rivers (Goulding and Carvalho, 1982; Mirande, 2010). This species is overexploited in nature, mainly in the Brazilian Amazon basin, and so, aquaculture currently supplies consumer markets in Brazil, Colombia, Peru, and Venezuela (Oliveira et al., 2012). The presence of tambaqui and its hybrids have been reported in several Latin American countries, in the United States of America, and in various countries in Asia, including China, Indonesia, Malaysia, Myanmar, Vietnam, Thailand, and Singapore, either introduced by accident or deliberately in fish farms (FAO, 2017, 2018; Nico and Neilson, 2018).

Studies involving manipulation of environmental factors and their effects on growth are scarce for Amazonian fish. For tambaqui, Oliveira and Val (2017) found a decrease in the feed efficiency of the animals submitted to the drastic scenario A2 (increase of 4.5°C and 850+ ppm of CO_2 in relation to the current levels) as predicted for the year 2100 by the IPCC (2007), suggesting increases in the cost of production due to the increase in food consumption and rearing time. Thus, in the coming decades, the great challenge will be to promote the development of techniques that ensure optimal fish growth rates under global warming scenarios (Baudron et al., 2014; Liang et al., 2018).

Therefore, considering that fish may present different growth patterns in the environmental scenarios foreseen for the near future, this study was designed to analyze if the exposure to different combinations between the photoperiod and the temperature can affect the Amazonian tambaqui. We hypothesized that the effect of photoperiod on the growth and physiological aspects of tambaqui is temperature dependent and that environmental manipulation is effective in reducing rearing time, ensuring better growth rates.

MATERIALS AND METHODS

Fish, Experimental Design and Facilities

All procedures and experimental manipulations used in this study were performed according to the Brazilian Guidelines for Animal Care and were approved by the Ethics Committee for the use of Animals of the Brazilian National Institute for Research of the Amazon (INPA), protocol number 026/2015. Juveniles of tambaqui were purchased from the Center for Technology, Training, and Production in Aquaculture (CTTPA, Manaus, Brazil) (1°55′07.7S/59°27′59.7W) and transported to the Laboratory of Ecophysiology and Molecular Evolution of INPA (LEEM/INPA). In the laboratory, the fish were kept in two 3000 L fiberglass tanks, supplied with flow thru water, under a 12:12 h light:dark (or L:D) photoperiod and temperature varying between 26 and 27°C for 2 weeks for acclimatization to local conditions. During this period, the fish were fed *ad libitum* with commercial feed of 2–4 mm (Nutripeixe Tr 36–36% protein, Purina Co., São Paulo, SP, Brazil), twice a day (at 9h and 16h) (**Table 1**). Feeding was suspended 48 h prior resettlement in the experimental tank.

After this period, juveniles weighing 16.22 ± 0.15 g and measuring 10 ± 0.04 cm ($N = 270$, mean ± standard deviation) were randomly distributed in 70 L tanks (80 × 50 × 40 cm, LxWxD) following a factorial scheme that included three photoperiods and three temperatures to evaluate the effects these variables on growth performance and physiological responses after 60 days. The photoperiods were: dark (D, 24 h dark), regular photoperiod of the Amazon (SNP, 12:12 L:D) and extended Amazonian photoperiod (PNP, 18:6 L:D). The temperatures

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Abbreviations: ADAPTA, Adaptations of Aquatic Biota of the Amazon; AOAC, Association of official analytical chemists; BSE, Before the Start of the Experiment; CAPES, Brazilian Coordination of Improvement of Personnel at Superior Level; CF, Condition Factor*; cf.*, Check out; CNPq, National Research Council of Brazil; CTTPA, Center for Technology, Training and Production in Aquaculture; D, Dark; ELISA, Enzyme Linked ImmunonoSorbent Assay; FAPEAM, Amazonas State Foundation Research; FCR, Feed conversion ratio; FI, Feed intake; INPA, Brazilian National Institute for Research of the Amazon; IPCC, Intergovernmental Panel on Climate Change; L, Light; LEEM, Laboratory of Ecophysiology and Molecular Evolution; MCH, Mean corpuscular hemoglobin; MCHC, Mean concentration of corpuscular hemoglobin; MCV, Mean corpuscular volume; nm, Nanometer; PER, Protein efficiency ratio; PNP, Extended Amazonian photoperiod; RBC, Red Blood Cells; S, Survival Rate; SEM, Standard error of mean; SGR, Specific Growth Rate; SNP, Regular photoperiod of the Amazon; WG, Weight gain.

TABLE 1 | Proximate composition of commercial feed applied in this study[a].

Component	Content (%)
Protein	35.4
Lipid	3.9
Ash	12.3
Crude fiber	2.7
Dry matter	4.1
Carbohydrates[b]	41.6

[a] *Bromatology analysis was carried in the Laboratory of Fish Nutrition at INPA following the* Association of official analytical chemists (AOAC) (1995) *recommendations.*
[b] *Carbohydrates = 100—(protein + lipid + ash + fiber).*

tested were 26, 29, and 32°C. These temperatures were set in accordance with preferred range of tambaqui in the wild (Araujo-Lima and Goulding, 1998). Thus, nine experimental conditions were established: D-26, D-29, D-32, SNP-26, SNP-29, SNP-32, PNP-26, PNP-29, and PNP-32. Three replicates ($n = 3$) of each experimental condition were employed.

The tanks were kept in an isolated room and were arranged on benches and covered with black plastic covers to avoid the contact of fish with the external luminosity. All tanks were supplied with 2 L.min^{-1} of aerated well water from a head tank. A chemical filter was positioned between the head tank and the experimental tank to reduce ammonia levels in the water. Fluorescent lamps (36 watts, AT T10, 5,600 K, ARTEK® Co, São Paulo, Brazil) were placed 50 cm above the surface of the water and controlled by timers (6610, DNI®, Brazil) set to start daily at 6 a.m and shut off according to experimental photoperiods. For the dark treatment (D), the benches received the lamps, but these were off during the experimental period. Heaters (Aquarium, H-606, Hopar®) and coolers coupled to a thermostat (TIC-17RGT, Full Gauge, ± 0.01 accuracy) were placed in the tanks to ensure the maintenance of the experimental temperatures. The food remains were siphoned through a hole in the lid of the tanks opened only for this operation.

Experimental Procedure and Sample Collection

After being transferred to the experimental tanks, the fish remained for 1 week under the same acclimation conditions (12L:12D, 26°C, 5.3 ± 0.10 mg O_2.L^{-1}, pH 6.40 ± 0.20, 9 ± 2.40 μS.cm^{-1}; 0.086 ± 0.01 mmol.L^{-1} Na^+; 0.026 ± 0.01 mmol.L^{-1} K^+). The initial health conditions of the animals were verified by sampling one fish per tank for hematological and biochemical analysis (Before the Start of the Experiment—BSE). After this period, temperatures were gradually changed at a rate of 1.0°C per day until reaching 29°C and 32°C, respectively. At the same time, the coolers coupled to the thermostats were activated to reduce the temperature to 26°C at the same rate. The temperature was stabilized within 3 days. Thus, on the fourth day (day 0 of the experiment), the exposure period to the experimental combinations, as indicated above, was started. During the experimental period, fish were fed a commercial feed of 2–4 mm (Nutripeixe Tr 36–36% protein, Purina Co, São Paulo, SP, Brazil), twice a day (9 a.m., 4 p.m., see **Table 1**). The unconsumed pellets were collected 30 min after feeding in each tank by means of siphoning. The traces were air dried and weighed to calculate feed intake (FI) and feed conversion ratio (FCR). The tank water was renewed daily at a rate of 20% to avoid increasing ammonia levels. The water quality was checked after the last feeding every day throughout the experimental period.

On days 15, 30, and 60, nine fish were collected, three animals per tank, which were anesthetized with buffered anesthetic (1 g.L^{-1} MS 222 + 2 g.L^{-1} $NaHCO_3$, Sigma Aldrich®, USA), measured with the aid of an ichthyometer with 0.1 cm of precision and weighed using an analytical balance (Model Marte BL3200H, Minas Gerais, Brazil) with 0.1 g of precision for the analyzes of the growth indices. Immediately after growth measurements, blood samples (1.5 mL) were collected from caudal vein using heparinized syringes (lithium heparin, Sigma Aldrich®, USA) for the determination of hematological and biochemical parameters. After each sampling period, fish marked with fluorescent elastomer (Northwest Marine Technology®, Shaw Island, Washington, USA) on the pectoral fin were transferred to the experimental tank to maintain biomass density.

Growth Parameters

Growth analysis was performed following the parameters described below:

Weight gain (WG, g) = *Final Weight (g)—Initial Weight (g)/number of fish per replicate*

Specific growth rate (SGR, %) = *100x [ln final weight (g)—ln initial weight (g)]/(days of feeding period)*

Feed intake (FI, g) = *total feed consumed (g)/number of fish per replicate*

Feed conversion ratio (FCR) = *feed intake (g)/weight gain (g)*

Condition factor (CF) = *weight (g)/length (cm)*$^{2.84}$ (2.84 corresponds to the regression coefficient for the growth of tambaqui populations in the wild (Araujo-Lima and Goulding, 1998)

Protein efficiency ratio (PER, %) = [*weight gain (g)/feed intake (g) x% protein ration*]×*100*

Survival Rate (S,%) = *100x (final number of fish/initial number of fish)*

Blood Analysis

After collection, the blood samples were stored in 2 ml Eppendorf bullets and kept on ice. Total blood aliquots were diluted in a solution of formaldehyde citrate (3.8 g $Na_3H_5O_7.2H_2O$, 2.0 mL 40% H_2O formaldehyde and distilled water q.s.p 100 mL) for RBC counts (RBC) using a Neubauer chamber under 40× magnification on a Motic Professional B5 optical microscope (Motic®, USA). Hematocrit was determined by the microhematocrit method described by Goldenfarb et al. (1971). The hemoglobin concentration was measured using the cyanometahemoglobin method described by van Kampen and Zijlstra (1961). The red cell index MCV (mean corpuscular volume), MCH (mean corpuscular hemoglobin) and MCHC (mean concentration of corpuscular hemoglobin) were calculated according to (Brow, 1976).

Plasma Metabolites

Plasma was obtained by centrifugation of whole blood in an Eppendorf centrifuge (model 5430R, Hamburg, Germany) at 1834 RCF for 7 min and stored at −80°C until analysis. Cortisol concentration was determined by the ELISA method using a commercial kit (Diagnostic Biochem Canada®, Canada) following the manufacturer's recommendations that were adapted for reading on a plate spectrophotometer (Spectra max Plus, model 384, Molecular Devices®, USA) at 450 nm. Cortisol concentrations are expressed as ng.mL^{-1}.

The glucose concentration was quantified by the enzymatic colorimetric method using a commercial kit (*In vitro*®, Minas Gerais, Brazil), following manufacturer's instructions adapted to a plate spectrophotometer (Spectra max Plus, model 384, Molecular Devices®, USA) at 500 nm. This method measures the oxidation of glucose caused by the enzyme glucose oxidase. Glucose concentrations are expressed in mg.dL^{-1}.

Cholesterol and triglyceride concentrations were also determined using a commercial kit (*In vitro*®, Minas Gerais, Brazil) following the manufacturer's instructions. Both protocols were adapted to a plate spectrophotometer (Spectra max Plus, model 384, Molecular Devices®, USA) and determined at 500 nm. The concentrations of both metabolites are expressed in mg.dL^{-1}.

Total protein levels were determined by the biuret method using a commercial kit (*In vitro*®, Minas Gerais, Brazil) following manufacturer's instructions adapted to a plate spectrophotometer (Spectra max Plus model, 384, Molecular Devices®, USA) at 550 nm. The concentrations of total proteins are expressed in g.dL^{-1}.

Water Quality

Dissolved oxygen (mg.L^{-1}), temperature (°C) and water pH were measured every day using YSI probes (YSI® 60 and 85 models, USA). Ammonia concentrations were determined according to the colorimetric method described by Verdouw et al. (1978) and are expressed in µmol.L^{-1}.

Statistics

All data are presented as mean ± standard error of the mean (SEM; $N = 9$; $n = 3$). Prior to the analyzes, normality and homogeneity of the variances were verified using the Sigma Plot 11.0 package (Systat Software Inc., USA). Data transformation was applied when the assumptions for parametric analysis were violated. Two-way ANOVA was used to test the effects of time and experimental combinations (photoperiod and temperature), and the presence or absence of interaction between these two factors on growth parameters and physiological responses. To evaluate the water quality and differences between treatments in relation to initial experimental group (BSE) during the experiment, a one-way ANOVA was performed. The Tukey test was used to determine the significance of the differences among the means. Significant differences were accepted when $p < 0.05$.

TABLE 2 | Water quality in tanks over the experimental period.

Time[1]	**Ammonia (µmol.L^{-1})**			**Dissolved oxygen (mg.L^{-1})**			**pH**			**Temperature (°C)**		
	T15	**T30**	**T60**	**T15**	**T30**	**T60**	**T15**	**T30**	**T60**	**T15**	**T30**	**T60**
TREATMENT												
D-26	0.28 ± 0.10	0.29 ± 0.01	0.26 ± 0.01	5.4 ± 0.10	5.9 ± 0.40	5.0 ± 0.20	5.4 ± 0.10	4.7 ± 0.10	4.9 ± 0.30	26 ± 0.10^{a}	26 ± 0.20^{a}	26 ± 0.10^{a}
D-29	0.22 ± 0.10	0.12 ± 0.01	0.29 ± 0.01	5.5 ± 0.10	5.0 ± 0.30	4.5 ± 0.20	5.7 ± 0.10	5.3 ± 0.04	4.8 ± 0.30	29 ± 0.10^{b}	29 ± 0.20^{b}	29 ± 0.10^{b}
D-32	0.13 ± 0.10	0.12 ± 0.01	0.17 ± 0.01	5.3 ± 0.10	5.0 ± 0.30	5.5 ± 0.40	5.5 ± 0.10	4.5 ± 0.20	4.8 ± 0.30	32 ± 0.01^{c}	32 ± 0.10^{c}	32 ± 0.20^{c}
SNP-26	0.22 ± 0.10	0.24 ± 0.01	0.22 ± 0.01	5.5 ± 0.10	5.7 ± 0.20	5.4 ± 0.20	5.5 ± 0.04	4.9 ± 0.20	4.6 ± 0.40	26.1 ± 0.10^{a}	26 ± 0.20^{a}	26 ± 0.10^{a}
SNP-29	0.20 ± 0.10	0.10 ± 0.01	0.27 ± 0.01	5.8 ± 0.10	5.2 ± 0.20	5.1 ± 0.20	5.8 ± 0.04	5.2 ± 0.04	4.8 ± 0.40	29 ± 0.10^{b}	29 ± 0.20^{b}	29 ± 0.10^{b}
SNP-32	0.17 ± 0.01	0.10 ± 0.01	0.11 ± 0.01	5.6 ± 0.10	5.2 ± 0.10	4.8 ± 0.30	5.2 ± 0.20	4.5 ± 0.10	4.8 ± 0.20	32 ± 0.10^{c}	32 ± 0.10^{c}	32 ± 0.20^{c}
PNP-26	0.14 ± 0.04	0.26 ± 0.10	0.28 ± 0.01	5.6 ± 0.10	5.5 ± 0.40	5.5 ± 0.20	5.4 ± 0.10	4.5 ± 0.04	5.0 ± 0.20	26 ± 0.10^{a}	26 ± 0.20^{a}	26 ± 0.10^{a}
PNP-29	0.24 ± 0.03	0.11 ± 0.01	0.30 ± 0.01	5.5 ± 0.10	5.0 ± 0.30	4.9 ± 0.20	5.7 ± 0.10	5.2 ± 0.10	4.8 ± 0.40	29 ± 0.10^{b}	29 ± 0.20^{b}	29 ± 0.10^{b}
PNP-32	0.11 ± 0.02	0.11 ± 0.01	0.16 ± 0.01	5.4 ± 0.10	5.2 ± 0.30	5.4 ± 0.40	5.6 ± 0.10	5.0 ± 0.20	4.7 ± 0.30	32 ± 0.10^{c}	32 ± 0.20^{c}	32 ± 0.20^{c}

Data are mean ± SEM ($N = 3$). Different lowercase superscript letters within the same column indicate significant differences to the treatments at the same experimental time ($P < 0.05$).

[1] T15, 15 days, T30, 30 days, T60, 60 days.

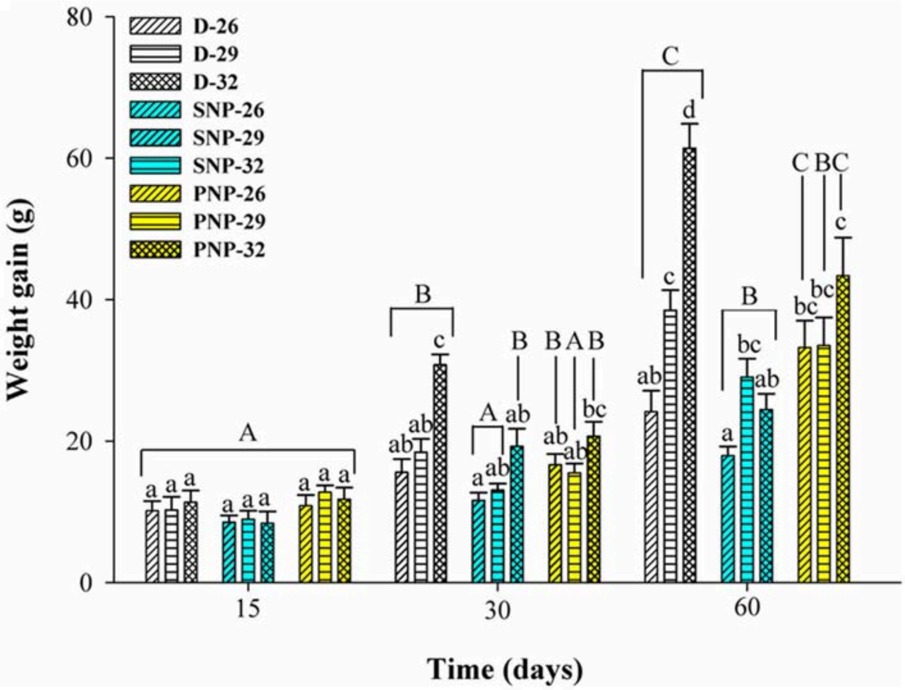

FIGURE 1 | Weight gain (g) of juveniles of *Colossoma macropomum* under controlled conditions of photoperiod and temperature. Data are mean ± SEM ($n = 3$). The different capital letters indicate significant differences in the same treatments over the experimental period ($p < 0.05$), while the lower-case letters indicate significant differences in the different treatments in the same experimental period ($p < 0.05$).

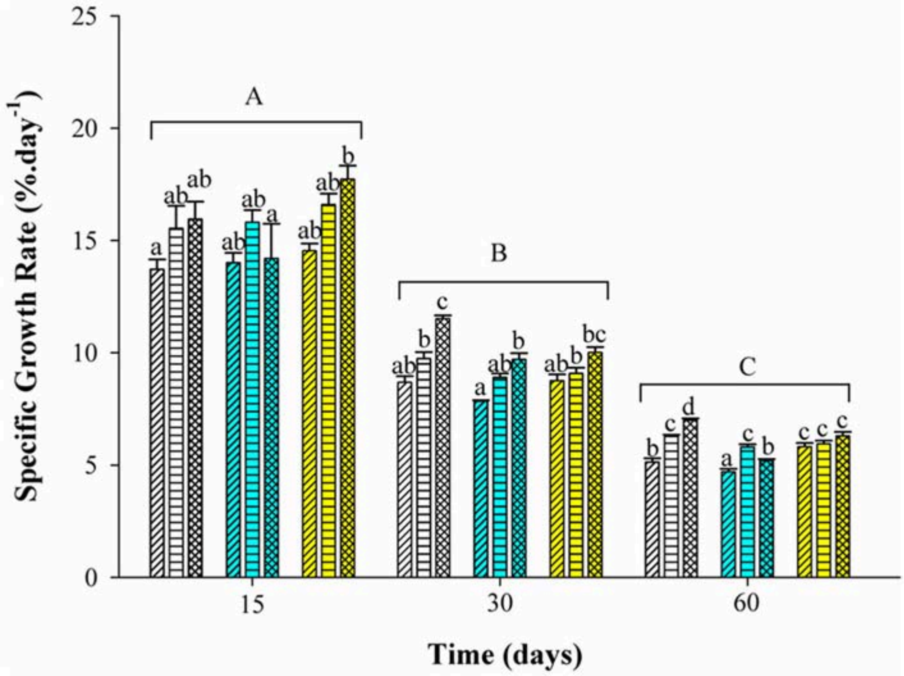

FIGURE 2 | Specific growth rate (%.day^{-1}) of juveniles of *Colossoma macropomum* under controlled conditions of photoperiod and temperature. Data are expressed as mean ± SEM ($n = 3$). Different lowercase letters indicate significant differences in the different treatments at the same experimental period ($p < 0.05$). The horizontal lines on the bars represent differences in experimental periods ($p < 0.05$).

RESULTS

Water Quality

The water quality are presented in **Table 2**. The levels of ammonia, dissolved oxygen, and pH presented no significant differences over the experimental period, while the temperature varied as we expected, according to the values preset for this study ($p < 0.05$).

Growth

Tambaqui performance was influenced by combinations of photoperiod and temperature as shown in **Figures 1**, **2** and **Table 3**. In our study, the increase in temperature combined with photoperiod had a great effect on growth. Overall results show an increase for WG, SGR, FI, CF, PER, and lower FCR for fish reared under D-32 conditions in contrast to the lower performance observed for fish reared under SNP-26 and SNP-32 conditions. PNP-fish at all temperatures had a similar performance, although the final WG, SGR, FCR, CF, and PER were lower than the D-32 fish, whose performance was also higher when compared to other treatments ($p < 0.05$). The increase of the photoperiod at lower temperatures, as observed for the treatment with PNP-26, increases FI and SGR, but is not compensated with better FCR, CF, and PER compared to fish at the same temperature in shorter photoperiods ($p < 0.05$).

Blood Parameters

The blood parameters of tambaqui juveniles under different photoperiod and temperature conditions are shown in **Table 4**. It was observed an increase in Hb, Ht, and RBC in fish raised at 32°C in D, SNP, and PNP, compared with fish at 26°C ($p < 0.05$), except for the PNP-26 treatment, where these variables were higher ($p > 0.05$, **Table 4**). At the end of the experiment, fish under PNP-29 had Hb, Ht, and RBC similar to fish grown at 26°C, although they remained similar to fish in the same photoperiod, for Ht and RBC, and for all other photoperiods at 32°C ($p > 0.05$). MCV, MCH, and MCHC were similar among treatments at 29 and 32°C over the experimental period. However, high VCM was observed for SNP-26 and PNP-26 compared to fish groups exposed to 29 and 32°C at 15 days; at 30 days, these differences were also observed between these two groups (SNP-26 and PNP-26). Lower MCH and MCHC were observed for fish under PNP-26 when compared to the SNP-32 group ($p < 0.05$). In general, the main differences between treatments and the group before the start of the experiment (BSE) for the hematological variables were verified at the highest temperatures and the prolonged photoperiod ($p < 0.05$).

Plasma Metabolites

Cortisol

An increase in cortisol levels was observed mainly at 30 days in all treatments (**Figure 3**). A similar pattern was observed among treatments in the same photoperiod, excluding the lowest level observed for the SNP-26 treatment when compared to the SNP-32 fish ($p < 0.05$). The increase in photoperiod and temperature were the main factors for the elevation of cortisol levels in tambaqui compared to BSE fish at the end of the experimental period ($p < 0.05$, see **Figure 3**).

Glucose

PNP-26 and SNP-32 treatments showed the most significant effect on plasma glucose levels of tambaqui (**Figure 4**). Glucose levels were significantly higher at 32°C for all photoperiods ($p < 0.05$). Compared to BSE, an overall increase of plasma glucose levels were observed.

Cholesterol and Triglycerides

Cholesterol and triglycerides varied between treatments (see **Table 5**). Elevated cholesterol levels were observed in PNP-32 fish compared to other treatments, except for 15 days for PNP-26 and for SNP-32 at 60 days ($p < 0.05$). In contrast, triglycerides were higher in the treatment of SNP-26 with remarkable differences in relation to fish of treatments D-32, SNP-32, and PNP-32 at 30 days ($p < 0.05$).

Total Proteins

Total protein levels in tambaqui plasma were similar among treatments ($p > 0.05$), except for fish under PNP-26 which exhibited high concentrations over the experiment, when compared to fish under the same photoperiod at 60 days and fish under darkness at all temperatures ($p < 0.05$) (**Table 5**). On the other hand, high levels of total proteins were observed only for PNP-26 and SNP-32 at the end of the experiment, in contrast to fish of the BSE group ($p < 0.05$).

DISCUSSION

Water Quality

The water quality showed no significant differences, except for the temperature that varied according to preset levels, as expected (**Table 2**). The observed variations of water quality remained within the range required for rearing tambaqui, as reviewed by several authors (Almeida-Val and Val, 1995; Araujo-Lima and Goulding, 1998; Souza-Bastos et al., 2017; Wood et al., 2017). For these authors, the rusticity of the species is based on its resistance to hypoxia, water acidity, and total ammonia, which preserves its growth performance in aquaculture.

Growth

Tambaqui growth varied according to the combination of photoperiod and temperature, as previously described in studies for temperate species such as *Salmo salar* L. (Knutsson and Grav, 1976), *Perca flavescens* and *Stizostedion vitreum* cf. *Sander vitreus* (Huh et al., 1976). These studies showed a positive relationship between the increase in daylight extension and the increase in temperature, and that photoperiod effects on growth were strongly modulated or dependent on the preferred environmental temperature of the species (Clarke et al., 1978; Imsland et al., 2007a). Photoperiod effects on tambaqui growth are modulated by temperature, as we hypothesized. However, different from other studies, darkness, when associated with higher temperatures (29 and 32°C for this study), is more efficient to promote better growth in tambaqui (**Figures 1**, **2** and **Table 3**). Thus, the best performance observed for the animals of the D-32

TABLE 3 | Feed intake (FI), feed conversion ratio (FCR), condition factor (CF), and protein efficiency ratio (PER) of juveniles of *Colossoma macropomum* at different experimental trials (D-26, D-29, D-32, SNP-26, SNP-29, SNP-32, PNP-26, PNP-29, and PNP-32).

Time (days)	**FI (g.fish^{-1})†**			**FCR**			**CF**			**PER**		
	T15	**T30**	**T60**	**T15**	**T30**	**T60**	**T15**	**T30**	**T60**	**T15**	**T30**	**T60**
TREATMENT[a]												
D-26	7.28 ± 0.30^{bc}	12.36 ± 0.60^{a}	25.50 ± 1.3^{a}	0.90 ± 0.04	0.93 ± 0.10	1.17 ± 0.10^{bc}	2.62 ± 0.04^{ab}	2.65 ± 0.10^{abcd}	2.63 ± 0.04^{abc}	3.26 ± 0.20	2.82 ± 0.20^{ab}	2.76 ± 0.20^{a}
D-29	9.22 ± 0.40^{d}	18.35 ± 0.50^{bcd}	38.01 ± 0.50^{c}	1.00 ± 0.20	0.93 ± 0.10	0.90 ± 0.04^{ab}	2.60 ± 0.01^{abA}	2.71 ± 0.03^{cdAB}	2.80 ± 0.04^{cdB}	3.15 ± 0.50	2.81 ± 0.20^{ab}	3.04 ± 0.20^{ab}
D-32	9.79 ± 0.50^{d}	22.03 ± 0.80^{d}	48.91 ± 0.50^{d}	0.90 ± 0.10	0.67 ± 0.02	0.68 ± 0.03^{a}	2.63 ± 0.10^{abA}	2.70 ± 0.10^{bcdA}	2.94 ± 0.04^{dB}	3.82 ± 0.40	3.78 ± 0.20^{b}	4.29 ± 0.20^{b}
SNP-26	6.52 ± 0.40^{b}	11.17 ± 0.40^{a}	25.31 ± 0.90^{a}	0.80 ± 0.10^{A}	1.0 ± 0.02^{AB}	1.24 ± 0.10^{cB}	2.59 ± 0.03^{ab}	2.62 ± 0.03^{abc}	2.50 ± 0.10^{ab}	3.57 ± 0.30^{A}	2.54 ± 0.10^{abB}	2.51 ± 0.20^{aB}
SNP-29	8.47 ± 0.40^{cd}	16.11 ± 0.20^{b}	34.91 ± 1.7^{bc}	0.92 ± 0.10^{AB}	0.93 ± 0.10^{B}	1.29 ± 0.10^{cC}	2.57 ± 0.10^{ab}	2.50 ± 0.03^{a}	2.63 ± 0.03^{abc}	3.16 ± 0.30	2.50 ± 0.10^{a}	2.54 ± 0.20^{a}
SNP-32	4.81 ± 0.10^{a}	12.68 ± 1.10^{a}	30.41 ± 0.90^{b}	0.99 ± 0.20^{A}	0.78 ± 0.10^{AB}	1.29 ± 0.10^{cB}	2.63 ± 0.10^{abA}	2.83 ± 0.02^{dB}	2.47 ± 0.10^{aC}	3.57 ± 0.90	3.24 ± 0.20^{ab}	2.47 ± 0.20^{a}
PNP-26	9.55 ± 0.50^{d}	17.25 ± 1.0^{bc}	39.28 ± 2.3^{cd}	1.16 ± 0.10	1.04 ± 0.10	1.09 ± 0.10^{bc}	2.64 ± 0.03^{ab}	2.51 ± 0.01^{ab}	2.52 ± 0.10^{ab}	3.00 ± 0.30	2.80 ± 0.30^{ab}	2.61 ± 0.20^{a}
PNP-29	9.98 ± 0.40^{d}	17.88 ± 0.50^{bcd}	39.29 ± 1.0^{cd}	0.84 ± 0.10	1.04 ± 0.10	0.87 ± 0.10^{ab}	2.51 ± 0.04^{a}	2.57 ± 0.10^{bc}	2.65 ± 0.04^{abc}	3.33 ± 0.20	2.53 ± 0.20^{a}	3.03 ± 0.20^{ab}
PNP-32	10.03 ± 0.50^{d}	21.51 ± 1.7^{cd}	40.81 ± 4.5^{cd}	0.87 ± 0.10	0.94 ± 0.04	1.13 ± 0.10^{bc}	2.73 ± 0.10^{b}	2.71 ± 0.03^{cd}	2.68 ± 0.03^{bc}	3.51 ± 0.50	2.81 ± 0.20^{ab}	3.37 ± 0.40^{ab}
TWO-WAY ANOVA[b]												
Time		**			**			ns			*	
Treatment		**			**			**			**	
Time x Treatment		**			**			**			ns	

[a] *Data are mean ± SEM ($N = 3$). Different superscripted uppercase letters in the horizontal lines indicate significant differences to the same treatments along of sampling times ($p < 0.05$). Lowercase letters in the same column indicate significant differences to the different treatments in the same experimental time ($p < 0.05$).* [b] **$p < 0.05$, **$p < 0.001$, ns, non-significant. †Indicate significant differences to all sampling times ($p < 0.05$).*

TABLE 4 | Hematological parameters of juveniles of *Colossoma macropomum* at different experimental trials (D-26, D-29, D-32, SNP-26, SNP-29, SNP-32, PNP-26, PNP-29, and PNP-32).

Time	Treatment	Hb (g.dL^{-1})	Ht (%)	RBC (10^6/mm^3)	MCV	MCH (pg)	MCHC (%)
BSE	Sample pool	6.30 ± 0.20	29.15 ± 0.70	1.80 ± 0.06	161.25 ± 2.20	34.80 ± 1.00	22.65 ± 0.40
15 days	D-26	6.00 ± 0.10^{aA}	25.75 ± 0.60^{aA}	1.60 ± 0.05^{aA}	161.10 ± 0.60^{cd}	35.40 ± 0.70^{ab}	22.20 ± 0.30^{abA}
	D-29	$8.60 \pm 0.20^{c*}$	30.60 ± 1.10^{bAB}	2.00 ± 0.07^{cd}	153.35 ± 3.50^{bc}	$40.40 \pm 0.80^{d*}$	$27.20 \pm 0.30^{dAB*}$
	D-32	$8.10 \pm 0.30^{cA*}$	32.00 ± 0.40^{bAB}	2.10 ± 0.06^{cdAB}	152.40 ± 3.00^{bc}	38.80 ± 0.50^{bcdA}	24.00 ± 0.30^{bcA}
	SNP-26	5.85 ± 0.20^{aA}	26.50 ± 0.60^{a}	1.60 ± 0.03^{aA}	174.50 ± 2.10^{eA}	36.70 ± 0.90^{bcA}	22.30 ± 0.55^{abA}
	SNP-29	$8.20 \pm 0.30^{c*}$	31.25 ± 0.80^{b}	2.00 ± 0.10^{cd}	148.85 ± 2.85^{ab}	37.70 ± 0.85^{abcd}	$25.10 \pm 0.60^{cdAB*}$
	SNP-32	$8.00 \pm 0.20^{cA*}$	31.70 ± 0.40^{bA}	2.00 ± 0.03^{cd}	148.10 ± 2.95^{abA}	$39.45 \pm 0.60^{cdA*}$	$25.30 \pm 0.50^{cd*}$
	PNP-26	7.10 ± 0.30^{bA}	31.75 ± 0.65^{b}	2.10 ± 0.05^{cd}	168.10 ± 3.40^{de}	35.00 ± 0.80^{a}	21.90 ± 0.30^{abA}
	PNP-29	$8.20 \pm 0.20^{c*}$	31.20 ± 1.10^{b}	1.90 ± 0.05^{bcA}	$145.40 \pm 2.50^{abA*}$	$40.40 \pm 1.10^{d*}$	$26.50 \pm 0.25^{dA*}$
	PNP-32	$8.20 \pm 0.10^{cA*}$	$33.40 \pm 0.50^{b*}$	2.15 ± 0.04^{dAB}	148.40 ± 1.90^{abA}	38.90 ± 0.70^{bcd}	24.70 ± 0.15^{cdAB}
30 days	D-26	7.00 ± 0.10^{abB}	27.40 ± 0.45^{aAB}	1.80 ± 0.03^{aB}	154.60 ± 2.00^{a}	37.80 ± 0.60^{ab}	24.60 ± 0.50^{abB}
	D-29	$8.20 \pm 0.10^{cd*}$	30.50 ± 0.60^{bA}	2.10 ± 0.07^{b}	159.50 ± 3.30^{ab}	$39.80 \pm 0.60^{ab*}$	$26.50 \pm 0.50^{abA*}$
	D-32	$7.50 \pm 0.30^{bcA*}$	31.75 ± 0.50^{bA}	2.00 ± 0.03^{bA}	159.20 ± 2.60^{ab}	37.75 ± 0.40^{abA}	23.50 ± 0.30^{aA}
	SNP-26	7.40 ± 0.20^{bB}	27.40 ± 1.10^{a}	1.70 ± 0.08^{aAB}	154.70 ± 2.75^{aB}	$39.70 \pm 1.00^{abB*}$	$25.40 \pm 0.30^{bB*}$
	SNP-29	$8.30 \pm 0.10^{cd*}$	32.75 ± 0.75^{b}	2.10 ± 0.08^{b}	155.00 ± 3.10^{ab}	37.80 ± 0.30^{ab}	23.90 ± 0.25^{abA}
	SNP-32	$8.00 \pm 0.20^{cdA*}$	31.00 ± 0.20^{bA}	2.10 ± 0.06^{b}	154.95 ± 3.00^{abAB}	$40.20 \pm 0.70^{bA*}$	$24.94 \pm 0.40^{ab*}$
	PNP-26	$8.10 \pm 0.20^{cdB*}$	32.40 ± 0.70^{b}	2.10 ± 0.08^{b}	166.30 ± 1.90^{b}	36.50 ± 0.80^{a}	23.10 ± 0.30^{aA}
	PNP-29	$8.50 \pm 0.10^{d*}$	$33.25 \pm 0.80^{b*}$	$2.10 \pm 0.05^{bB*}$	148.60 ± 2.60^{abAB}	$39.65 \pm 0.90^{ab*}$	$25.70 \pm 0.20^{abB*}$
	PNP-32	$7.55 \pm 0.20^{bcA*}$	32.60 ± 1.00^{b}	2.10 ± 0.04^{bA}	155.65 ± 2.00^{abAB}	39.00 ± 1.00^{ab}	24.10 ± 0.50^{abA}
60 days	D-26	$8.10 \pm 0.30^{aC*}$	29.10 ± 0.60^{abB}	1.80 ± 0.07^{aAB}	155.50 ± 2.50	37.80 ± 1.80^{a}	$25.70 \pm 0.50^{B*}$
	D-29	$8.60 \pm 0.10^{ab*}$	$32.80 \pm 0.50^{cB*}$	$2.10 \pm 0.03^{c*}$	155.80 ± 1.55	$41.70 \pm 0.60^{bc*}$	$26.70 \pm 0.10^{B*}$
	D-32	$9.00 \pm 0.20^{bB*}$	$34.30 \pm 0.20^{cB*}$	$2.20 \pm 0.05^{cB*}$	160.90 ± 3.00	$42.80 \pm 0.80^{bcB*}$	$26.60 \pm 0.30^{B*}$
	SNP-26	$7.80 \pm 0.20^{ab*}$	28.50 ± 0.80^{ab}	1.80 ± 0.05^{abB}	157.10 ± 1.60^{B}	$39.25 \pm 0.90^{abAB*}$	$25.60 \pm 0.60^{B*}$
	SNP-29	$8.70 \pm 0.40^{ab*}$	$32.90 \pm 0.50^{c*}$	$2.20 \pm 0.04^{c*}$	152.70 ± 2.70	38.50 ± 0.95^{ab}	$25.85 \pm 0.90^{B*}$
	SNP-32	$9.25 \pm 0.20^{bB*}$	$34.50 \pm 1.00^{cB*}$	$2.20 \pm 0.05^{c*}$	158.80 ± 3.80^{B}	$43.10 \pm 1.00^{cB*}$	25.90 ± 0.50*
	PNP-26	$8.55 \pm 0.10^{abB*}$	$32.50 \pm 0.60^{c*}$	2.10 ± 0.03^{c}	162.30 ± 2.65	$40.20 \pm 0.50^{abc*}$	$25.60 \pm 0.50^{B*}$
	PNP-29	$7.90 \pm 0.20^{a*}$	31.50 ± 0.20^{bc}	2.00 ± 0.02^{bcAB}	155.60 ± 1.30^{B}	38.50 ± 0.75^{ab}	$25.60 \pm 0.30^{ab*}$
	PNP-32	$9.10 \pm 0.15^{bB*}$	$34.10 \pm 0.60^{c*}$	$2.20 \pm 0.05^{cB*}$	160.10 ± 3.40^{B}	$40.90 \pm 0.50^{abc*}$	$25.90 \pm 0.40^{B*}$
TWO-WAY ANOVA							
Time		***	***	***	*ns*	***	***
Treatment		***	***	***	***	***	***
Interaction		***	**	*n.s*	***	**	***

Data are mean ± SEM (N = 3). Different underlined capital letters in the columns indicate significant differences in the same treatments over the sampling period (p <0.05). The lowercase letters in the columns indicate significant differences in the different treatments for the same experimental time (p <0.05). Hb, hemoglobin; Ht, hematocrit; RBC, erythrocyte count; MCV, mean corpuscular volume; MCH, mean corpuscular hemoglobin; MCHM, mean corpuscular hemoglobin concentration.

**indicate significant differences compared to the initial experimental group (BSE); $^{**}p < 0.05$; $^{***} p < 0.001$; ns, no significant. D, darkness; SNP, regular photoperiod of the Amazon; PNP, extended Amazonian photoperiod.*

treatment, when compared to the other treatments, is explained by the natural life history of the studied species. In wild areas, tambaqui lives near or under aquatic vegetation and in forest-shaded water bodies where it finds shelter, food, and poor lighting in the muddy waters of Amazonian floodplains (Araujo-Lima and Goulding, 1998). Our data contrast with Mendonça et al. (2012) that recommended 15-h or more of light for a better growth performance of tambaqui. We believe that the darkness associated with temperatures above 30°C offer better conditions for better growth, since they mimic the light and temperature conditions found in nature and in fish farms, especially in the dry season, when Secchi disk reads are 20 cm (Sioli, 1984; Araujo-Lima and Goulding, 1998). Our study demonstrates that such effects appear to be persistent in laboratory and field conditions, as also observed for *Gadus morhua* (Atlantic cod) by Imsland et al. (2007b).

Similar growth rates were recorded in the same photoperiod of the SNP-26 animals and higher growth rates in relation to D-26 and SNP-26 (**Figures 1**, **2** and **Table 3**). A growth-stimulating effect has been reported in continuous light at low temperatures for species such as *Hippoglossus hippoglossus* L. and *S. salar* (Jonassen et al., 2000; Lohne et al., 2012; Handeland et al., 2013). According to the findings of Døskeland et al. (2016), the magnitude of these effects is inversely related to the increase in temperature indicating higher efficiency for animals raised at low temperatures when in continuous light, than at temperatures close to the optimum of the species. Even not testing a continuous light condition, the increase in the natural photoperiod found in nature by the species indicated the same effect in our study for tambaqui, although it was not accompanied by good indicators of food efficiency and body condition. Thus, our data contrast with the results of Imsland et al. (2007a) who reported lower growth rates for *Gadus morhua* raised in continuous light and low temperatures compared to those animals raised at 10 and 13°C in the same photoperiod, as the growth rates for tambaqui were similar over time (**Figures 1**, **2** and **Table 3**).

In the treatments where it was applied the natural photoperiod found by tambaqui in nature, the feed efficiency was compromised, as previously described by Aride et al. (2006). Thus, in our study, the best feed conversion for the D-32 group may be associated with the fact that the animal is prepared to process the food near or at night. We believe that exposure to darkness, associated with increased temperatures, promotes an optimization of digestive enzyme activities, and absorption of nutrients from the ingested food. Previous studies with tambaqui and pirapitinga *Piaractus brachypomum* support our hypothesis (Baras et al., 1996; Van der Meer et al., 1997). Thus, the increase in protein and condition factor efficiency was correlated with the increase in body mass as a consequence of better conversion of the food after 30 days (**Table 3**). The maintenance of high food intake in fish raised under the Amazon natural photoperiod, which presented a lower performance than the D-32 group, occurred due to the increase in the energetic costs due to the longer time for social contact, swimming, and competition for food. Thus, our data are in agreement with the observations of Adewolu et al. (2008) when they suggested a lower performance for the African catfish *Clarias gariepinus* subjected to natural photoperiod (12L: 12D) and continuous light. In addition, our personal observations suggest that these behaviors are more influenced by the temperature increase because the smaller fish take more time to obtain the food in relation to the larger ones, pointing out the existence of hierarchy of dominance associated with the size of the animals.

Physiological Indexes

Blood reflects the physiological state of animals in the face of environmental challenges (Zhou et al., 2009). The increase in water temperature tends to cause elevation of blood oxygen transport capacity suggesting a greater need for oxygen transfer. Under hypoxemic conditions or high demand for oxygen, splenic contractions followed by release of young erythrocytes improve oxygen transfer (Houston and Murad, 1995). However, the associated effects between photoperiod and temperature on these responses need to be further clarified.

Our study shows that the increase in temperature associated with all photoperiods caused an increase of RBC, Hb, Ht, and corpuscular constants (**Table 4**). These data are in agreement with those of Valenzuela et al. (2008) who observed an increase for RBC, Hb, and Ht of rainbow trout *Oncorhynchus mykiss* under 12L: 12D and under continuous light at warmer temperatures (18°C), suggesting that respiratory capacity is temperature dependent. Surprisingly, our study also showed that prolonged photoperiod at lower temperatures cause hemoconcentration. We believe that changes in blood properties occurred in response to increased respiratory demand due to additional costs with activities such as swimming, digestive needs, and social contact (Chudzik and Houston, 1983).

Fish under stressful conditions exhibit elevated levels of glucose and cortisol, which compromise vital activities (Barton and Iwama, 1991; Barton, 2002). Several studies reported acute stress conditions after handling, short exposure or even absence of photoperiod variation (Biswas et al., 2006, 2008; Bani et al., 2009; Veras et al., 2013). The increase in cortisol levels, for all treatments, is strongly influenced by the increase in temperature after 30 days (**Figure 3**) and suggests that exposure time is a stressful condition itself. It is noteworthy that in nature, fish can look for places where their vital activities are optimal. In this study, the impossibility of choosing environmental optima and the need to mobilize energy more quickly for the supply of metabolic needs under stressful conditions triggered such responses. These effects are more evident both when the photoperiod is increased as in the present study and when the temperature is increased as observed by Jaxion-Harm and Ladich (2014) for the common carp *Cyprinus carpio*.

The elevation of glucose levels for the PNP-26 and PNP-32 animals suggests increased energy mobilization (**Figure 4**). The slight increase for the SNP-26 fish, at 30 and 60 days, and the PNP-26 may be associated with the feeding regime (see **Table 1**). In addition, fish reared at 29 and 32°C showed lower levels of glucose (**Figure 4**). The data of Biswas et al. (2004) and Biswas and Takii (2016) did not show differences in glucose levels for *Oreochromis niloticus* and *Oplegnathus fasciatus* submitted to intermittent photoperiods for 3 months and also different luminosity. Our study, however, shows that higher temperatures combined with shorter photoperiods promote a better use of glucose and that longer photoperiods increase the energy cost for tambaqui when associated with different temperature levels.

We observed that fish at lower temperatures tended to maintain high triglyceride levels compared to the other treatments, regardless the photoperiod interval (**Table 5**). So, this elevation may have ensured greater thermal stability and protection to the animals in these temperatures due to the time of exposition and impossibility of the animals to move to confortable temperatures under the experimental conditions, as they would do in nature (see **Figure 4**). However, our data suggest that the elevation of cholesterol levels in the fish reared under PNP-32 is a result of the impact caused by the combination of the higher temperature and photoperiod. For tambaqui, in contrast to what has been suggested for marine and temperate species, the simultaneous elevation of photoperiod and temperature causes physiological impacts that do not ensure good conditions for fish growth, explaining the lower growth of animals under these conditions compared to the animals in the dark at 32°C.

Plasma total protein levels in this study were relatively stable (**Table 5**). Fish under PNP-26 maintained the highest levels of plasma protein in contrast to other treatments (**Table 5**). Contrary to what we have observed, Sala-Rabanal et al. (2003) found lower protein levels for *Sparus aurata* maintained at 8°C for 20 days. Tambaqui under the present experimental protocol may have increased plasma protein levels due to the reduced use

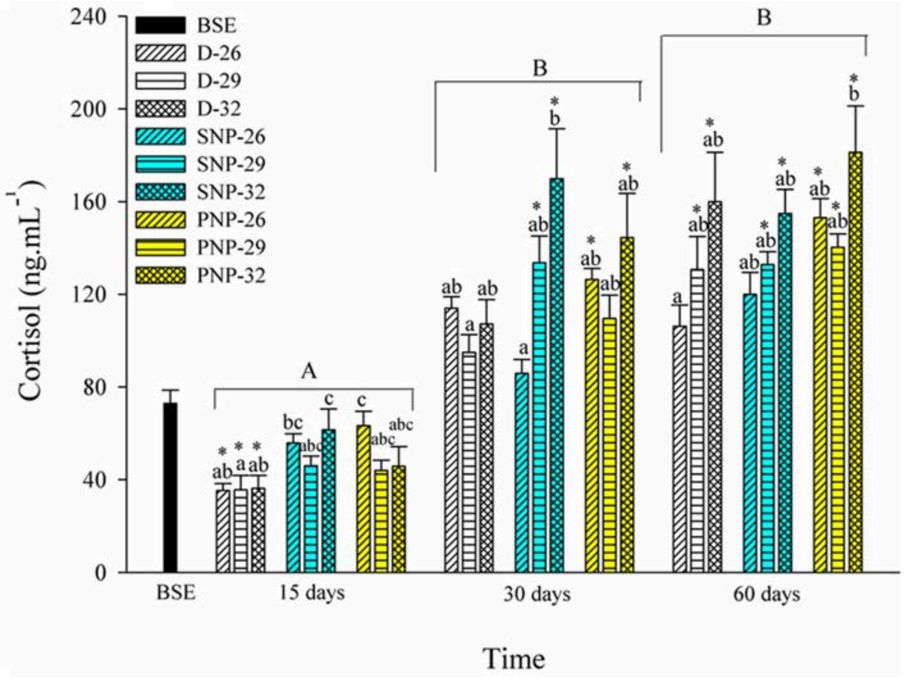

FIGURE 3 | Plasma cortisol of juveniles of *Colossoma macropomum* under controlled conditions of photoperiod and temperature. Data are expressed as mean ± SEM ($N = 3$). Different lowercase letters indicate significant differences between treatments at the same experimental period ($p < 0.05$). The horizontal lines on the bars represent differences in experimental periods ($p < 0.05$). * Indicate differences of the treatments in relation to BSE group.

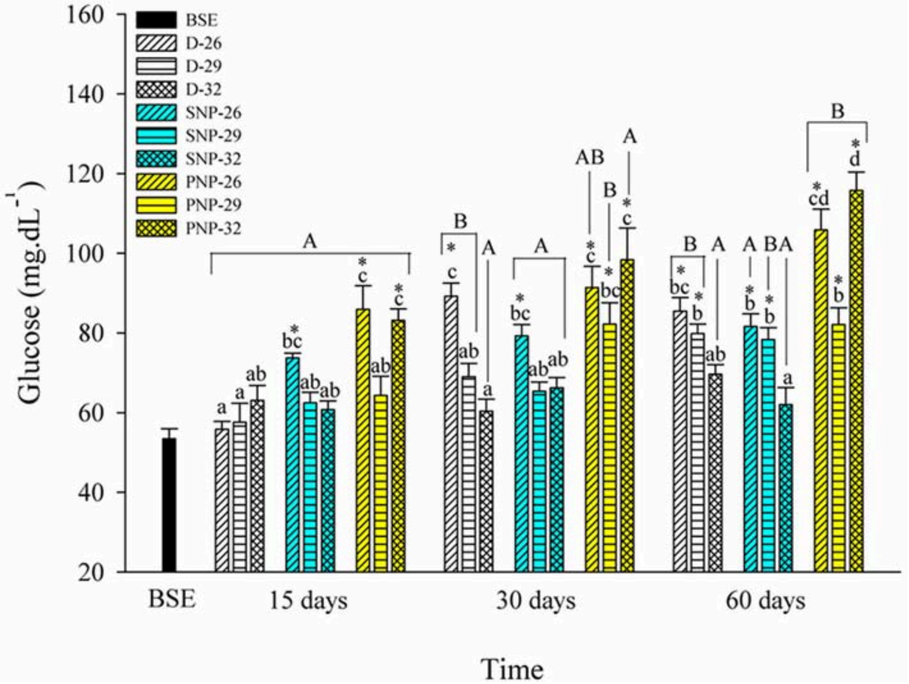

FIGURE 4 | Plasma glucose of juveniles of *Colossoma macropomum* under controlled conditions of photoperiod and temperature. Data are expressed as mean ± SEM ($N = 3$). The different capital letters indicate significant differences in the same treatments over the experimental period ($p < 0.05$), while the lowercase letters indicate significant differences in the different treatments in the same experimental period ($p < 0.05$). * Indicate differences of the treatments in relation to BSE group.

TABLE 5 | Plasma cholesterol, total proteins, and triglycerides of juveniles of *Colossoma macropomum* at different experimental trials (D-26, D-29, D-32, SNP-26, SNP-29, SNP-32, PNP-26, PNP-29, and PNP-32).

Time (days)	**Cholesterol (mg.dL^{-1})**			**Total protein (g.dL^{-1})**			**Triglycerides (mg.dL^{-1})**		
	T15	**T30**	**T60**	**T15**	**T30**	**T60**	**T15**	**T30**	**T60**
BSE†	58.10 ± 1.50	2.55 ± 0.06	201.50 ± 6.50						
D-26	62.50 ± 3.30^{a}	61.30 ± 1.90^{a}	57.90 ± 1.10^{a}	2.25 ± 0.07^{aA}	2.20 ± 0.08^{aA}	2.50 ± 0.09^{abB}	124.00 ± 3.45^{bcA*}	261.20 ± 3.60^{deC}	211.90 ± 6.80^{bcB}
D-29	68.80 ± 1.30^{abc*}	62.80 ± 0.80^{a}	64.00 ± 1.95^{ab}	2.30 ± 0.02^{abA}	2.60 ± 0.06^{bB}	2.50 ± 0.09^{bcAB}	106.20 ± 4.80^{abA*}	199.00 ± 10.30^{bcB}	178.65 ± 12.50^{abB}
D-32	67.50 ± 1.40^{abcA}	75.80 ± 1.80^{bB*}	67.30 ± 1.70^{abcA}	2.20 ± 0.05^{aA}	2.50 ± 0.06^{bB}	2.55 ± 0.04^{bcB}	99.60 ± 5.40^{abA*}	172.80 ± 5.40^{abB}	182.65 ± 6.00^{abB}
SNP-26	72.60 ± 2.90^{abc*}	73.00 ± 1.00^{b*}	66.40 ± 1.00^{abc}	2.60 ± 0.08^{bcA}	2.70 ± 0.06^{bcA}	3.10 ± 0.07^{deB*}	169.30 ± 11.20^{deA}	318.40 ± 6.60^{eB*}	304.90 ± 22.70^{dB*}
SNP-29	71.80 ± 2.80^{abcA*}	72.90 ± 1.95^{bA*}	63.70 ± 2.40^{abB}	2.40 ± 0.05^{abcA}	2.80 ± 0.08^{bcB}	2.80 ± 0.05^{cdB}	184.10 ± 10.40^{e}	161.30 ± 7.20^{ab}	185.80 ± 10.00^{ab}
SNP-32	63.50 ± 1.80^{abA}	71.10 ± 0.60^{abB*}	76.20 ± 2.10^{cdB}	2.30 ± 0.05^{abA}	2.60 ± 0.08^{bB}	3.00 ± 0.10^{deC*}	138.50 ± 8.50^{cdA*}	179.10 ± 5.70^{abB}	176.10 ± 8.10^{abB}
PNP-26	74.60 ± 1.80^{cdAB*}	79.10 ± 2.00^{bB}	68.60 ± 2.30^{bA*}	2.60 ± 0.07^{cA}	2.95 ± 0.08^{cB}	3.20 ± 0.04^{eC*}	168.00 ± 6.90^{deA}	247.80 ± 12.20^{cdB}	249.60 ± 19.30^{cdB}
PNP-29	73.10 ± 2.40^{bcA*}	75.40 ± 2.60^{bA}	63.30 ± 1.70^{abB}	2.50 ± 0.07^{abcA}	2.80 ± 0.09^{bcB}	2.35 ± 0.10^{abA}	140.80 ± 3.30^{cdA*}	167.95 ± 11.50^{abA}	228.90 ± 16.00^{cdB}
PNP-32	83.50 ± 2.80^{dA*}	96.25 ± 5.50^{cB}	80.25 ± 2.70^{dA*}	2.40 ± 0.04^{abcA}	2.70 ± 0.08^{bcB}	2.40 ± 0.10^{abA}	99.80 ± 6.00^{abA*}	189.00 ± 14.00^{abB}	178.80 ± 7.50^{abB}
TWO-WAY ANOVA									
Time		**			**			**	
Treatment		**			**			**	
Interaction		**			**			**	

Data are mean ± SEM (N = 3). Different underlined capital letters in the horizontal lines indicate significant differences in the same treatment over the sampling periods ($p < 0.05$). The lowercase letters in the same column indicate significant differences for different treatments at the same experimental period ($p < 0.05$). *Indicate significant differences compared to the initial experimental group (BSE); $^{**}p < 0.001$. D, darkness; SNP, regular photoperiod of the Amazon; PNP, extended Amazonian photoperiod.

of available proteins in the diet, which did not result in different growth rates as observed for SNP-32 and SNP-26 fish (**Table 5**).

Seasonal and estuarine species have their growth rates controlled by seasonal changes resulting from increased photoperiod and environmental temperatures in the summer and spring. However, this pattern is not similar among species, since the potentiating effect of growth promoted by periods of prolonged or continuous light may become limited at elevated temperatures (Lohne et al., 2012; Døskeland et al., 2016). In natural environments, the photoperiod affects fish development, in addition to plankton productivity and migration, an important food source, and oxygen producer in these ecosystems. Nowadays, anthropogenic activities, pollution levels and global warming potentiate the harmful effects of temperature on aquatic communities (Harley et al., 2006). The decline in productivity in marine regions, changes in migratory patterns, animal metabolic stress, and increased mortality are expected effects in the coming years, resulting in direct impacts on fisheries and aquaculture industries (Brander, 2007). Our results, in this context, show that fish exposure to temperatures out of the ranges occurring in their pristine habitats, even for a short period of time, reduce growth. From a climate change perspective, protocols to improve performance of captive animals under controlled conditions are needed to ensure the supply of protein in the near future, contributing to food security.

CONCLUSIONS

The general data of this work showed that the growth and the physiological responses of the tambaqui are adjusted according to photoperiod and the temperature. For this species the simultaneous increase of photoperiod and temperature causes hemoconcentration, higher levels of stress, and loss of food efficiency in contrast to marine, and estuarine species. Due the great metabolic costs in these conditions growth performance is not compensated for, and is not recommended as an adequate condition for rearing the species. Considering that tambaqui lives near its thermal limits, an association of increased photoperiod with low or high temperatures has a significant impact on the development of this species that grows better in the dark warmth (between 29 and 32°C).

AUTHOR CONTRIBUTIONS

RA designed the work, performed the experiment, the data collection, analysis, and wrote the manuscript, JS helped to perform the experiment, the collection of samples, and discussed the data, and AV designed and supervised this work, obtained the financial support, discussed the data, and revised the manuscript.

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Predicting Which Species Succeed in Climate-Forced Polar Seas

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Understanding the mechanisms which determine the capacity of any species to adapt to changing environmental conditions is one of the foremost requirements in accurately predicting which populations, species and clades are likely to survive ongoing, rapid climate change. The polar oceans are amongst the most rapidly changing environments on Earth with reduced regional sea ice duration and extent, and their fauna's expected sensitivity to warming and acidification. These changes potentially pose a significant threat to a number of polar fauna. There is, therefore, a critical need to assess the vulnerability of a wide range of species to determine the tipping points or weak links in marine assemblages. Knowledge of the effect of multiple stressors on polar marine fauna has advanced over the last 40 years, but there are still many data gaps. This study applies ecological risk assessment techniques to the increasing knowledge of polar species' physiological capacities to identify their exposure to climate change and their vulnerability to this exposure. This relatively rapid, semi-quantitative assessment provides a layer of vulnerability on top of climate envelope models, until such times as more extensive physiological data sets can be produced. The risk assessment identified more species that are likely to benefit from the near-future predicted change (the winners), especially predators and deposit feeders. Fewer species were scored at risk (the losers), although animals that feed on krill scored consistently as under the highest risk.

Keywords: climate change, ecological risk assessment, vulnerability, physiological niche, sea ice, food webs

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INTRODUCTION

Amongst the foremost scientific questions of the Anthropocene are which populations, species and clades will survive sustained, rapid climate change and which mechanisms underpin their sensitivity (Pennisi, 2005). Previous mass extinctions have led to massive faunal shifts whereby 5–29% of the original species dominate the remaining fauna, leading to a global "biotic homogenization" (McKinney and Lockwood, 1999). Likewise current impacts seem to be following a "few winners, many losers" pattern, with most of Earth's monitored species showing large scale declines (70% of global bird species; Collar et al., 1994), but with some taxa, such as ducks (Anatidae) and grasses (Poaceae), increasing and thus more likely to be over-represented in future patterns of biodiversity. The species that tend to dominate after such extinctions share features of high genetic and/or physiological diversity, broad geographic ranges, high dispersal, broad capacities and tolerances (eurytopic species), small body sizes, high fecundity, and, in the Anthropocene, a positive association with human societies (McKinney and Lockwood, 1999). Currently the most intense and rapid climate forcing has occurred in parts of Earth's high latitudes, many of whose fauna have few of those typical "winner" features.

The polar regions, particularly the Southern Ocean and Antarctica, have had comparatively little direct human impact on their biota. In the previous century there was a drastic over-exploitation of fish, seals and whales, which has led to some dramatic disruption of higher trophic levels (Miller, 1991). What we know of the fauna from the Southern Ocean continental shelf suggests they share many of the traits, identified by McKinney and Lockwood (1999), which make them more likely to be losers rather than winners. The rich biota there show high levels of endemism, ranging from 37% in hexacorals to 70% in gastropods (De Broyer et al., 2014) and therefore generally have restricted geographic ranges. Growth in cold water is slow and many ectotherms have long life spans and long generation times, which act to reduce the chances for adaptive change (Peck, 2011). Many Antarctic ectotherms have also evolved specific adaptations to cope with life in the Southern Ocean, such as antifreeze proteins (DeVries, 1971) and lack of hemoglobin (Ruud, 1954), which give them narrow tolerance ranges; they are classically stenotopic. Body size spectra vary considerably with clade (small in mollusks Hain and Arnaud, 1992, large in amphipods Chapelle and Peck, 1996) but fecundity is typically low (Pearse et al., 1991).

The physiological and biological capacity of all animals and plants has evolved to cope with their experienced environmental variability (e.g., Clarke and Crame, 1992). The Southern Ocean is one of the most constant surface environments in terms of annual temperature and salinity range but one of the most variable in terms of photoperiod, disturbance and phytoplankton abundance (so food availability for secondary production) (Clarke, 1988). This physical environment, although relatively constant for more than 4 million years, nevertheless has regular massive perturbations in the form of glaciation cycles (driven by variations in the Earth's orbit, with 41 and 101 kyr cyclicity). Glaciations have varied in magnitude and duration but in each the expansion and contraction of grounded ice sheets has changed the size and geography of continental shelves drastically (as grounded ice covers much of the continental shelves). Thus life in the Southern Ocean has experienced considerable past stresses, within interglacial periods (e.g., warming, freshening, sedimentation and iceberg disturbance) but especially in transitions to and from glaciation. The impact of modern and near future change has to be set against the backdrop of those historic "norms" of stress and resultant habitat shifts.

Modern change is mainly driven by increasing atmospheric CO_2 and other "greenhouse" gas emissions but also ozone depleting chemicals. Salinities, UV irradiation and wind patterns have already begun to alter in the Southern Ocean and sea temperature (IPCC, 2013) and *p*H are predicted to change considerably (Orr et al., 2005). Aragonite saturation may become one of the biggest stresses affecting polar seas, due to lower initial saturation levels and greater dissolution of atmospheric CO_2 into cold waters (Gutt et al., 2015). Secondary physical impacts to air temperature and the influx of deeper, warmer water masses have included extensive sea-ice changes, glacier retreat, ice shelf collapses and sea level rise (Cook et al., 2005, 2016). Investigating the effect of multiple stressors on life in the Southern Ocean has been identified as one of the 80 priority questions for future scientific research (Kennicutt et al., 2014). The effect of interaction of such variables on organisms have been little considered to date, but the impacts of some of these stressors have been studied in some detail—both in terms of manipulations and field observations. Most direct experimentation has involved temperature or *pH*. Stresses to organisms in polar regions (and elsewhere) from changing climate are not isolated from other stressors. Their impact occurs in combination with, and can be altered by, other stresses, such as harvesting (fishing), pollution, non-indigenous species (NIS) and habitat alteration. However, compared with elsewhere on Earth these are all minimal, although top predator harvesting has been high in the past, plastic pollution is increasing (Barnes et al., 2018) and the threat of NIS establishment growing.

The Southern Ocean has an important fauna, with massive stocks of krill (*Euphausia superba*), is home to 99% of southern polar species and is the only place on Earth left where all the established fauna are native. However, there are more reports of non-native species that could become established, such as decapod crustaceans (Aronson et al., 2015) and mussels (Lee and Chown, 2007), as climate changes. In the near future, it has been suggested that 86% of the Southern Ocean's area may be impacted by 2–3 overlapping stressors (Gutt et al., 2015). In contrast, there is little evidence of change or a trend in physical change in the ocean around East Antarctica (i.e., the majority of the Southern Ocean). There remains considerable uncertainty and divided opinions on the level of vulnerability of its fauna (Barnes and Peck, 2008). As elsewhere stressors are likely to impact organisms in different ways, for example all marine invertebrates are ectothermic, whilst all marine mammals and birds are endothermic. As such, they will experience different types of stress within the Southern Ocean, the magnitude of which will vary as the environment changes. Ectotherm physiology is more directly affected by the physical environment, such as temperature and ocean acidification (OA). The environment will have less of a direct effect on endotherms but more of a cascading effect through impacts on food webs. However, several polar endotherms give birth on sea ice, feed through sea ice, or utilize sea ice to haul out for periods of rest. The many organism types and species directly associated with sea ice are likely to be amongst those which will lose out most to sustained climate change.

Polar ecosystems are often considered simpler than those at lower latitude and certainly have less direct anthropogenic stressors. However, even in the Southern Ocean the complexity of ecosystems means that it is only possible to have a partial understanding of all the interactions between environment and species. This in turn limits our ability to determine the structure and stability of the food web and nutrient cycles. In these data-deficient situations managers need to use tools that allow vulnerability to be assessed. Risk Assessment is a formal process of identifying the hazards, or risks, identifying the extent of the exposure (exposure assessment), the sensitivity to that risk (dose-response assessment), and where possible, suggesting measures to manage or mitigate that risk (Karr and Chu, 1997). While this is a standard procedure to ensure human health in the work place, the risk assessment framework is increasingly being applied to ecological systems (Karr and Chu, 1997; Holsman et al., 2017)

TABLE 1 | Description of climate risk factors.

Ocean acidification	The reduction of pH of the ocean caused primarily by the uptake of atmospheric CO_2.
Sea ice	The reduction in the duration and extent of sea ice.
Temperature	Warming of the ocean.
Ice scour	The increase in the frequency of iceberg impacts on the sea floor.
Ice shelf collapse	The break-up of sheets of floating ice that are permanently attached to a land mass
Sediment	The increase in sedimentation of glacial flour (ground rock)
Glacial retreat	The geographic retreat of glacier fronts
Snowfall	Precipitation as snow that covers the land

TABLE 2 | Scoring of expected species response to change based on the literature review.

Score	Prediction
+2	2 positive responses to change
+1	1 positive response to change
0	No response
−1	1 negative response to change
−2	2 negative responses to change
N/A	Not applicable
	Blank cells indicate the effect is not known

to assess which risks will cause maximum disruption to the ecosystem or have the greatest socio-economic impact. The level of complexity that can be included in ecological risk assessments will vary depending on data availability. In the best described environments detailed approaches, such as the NatureServe Climate Change Vulnerability Index (Young et al., 2015), can be employed. In data-deficient ecosystems, expert opinion can provide qualitative assessments of relative risk, allowing rapid, but crude, assessments to be made (Holsman et al., 2017). These may be sufficient to determine priorities for further monitoring or data collection efforts.

This study aims to combine advances in ecological risk assessment with improved data availability for exposure and vulnerability to climate change of Antarctic marine animals. Here we risk assess which Southern Ocean species are likely to be most and least impacted, using model forecast projections of climate change and what is currently known of organismal responses to physical change to date. In this way we identify the exposure to climate change risk and combine this with vulnerability to that exposure to build a risk assessment matrix that will help define priorities for future research and management actions.

MATERIALS AND METHODS

The risk assessment was conducted in two stages. First, there was a comprehensive meta-analysis of the literature from which the environmental factors that determine risk exposure of Antarctic marine fauna were extracted. We reviewed how these factors are projected to alter through the effects of climate change on the Antarctic near shore marine environment. This information was then used to assess the positive and negative effects of each of these stressors to individual species.

Literature Review

A comprehensive search of the literature was conducted to identify the current state of knowledge of the risks to Antarctic marine fauna and how these risks are predicted to change. These factors included environmental factors that are already in flux and/or are projected to change with climate (**Table 1**). The literature review also took into account some of the drivers underlying these factors, such as the link between the ozone hole and strengthening winds.

Risk Assessment

From the literature meta-analysis, it was determined that advances in knowledge of the vulnerability to climate change exposure, a semi-quantitative rank-based exposure-sensitivity assessment could be applied to Antarctic marine fauna. We applied the level 2 risk assessment of Holsman et al. (2017), which aims to identify the highest risk components of the ecosystem that can then be prioritized for more detailed analyses.

Literature that provided experimental evidence of responses to risk factors was used to score the risk. A positive (+1), negative (−1) or no expected response (0) was scored for each risk factor for which there was available literature (**Table 2**). So, a score of +2 indicates that there was literature evidence for two positive responses to the predicted change in that factor. These scores were summed for each species to predict the total risk for each species.

Due to their long generation times, many polar marine ectotherms have low adaptive potential (Peck, 2011), which is therefore excluded from this analysis. Due to fundamental differences in vulnerability we consider ectotherms and endotherms separately. For the marine endotherms, sufficient information is known about the key components of their diet. It was therefore possible to estimate not only the direct risk of exposure to climate change, but the indirect effects through the food web as well. These direct and indirect scores were summed to create the final assessment.

RESULTS

Literature Review: Defining Risk Exposure and Vulnerability to Climate Change

Temperature

To date marine temperature rises have only been associated with the shallowest 20 meters of the Bellingshausen and Scotia seas (Meredith and King, 2005). In general, therefore, species most likely to be at risk are those with geographic ranges restricted to shallow shelf depths in this region and with narrow temperature envelopes. Many Antarctic marine ectotherms are considered "stenothermal," with many recorded to have poor capacity to cope with even modest increases in temperature (Pörtner, 2002). Small rises in temperature can drive increased growth of some species, but performance gains are no longer clear with even as little as a 2°C rise above ambient sea temperatures (Ashton et al., 2017).

Temperature rise has been widely considered to be one of the greatest risks to Antarctic marine ectotherms, as they have been shown to have long term lethal temperature limits and limits for activity only 0–5°C above currently experienced maximum environmental temperature (Peck et al., 2014). Whilst global air temperature increases have dramatically slowed or even halted in recent years, future warming of the ocean (Smith, 2016) and the atmosphere (IPCC, 2013) is predicted. Climate envelope models, based on species distributions and their currently experienced annual temperature ranges, were combined with projected warming to predict how species ranges will shift (Griffiths et al., 2017). However, while climate envelope models give a measure of exposure, they need to be overlain by a layer of vulnerability based on known physiological tolerance. While many of the species living in the shallow Antarctic are eurybathic, with distributions that stretch well below these surface waters, their population densities are often at their highest in the shallowest 20 m, e.g., the limpet, *Nacella concinna*, the urchin, *Sterechinus neumayeri* and the sea cucumber, *Heterocucumis steineni*. In unusually calm conditions the temperature of the surface 5 m of the ocean have been recorded to reach 4°C (Morley pers obs.), a temperature that is above the thermal limit for several critical physiological functions of *N. concinna* (Peck et al., 2004; Morley et al., 2012). So, whilst individuals living in deeper water are unlikely to be affected by surface warming, the vast majority of the populations of these shallow water species will. These are all hugely abundant species in the shallow Antarctic ecosystem, so even if their populations can persist in the face of surface warming, any reduction in numbers in the shallows is likely to have major impacts through these food webs. However, marine warming has other indirect effects, such as reduction of sea ice, melting of ice shelves and lubricating the underside of glaciers, as well as reducing the duration of "winter" (Barnes, 2017a). Reduction of sea ice and the period of time when the sea is at freezing temperatures could both lead to increased light penetration into surface waters and therefore increased primary productivity (Barnes, 2015) amongst other effects.

pH

As in other oceans, gases dissolve into and out from the Southern Ocean in equilibrium with partial pressures in the atmosphere above them. Increased atmospheric CO_2 concentrations have driven small and large net absorptions in the Southern and Arctic Oceans respectively (Sabine et al., 2004). These lower *pH*, causing OA, are predicted to have one of the major anthropogenic impacts on marine species, particularly those that rely on synthesizing calcified exoskeletons (Bray et al., 2014). As liquids can hold more gas with lowered temperature, it was thought that polar ocean fauna would be more impacted by OA than in other oceans (Guinotte and Fabry, 2008). However, recent studies have shown that the *pH* of the seas off the Western Antarctic Peninsula (WAP) have not (yet) acidified rapidly, and have a high spatial and temporal variation from *pH* 7.6–8.3 (Bjork et al., 2014; Collard et al., 2015). With large seasonal variation in the pattern of deep CO_2-rich water upwelling to the surface of the Southern Ocean (Takahashi et al., 2009), marine animals may therefore have evolved the flexibility to cope with this high level of variability in their environment (Suckling et al., 2015; Morley et al., 2016).

There have been concerns that reduced ability to synthesize carbonate (particularly aragonitic) shells might leave some species vulnerable to predators. There are few durophagous (crushing) predators in the Southern Ocean, and only in a few locations are they abundant, but despite some high impact opinion-based science reports and popular headlines, there is little or no evidence to support any increased predation response to date (Griffiths et al., 2013). The strongest evidence for OA impacts is on thinly shelled, pelagic pteropod mollusks (Bednaršek et al., 2012). Although the carbonate compensation depth (CCD) is expected to become shallower, the high eurybathy in Antarctic marine species (compared with lower latitude species) found to date (Brey et al., 1996) shows that populations occur below this horizon already. The Antarctic fauna is still poorly described and new scientific samples from deep shelf and slope depths are still increasing the known bathymetric (and geographic) ranges of species (e.g., bryozoans in Barnes and Kuklinski, 2010). Thus, whilst it is possible that the Southern Ocean may be disproportionately impacted it may also be that much, or even most, of the fauna is fairly robust to this. Perhaps the most important question is how will primary production—phytoplankton (necessarily near surface)—be affected by lowered *pH*?

Salinity

The Southern Ocean is a high salinity region and sea surface change-trends are hard to interpret because they are so closely connected to changes in the timing and geography of sea ice formation and melt. Warming can directly drive salinity change through melt waters but also indirectly affect freshening through sea ice increases or reductions. Salinity has changed in the Bellingshausen Sea due to a dramatic reduction in winter sea ice formation, reducing the extent of summer melting. This has led to an increase in summer salinity of surface waters (Meredith and King, 2005). During the second half of the twentieth century the increased precipitation, reduced sea ice production and increased melting of the West Antarctic ice sheet has, conversely, led to a freshening of the surface waters of the Ross Sea (Jacobs et al., 2002). Unlike in the Arctic, Southern Ocean salinity changes have been small and there is little evidence of this being an important near-future stressor to Southern Ocean fauna. The exception to this is near coastal systems (fjords, shores and surface waters) around West Antarctica, as rapidly retreating glaciers pass their grounding lines and melt water flows from under thinning ice shelves (such as Thwaites Glacier).

Ozone Losses Leading to Increased UV and Strengthening Wind

Use of industrial chlorofluorocarbons during the twentieth century led to a thinning of the ozone layer and the development of a late winter and spring "ozone hole" over the Antarctic (Solomon, 1990). This has had several effects on marine animals living in the shallows in the Antarctic Peninsula region. The reduced protection by ozone has led to an increase in exposure to UV-radiation (Karentz and Bosch, 2001). Although UV only penetrates through the first few tens of meters of seawater, it can have damaging effects on marine organisms from phytoplankton through to benthic invertebrates and fish (Karentz and Bosch, 2001). The impact on the atmosphere has also led to strengthening winds that have caused an increase in sea ice in regions of East Antarctica but large losses of sea ice and ice shelves on the WAP (Thompson et al., 2011; Holland and Kwok, 2012). Barnes et al. (2011) hypothesized that the main cause of recent rapid increases in growth by Ross Sea shelf benthos (bryozoans) was increased winds maintaining ice-free areas (polynyas) within the sea ice. Maintaining open water areas in turn increased light and enhanced longer blooms of their phytoplankton food (Arrigo et al., 2008).

Food Availability

One of the few demonstrable responses to physical change to date has been distributional, timing, duration and compositional changes in phytoplankton productivity (Arrigo et al., 2008). The nature of phytoplankton change seems to be complex and climate-mediated trends remain unclear. If composition does alter from diatom domination to more smaller and naked cells (e.g., ciliates and flagellates), this could enhance growth in primary consumers (such as suspension and deposit feeders). New coastal (highly productive) phytoplankton blooms now occur where glaciers have retreated and ice shelves have collapsed (Peck et al., 2010a). Longer abundances of (phytoplankton) food have also been strongly correlated with sea ice losses and driven widespread increased growth performance of benthos (Barnes et al., 2016). These new and longer blooms have resulted in significant increases of benthic carbon accumulation on the West Antarctic seabed, leading to an important negative feedback on climate change (Barnes, 2015). Whilst marine warming and sea ice losses may sustain increases in phytoplankton availability, UV increases, OA and freshening are likely to impact near surface algal species. Altered sea ice patterns are likely to strongly influence assemblages directly linked to (the considerable) seasonal sea-ice algae build-ups. Thus changing food availability is likely to generate quite a number of winners and losers depending on geography—primary consumer winners on shelves underlying ice shelf collapses and major sea ice reductions but losers associated with sea ice algae and associated productivity.

Warming may also act to reduce the duration of the "winter fast" of ectotherms but this is not necessarily positive for all species. The cold winter period may be essential for some Antarctic marine ectotherms, allowing them to use the period of low maintenance metabolic costs to, for example, channel the energy gained through the summer into growth. The brachiopod *Liothyrella uva* is thought to use all of its physiological capacity to process food during the summer, such that growth can only occur during winter, decoupled from feeding (Peck et al., 1997). In strong contrast other similar (but colonial) suspension feeding animals, such as the bryozoan *Cellarinella watersi*, undertake growth throughout the summer but cease growth as soon as food is less available (Barnes, 1995). If changes in sea ice duration affect the characteristics of the phytoplankton bloom (Venables et al., 2013), or shorter winters reduce the period of minimum maintenance metabolism, then animals may not gain enough energy during the limited feeding period to survive through the following winter.

Glacier Retreat

Widespread glacial retreat is perhaps the most directly observed and publicly conscious impact of climate change. The proportion of West Antarctica in retreat has drastically increased, as has the rate of glacial retreat (Cook et al., 2005). The impact of some of these, particularly the Pine Island and Thwaites glaciers, have far-reaching consequences on shelf water masses, sea level rise and even West Antarctic Ice sheet stability (Vaughan et al., 2011). The impacts of such are less well-documented in the Southern Ocean than in the Arctic, although Sahade et al. (2015) detailed strong nearshore ecosystem responses to glacial retreat in Maxwell Bay, King George Island. There they found the resultant sedimentation was the key factor driving assemblage change with losers being suspension feeders, such as the ascidian *Molgula pedunculata*. In contrast infaunal deposit feeders which were able to persevere with high sediment loading e.g., *Laternula elliptica* had fewer space and food competitors (e.g., Philipp et al., 2011; Sahade et al., 2015).

Sea Ice Losses and Habitat Availability

Changes in the seasonal extent of sea ice influence habitat availability, albedo, light availability, primary productivity, abundance and species composition. The duration of the fast ice component (winter sea surface freeze) has an important role in minimizing disturbance through "locking in" icebergs, preventing movement and thereby reducing seabed scour. Remote-sensed imaging suggests that regional sea ice (mainly fast ice) losses are one of the most measurable impacts of climate change at the poles to date. At Ryder Bay, WAP, this has approached 5 days less of fast ice per year for the last 2 decades, strongly inversely correlated with the number of ice scour events on the seabed (Barnes and Souster, 2011). Although sea ice losses lead to higher benthic mortality in the shallows, this is more than compensated for in terms of biomass or zoobenthic carbon stocks by increased growth in deeper water due to longer phytoplankton blooms (Barnes, 2017a). As with most, if not all stressors, changes in seabed scouring levels affect marine species differently; although 99% of individuals may be killed in a scour event this also provides carrion and opens up new habitat space. Losers from intense scouring are slow growing and slow maturing species like the brachiopod *Liothyrella uva*, corals and sponges, whereas pioneers, such as polychaete worms, bryozoans and scavengers, such as the nemertean worm *Parbolasia corrugatus* and echinoderms *Odontaster validus* and *Sterechinus neumayeri* benefit. The biggest winners from the combination of sea ice losses and slightly raised temperatures could be macro-algae, through extending their richness, productivity and range further south.

Changes in sea ice duration and extent correlate with population processes of many Southern Ocean species and, in particular, the biomass and distribution of Antarctic krill

(*Euphausia superba*), a key species linking primary production to upper-trophic levels (Atkinson et al., 2004; Trathan et al., 2007). Sea ice provides an important habitat for Antarctic krill, the young of which feed on algae growing on the underside of the sea ice. As such the annual change in sea ice duration and extent is a key influence on krill population dynamics, particularly in the WAP region, which is an important spawning ground for this species (Quentin and Ross, 2001; Murphy et al., 2007). Indeed, the loss of sea ice on the WAP led to a 70% reduction in krill around South Georgia between 1975 and 2003 (Atkinson et al., 2004). It is, however, possible that rather than (krill) reduction, much of the krill biomass is following the changing position of the marginal sea ice zone (whereas the positioning of scientific measurements is more restricted) (Brierley et al., 2002).

Recent studies from a number of sites located across the WAP and Scotia Sea region have provided strong evidence of shifts in the distribution of both Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarctica*) penguin populations (Croxall et al., 2002; Dunn et al., 2016). However, the role played by sea ice dynamics in influencing the population trends of upper-trophic predators (both pagophilic and pagophobic) is complex. Recent research has suggested sea ice dynamics play a key role in influencing juvenile over-winter survival in pygoscelid penguins not simply through a direct effect on habitat availability, but rather by influencing the availability of Antarctic krill (Hinke et al., 2007; Lynch et al., 2012). By acting as a mediating link between predators and prey, sea ice can exert a key influence on predator-prey relationships; episodic recruitment levels of krill reflect the temporal variation not only in duration and extent, but also in advance and retreat of sea ice (Quentin and Ross, 2003; Trathan et al., 2007). The relationship between sea-ice conditions and trophic-mediated variability has been reported in long-term studies of population size and breeding success in Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. These studies have revealed an inverse relationship between breeding success and sea surface temperatures (Forcada et al., 2005, 2008). The increase in positive temperature anomalies associated with increasing ENSO events has increased environmental variability and led to less predictable and limited availability of krill. This has increased the fitness costs of breeding fur seals and led to the loss of life history buffering. However, the role played by sea ice dynamics in influencing the population trends of upper-trophic predators is complex. There is evidence that both greater and lesser winter sea ice extent improved the breeding success of snow petrels (*Pagodroma nivea*), although adult survival has been strongly correlated with years of extensive sea ice (Croxall et al., 2002).

Ecological Risk Assessment

Marine Ectotherms

Of the 21 species assessed, 15 were predicted to be winners in the face of climate change and 4 scored a neutral summed response. Summed negative responses were only predicted for two species. The species predicted to be at most risk were the amphipod *Paracerodocus miersi* and the brachiopod *Liothyrella uva* (**Table 3**). The species expected to be at least risk from the changes in the Southern Ocean were the generalist predator/scavengers *Ophionotus victoriae* and the starfish, *Odontaster validus*.

However, most species were predicted to have a negative response to at least one environmental factor. Only *Odontaster validus*, *Parborlasia corrugatus* and gelatinous zooplankton were predicted to have positive responses for every risk factor that could be scored.

Marine Ectotherm Trophic Guilds

All marine ectotherm trophic guilds were predicted to benefit, or not be affected, in the case of grazers, by the changes in the environment of the Southern Ocean (**Table 4**). Deposit feeders and scavengers were the functional groups expected to benefit most from the changes.

Marine Endotherms

Three marine endotherms were scored with positive summed responses and three with negative overall responses to climate change (**Table 5**). However, only *Eubalaena australis* and *Aptenodytes patagonicus* had summed positive or neutral responses for both direct and indirect risk factors, and only *E. australis* had no negative scores for any of the environmental factors. Most of the negative risk was realized through the food web as indirect risk factors.

DISCUSSION

Ectotherms

The ectotherms considered most at risk were species, such as the *Liothyrella uva,* the clam, *Laternula elliptica* and the amphipod, *Paracerodocus miersi* (**Table 3**). All three species are amongst the most temperature-sensitive, with both long term limits and burrowing limits of *L. elliptica* having an upper temperature of between 2 and 3°C (Peck et al., 2004) and both *L. uva* and *P. merseii* were unable to acclimate to 3°C. Contrasting with this thermal sensitivity, *L. elliptica* has been found living in the intertidal zone at James Ross Island, where sediment temperatures were as high as 7°C (Waller et al., 2017). However, intertidal temperatures are only this high for a few hours, during low water in summer. *L. elliptica* exhibits acute capacity for physiological resistance, producing heat shock proteins at 6–8°C and are able to survive, in winter, for more than 36 h without breathing (Morley et al., 2007). The ability to survive short-term events, such as heat waves in summer and short-term intertidal exposure, is very different to vulnerability in the face of projected climate change. While limited warming has been observed in the shallow Western Antarctic Peninsula, all three of these animals have exoskeletons, and although studies to date have shown they are robust to reductions in seawater pH (Cross et al., 2015; Suckling et al., 2015; Morley et al., 2016), continued acidification is, however, predicted to increase the cost of making shells. Suspension feeders, such as *L. elliptica* and *L. uva* are expected to benefit from the break-up of ice shelves, increasing the area where spring phytoplankton blooms can occur (Peck et al., 2010a), increasing available habitats. The negative effect of reduced sea ice and ice shelf collapse is that iceberg scour will increase (Barnes, 2017b), increasing mortality in benthic communities in

TABLE 3 | Risk assessment matrix for Polar marine invertebrate taxa.

	Stress	OA	Sea ice	Temp	Ice scour	Ice shelf collapse	Sediment	Glacial retreat
Expected direction		+	−	+	+	+	+	+
Species	**Risk**							
Ophionotus victoriae (Brittlestar)	6		1	−1	1	2	1	2
Odontaster validus (Starfish)	5		1	1	1	1		1
Parborlasia corrugatus (Worm)	5		1		2	1		1
Molgula (Sea squirt)	5		1	1	1	1	−1	2
Gelatinous zooplankton	4	1	1		N/A	1		1
Aequiyoldia eightsi (Clam)	4	−1	1	1	−1	1	1	2
Sponges	3		1	1	−1	1	−1	2
Spirorbid Polychaetes (Fan worms)	3	−1	1	1	1	1	−1	1
Sterechinus neumayeri (Urchin)	3		0	1	1	1	−1	1
Nacella concinna (Limpet)	3		1	−1	1	1		1
Fenestrulina rugula (Bryozoan)	2	−1	1	1	1	1	−2	1
Glyptonotus antarctica (Sea slater)	2			−1	1	1		1
Cnemidocarpa verrucosa (Sea squirt)	2				1	1	−1	1
Paralomid decapods (Crabs/shrimps)	2	−1		1	0	1		1
Whip corals	2	−1	1	1	−1	1		1
Cellarinella nutti (Bryozoan)	0	−1	1	1	−1		−1	1
Pycnogonida (Sea spiders)	0			−1				1
Pteropods (Sea angels)	0	−1						1
Beania erecta (Bryozoan)	0		0	1	−2	1	−1	1
Liothyrella uva (Lantern shell)	−1	−1	1	−1	−1	1	−1	1
Laternula elliptica (Clam)	−1	−1	1	−1	−1		−1	2
Euphasia superba (Krill)	−2	−1	−1			1		
Paracerodocus miersi (Amphipod)	−2	−1		−1	−1			1

Colors from green to red are used to indicate increasing risk.

the upper ∼100 m. Filter feeders are also, in general, expected to be negatively impacted by increased sedimentation from the increased melting of glaciers (Sahade et al., 2015). However, because of the impacts of sedimentation, ice scour and ocean acidification on benthic suspension and grazing species, these functional groups were predicted to be the ones to benefit least from the change in environmental factors (**Table 4**).

In general sediment dwellers, such as deposit feeders, e.g., *Aequiyoldia eightsii*, are likely to benefit (**Tables 3**, **4**) because large areas of suitable soft sediment habitat are opening up on open shelf (from ice shelf break up) and along fjords (from glacial retreat). The ectotherm taxa that are predicted to benefit most from climate change, using our risk matrix, were suspension feeders, such as gelatinous zooplankton (salps and jellyfish), sponges and benthic predators and scavengers, such as *Odontaster validus* and *Sterechinus neumayeri*. The suspension feeders will benefit through the increased phytoplankton blooms, whereas the benthic predators will benefit from the mortality caused by increased ice berg scours. They are opportunistic predators who quickly move into recent ice berg scours to feed on dead and decaying organisms (Dunlop et al., 2014) and possibly surface microbial communities that will take advantage of the turned over nutrients. Smaller non-diatom phytoplankton may benefit as there is some evidence that they are increasing along parts of the WAP, coinciding with diatom decreases (Sailley et al., 2013). Other potential beneficiaries would include non-indigenous species invaders, with increased transport opportunities (more shipping and plastic) and less severe conditions enhancing establishment success—this would likely lead to strong negative impacts on surrounding native species.

Marine Ectotherm Trophic Guilds

The impacts of climate change are expected to have a greater effect on calcareous suspension feeders because of the impact of ocean acidification and the increased ice berg scour due to the loss of sea ice and ice shelves (**Table 4**). This negative impact is predicted to outweigh the positive effects of increased primary productivity in the shallows, but the reverse may be true in deeper water (which covers most of the shelf). The greater disturbance has already had a profound effect on shallow water Antarctic benthos (Barnes, 2017b). The community structure has been altered toward favoring pioneers, particularly a single bryozoan species, *Fenestrula rugula* (Barnes et al., 2014). The favoring of pioneer species was also found when the temperature of the colonizing substratum was raised by 1°C (Ashton et al., 2017), with the same pioneering bryozoan increasing its growth rate to dominate the available space. Within each of these guilds there

TABLE 4 | Matrix summarizing the risk for different marine ectotherm functional groups.

	Stress	OA	Sea ice	Temp	Ice scour	Ice shelf collapse	Sediment	Snowfall	Glacial retreat
Expected direction		+	–	+	+	+	+	+	+
Species	**Risk**								
Deposit feeders	5	0	1	1	–1	1	1		2
Scavengers	4		1	1	1	1			0
Predators	3		1		1	1			
Non-Calcareous Benthic Suspension Feeders	2	0	1	1	–1	1	–1		1
Calcareous Benthic Suspension Feeders	1	–1	1	1	–1	1	–1		1
Grazers	0	–1	1	1	–1	1	–1		0

Colors from green to yellow are used to indicate increasing risk.

will clearly be winners and losers, with selection for species with rapid growth rates, early reproduction and rapid colonization. Longer phytoplankton blooms, with more smaller cells, are likely to benefit suspension and deposit feeders in deeper water as they will get longer meal times and more growth (Barnes, 2017a).

Deposit feeders are expected to benefit as they will receive more organic material from longer phytoplankton blooms, more habitat and the increased melt water from glaciers, which increases the input of glacial flour into bays and subsequent benthic sedimentation (Sahade et al., 2015). For example, in Potter Cove, King George/25 de Mayo Island in the South Shetland Islands, there has been a shift away from a filter feeder-dominated community to a more mixed community. This shift is thought to be due to the increased sedimentation clogging filter mechanisms benefitting species with alternate feeding modes (because of reduced competition for space and resources).

The increased mortality from increases in ice-berg scour is one of the key attributes that suggests scavengers and generalist predators are one of the trophic guilds that are predicted to benefit, at least in the medium term, from climate change. If, however, one of the key prey species (such as the limpet *Nacella concinna*) disappears from the shallows, then the success of these predators in the shallows will depend of the balance of prey availability and if a suitable prey species takes over. We do not have enough information to understand the indirect effects of climate change on marine ectotherms.

Endotherms

The most vulnerable endotherm to the direct effects of climate change in this study was the emperor penguin, *A. forsteri* (**Table 5**). It is vulnerable due to loss of its breeding habitat on sea ice and ice shelves. *A. forsteri* do not feed on krill and it is possible that the abundance of their fish prey will increase in open water, but this is currently unknown. All species that breed on land, or on ice, are expected to be affected by increased snowfall, linked to warming atmospheric temperatures (Thomas et al., 2017). Of course this will be countered by the increased number of melt days during summer (Barrand et al., 2013), however, it is the date at which the snow accumulation melts out on historical sites for penguin colonies that determines the time of the start of the breeding season (Trivelpiece and Fraser, 1966).

The endotherm that is predicted to gain most from the direct effects of climate change is the king penguin, *Aptenodytes patagonicus*. It is not a krill but a fish feeder and its main food, myctophids, are likely to benefit from reduced sea ice and collapses in ice shelves, which will lead to increased areas for primary productivity (Sailley et al., 2013). Increased knowledge of the strength of food web interactions will improve the layer of physiological vulnerability by adding the complexity of these interactions. *A. patagonicus* also nests on glacial plains in front of glaciers. As these glaciers recede, the area available for the breeding colony will increase, reducing competition for space within the breeding colony and ultimately improving breeding success.

The indirect effects of climate change, those that act through the food chain, have already been assessed through the marine ectotherms, where ice-associated food, such as *E. superba*, is expected to suffer. When these indirect effects are considered, the krill feeding sea ice-associated penguins, *Pygoscelis adeliae* and *P. antarctica* are assessed to be most at risk. This risk is, however, mitigated by the potential that the distribution of these penguins and their prey are migrating south, and their populations are in fact stable.

For cetaceans, the krill feeders are expected to do badly, e.g., the humpback whale, *Megaptera novaeangliae*, due to the reduction in krill populations. However, if, as for the penguins discussed above, krill populations have not reduced but simply tracked the southern trajectory of the ice, then this risk may be substantially reduced. For non-*E. superba* feeding cetaceans, such as the southern right whales *Eubalanus australis*, the prospects are favorable, as their main food—copepods—may be one of the species that benefits from the increase in open water and increased primary productivity. This may be one of the species that continues its current rate of recovery from the historical impacts of human exploitation (Jackson et al., 2016).

TABLE 5 | Risk assessment matrix for marine endotherms.

			Stress	**OA**	**Sea ice**	**Temp**	**Ice shelf collapse**	**Snowfall**	**Glacial retreat**
			Expected direction	+	−	+	+	+	+
Species	**Total risk**		**Risk**						
Eubalaena australis (Southern right whale)	4	Direct	1			1			
		Indirect	3		1	1	1		
Aptenodytes patagonicus (King penguin)	3	Direct	3		1	1	1	−1	1
		Indirect	0						
Megaptera novaeangliae (Humpback whale)	1	Direct	4		1	1	1		1
		Indirect	−3	−1	−1	−1			
Arctocephalus gazelle (Fur seal)	0	Direct	1			1	1	−1	
		Indirect	−1	−1	−1	−1			
Orcinus orca (Pack ice killer whale)	0	Direct	2		−1	1	1		1
		Indirect	−2	−1	−1	−1			1
Aptenodytes forsteri (Emperor penguin)	−2	Direct	−2		−1	1	−1	−1	
		Indirect	0						
Pygoscelis adeliae (Adèlie penguin)	−4	Direct	−1		−1	1		−1	
		Indirect	−3	−1	−1	−1			
Pygoscelis Antarctica (Chinstrap penguin)	−4	Direct	−1		−1	1		−1	
		Indirect	−3	−1	−1	−1			

Both direct and indirect (through the food web) effects are reported and summed. Colors from green to red are used to indicate increasing risk.

Species Range Shifts and Invasions

Most Antarctic marine ectotherms have nowhere colder to migrate to Peck (2005). There may be some additional open water habitats created when ice shelves collapse, and the break-up of the Ross ice shelf (if it happens) would create the furthest south open water, but the geographic migration potential is extremely low. For example, there is evidence that most benthic ectotherms on South Georgia's outermost shelf have made little progress reinvading the inner shelf after the Last Glacial Maximum more than 20 kya (Barnes et al., 2016). An analysis of species range limits within the Southern Ocean suggested that this location, South Georgia, was amongst the most likely places to detect climate-forced range shifts (Barnes et al., 2009). A recent study based on climate envelope models predicted a 79% reduction in suitable temperature habitat under predicted climate change (Griffiths et al., 2017). When a layer of physiological tolerance is overlain on this projected climate envelope, this potential reduction is expected to be more severe. However, there is an argument that East Antarctica is one of the least changing environments and, in combination with eurybathy, species on the majority of the Antarctic shelf have the least need to migrate (Barnes and Peck, 2008).

The Southern Ocean is bordered by the major southern hemisphere continents South America, Africa and the Australasia. The Antarctic circumpolar current and the sharp temperature gradient across the polar front currently act as a rarely permeable barrier to a range of cold temperate fauna that are living at the northern edge of the Southern Ocean (Clarke et al., 2005). These will have increased potential to migrate south and colonize the Southern Ocean as it continues to warm. There are currently no marine invasive species in the Southern Ocean, but species, such as the Patagonian gastropods *Nacella magellanica* and Siphonaria spp. will have increased chances to make it across the Drake Passage and particularly to the northern Antarctic Peninsula and the northern islands. Species that can raft across the polar front by hitching a ride on floating seaweed, megafauna, plastic or ships are likely to be the first invasives (Lewis et al., 2006; González-Wevar et al., 2018).

Human Impacts

Human society is geographically distant, so anthropogenic associations are limited to a few introduced terrestrial species and the impacts of harvesting. The current impacts of human activity are, however, global and are encroaching into Antarctica (Gutt et al., 2015). The number of tourist and scientific vessels is ever increasing, as is the level of plastic in the ocean (Barnes et al., 2018). These increase the number of available vectors for invasive species to reach the Antarctic (Lee and Chown, 2007). Currently, all fisheries within polar waters around Antarctica—including the harvesting of Antarctic krill (*Euphausia superba*)—take place under the management of the Commission for the Conservation of Antarctic Marine Living resources (CCAMLR). Central to the management policies of CCAMLR is the ecosystem approach it employs to determine the setting of catch limits. This entails utilizing scientific data collected from a range of marine higher predators including seabirds, penguins, seals and whale species to ensure that management of its various fisheries takes into account the requirements of such krill-dependent predators. Nevertheless, as noted by Trathan et al. (2015), the advent of more efficient krill extraction technology, together with the opening up of new consumer markets for what is currently one of the last remaining large exploitable sources of marine protein, would all indicate a likely future expansion of this fishery. Unless carefully controlled, impacts on predator species including penguins and seals could be significant (Warwick-Evans et al., 2018). For example, limited availability of Antarctic krill around South Georgia, in this case driven by increasing environmental variability, is already negatively impacting breeding Antarctic fur seals through loss of life history buffering (Forcada et al., 2008). Further reductions in krill availability caused by increased catch limits for fisheries would be likely to compound this process, adding to the fitness costs of fur seals and in particular breeding females.

Incorporating Greater Complexity Into Ecological Risk Assessment

From the available literature the responses of Antarctic marine fauna allowed a semi-quantitative risk assessment of the impact of climate change. These assessments will clearly be improved as more data are published. Our risk assessment only scored a positive or negative response to each factor. The assumption that each factor should be equally weighted is unlikely to be realistic and, as has already been discussed, the effect of some factors, such as temperature, are thought to be more important to Antarctic marine ectotherms than other factors, such as ocean acidification.

It is also important to integrate knowledge of interactions through the food web, increasing the accuracy with which marine ectotherms can be risk assessed. The inclusion of indirect factors into the risk assessment for endotherms is the first stage in building more comprehensive risk assessments. For example, temperature and other environmental factors are known to influence the nutritional quality of prey as well as the nutritional requirements of predators. Incorporating nutritional ecology into assessments of climate change effects (Rosenblatt and Schmitz, 2016; Machovsky-Capuska et al., 2018) is just one of the improvements that will become possible as data availability increases. Our knowledge of the importance of factors that are likely to mitigate or even feedback against climate change, can be incorporated in more complex assessments.

Mitigating Factors

The major mitigation against climate change is carbon sequestration. Most carbon that is genuinely sequestered (i.e., buried and ultimately converted into rock) happens at the seabed. Although many low-latitude habitats, such as forests, kelp forests, seagrass beds and mangrove swamps (amongst others) are efficient at carbon capture and storage, they may provide poor negative feedbacks (on climate). This is because they are all decreasing as sinks (because of area loss) and not much of the carbon is buried. Benthos on polar and subpolar shelves in contrast are minor sinks in terms of carbon capture and storage values, but substantial in terms of sequestration and as a negative feedback mechanism (Barnes et al., 2018). This is because they store carbon at the seabed interface (i.e., site of burial) and are increasing their growth and carbon storage as a result of reductions in sea-ice, leading to longer phytoplankton blooms (Barnes, 2015); increasing habitat due to both glacial retreat (Cook et al., 2005) and ice shelf collapse (Peck et al., 2010a); as well as giant iceberg activity (Duprat et al., 2016; Barnes et al., 2018).

Along with many Antarctic marine ectotherms, Antarctic demosponges were thought to live life in the slow lane (Dayton et al., 1974). However, recently sponges have been found to respond rapidly to the opening up of new areas of the ocean (Fillinger et al., 2013) that now receive enough light for primary productivity to occur in summer, after events, such as ice shelf collapse (Peck et al., 2010a). Whilst the greater-than-expected plasticity of sponges may be linked to their symbiotic communities (Morley et al., 2016), other taxa, such as ascidians and bryozoans have also been found to grow and colonize rapidly under these altered conditions (Barnes et al., 2011).

Whilst many studies have investigated the effects of climate stressors on either adults or during fertilization and development, few studies have utilized long term incubations to investigate the effect of acclimation in adults, or during development. Recent experiments using Antarctic marine ectotherms have found that acclimation capacity is poor, but if adults are able to adjust their physiology, it can take 5–9 months for acclimation to occur (Peck et al., 2010b, 2014). After these long-term incubations, some Antarctic ectotherms exhibit unexpectedly high acclimation capacities (Morley et al., in press). Also, one of the few studies to incubate adults long term (18 months), through the majority of gonad development, found that after 8 months, adult *Sterechinus neumayeri* were fully acclimated to a combination of OA and elevated temperature treatments (Suckling et al., 2015). This study also found that the hatching and larval survival of adults spawned after 17 months of exposure to altered conditions was not significantly affected by these treatment combinations (Suckling et al., 2015).

The impact of altered conditions during adult and embryo development can lead to cross-generation changes in physiological plasticity (Donelson et al., 2011; Salinas et al., 2013). These changes can be fixed in future generations, so-called epigenetic effects, even if environmental stressors are removed (Klironomos et al., 2013). Also, there is the possibility for selection to occur rapidly, with larvae with more tolerant phenotypes surviving through to the next generation, all of which can lead to rapid evolution, even in long-lived species (Thompson, 1998). The projected warming combined with the stenotypic nature of the fauna suggests that population genetic studies within the Southern Ocean may yield the best evidence of selection for more tolerant phenotypes. Due to the extended time to reach maturity for some Antarctic marine ectotherms (Peck, 2011) we are not aware of any multi-generational studies that have been conducted in the Antarctic. If such rapid evolutionary change can occur in the Antarctic, then it has the potential to mitigate many of the impacts predicted due to climate change (Zizzari and Ellers, 2014; Donelson and Munday, 2015).

The earth is currently in an interglacial period, with warming temperatures, but the shelf seas around the Antarctic have been almost completely covered by ice during recent glacial maxima (Clarke and Crame, 1989). The requirement to migrate on and off the shelf is thought to have been driven by glacial-interglacial cycles, resulting in many of the surviving Antarctic shelf species having eurybathic distributions (Brey et al., 1996). Eurybathy may not only have allowed species a refuge from glaciation but may now also provide a refuge from many of the impacts of climate change (which are mainly occurring toward the surface waters).

In contrast to the dramatic message of more losers than winners gained from single factor studies, when multiple factors are considered the resilience of many Antarctic marine species is highlighted. However, while the understanding of the relative effects of different stressors is improving, more information is required to improve the accuracy of such risk assessments. This will be further improved when the vulnerability of links within the food web can be described in detail, allowing the true vulnerability of Antarctic marine fauna to be more completely assessed. These principles are not unique to the Antarctic and the principles outlined above can be applied across latitudes and systems where data is limited.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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The Influence of Abiotic Environment and Connectivity on the Distribution of Diversity in an Andean Fish Fluvial Network

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The distribution of Andean freshwater fishes is the result of the interaction of historical and contemporary factors such as basin geomorphology and the physicochemical characteristics of water bodies. Dramatic changes along river networks due to waterfalls or dams generate abrupt changes in longitudinal slopes that function as ecological barriers to dispersal and thus have an effect on the composition and richness of fish assemblages. We expect the amount of variation in beta diversity along the elevation gradient (between 700 and 3,500 m a.s.l.) of the eastern slope of the Cauca River basin to be explained by changes in the aquatic environment and connectivity among sites. We measured connectivity in terms of the distance along the stream channel between sampling sites considering changes in slope. We used a Generalized Dissimilarity Model (GDM) to evaluate the contribution of connectivity and other water mass characteristics (dissolved oxygen, pH, conductivity, temperature, and elevation) in predicting changes in beta diversity. The GDM models explained 33% of the total deviance in species turnover, suggesting that there are additional variables that have not been considered, such as available habitats along the rivers. Elevation was the variable with the largest relative importance in the model and connectivity explained only seven percent of the total variance when all sites were included. However, when only the sampling sites in the headwater streams were included (the most geographically isolated sites), the GDM models explained 51% of the total deviance and the contribution due to connectivity increased. Isolation of stream headwaters, in conjunction with extreme conditions present at high elevations may influence the fish assemblage turnover. Our results provide evidence that elevation has a strong influence on beta diversity of Andean fish assemblages. Species turnover upstream above 1,200 m a.s.l. is strongly influenced by channel connectivity and there are additional environmental variables that need to be included in the models to improve their prediction power.

Keywords: tropics, freshwater, beta diversity, river connection, teleostei

INTRODUCTION

Freshwater fish represent nearly 10% of all vertebrate species in the world (Vari and Malabarba, 1998) and each continent has a distinctive fauna, which is the result of a long geological history of isolation due to physical barriers and the adaptation of each of the various groups to particular biotic and abiotic environmental conditions (Lévêque et al., 2008). The composition and structure of communities has also been associated with elevation gradients and changes in environmental factors along the cline. The pattern observed has been a decrease in species richness and increase of endemism with the increase in elevation (Lomolino, 2001). At a local scale, the composition of fish communities has been the result of these same conditions (Albert and Carvalho, 2011); however, their relative importance varies (Cilleros et al., 2016). In the South American Andes, for instance, studies on fish assemblages have identified elevational climatic gradients as the main drivers of change in composition and species richness (Pouilly et al., 2006; Jaramillo-Villa et al., 2010; Carvajal-Quintero et al., 2015; De La Barra et al., 2016). These analyses did not consider connectivity throughout the channel within a basin as a possible factor that could contribute to shaping the composition of fish assemblages.

The dendritic nature of fluvial networks creates preferential or obligatory connections for fish and aquatic taxa (Cote et al., 2009); thus, the spatial positioning of habitats within a river network could play a crucial role in the way communities are structured through processes of dispersal and environmental selection (Altermatt, 2013). Furthermore, longitudinal fragmentation, known as the natural discontinuity of fluvial networks, caused by natural waterfalls and rapids may act as ecological barriers which limit the process of fish dispersal and even promote speciation events in fragmented sub-drainages (Dias et al., 2013). As a result, the degree of connectivity within a given fluvial network should be an important mechanism that promotes speciation, extinction, and migration in evolutionary time-scales (Dias et al., 2013).

Both theoretical and empirical studies show that dispersal through dendritic systems exerts an influence on the spatial distribution of diversity (Altermatt, 2013). Evidence from fish communities at high elevations in the Andes suggests that headwater streams have different compositions despite having similar environments (Carvajal-Quintero et al., 2015). Therefore, the connectivity of the fluvial network could play an important role in the composition of these assemblages. With this in mind, this study analyzes the variation in the composition of fish communities in the Cauca River basin (northern Colombia's second most important river) considering the local environmental conditions along the elevational gradient, and also quantifies the spatial connectivity between fish assemblage locations.

Beta (β) diversity, defined as the temporal or spatial variation in species composition, provides a fundamental tool to quantify the distribution of diversity at a regional level, which has implications in ecosystem functioning and conservation (Socolar et al., 2016). β diversity may reflect two types of phenomena: spatial species turnover and community nestedness (Baselga, 2010). Nestedness occurs when the sites with less species richness are a subgroup of species that are present in successively richer sites, whereas turnover is when a species in a specific site is substituted by other species (Leprieur et al., 2011). This partition of β diversity into its independent components makes it possible to find suitable spatial conservation strategies that cannot be identified through the analysis of general β diversity (Angeler, 2013). For example, if the largest part of β diversity refers to nested communities, this would allow for the prioritization of a small number of sites with more species, whereas a high turnover would require the conservation of a greater amount of sites, though not necessarily the richest (Baselga, 2010; Guareschi et al., 2015; Loiseau et al., 2017).

Understanding the effects of the local abiotic conditions in conjunction with connectivity in dendritic systems at the local and regional levels is necessary in order to have a better grasp on ecosystem ecology and how it can be managed effectively (Barletta et al., 2010). With this in mind, in this study we seek to (i) quantify β diversity and its two components (turnover and nestedness) amongst local fish communities, and (ii) determine the contribution of fluvial connectivity, elevation, and physicochemical water conditions to explain the variation in β diversity of the fish fauna along the Cauca River basin in the northwestern Andes. We expect species turnover to be determined largely by changes in elevation gradient as has been reported by other authors (Carvajal-Quintero et al., 2015; De La Barra et al., 2016), and that fluvial connectivity and water conditions complement the importance of elevation as a predictor of species turnover amongst Andean fish assemblages. Finally, we expect a special importance of connectivity for headwater fish assemblages that are the most isolated and often with a highly differentiated biota (Albert and Carvalho, 2011; Carvajal-Quintero et al., 2015).

MATERIALS AND METHODS

Study Area

Colombia is a topographically diverse country, where the western region is predominantly mountainous as the Andes subdivide into three mountain ranges separated by two valleys through which the Magdalena and Cauca rivers run. Our study takes place in the Cauca River basin, specifically between 4°47′54″-5°32′21″N and 75°59′53″-75°16′34″W (**Figure 1A**). This region is characterized by a bimodal rainfall pattern and is made up of numerous valleys, plateaus, and smaller mountain ranges which result in varying climates ranging from temperate in the mountains to warm, semi-humid climates in the Cauca valley. We used 45 sampling sites between 700 and 3,500 m a.s.l. along the main Cauca River basin and in its tributary basins, including Risaralda, Campoalegre, Opiramá, Tapias, Pozo, and Supía rivers.

Sampling

This study was carried out with recommendations and approval of the Ethics Committee for Animal Experimentation from the Universidad de Antioquia (CEEA). Fish were captured during the first low-flow period of 2015 between February and March in longitudinal transects of 100 meters. The fishing effort at each site

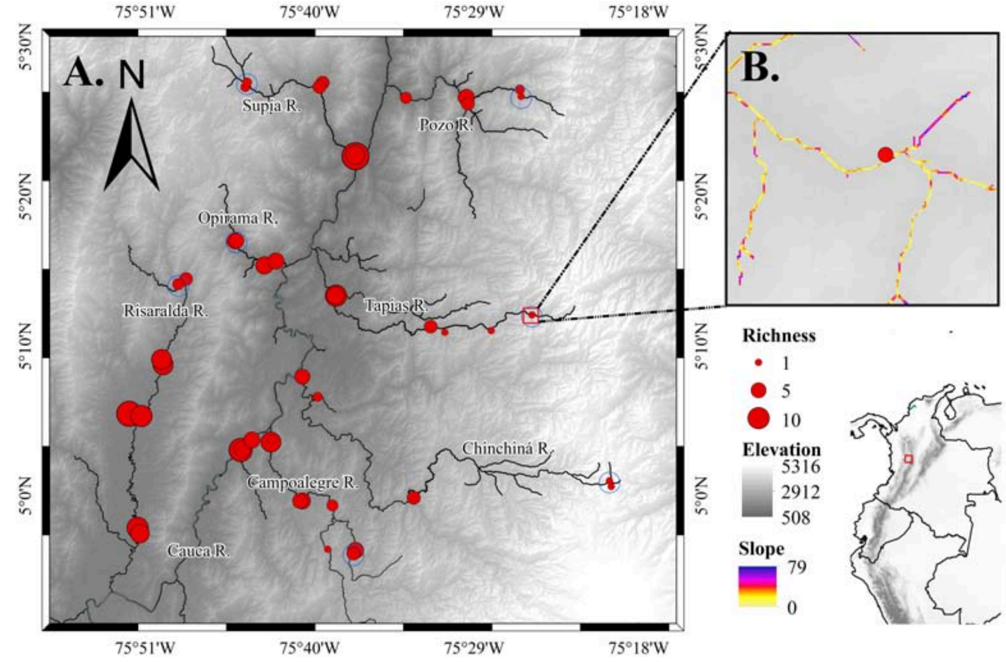

FIGURE 1 | (A) Hydrographic network of the study area. Circle size indicates species richness at each sampling site. Blue circles indicate sites that were used as headwater streams in the GDM. **(B)** Cost surface.

consisted in 30 throws using cast nets with different mesh sizes (0.5, 1, 2 cm) and an area sweep for 60 min using electrofishing.

All captured specimens were recorded; some were released, while others were fixed in 10% formaldehyde, taken to the lab, stored in 75% alcohol, and identified using taxonomic keys and compared with identified specimens and deposited in the fish collection of the Universidad de Antioquia CIUA. The identified records are available from the Global Biodiversity Information Facility (URL: https://www.gbif.org).

Each site was georeferenced and the following environmental variables were recorded using a Multi-Probe System (YSI 556 MPS): dissolved oxygen (mg/l), water temperature (○C), pH, and conductivity (µScm−1) (see **Table S1** in Supplementary Material). Even though sampling effort was the same for all sites, we conducted individual based rarefaction curves for each site to get an idea of sampling efficacy using the Vegan package (Oksanen et al., 2018) in software R (R Core Team, 2018).

Connectivity

For the purpose of this study, we defined connectivity among sampling sites as the degree in which the fluvial network facilitates or prevents movement between them (Tonkin et al., 2018). We used the measure of effective resistance, based on electrical circuit theory, as an indicator of connectivity between two sites. A high resistance value indicates little connectivity between sites. To quantify resistance, we generated a cost surface with low resistances assigned to habitats that are most permeable to movement, and high resistances assigned to poor dispersal habitat or to movement barriers (Shah and McRae, 2008). To accomplish this, we used the elevation raster available from the PALSAR radar system at a spatial resolution of 12.5 m to calculate slope angles in degrees, and determined drainages (**Figure 1B**) using the hydrology toolset from ArcMap 10.2 software (ESRI, 2011). The final cost surface was the result of the sum of both surfaces. Since the drainages are used for transit, all cells along the drainage were assigned a value of 1 while all other cells were discarded. The slope values varied from 0 to 90 degrees, where a 90-degree watercourse slope is vertical.

With the cost surfaces along the drainage system we calculated the fluvial network resistance to organism movement, with the software Circuitscape (Shah and McRae, 2008). This program calculates the connectivity between sites based on an analogy with electrical circuit theory, (McRae and Shah, 2011). Connectivity is quantified as the amount of current conducted from one site to another. The resistance of a resistor is the reciprocal of its conductance and can be thought of as representing isolation or movement cost between nodes. This measure considers not only the least cost path but all possible paths between a pair of sites, which might be more suitable as a measure of connectivity in biological systems (McRae et al., 2008). In our particular case, we used the program output file that reporting effective resistances between all pairs of focal nodes in the pairwise model.

Beta-Diversity Patterns

In order to identify whether the longitudinal fragmentation caused by changes in elevation influences β diversity among fish communities, we calculated the Sorensen dissimilarity index (βsor) and its components: turnover (βsim) and nestedness (βnes; Equation 1) using the Betapart package (Baselga and Orme, 2012) in R software (R Core Team, 2018). This index is based on presence-absence matrices and determines which of the components (βsim or βnes) underlies variations in β diversity through the following equation:

$$\beta_{sor} = \beta_{sim} + \beta_{sne} \equiv \frac{b+c}{2a+b+c} = \frac{b}{b+a} + \left(\frac{c-b}{2a+b+c}\right)\left(\frac{a}{b+a}\right)$$

where *βsor* is the Sorensen dissimilarity and is made up of the Simpson similarity (*βsim*), which consists of the substitution of species in one site for different species in another site (species replacement) describing a spatial turnover that is not influenced by differences in the species richness of each community, and βnes, which is the nestedness that occurs when sites with less species richness are a subgroup of the species at the sites with higher species richness (Leprieur et al., 2011; Baselga and Orme, 2012).

GDM

To explore which potential environmental and spatial variables may drive the variation in β diversity (βsor) among sites, we used a Generalized Dissimilarity Model (GDM). A GDM is a technique, which allows one to model the spatial variation in biodiversity based on the variation in environmental conditions, including means of spatial isolation, such as geographic distance. The model can predict the change in the composition of communities, based on a curvilinear relationship with the predictor variables (Ferrier et al., 2007). This type of relationship between change in composition and change in the ecological environment is more adequate since betadiversity reaches a maximum when two sites do not share species while ecological dissimilarity can always increase. In its traditional version, this model uses pairs of geographical coordinates to calculate distances in a straight line. This would not fit our purpose since we were interested in calculating distances along the drainage network and considering slope effects. Thus, we used the resistance matrix derived from Circuitscape as input in a non-metric multidimensional scaling (NMDS) analysis with the aim of transforming the resistance matrix into points on a two-dimensional space. The coordinates obtained through NMDS for each of the points were used to calculate euclidean distances for the GDM model. In addition to the distances calculated, the following continuous predictor variables were used in the GDM: dissolved oxygen, pH, elevation, and conductivity.

Two models were constructed; one used all 45 sampling sites, while the other only used the farthest sites from each of the drainage branches (seven sampling sites). The first model sought to capture variables that allow predicting most of the variation in the fish community composition, whereas the second model sought to evidence the isolation effect generated by the distance and accumulation of physical barriers for fish displacement.

RESULTS

In the 45 sampling sites, 2,475 specimens were recorded from 43 species grouped in five orders, 13 families, and 29 genera. The rarefaction curves from most sampling sites presented asymptotic behavior (see **Figure S1** in Supplementary Material), which can be interpreted as evidence that sampling was representative, at least during the time intervals in which samples were taken. The greatest species richness (16 species) was found in the Supía River at 759 m a.s.l., whereas the sites where only one species was collected were at elevations above 1,400 m a.s.l., including La Leona stream, and the high parts of Pozo River, Tapias River, and Chinchiná River (see **Table S1** in Supplementary Material, **Figure 1**). Headwater fish assemblages had on average two species and were characterized by a prevalence of species of the genus Astroblepus (60%).

The average β diversity (βsor) among all sites was 0.93 ± 0.002, and the beta diversity component due to turnover (βsim) was 0.867 ± 0.007, while the component due to nestedness (βnes) was only 0.063 ± 0.006. The same pattern was observed when performing the analysis only with the headwater sites. Average beta diversity (βsor) was 0.8184 ± 0.03, and turnover (βsim) was the most important component (0.6860 + 0.05), while nestedness (βnes) was relatively low (0.13 + 0.25). In other words, the replacement of species is the component that most contributes to the general beta diversity of the area (**Figure 2**). The low percentage of β diversity that was not originated by differences in species composition is related to nestedness.

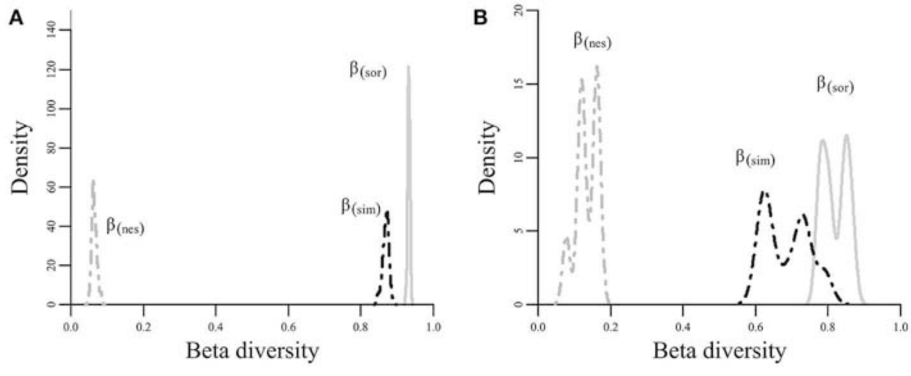

FIGURE 2 | Density plots with the distribution of general beta diversity (βsor, solid line) and its nestedness component (βnes, dashed gray line) and turnover component (βsim, dashed black line). **(A)** Results for all sampling sites and **(B)** results for headwater stream sites only.

The GDM conducted for all sampling sites explained 33.14% of the total deviance in β diversity, whereas, if conducted using only the farthest sampling sites in each of the sub-basins, 51% of the deviance was explained.

In terms of the relative importance of each predictor variable, results differed between models (**Figure 3**). In the model including all sampling sites, the most important variable was elevation, followed by pH, dissolved oxygen, and resistance last, whereas in the model that used only headwater stream sites, resistance was the most important variable, followed by elevation. Conductivity does not seem to contribute to either of the models as all of the coefficients assigned to this I-spline equaled 0.

DISCUSSION

Results of our study support the hypothesis that both environmental gradients and connectivity exert an effect on the composition of fish communities, but their relative contributions vary along the drainage system. Connectivity exerts a greater contribution to explain beta diversity when only headwater streams are used, while changes in elevation explain variation among most other sites. This is partly related to the contrasting structure of river networks between high and low elevation sites. While there is a high degree of connectivity in water systems in lowland areas (e.g., <500 m), rivers and streams in the Andes are isolated and discontinuous (Schaefer, 2011) partly due to waterfalls and chutes that act as natural barriers within the fluvial network that affect the degree of connectivity and configure permeability and the availability of habitats for freshwater organisms (Rahel, 2007; Dias et al., 2013). As a result, the degree of connectivity within a fluvial network is an important mechanism that promotes speciation, extinction, and migration in evolutionary time-scales (Dias et al., 2013), with particular relevance in headwater streams. On the other hand, changes in elevation, which are related to changes in temperature, vegetation, and substrate conditions, may exert significant differential selective pressures that account for a major part of the variation in fish assemblage composition. Unlike elevation and connectivity, which significantly contribute to explain the variation in β diversity in this system, changes in local physicochemical water conditions, such as pH, dissolved oxygen, and temperature, seem to contribute little (**Figure 3**). The high variability of the water conditions at sampling sites is associated to seasonal precipitation changes, soil types, and the riparian forest cover, amongst others, which were not measured in this study. This variation could have reduced the influence of these variables in the model.

Beta diversity among the fish communities of the Cauca River basin was mainly characterized by strong species replacement. Our results support those obtained by Leprieur et al. (2011) on a global scale, where the variation in β diversity in South America is mainly caused by turnover. This same result was found in other studies conducted in freshwater systems at the local level where the dominant component in terms of β diversity is turnover and where the nestedness component is generally low (Tisseuil et al., 2012; Angeler, 2013; Jamoneau et al., 2018). The nestedness component is characteristic of lowland communities (Granado-Lorencio et al., 2012; <500 m, Henriques-Silva et al., 2018), and has been observed in other water organisms, such

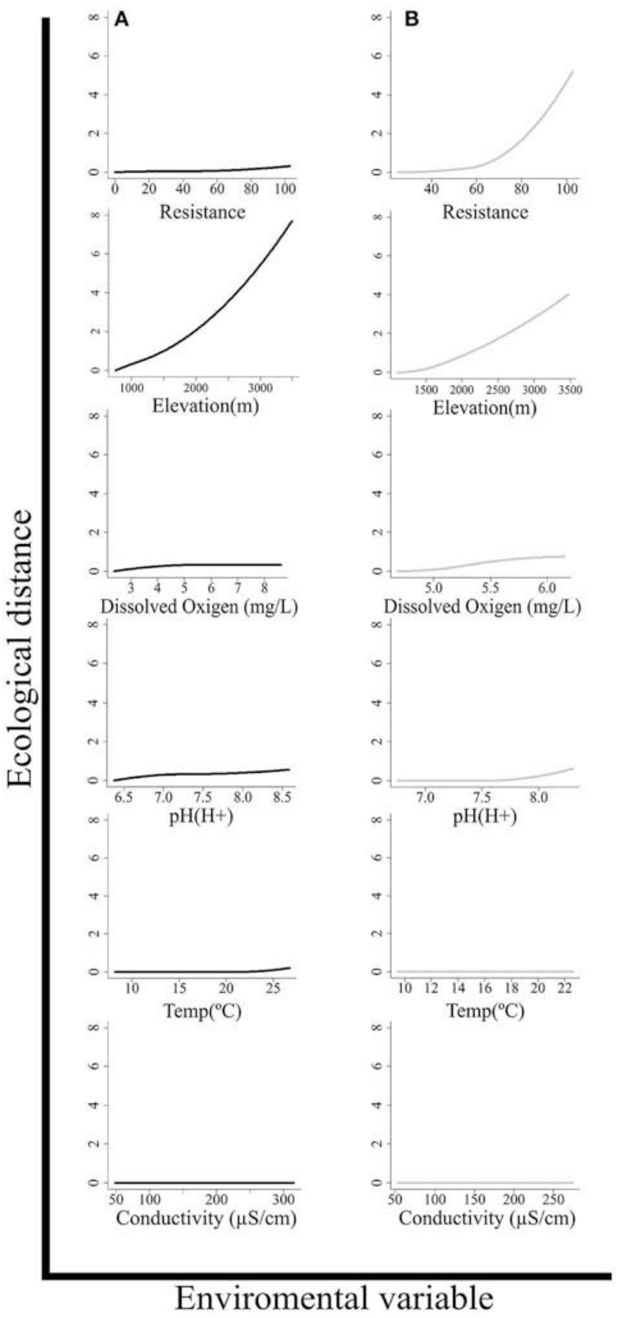

FIGURE 3 | I-splines generated for each environmental variable from the GDM model to predict beta diversity. The maximum height of each curve indicates the magnitude of turnover in fish communities with respect to that variable. The relative magnitude among variables within a model is indicative of the relative importance among variables to explain the changes in β diversity while maintaining the remaining variables constant. The form of each function indicates the rate of turnover throughout the gradient. **(A)** Results of model with all sampling sites **(B)**, and results only including only headwater stream sites.

as diatoms (Jamoneau et al., 2018). According to the network position hypothesis (Brown and Swan, 2010), the communities of downstream stretches are increasingly influenced by effects of mass due to their position in the fluvial network, which facilitates dispersal. Migratory fish are a good example of species with strong dispersal capacity that can homogenize fish assemblages especially at low to intermediate elevations (Ríos-Pulgarín et al., 2008; Jiménez-Segura et al., 2014). Only one migratory species—Brycon henni—was recorded in this survey and is characterized by short, lateral migration patterns (Builes and Uran, 1974). We recovered a low nestedness component because our sampling sites were located at elevations above 700 m. The spatial patterns of beta diversity evidenced are consistent with a scenario of differential selection along the elevation gradient that suggests a steady change in composition along the gradient (Vellend, 2016), and isolation in conjunction with extreme selective pressures at headwater sites.

In this study we found an important contribution of βsim to β diversity, which is often associated with climatic gradients (McCain, 2005; Bryant et al., 2008). Nonetheless, we propose that aside from the contribution of climate gradients, connectivity due to the dendritic structure of the basins and principally driven by headwater assemblages (Tonkin et al., 2018) also contributes to the high relative importance of turnover. Headwater sites are characterized by low species richness (**Figure 1**) but very distinctive compositions. Headwater assemblages are important because, even though they present low α diversity, they contribute to a high γ diversity with a group of endemic species (Clarke et al., 2008; Carvajal-Quintero et al., 2015). In the case of the Andes, the headwater communities are mainly composed of species belonging to the genera Astroblepus and Trichomycterus (Barletta et al., 2010; Jiménez-Segura et al., 2016), which have been recorded at up to 3,300 m a.s.l (Maldonado et al., 2011). Besides the importance of these assemblages due to their distinctive composition, the functional traits present in these species reflect unique adaptations required by the fish in order to inhabit water bodies characterized by extreme environmental conditions, such as low temperatures, high slopes, and fast-flowing waters. Fish from the Astroblepus genus are characterized by depressed bodies, lips specialized for adhering to substrates, dorsolateral eyes, and well-developed pectoral, pelvic, and caudal fins, which provide greater stability on the substrate and allow for rapid, explosive movements (De Crop et al., 2013; Conde-Saldaña et al., 2017). This genus presents a complex history where divergence and dispersal along the drainage basins are the main factors explaining their distribution; they are usually species that are endemic or unique to a particular river or its adjacent systems (Schaefer et al., 2011).

Defining conservation areas to protect species as well as endemisms within fluvial networks, should consider not only the number of drainages but also the probability of connection among them. Our results indicate that low-order drainages are the most isolated and present a number of endemic species. The challenge lies not only in determining how many patches to conserve, but also which ones. In Colombia, ca. 25,711 km^2 at elevations above 1,000 m are under some type of protection. Thus, an important next step is to identify the water bodies that exist within the current protected areas and determine whether it is necessary to complement the existing reserve network with new areas or if the current protected network is accomplishing our conservation goals. It is important to keep in mind that our analyses were conducted in a small part of the central branch of the Andes and that the ichthyofauna of the other two branches may differ in terms of species composition (Jiménez-Segura et al., 2014). Therefore, it will be necessary to increase the extent of this analysis in order to obtain a broader perspective on the conservation strategies that must be implemented in the northwestern Andean region.

In conclusion, we identified patterns in the spatial distribution of β diversity that support a role for environmental gradients and connectivity at the local level, and we suggest that the effects of connectivity are magnified in headwater streams. Even though most studies along mountain sides identify climate gradients as ultimate drivers of variation in community properties, we were able to unmask the effects of other variables such as connectivity among sites, considering that euclidean geographic distances are not adequate to describe the complex structure of fluvial networks (Henriques-Silva et al., 2018). Our models explained only 33 and 51% of the variation in β diversity, which suggests that there may be other variables that have not yet been considered; for example, our analyses did not take into account the one-directional flow of water nor other environmental variables, such as the watercourse width, depth, and stream bed composition. We suggest that future studies include these variables as well as the interaction between topography and water mass (water level and average velocity of the water bodies). Regarding composition, it is important to take samples during other seasons and at lower elevations in order to detect the influence of migratory species, which, due to their movement capacity, would participate in different communities depending on the time of year. Continuing to model these scenarios will improve our understanding of the system behavior and allow us to identify the possible effects of basin fragmentation and climate change in Andean fish communities.

AUTHOR CONTRIBUTIONS

All authors conceived the presented idea. JP suggested the type of analysis and wrote parts of the manuscript. JH-P performed the analysis. LJ-S helped in data interpretation and wrote parts of the manuscript. DR-S provided orientation in the manuscript style. All authors discussed the results and contributed to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2019.00009/full#supplementary-material

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How Far Upstream: A Review of Estuary-Fresh Water Fish Movements in a Large Neotropical Basin

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The present study comprises the first systematic analysis of the limits of upstream movement by some fish species that use the estuarine area of the Patos Lagoon basin in southern Brazil. The Sinos River sampling program included 86 sites, sampled from 1998 to 2014, covering lowland stretches and headwater streams. The Guaíba sampling program was conducted from February 2011 to March 2013 and comprised 59 independent samples. Six fish species using estuarine areas occur in the upper Patos basin, 250–500 km from the Patos Lagoon outlet to the Atlantic Ocean. *Parapimelodus nigribarbis* specimens ranged from 11.3 to 18.9 cm (median = 13.3 cm) in length, i.e., were adults (Sinos, *n* = 459; Guaíba, *n* = 149). The species was captured almost 500 km from the Patos outlet, as far as 180 km upstream in the Sinos main channel. In Guaíba Lake, the species was captured mainly in autumn, although it was more abundant in winter and spring in the Sinos River. *Lycengraulis grossidens* was captured in the Sinos Basin, restricted to the lower stretches in spring and summer months (*n* = 7). In Guaíba Lake (*n* = 134) the species occurred throughout the lake and year-round, and was ten times more abundant in spring. Most specimens were adult (8.2–26.9 cm, median = 20.0 cm). Most *Micropogonias furnieri* individuals (*n* = 63) were juveniles (10.7–33.4 cm, median = 14.2 cm). The species was not captured in the Sinos Basin. In Guaíba Lake *M. furnieri* occurred predominantly in the southernmost part (downstream) and was more abundant (>10×) in winter. *Genidens genidens* (*n* = 27) was captured only in summer in the southern part of Guaíba Lake (closest to the outlet). Most individuals were adults (24.5–34.0 cm, median = 27.8 cm). *Genidens barbus* (*n* = 7) was restricted to spring and summer months and was captured only in southern (near-outlet) parts of Guaíba Lake, comprising mainly large juveniles and adults (31.5–68.0 cm, median = 37.9). *Mugil liza* (*n* = 13) appeared in spring in relatively low abundances but was widespread throughout Guaíba Lake during the summer. The species was not captured in the Sinos sampling program. The size profile comprised specimens nearing maturity (34.3–45.5 cm, median = 38.9 cm). Finally, we suggest possible biological cycles for these species that combine these new distribution data with published information.

Keywords: estuarine fish, ecosystem connectivity, amphidromous, anadromous, catadromous, potadromous

INTRODUCTION

The study of fish migration patterns, due to their complexity, has been a challenge for centuries. Difficult to follow, fish can move among marine areas, estuaries and fresh waters to reproduce, locate nursery grounds or feed. These migrations, which may include entire populations or only parts of them, can transfer huge amounts of biomass and energy between ecosystems, and have important ecological, economic and social implications (Chapman et al., 2012b; Metcalfe and Craig, 2012).

The coastal landscape of southern Brazil is an interesting example. As a consequence of disrupted research programs, a full understanding of the biological cycles of migratory fish along the Patos Lagoon system suffers from several lacunae, especially concerning the upstream distribution limits and seasonal movement cycles of migratory species. The present study analyzed the distribution patterns of six fish species, from the upper Patos Basin (Guaíba Lake and Sinos Basin) to the Patos Lagoon outlet to the Atlantic Ocean, covering distances of 250–500 km: *Lycengraulis grossidens* (Engraulididae), *Mugil liza* (Mugilidae), *Micropogonias furnieri* (Sciaenidae), *Parapimelodus nigribarbis* (Pimelodidae), *Genidens genidens* and *Genidens barbus* (Aridae).

The Atlantic sabretooth anchovy *L. grossidens* occurs from Belize to southern Argentina (Golfo San Matías; Mai and Vieira, 2013). The species is eurytopic, with records from fresh waters to the coastal shelf (Whitehead et al., 1988; Barletta et al., 2010), and can reproduce in both fresh and brackish water (Mai and Vieira, 2013). Reproduction is reported for spring and summer months in the southern part of its range. *L. grossidens* has been classified as a freshwater resident, anadromous, marine migrant, estuarine resident, catadromous, or semi-catadromous (see Mai and Vieira, 2013 for review) and most recently as facultatively amphidromous (Mai et al., 2014).

The gray mullet *M. liza* is a typical catadromous fish, widely distributed along the western Atlantic coast of South America (Menezes et al., 2010). Its life cycle comprises reproductive migrations each autumn from Argentina and southern Brazil, to spawn between northern Santa Catarina and Paraná (Lemos et al., 2014). Along the species' distribution range, the Patos Lagoon is the main nursery habitat and an inland fishery ground (Vieira, 1991; Vieira and Scalabrin, 1991; Lemos et al., 2014).

The whitemouth croaker *M. furnieri* occurs in the western Atlantic Ocean, from the Caribbean Sea to the northern Argentine coast (Isaac, 1988). In southern Brazil, this croaker can be found from the marine surf zone and continental shelf to the upper (freshwater) zone of the Patos Lagoon, with a spring-summer migration to reproduce in brackish waters (Muelbert and Weiss, 1991), using estuaries as nursery grounds (Costa et al., 2014) in a pattern of anadromy.

The mandí catfish *P. nigribarbis* is restricted to the Patos Lagoon basin (Lucena et al., 1992) and is recorded year-round in the estuarine (Vieira and Castello, 1997; Garcia et al., 2003) and freshwater areas of Patos Lagoon (Bertaco and Becker, 2000). The species shows higher gonadosomatic indexes (GSI) in spring and summer (Fontoura et al., 2018). Based on monthly samples with gill nets and beach seines in limnetic zones, Bertaco and Becker (2000) identified that the species was more abundant in spring and summer, proposing a seasonal species movement from nearshore to deeper water in Guaíba Lake, with the fish occupying nearshore areas in spring and summer and deeper water in autumn and winter (potamodromy; Chapman et al., 2012b). Garcia et al. (2003), sampling with beach seines, also inferred an increased abundance in spring and summer in the Patos estuary. Nevertheless, the presence of larvae recorded for estuarine areas (Muelbert and Weiss, 1991) and the upstream seasonal cycles of abundance also suggests possible semi-anadromy (*sensu* Chapman et al., 2012b).

The white sea catfish *G. barbus* occurs on the coasts and estuaries of South America, from Bahia in northeastern Brazil to San Blás on the central Argentine coast (Velasco et al., 2007). The life cycle of the species has been described for the Patos Lagoon (Reis, 1986; Haimovici, 1997). This catfish migrates from coastal waters to estuarine areas at the end of winter for reproduction, seeking oligohaline waters for spawning (anadromy). The males mouth-breed the eggs and juveniles for about 2 months. From December on, catches in the estuaries rapidly decrease, suggesting a return to coastal waters.

The guri sea catfish *G. genidens* ranges from Ceará in northeastern Brazil to the central Atlantic coast of Argentina (Acero and Bentancur, 2010). The species' life cycle in Patos Lagoon is poorly known but may be similar to that of *G. barbus*.

The present study aimed to contribute to the understanding of the biological cycles of *L. grossidens*, *M. liza*, *M. furnieri*, *P. nigribarbis*, *G. genidens* and *G. barbus*. We present the first systematic records of upstream distribution limits for these fish species using the Patos Lagoon estuary, combining new data with available information to describe consensus information and aspects that are still in need of attention.

MATERIALS AND METHODS

The Patos Lagoon (<8 m deep) is 250 km long and 60 km wide (~10,000 km^2), dominated by fresh to oligohaline waters (**Figure 1**). The estuarine area is generally limited to the

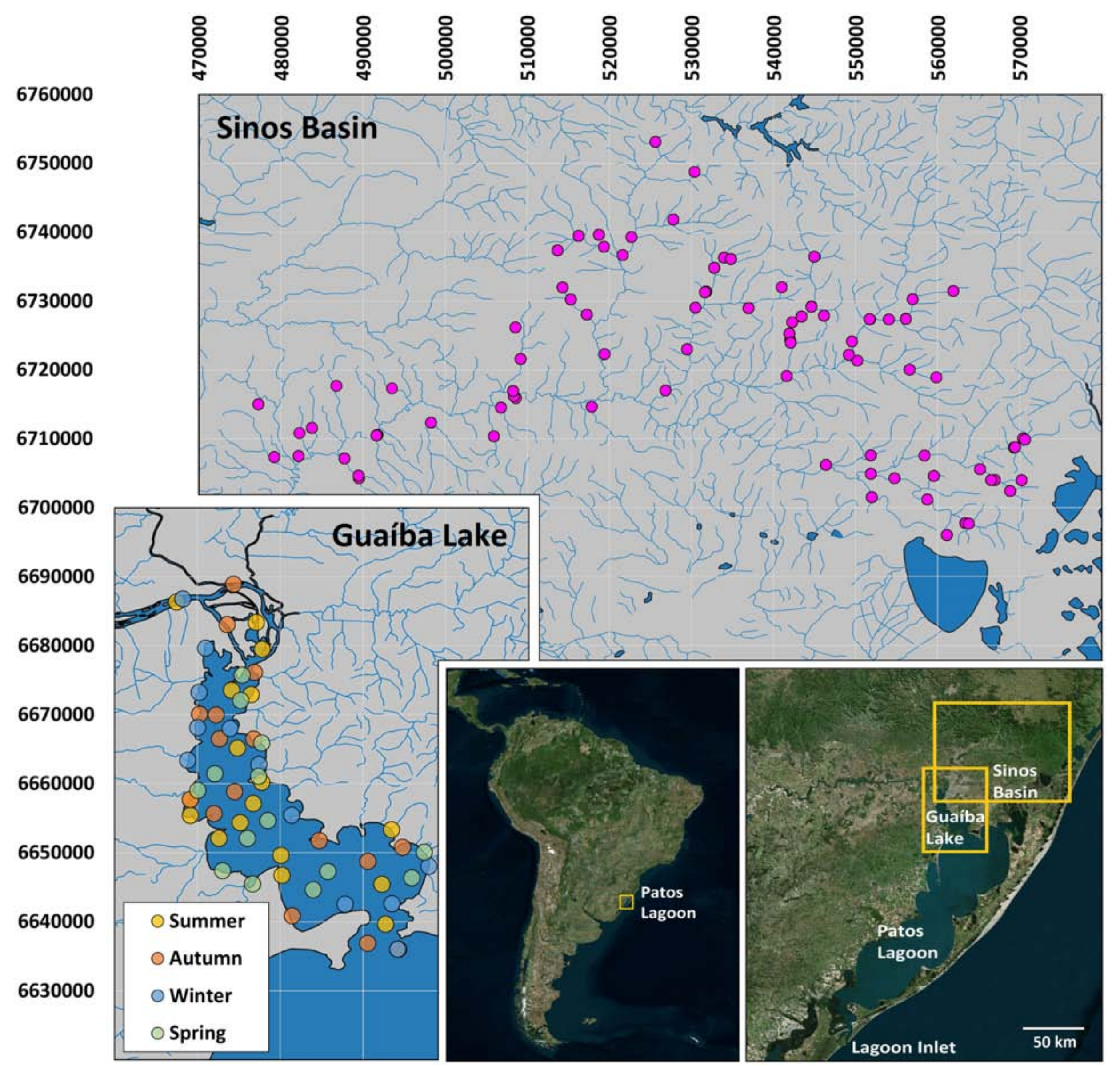

FIGURE 1 | Areas sampled in the Patos Lagoon basin, comprising 86 sampling sites visited seasonally in the Sinos Basin (1998 through 2014); and 59 sampling sites, each sampled once in Guaíba Lake (2011 through 2013). See text for details of sampling methods. Vector maps from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). Satellite compositions from Bing Satellite Aerial, Open source plugin, QGIS. 22J UTM coordinates.

southern 10%, although the upper limit of the saline waters shifts seasonally. Guaíba Lake on the northwestern edge of the Patos Lagoon is 50 km long and 19 km wide (∼500 km^2), and most of the lake is shallower than 3 m. A deltaic system on its northwestern upstream border is formed by incoming rivers (Jacuí, Caí, Sinos and Gravataí). The Sinos River basin, 210 km long and up to 600 m a.s.l., is a small part of the area where fish move to and from the Patos Lagoon estuary. The artisanal fishery, organic pollution and other widespread environmental impacts of a large metropolitan area (over 4 million inhabitants) are the main pressures on the fish populations. A general overview and assessment of the conservation status of the Patos Lagoon system were provided by Fontoura et al. (2016).

The Sinos River sampling program comprised 86 sites that were sampled monthly during several projects from 1998 through 2014, extending from lowland stretches to the headwaters (**Figure 1**). In the Sinos River main channel, fish were captured by 1-h electrofishing by boat and a 7.5 kW (750 V) unpulsed direct-current generator along both banks, and with a set of 7 gill nets set out for approximately 16 h from early afternoon to the next morning (all nets were 20 m long with mesh sizes 15, 20, 25, 30, 35, 40, and 50 mm, adjacent knots; the 15–25 mm gillnets measured 1.5 m high and the 30–50 mm gillnets were 2.0 m high).

In the smaller tributaries, fish were captured by 1-h electrofishing (2 kW, 750 V, unpulsed direct current).

The Guaíba sampling program extended from February 2011 to March 2013 and comprised 59 sampling sites, each sampled only once. Although samples were not replicated at the same site along Guaíba Lake, the sampling program was designed to allow wide sampling coverage, comprising combinations in space (upstream, downstream, shallow and deep water) and time (year, season) (**Figure 1**). Fish were captured using surface and bottom gillnets (60 m long), each comprising a set of 12 different mesh sizes (5-m panels, 1.5 m high, mesh sizes of 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, and 70 mm, adjacent knots). Fishing time was approximately 20 h, from early afternoon to the next morning. Fish from the Guaíba sampling program were measured (total length) to the nearest millimeter. Additional distribution records were obtained from public databases of museum records[1].

RESULTS

Six fish species recorded for the estuarine area of the Patos Basin are also present in the limnetic areas sampled (Guaíba Lake and the Sinos River Basin), over distances of 250–500 km from the Patos Lagoon outlet to the Atlantic Ocean: *L. grossidens* (Engraulidae), *M. liza* (Mugilidae), *M. furnieri* (Sciaenidae), *P. nigribarbis* (Pimelodidae), *G. genidens* and *G. barbus* (Aridae). Of these, only *P. nigribarbis* and *L. grossidens* were captured in the Sinos Basin (**Figure 2**). Information on fish size profiles is available for the Guaíba Lake samples (**Figure 3**), where all the species were detected.

The mandí catfish *P. nigribarbis* had the widest distributional range, up to almost 500 km from the Patos outlet, 180 km upstream in the Sinos River basin (n = 459, **Figure 2**). In the Sinos River main channel, this catfish was present year-round, in higher abundance (>10×) in winter and spring. In Guaíba Lake (n = 149), the species was captured in autumn in deeper water, except for a few specimens collected in summer (**Figure 4**). The size profile of *P. nigribarbis* included fish in the range of 11.3 to 18.9 cm (median = 13.3 cm), i.e., adults. Museum records extend as far as 588 km upstream (from the Patos outlet to the Atlantic Ocean) in the Taquari Basin (Museu de Ciências e Tecnologia da PUCRS, MCT 38912) or 694 km in the upper Jacuí River (Museu de Ciências e Tecnologia da PUCRS, MCT 23770).

In the Sinos River Basin, the Atlantic sabretooth anchovy *L. grossidens* was limited to the lower stretches in spring and summer months, in relatively low abundances (n = 7). In Guaíba Lake, *L. grossidens* occurred throughout the lake and year-round, although it was tenfold more abundant in spring (n = 134, **Figure 5**). The size profile comprised mainly adult specimens (8.2–26.9 cm, median = 20.0 cm). Museum records extend as far as 400 km upstream (from the Patos outlet to the Atlantic Ocean) in the Taquari Basin (Museu de Ciências e Tecnologia da PUCRS, MCP 19468).

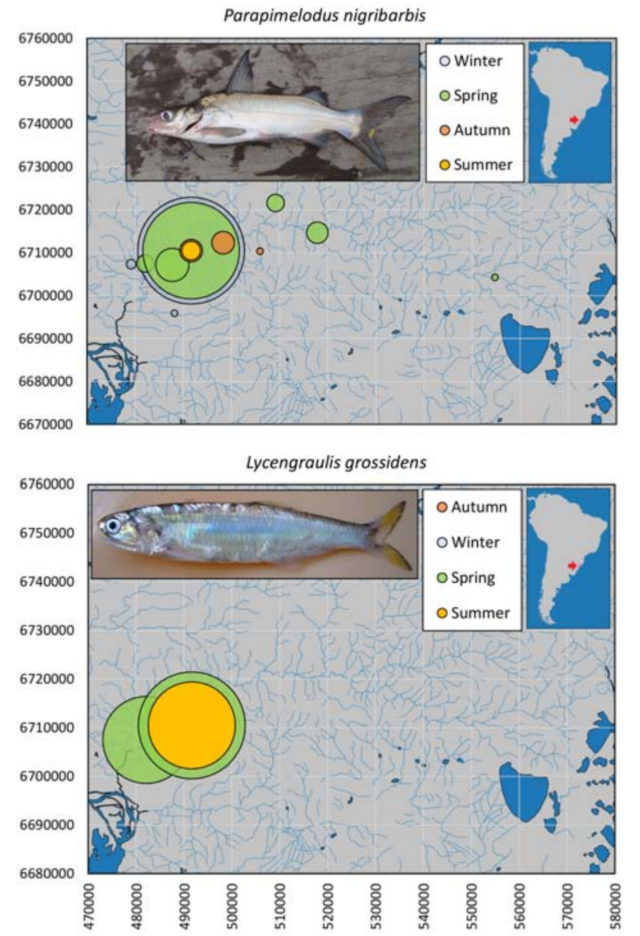

FIGURE 2 | Spatial and seasonal relative abundances of *Parapimelodus nigribarbis* (n = 459) and *Lycengraulis grossidens* (n = 7) in the Sinos River basin, southern Brazil. Bubble area proportional to number of captures per site. Fish photographs from Timm, C.D. available at Fishbase.com. Vector map background from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). 22J UTM coordinates.

Mainly juveniles of the whitemouth croaker *M. furnieri* were captured (10.7–33.4 cm, median = 14.2 cm). Croakers were caught in all seasons in the southernmost portion of Guaíba Lake (n = 63), although they were more abundant (>10×) during winter months (**Figure 6**). Museum records of *M. furnieri* in the northern limnetic distribution comprised individuals captured in summer (n = 3, MCP 3700, UFRGS 1056 and 8481), autumn (n = 4, MCP 25583, 2583, 16334 and 27439) and winter (n = 3, MCP 28043, 28045 and 28044), with no recorded capture in spring.

The guri sea catfish *G. genidens* (n = 27, **Figure 7**) was captured only in summer, downstream from the middle Guaíba Lake and increasing in relative abundance toward the Patos Lagoon, although there is one museum record upstream in northern Guaíba Lake in November (UFRGS 5819). The size profile comprises adult individuals (24.5–34.0 cm, median = 27.8 cm).

The few individuals of the white sea catfish *G. barbus* (n = 7, **Figure 8**) were sampled in spring and summer months, only in downstream areas of Guaíba Lake, and comprised mainly large

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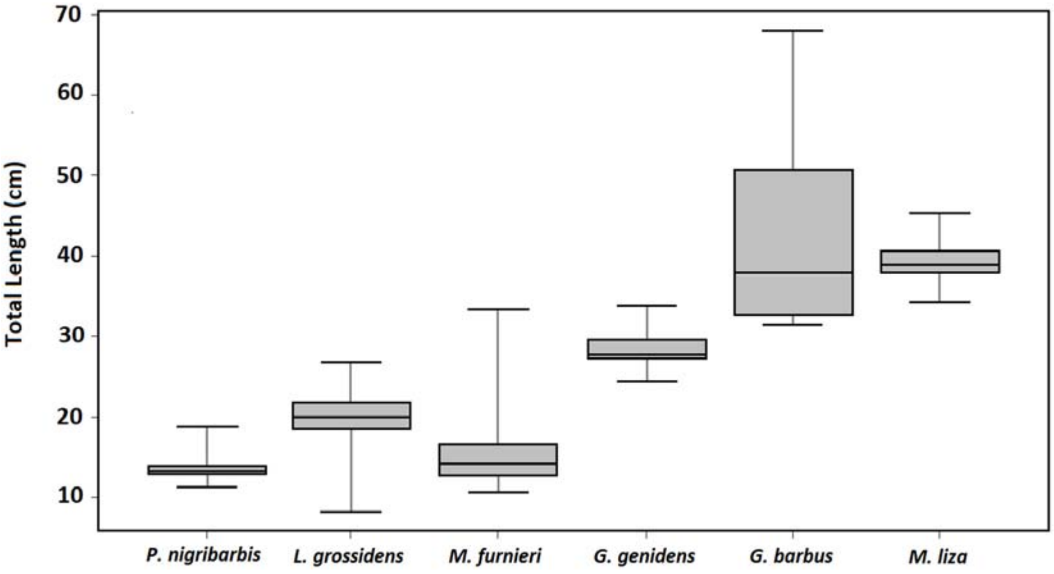

FIGURE 3 | Boxplot of the size profiles (total length, cm) of *Parapimelodus nigribarbis, Lycengraulis grossidens, Micropogonias furnieri, Genidens genidens, Genidens barbus* and *Mugil liza* sampled in Guaíba Lake, southern Brazil.

juveniles and adults (31.5–68.0 cm, median = 37.9 cm). One museum record documents the species in northern Guaíba Lake in October (MCP 3763).

Finally, the gray mullet *M. liza* ($n = 13$, **Figure 9**) appeared in spring and was widespread in the entire Guaíba Lake during the summer, although with no captures in the Sinos River sampling program. The size profile comprised specimens at the borderline of maturity (34.3–45.5 cm, median = 38.9 cm). Museum data for the species in Guaíba Lake record its presence between November (UFRGS 17771) and March (MCP 14702), with no records in the tributary rivers.

DISCUSSION

The mandí catfish *P. nigribarbis* feeds on plankton, using filiform and closely spaced gill rakers (Almeida et al., 2013). Marques et al. (2007) found that females measuring 8 cm (total length) and above had developing ovaries, and estimated the size at first maturity as 13.7 cm. In estuarine areas, *P. nigribarbis* larvae were identified in spring and summer plankton surveys by Muelbert and Weiss (1991).

In monthly samples taken with beach seines in the southern part of Guaíba Lake, Lucena et al. (1994) failed to identify any clear temporal pattern for the species. On the other hand, Bertaco and Becker (2000) observed a seasonal pattern of abundance, although with marked year-to-year variability. According to these authors, the species was present year-round but was more abundant in spring and summer. Bertaco and Becker (2000) proposed a seasonal species movement (potamodromy; Chapman et al., 2012b) from shallow to deeper water in Guaíba Lake, with the fish occupying nearshore areas in spring and summer and deeper water in autumn and winter.

In analyzing reproductive patterns in Guaíba Lake from gillnet captures, Fontoura et al. (2018) found increased GSI values in spring and summer. Nevertheless, the mean GSI values were far below the maximum GSIs recorded, suggesting that the species migrates outside the sampling areas (depth > 1.5 m) for spawning.

Based on the available information, the life cycle of *P. nigribarbis* is still obscure. Apparently the species reproduces both in estuarine lentic areas (Muelbert and Weiss, 1991) and far upstream in lotic reaches, as evidenced by the occurrence of larvae in the Jacuí River (November 2017; Santo Amaro Dam; 29.947°S; 51.893°W; D.A. Antonetti and D.R. Tataje, personal communication).

The evolution of the coastal plain of Rio Grande do Sul provides an interesting natural experiment concerning the evolution of species occupancy (**Figure 10**). The coastal plain is about 600 km long, wide and flat, and has undergone a cycle of oceanic transgressions and regressions during the Pleistocene and Holocene, which gave rise to a complex lagoon system (Rosa et al., 2017). The so-called Barrier I was formed 325 ka ago as a sandy dune system during the first recorded oceanic transgression. Barrier II was formed at 230 ka and Barrier III at 125 ka. Barriers I and III now delimit a plain area (with Barrier II between) connecting the northern Patos Lagoon to the Barros Lagoon (**Figure 10**). This flat area, drained by the Capivarí River (between Barriers I and II) experienced cycles of expansion and retraction of the northern boundary of the Patos Lagoon, reflecting sea-level fluctuations (rises of 9 m at 230 ka, 8 m at 125 ka, and 3 m at 8 ka; Rosa et al., 2017).

The southern boundary of Barros Lagoon lies at an altitude of about 18–25 m a.s.l. (**Figure 10**), high enough to keep the Barros Lagoon separated from the Patos Lagoon in the last 230 ka, although potentially connected by a lagoon spill. Nowadays,

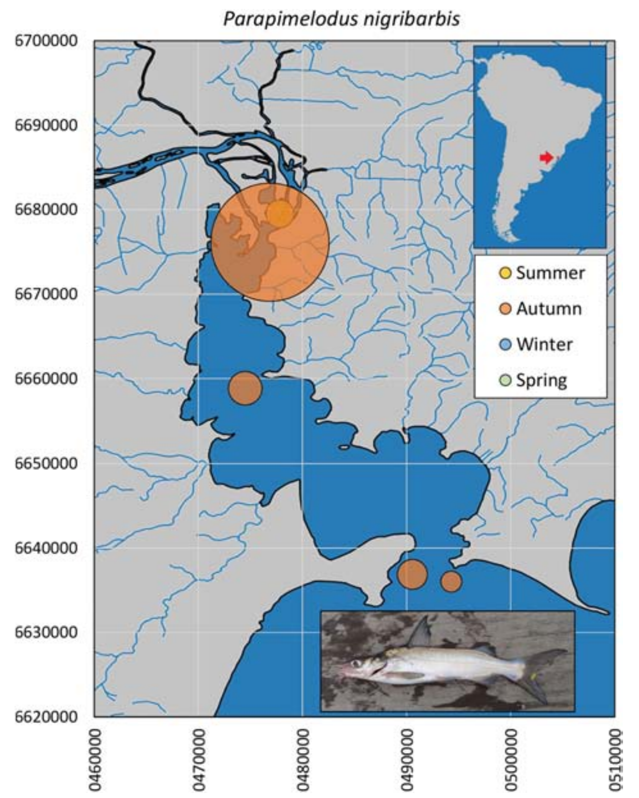

FIGURE 4 | Spatial and seasonal relative abundance of *P. nigribarbis* in Guaíba Lake, southern Brazil. Bubble area proportional to number of captures per site (*n* = 149 individuals). Fish photograph from Timm, C.D. available at Fishbase.com. Vector map background from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). 22J UTM coordinates.

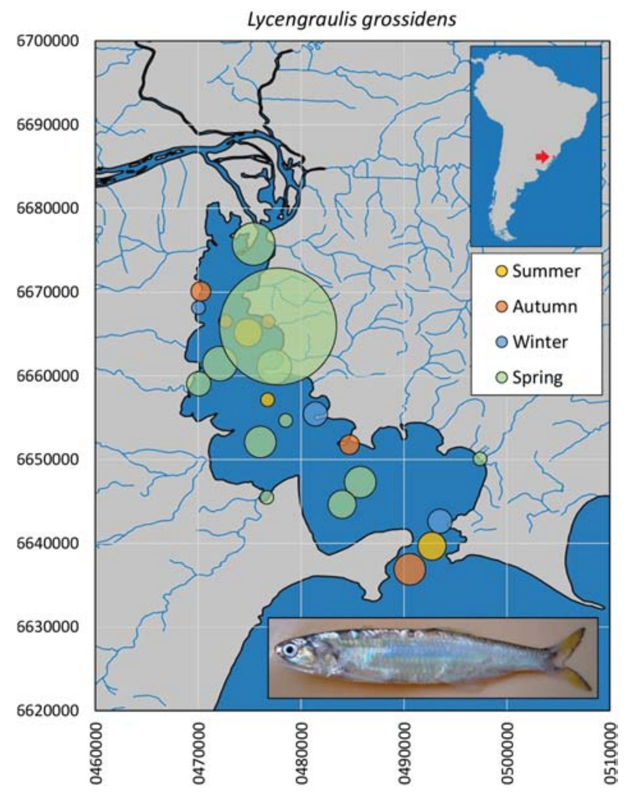

FIGURE 5 | Spatial and seasonal relative abundance of *L. grossidens* in Guaíba Lake, southern Brazil. Bubble area proportional to number of captures per site (*n* = 134 individuals). Fish photograph from Timm, C.D. available at Fishbase.com. Vector map background from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). 22J UTM coordinates.

Barros Lagoon is isolated, receiving only very small tributaries from the Serra Geral coastal mountain range. The ancient connection with the Capivarí River has been completely modified by extensive land use for rice farming, including a network of irrigation channels and water pumping from Barros to rice fields. Nevertheless, before human occupancy, there was probably a connection to the Capivarí basin during winter months, when the lagoon level was higher, and a probable isolation in summer, with increased evaporation and reduced rainfall.

Among the species examined here, only *P. nigribarbis* has been recorded in Barros Lagoon (Museu de Zoologia da Universidade Estadual de Londrina, MZUEL 8426; Museu de Ciências e Tecnologia da PUCRS, MCT 000013907), suggesting that the species is able to reproduce in isolated lakes with no brackish water or any movement to a river channel (landlocked population). In this regard, the high abundance in spring at both ends of its distribution, the Sinos River and the estuary, and spring upstream distribution records in the Taquarí and Sinos rivers, all suggest no clear pattern of upstream-downstream movements. On the other hand, Oldani et al. (2007) recorded *Parapimelodus valenciennis* as a dominant species passing through the Borland fishpass at Salto Grande Dam on the Uruguay River, which suggests some degree of upstream-downstream movement for this congener of *P. nigribarbis.*

At this time, the original suggestion by Bertaco and Becker (2000), of movements from shallow to deeper water, is certainly possible. The information gaps indicate the need for additional sampling programs to reach a full understanding of *P. nigribarbis* biology, including larval surveys and a program of seasonal sampling with both seines and gillnets along the full gradient of the Patos Lagoon, from a large tributary (including marginal lagoons) to the estuarine region. In addition, otolith lifetime transects of Sr:Ca and Ba:Ca could be very informative to identify any movement from fresh to more-saline waters (Chapman et al., 2012b). Although *P. nigribarbis* could be found from estuarine waters to far upstream in seasonal patterns of abundance, with the sampling gear used, the species cannot be classified as diadromous and is apparently an opportunistic potamodromous planktivorous fish that reproduces throughout its distributional range.

A recent review of the Atlantic sabretooth anchovy *L. grossidens* biology was presented by Mai and Vieira (2013). Reproduction of the species is reported for spring and summer months, and the size at first maturity is estimated

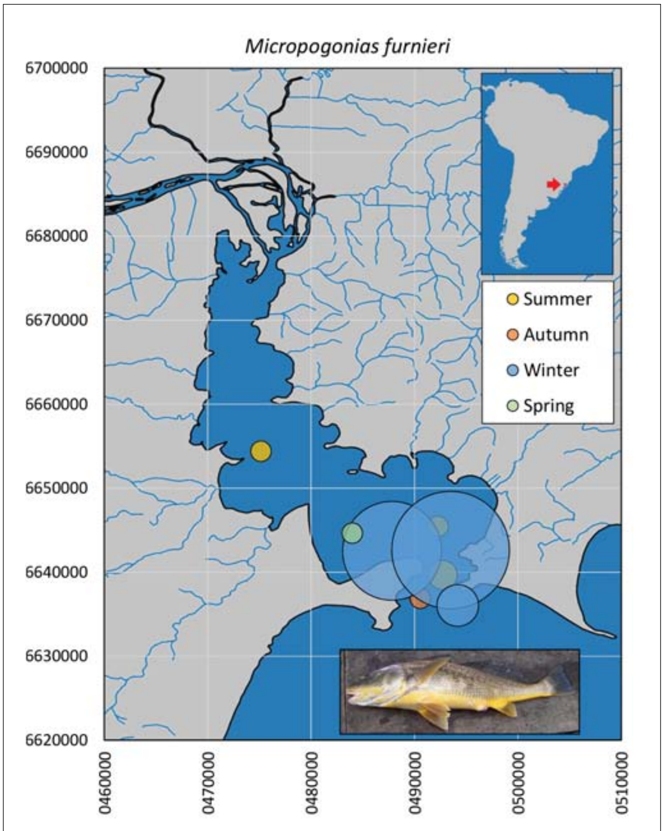

FIGURE 6 | Spatial and seasonal relative abundance of *M. furnieri* in Guaíba Lake, southern Brazil. Bubble area proportional to number of captures per site ($n = 63$ individuals). Fish photograph from Timm, C.D. available at Fishbase.com. Vector map background from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). 22J UTM coordinates.

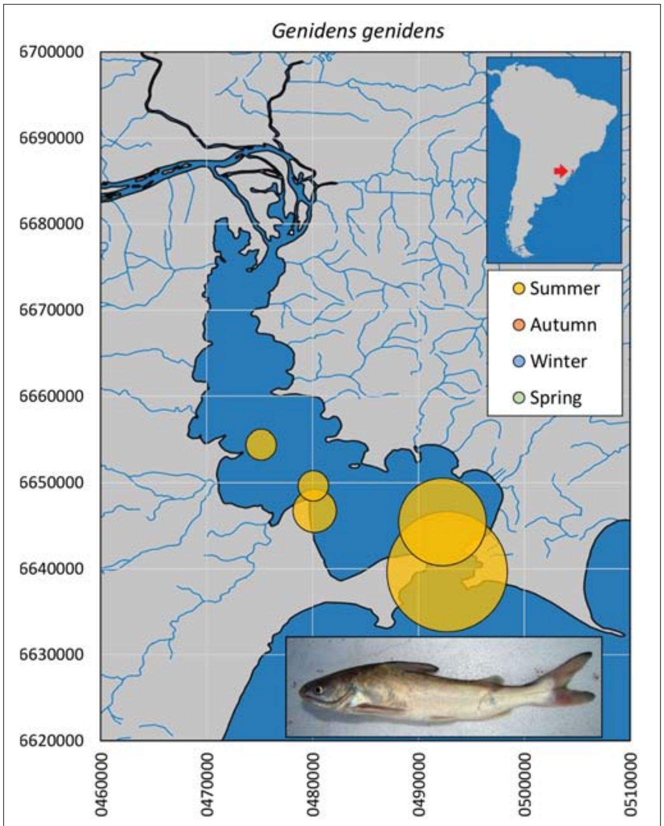

FIGURE 7 | Spatial and seasonal relative abundance of *G. genidens* in Guaíba Lake, southern Brazil. Bubble area proportional to number of captures per site ($n = 27$ individuals). Fish photograph from Timm, C.D. available at Fishbase.com. Vector map background from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). 22J UTM coordinates.

in the 8.0–13.3 cm range (total length) (Mai and Vieira, 2013). The species shows a marked shift in feeding habits, changing at ∼10 cm from planktivorous to ichthyophagous (Fontoura et al., 2015).

Lycengraulis grossidens is eurytopic in fresh to coastal waters (Whitehead et al., 1988; Barletta et al., 2010) and was classified as facultatively amphidromous by Mai et al. (2014). Although described as an estuarine reproducer, the species is presumed to spawn in fresh water because larvae (reported as *Lycengraulis olidus*) have been found immediately downstream from the Salto Grande Dam on the Uruguay River, roughly 370 km upstream from the Uruguay-Paraná Delta (Fuentes et al., 2016).

By analyzing the Sr:Ca and Ba:Ca ratios, Mai et al. (2014) identified at least four distinct patterns of habitat use for *L. grossidens*: freshwater residents, estuarine/marine residents, and two distinct diadromous/nomadic types. Nevertheless, even the so-called freshwater stocks are not completely isolated. Oldani et al. (2007) reported *L. grossidens* as a dominant species in the Borland fishpass system at the Salto Grande Dam on the Uruguay River, although they provided no information on the direction of the movements. Unfortunately, live-time Sr:Ca and Ba:Ca ratios for *L. grossidens* in the Uruguay River were reported for only one specimen by Mai et al. (2014). They found a marked change in the Sr:Ca and Ba:Ca ratios measured before and after the first annulus. Younger fish showed higher ratios of Ba:Ca and Sr:Ca, typical of freshwater development; but after the first annulus, the Ba:Ca and Sr:Ca values became more similar, suggesting a possible movement between habitats or an ontogenetic shift in ion absorption-deposition.

Mitochondrial DNA analysis (control region, 1017 bp) of fish from estuarine areas in southern Brazil (Patos Lagoon and Mampituba River), the La Plata estuary and a landlocked population in the Uruguay River (Mai et al., 2016) revealed increased haplotype diversity in estuarine samples. Although most fish from the Uruguay River grouped together with all estuarine *L. grossidens*, Mai et al. (2016) found a clade of low diversity and exclusive haplotypes in the Uruguay River samples, a clade segregated from estuarine samples (except for one individual) and closer to the outgroup (*Lycengraulis poeyi*). According to Mai et al. (2016), the haplotype structure suggests that the Uruguay population is an ancestral lineage and the phylogenetic history is compatible with a north-to-south

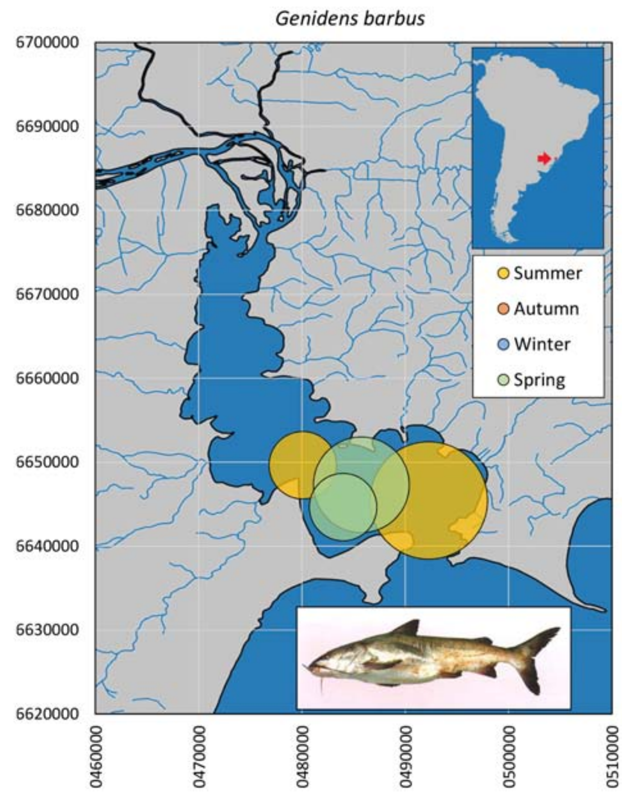

FIGURE 8 | Spatial and seasonal relative abundance of *G. barbus* in Guaíba Lake, southern Brazil. Bubble area proportional to number of captures per site (7 individuals). Fish photograph from Sverlij, S. available at Fishbase.com. Vector map background from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). 22J UTM coordinates.

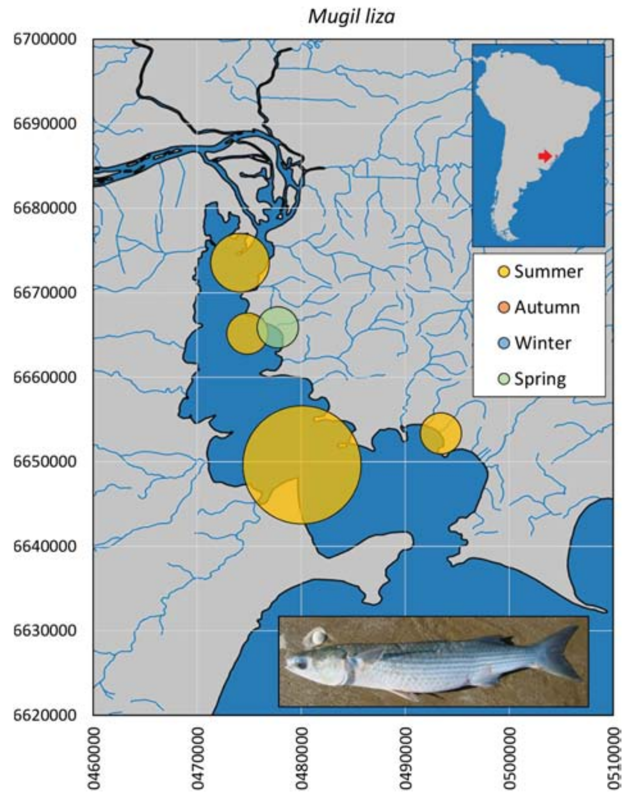

FIGURE 9 | Spatial and seasonal relative abundance of *M. liza* in Guaíba Lake, southern Brazil. Bubble area proportional to number of captures per site (13 individuals). Fish photograph from Timm, C.D. available at Fishbase.com. Vector map background from FEPAM open database (http://www.fepam.rs.gov.br/biblioteca/geo/bases_geo.asp). 22J UTM coordinates.

continental colonization route from the Amazon to the Paraná-Uruguay basins. In this respect, the transition to estuary and coastal regions would be a new evolutionary event.

Nevertheless, a broader interpretation of the distribution pattern of the species could go in another direction. Considering the coastal lagoons of Rio Grande do Sul, *L. grossidens* is not present in Barros Lagoon, although presumed to be present (as *P. nigribarbis*) in regard to the ancient Barros-Patos connection. The species is also absent from other isolated coastal lagoons (L.H. R. Rodrigues, personal communication) that were formed in the last oceanic regression around 5–8 ka ago, although present in lagoons with some connection to the sea. Therefore, the question arises of why the species disappeared from closed coastal lagoons where it was presumed to be present some time ago (hundreds or thousands of years), but is still present as a landlocked population in the Uruguay River?

One hypothesis is that the species is able to reproduce successfully in fresh water, a hypothesis supported by the presence of larvae immediately downstream from Salto Grande Dam (we assume that larvae will not migrate > 300 km upstream from estuarine areas, swimming against strong river currents). This hypothesis was suggested long ago, during a sampling program in the Fortaleza Lagoon (30.130°S, 50.234°W) in 1992, when specimens of *L. grossidens* only 4.0 cm long were found upstream from a small dam (~1 m high) that obstructed the route from estuarine areas only 10 km downstream. Although a 1-m leap is easy for many fish species, this is probably not the case for *L. grossidens* individuals only 4 cm long, as they are proportionally very long and fragile.

A possible hypothesis is that in freshwater conditions, eggs and larvae are under increased stress, with consequently reduced viability. This hypothesis could explain why the species is now absent from isolated coastal lagoons, although it had the opportunity to colonize them within the last few thousand years. This hypothesis also explains the lower haplotype diversity in the Uruguay River in comparison with estuarine samples, a result of possible selective pressures. In this regard, the exclusive haplotypes in the Uruguay River could be the result of strong selection pressures, making some haplotypes frequent that in estuarine areas are rare and therefore are not collected. This hypothesis also agrees with the higher haplotype diversity in estuarine areas.

However, why did Mai et al. (2016) conclude exactly the opposite, inferring that the Uruguay River stock is an ancestral

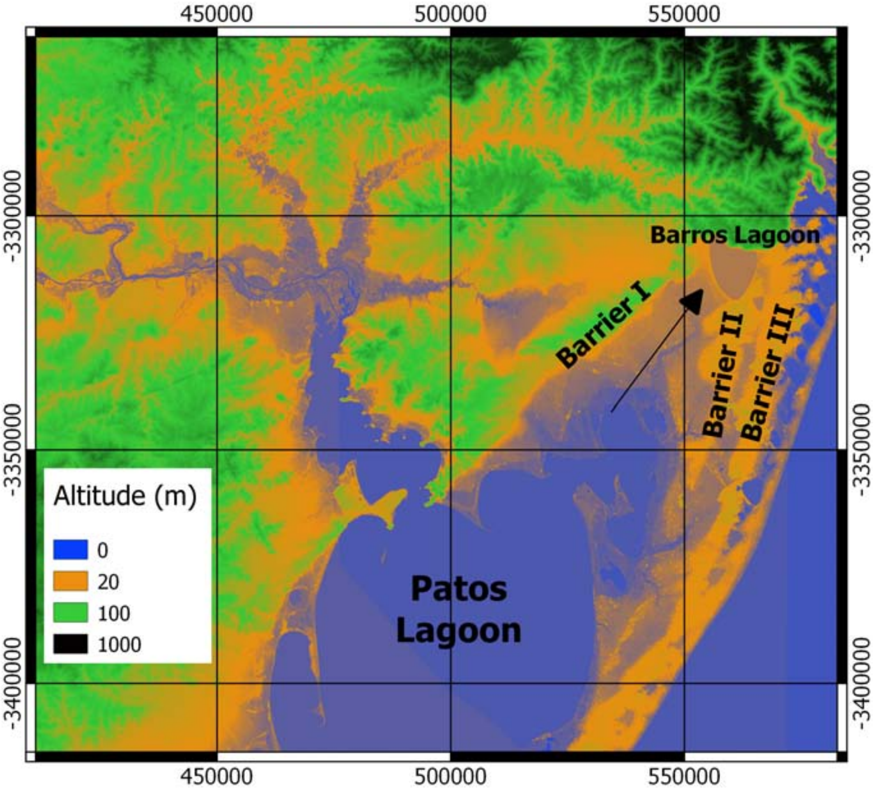

FIGURE 10 | Northern Patos Lagoon and depositional sand barriers from marine transgressions and regressions during the Pleistocene. Barriers I, II and III were formed at 325, 230 and 125 thousand years, respectively (Rosa et al., 2017). Arrow indicates a possible connection between Patos Lagoon and Barros Lagoon through lowland areas. Digital Elevation Model at 30 × 30 m resolution (EPSG:32622 – WGS 84/UTM zone 22N – Projected).

lineage after applying several tools for genetic analysis? This could be because these authors interpreted their data as populations in Hardy–Weinberg equilibrium, which is probably not true for the Uruguay stock. If we are correct, the Uruguay population above Salto Dam could be suffering from selective pressures, especially on the egg and larval stages, and could become extinct in the near future, as in the isolated coastal lagoons of Rio Grande do Sul. The extinction process could last from hundreds to thousands of years, but is a plausible scenario.

Concerning the data analyzed in the present study, *L. grossidens* was restricted to lower stretches of the Sinos River in spring and summer months, while present year-round throughout the lake in Guaíba Lake, although tenfold more abundant in spring, indicating seasonal movement. Although we used gillnets exclusively, Lucena et al. (1994) used beach seine nets (5-mm mesh) in monthly samples, with larger catches in autumn and spring, and caught several individuals as small as 4 cm in April 1990. These tiny specimens either hatched in fresh water or migrated > 200 km from estuarine waters.

Nevertheless, as for *P. nigribarbis*, these information gaps require further investigation, and programs to sample plankton from the upper Patos basin to the estuarine region should be developed in the future. Although this complex species continues to defy our understanding, it seems that *L. grossidens* is a partial migrator *sensu* Chapman et al. (2012a), and also has a very versatile lifestyle (life-history polymorphism), with part of the population migrating from fresh water to estuaries for spawning (semi-catadromy), some remaining in fresh water (with no identified movement pattern), and some moving from marine environments to brackish waters for spawning (semi-anadromy) (Chapman et al., 2012b; Mai and Vieira, 2013, Mai et al., 2014). However, as the movements involve reproduction, it seems more appropriate to classify the species as facultatively diadromous instead of facultatively amphidromous *sensu* Mai et al. (2014).

The whitemouth croaker *M. furnieri* is classified as an estuarine-dependent species and can be found from the upper limnetic part of the Patos Lagoon to the adjacent marine surf zone and shelf, using estuaries as nursery grounds (Costa et al., 2014). Size at sexual maturity is in the range of 18–20 cm (Castello, 1986), with a spring-summer migration to reproduce in saline waters (Muelbert and Weiss, 1991).

Costa et al. (2015) modeled the spatial and temporal distribution patterns of the species in the estuarine area of the Patos Lagoon. Maps of the presumed distribution were presented for different size classes and season of the year. Although the authors studied a limited area, comprising roughly the southernmost 10% of the lagoon (estuary), there was a clear spatial distribution pattern, with small individuals in both the 30–90 mm and 90–160 mm ranges expanding their distribution northward to less-saline waters in winter and spring.

Records from museum specimens for *M. furnieri* in the core of the Patos Lagoon are sparse (MCP 9121–9124, 9141), except for the north (Guaíba) and south (estuary) ends. Dated samples (n = 10) from the northern limnetic distribution comprised individuals captured in summer (n = 3, MCP 3700, UFRGS 1056 and 8481), autumn (n = 4, MCP 25583, 2583, 16334 and 27439) and winter (n = 3, MCP 28043, 28045 and 28044), with no catches recorded in spring. Lucena et al. (1994), from monthly samples taken with a beach seine in southern Guaíba Lake, recorded only two captures of *M. furnieri* in autumn. In a more-recent sampling program, using surface and bottom gillnets (adjacent knots: 35, 40, 45, 50, 55, 60 and 65 mm), Ceni et al. (2016) captured *M. furnieri* in the northern Patos Lagoon in the size range of 10–55 cm (total length). The species was present year-round and was 3–4-fold more abundant from August to October. Summarizing the available information, *M. furnieri* is well distributed along the Patos Lagoon and Guaíba Lake, although with no recorded occurrence in tributary rivers forming the Guaíba Delta. Even though it is present year-round in both limnetic (lagoon and lake) and estuarine areas, there is a pattern of spring and summer migration to reproduce in more-saline waters.

The available data add new evidence to clarify the general pattern for the spatial and temporal distribution of *M. furnieri*. First, the species does not move toward the rivers forming the Patos Basin, as no specimens were caught in the extensive Sinos River sampling program, in agreement with its absence from museum collections. Unfortunately, the smallest mesh size used by Ceni et al. (2016) was 35 mm (adjacent knots), and direct comparison of the species size profile with the present samples (taken using mesh sizes from 15 mm) is not possible. Nevertheless, it is clear that *M. furnieri* could be present in the northern Patos Lagoon and Guaíba Lake during all months of the year, from juveniles to adults, although mostly juveniles occur in southern Guaíba Lake in winter. The anadromous migration pattern could be more complex, with possible partial migration. Movement from coastal waters to the estuary for spawning is well established (Muelbert and Weiss, 1991), but the seasonal estuarine pattern proposed by Costa et al. (2015) is more complex than described, as the species could spread far beyond into fresh waters. A general pattern of higher winter abundance in northern fresh waters prior to a spring spawning in the estuary suggests a more-complex migration pattern. Also, the presence of adult *M. furnieri* in the northern Patos Lagoon year-round (Ceni et al., 2016) suggests a more intricate pattern of habitat occupation (life-style polymorphism), with adult individuals not returning to the sea after reproducing, and perhaps spending their entire lives in fresh to brackish waters. Analysis of the Sr:Ca and Ba:Ca ratios is needed to resolve these questions, and a full understanding of *M. furnieri* life history is still to come.

Three species of marine catfishes have historically been recorded in Patos Lagoon: *G. barbus, G. genidens* and *Genidens planifrons* (Chao et al., 1985; Reis, 1986), although only *G. barbus* and *G. genidens* were captured in Guaíba Lake in the present study. According to Brazilian regulations (Portaria MMA 445/2014) *G. barbus* is considered Endangered (EN) and *G. planifrons* Critically Endangered (CR), with captures and trade forbidden (RS State Law No. 5 797, 2014).

Ceni et al. (2016), describing the artisanal fishery in the northern Patos Lagoon, reported that *G. barbus* had a 25-fold larger captured biomass than *G. genidens*. In the present study, both species were captured in small numbers in the southern Guaíba Lake, although *G. genidens* was far more abundant (*G. genidens,* n = 27; *G. barbus,* n = 7). The biomasses for the two species were quite similar (∼ 6 kg), suggesting that the artisanal fishery targets *G. barbus* in the northern Patos Lagoon by selecting larger gillnet mesh sizes.

Genidens barbus is a typical anadromous species, migrating from coastal to estuarine waters for spawning, where the males mouth-breed eggs and juveniles (Reis, 1986; Haimovici, 1997). Nevertheless, the seasonal patterns of occurrence of *Genidens* catfishes in the northern Patos Lagoon and Guaíba Lake are still obscure, with contradictory information. Milani and Fontoura (2007), monitoring fishery landings of marine catfish (*Genidens*, but with no species identification) identified captures during all months of the year, but with no clear pattern in the 2002 survey, although they reported higher landings from May through September in 2004. This contradictory result was explained by a moderate El Nino in 2003–2004, which caused higher rainfall in southern Brazil and may have affected the *Genidens* reproductive and migratory cycles.

Ceni et al. (2016), monitoring an artisanal fishery in the northern Patos Lagoon, also observed that both *G. barbus* and *G. genidens* were present during all months of the year, with higher abundances from August through January. This cycle agrees with the descriptions by Reis (1986) and Haimovici (1997), but conflicts with the higher abundances in May through September reported by Milani and Fontoura (2007) in 2004 landings.

In the present study, *G. genidens* was captured only in summer (mainly January and some in February) in the southern Guaíba Lake, whereas *G. barbus* was captured in spring and summer (beginning of December through January). Both species were captured in the downstream areas of Guaíba Lake, and none in the Sinos River. By checking museum records, more upstream movements for both species were identified, with recorded occurrences in the northern Guaíba Lake in October and November (*G. barbus,* MCP 3763; *G. genidens,* UFRGS 5819).

The low captures of both species are not sufficient to establish a clear cycle of occurrence, but one must note that some specimens were caught in the far-upstream part of the range just when the described reproductive cycle would predict movement to coastal waters (Reis, 1986; Haimovici, 1997). The available data and the landings reported by Milani and Fontoura (2007) suggest that the migratory cycles of *Genidens* species could be much more complex than previously described, with remarkable plasticity in the way that individuals respond to environmental factors. Although both species could be classified as anadromous, they show complex movement patterns that may include partial migration.

The life cycle of the gray mullet *M. liza* comprises reproductive migrations each autumn from Argentina and southern Brazil to spawn between northern Santa Catarina and Paraná (Lemos et al., 2014), with juveniles migrating to estuarine areas to grow, in a typical catadromous strategy (Vieira, 1991; Vieira and Scalabrin, 1991; Lemos et al., 2014).

The present data show that *M. liza* was present throughout Guaíba Lake during spring and summer, although not caught in the Sinos River. Occurrence data from museum specimens record its presence from November (UFRGS 17771) to March (MCP 14702) in Lake Guaíba, with no records in tributary rivers. Interestingly, the species was present in the Dilúvio River, a small and very eutrophic channeled river receiving Porto Alegre city drainage and untreated domestic sewage. The reason that *M. liza* (with the introduced cf. *Oreochromis niloticus*) is attracted to these heavily polluted waters is unknown, but probably related to organic-rich sediments (cf. YouTube videos of *M. liza* caught in the Dilúvio River)[2,3].

Milani and Fontoura (2007) reported captures of *M. liza* in the northern Patos Lagoon during all months of the year, but with a marked increase from October through February, mainly during the fishery closed season (November 1 to January 31 in the northern Patos Lagoon). On the other hand, in a more recent survey, Ceni et al. (2016) did not record captures during the closed season. The mullet was captured by the artisanal fleet from February to October and was 5–6 times more abundant from August through October (280 individuals 10,000 m^{-2} day^{-1}). If one compares scientific captures with a set of mesh sizes, including smaller mesh sizes than are usually used by the artisanal fishery, *M. liza* showed increased captures from February to April, probably mainly sub-adults. In this regard, this mullet is present year-round in fresh waters, mainly lentic ones, with lower abundances of adults during the autumn and winter when most adults are moving to coastal waters for spawning. Although this general cycle has been described previously, the upstream limits of the mullet in the Patos Lagoon are now better documented.

Finally, the new data presented here and comparison with information available in the literature improved the understanding of the movements of fish between fresh, estuarine and ocean waters. Nevertheless, some information gaps are still in need of further investigation, especially the midsection of the large Patos Lagoon and its main tributary, the Jacuí River. For both, systematic sampling programs directed toward all life stages, larvae, juveniles and adults, are mandatory to fill the existing lacunae in knowledge, for a better understanding of fish biology and to support environmental management policies.

ETHICS STATEMENT

This research was approved by the Comissão de Ética no Uso de Animais (Ceua – PUCRS) and all animal collections were approved by IBAMA.

AUTHOR CONTRIBUTIONS

NF organized the Guaíba sampling project and prepared the first version of the manuscript. US performed the Sinos River sampling project and revised the manuscript. TA and TS conducted the Guaíba sampling program, sampling trial, and organization, and revised the manuscript. JP organized the Sinos data set and revised the manuscript. DA participated in the Sinos River sampling program and revised the manuscript.

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[2] https://www.youtube.com/watch?v=W25yUE7BdZc

[3] https://www.youtube.com/watch?v=txMejbrZDtQ

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frontiers in Marine Science

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Geomorphological Classification of the Benthic Structures on a Tropical Continental Shelf

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Geomorphological research offers a valuable first step to understand the complexity of seafloor patterns that are likely to support particular fauna, thereby providing value for future targeted studies on benthic communities and habitats. The objective of this study is to perform a geomorphological classification of a tropical continental shelf, located in the north of the State of Pernambuco, Brazil, using Benthic Terrain Modeler (BTM), as a first step to characterize benthic habitats. The classification of the seabed is based on the bathymetry, broad-scale and fine-scale BPI (Benthic Positioning Index), seafloor slope, and a decision table containing definitions and thresholds appropriate to the data input. The relationships between morphology and the deposition of surface sediments were also investigated. Results from the BTM analysis revealed eight types of benthic structures: Flat Plains, Depressions, Gentle Slopes, Steep Slopes, Flat Ridge Tops, Rock Outcrop Highs, Local Pinnacles in Depressions and Local Pinnacles on Broad Flats. The results from this study may therefore assist in selecting priority areas to investigate, supporting better marine spatial planning in the region, and, in the future, collaborating to determine biodiversity patterns in Brazilian waters.

Keywords: potential habitats, Benthic Terrain Modeler, terrain attributes, single-beam echosounder, tropical Atlantic Ocean

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INTRODUCTION

Geomorphological research is a tool to understand the complexity of seafloor patterns. These patterns can condition a number of environmental characteristics, such as light incidence, exposure to currents and waves, nutrient availability, substrate, erosion, or sediment deposition (Post, 2008; Verfaillie et al., 2009; Harris, 2012), providing a range of spatiotemporal influences on the habitat suitability of an area for benthic fauna and flora (Post et al., 2011; Lecours et al., 2015).

Within the context of seafloor habitat mapping, the term "habitat" has been defined and used in various ways (Brown et al., 2011). For example, Harris and Baker (2012) define benthic marine habitats as geographically distinct areas of the seafloor, where physical characteristics are associated with species or communities that occur consistently together. Similarly, other studies have utilized (geo) statistical methods to examine the relationship between physical, chemical and biological characteristics of the seafloor to spatially define habitats with similar characteristics (e.g., Brown et al., 2012; Lecours et al., 2016). Spatial scale in defining habitat is often a complicating factor (see discussion in Lecours et al., 2015), with several seafloors habitat mapping studies now adopting a landscape-scale approach analogous to mapping biophysical patterns in the terrestrial environment. This broad-scale approach, often underpinned by acoustic seafloor mapping data validated with *in situ* ground validation, is often referred to as "seascape" (Pittman et al., 2007), or "benthoscape" mapping (Zajac et al., 2003; Zajac, 2008; Brown et al., 2012).

"Potential habitat," as proposed by Greene et al. (2005), describes a set of distinct physical seafloor conditions (e.g., landforms, texture, etc.) without incorporating any *in situ* geological/biological ground validation data. Specific associations between the seafloor biology and the physical attributes may not be known at the initial stage of defining and mapping the potential habitats of a study site, but may be investigated at some stage in the future to define "actual habitats" (Greene et al., 2007). Potential habitat mapping, accomplished through terrain attributes, offers a robust methodology to understand the spatial distribution and complexity of benthic habitats where ground validation data is scarce (Rinne et al., 2014). It is also a valuable means of highlighting species-environment relationships routinely integrated into environmental studies around the world (Lecours et al., 2016) which, until now, have been lacking for the South Atlantic Ocean (Harris and Baker, 2012). The benthic structures describe features of seafloor geomorphology, which can be determined using spatial statistical analysis available within various Geographic Information System (GIS) software packages.

In this study, the benthic structures and their distribution on a tropical continental shelf, located in the north of the State of Pernambuco – Brazil, were investigated through geomorphological classification. Furthermore, the relationships between morphology and the deposition of surface sediments were also investigated, aiming to present the first potential benthic habitats classification for this tropical area, particularly important for ecosystem studies, since the morphology affects the distribution of benthic communities.

The study area (91 km^2) is located on the continental shelf between the coastline and the 20 m isobaths, in the northern region of the Port of Recife (Pernambuco–Brazil) (**Figure 1**). In this area, the continental shelf is 34 km wide to a maximum depth of 60 m (Camargo et al., 2015). The characteristics of the Pernambuco continental shelf are a reflection of the low continental sedimentary contribution, of the predominant tropical climate (Goes and Ferreira, 2017) and tectonism (Vital et al., 2005). Its shallow depth is related to the inefficiency of the marine processes in recent geological periods (Manso et al., 2004).

One of the main features of the northeastern Brazilian coast and continental shelf is the peculiar characteristics of coral reef and beachrock features parallel to the main shoreline axis (Laborel, 1965; Dominguez et al., 1990; Maida and Ferreira, 1997; Costa et al., 2016; Leão et al., 2016). On the shallower portion of the Pernambuco continental shelf, the presence of beachrocks is a striking feature in the landscape. These sedimentary rocks are intertidal in the shallower parts running parallel to the shoreline, and are exposed during low tides, while remaining completely submerged at greater depths (Mabesoone, 1964; Laborel, 1970; Maida and Ferreira, 1997). The topography of the continental shelf includes both positive and negative features (reef banks of various origins, channels, among others), and the micro relief is a direct response of the seafloor to the prevailing hydrodynamic conditions (Araújo et al., 2004; Costa et al., 2016).

MATERIALS AND METHODS

Bathymetric Data

The bathymetric database consists of single-beam echosoundings, collected in the scope of MAI Project (Financiadora de Estudos e Projetos [FINEP] and Universidade Federal de Pernambuco [UFPE], 2009). It was performed using a single-beam echosounder, operating at 200 kHz and integrating a Garmin 298 GPS with antenna for navigation and positioning, at a sampling rate of three soundings per seconds. For this study, 110 profiles were conducted between the coastline and the 20 m isobaths (**Figure 1**). These profiles were arranged perpendicular to the main axis of the coast and were spaced at approximate intervals of 200 m. All depth values were adjusted for tidal variation using tidal prediction form the Brazilian Hydrographic Service.

All bathymetric data (55,102 points) were pooled and submitted to a natural neighbor interpolation method to create a raster surface with 10 m cell size, to generate a digital bathymetric model (DBM) of the seafloor. This cell size was chosen because it best represented the existing conditions in the bathymetric profiles. Other tests were performed, with cells of 20, 40, and 100 m, in which loss of resolution was observed when comparing the interpolated surface to the bathymetric profiles of the area.

Increased survey density and use of multibeam echosounders provide the opportunity for higher reliability hydrographic survey, which would improve identification of seafloor morphology. The existing data set, with widely spaced survey lines, generates anisotropic effects in the spatial interpolation, creating artifacts, which are present in the final digital elevation model of the seafloor. This is an inherent issue related to the available survey data set. It should be noted that in a study comparing the accuracy of single-beam echo-sounder (SBE) against multibeam echo-sounder (MBE), it was found that maps produced with data acquired with the first have an average of 84% accuracy, while the second 91% (Parnum et al., 2009). We therefore consider the accuracy of the data for this study fit for purpose, allowing the first broad-scale.

Terrain Attributes Derived From Bathymetric Data

Terrain attributes can be quantitatively measured in a three-dimensional space and related to wildlife dynamics, making for the well-established field of geomorphometry (Bouchet et al., 2015). Then, these attributes derived from bathymetric data can be used as proxies for habitat studies (Bargain et al., 2018). As shown in the Digital Bathymetric Model (DBM) (**Figure 2**), terrain attributes such as seafloor slope and Bathymetric Position Index (BPI - at fine and broad-scales) were derived using the Benthic Terrain Modeler (BTM), an extension to ArcGIS (versions 10.x).

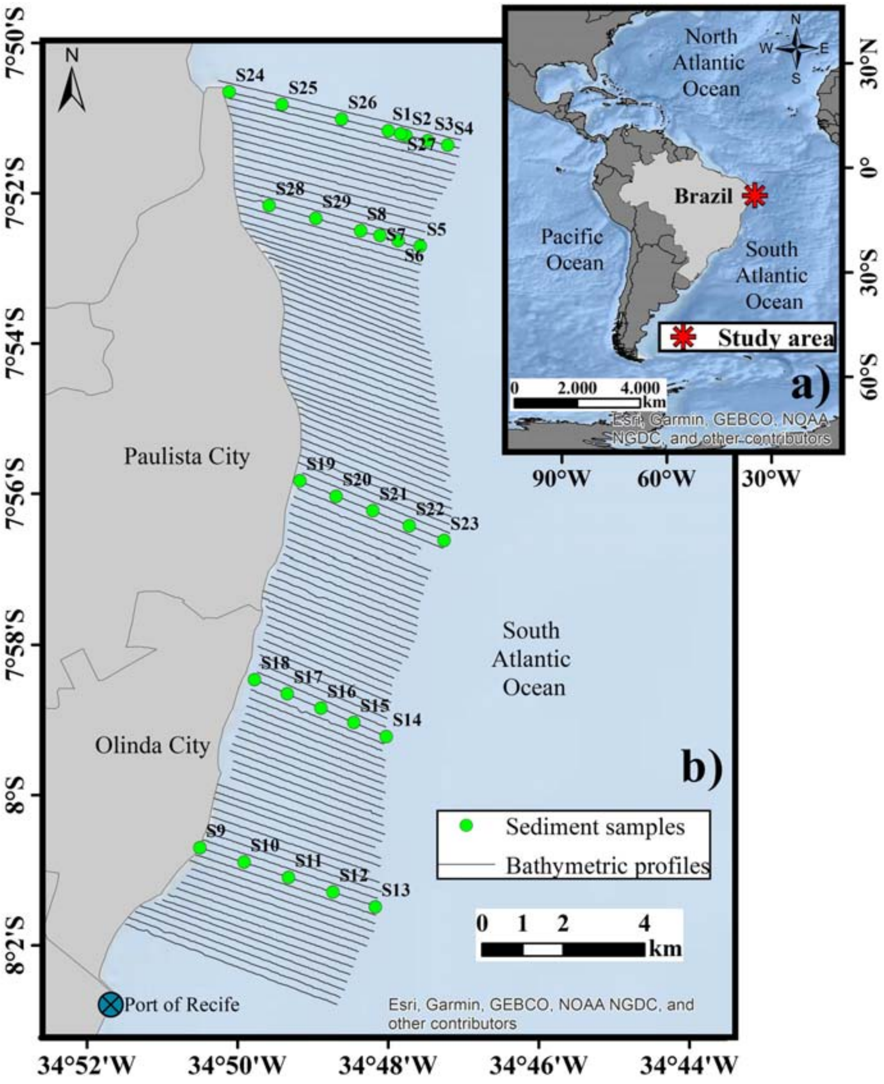

FIGURE 1 | (a) Location map of the study area; **(b)** Bathymetric profiles surveyed and sediment samples at the study area.

Benthic Terrain Modeler is a GIS classification approach, which uses a combination of derived terrain attributes to segment the seafloor into geomorphic classes. It was developed by the Department of Geosciences of Oregon State University in collaboration with the National Oceanic and Atmospheric Administration (NOAA) GIS Integration and Development Program (Wright et al., 2005; Lundblad et al., 2006). Slope is defined as a gradient toward the maximum slope of the ocean floor (Lundblad et al., 2006; Jerosch et al., 2015). Expressed in degrees, it is understood as a fundamental ground attribute to the analysis of the seafloor, whereas the slope of the terrain exerts influence on the currents, influencing the rate of erosion in a given area and allowing different adjustments to the distribution of organisms (Kostylev et al., 2003). BPI is a measure of relative elevation of the general marine landscape. It calculates, on user-defined scales, the difference between the elevation of a DBM focal cell relative to the average elevation of surrounding cells (Erdey-Heydorn, 2008; Jerosch et al., 2015). Negative BPI values mean that focal cells have lower values than the surrounding cells, configuring structures such as valleys. Positive BPI values mean that focal cells have higher values than their surrounding ones, forming structures such as ridges. BPI values close to zero are related to flat or constant slope areas (Lundblad et al., 2006).

Once BPI data sets were created at both fine and broad-scales, the next step in the classification process was to standardize the values of these raster data sets, because the elevation tends to be spatially auto-correlated (Weiss, 2001; Erdey-Heydorn, 2008). These BPI data were standardized by subtracting the mean value of the BPI data from each BPI data point and dividing by the standard deviation; in this way the BPI data point had a value of 0 and the standard deviation had a value of −1/1. The standardized value of each data point was then multiplied by 100 (Wienberg et al., 2013). This allows for the same basic equations to be used to classify any scale combinations of BPI grids. The

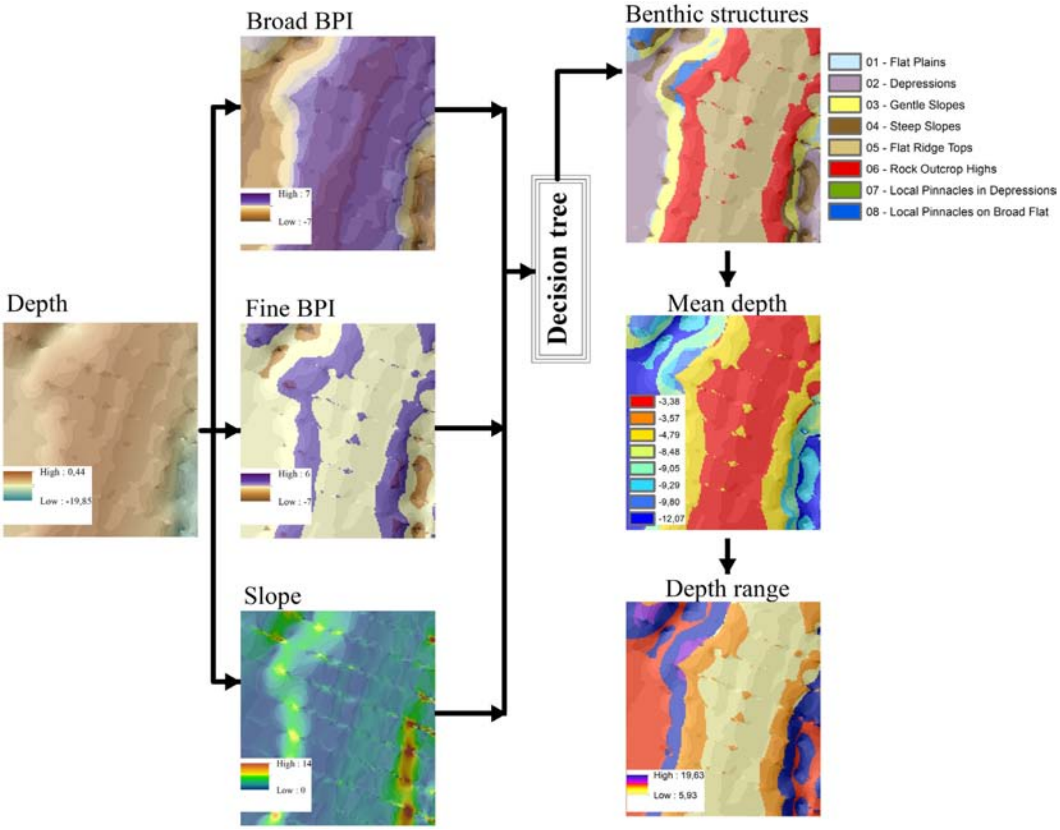

FIGURE 2 | Flow chart of morphology classification scheme using terrain attributes for the study area. The final products (last image column) represent the topographical characteristics based on bathymetry and derived products (BPIs and slope).

exact breakpoints among classes can be manually chosen to optimize the classification for a particular landscape and problem (Weiss, 2001). Therefore, conclusions about the structure of the overall seascape were produced with spatial analysis by applying an algorithm that combines standardized BPI grids of different scales with slope and bathymetry (Lundblad et al., 2006).

Geomorphological Classification

The geomorphological classification is based on the ensemble analysis between DBM, broad-scale and fine-scale of the Bathymetric Position Index (BPI), and slope (**Figure 2**). A decision table containing definitions and thresholds is applied to the data to classify the existing benthic structures in the study area (**Table 1**). The decision table used in this work is based on and adapted from previous works (Lundblad et al., 2006; Erdey-Heydorn, 2008; Wienberg et al., 2013), and defines eight benthic structure/potential habitats. These are Flat Plains (ID 01), Depressions (ID 02), Gentle Slopes (ID 03), Steep Slopes (ID 04), Flat Ridge Tops (ID 05), Rock Outcrop Highs (ID 06), Local Pinnacles in Depressions (ID 07), and Local Pinnacles on Broad Flats (ID 08).

In order to obtain BPI in broad and fine-scales, inputs such as those from the literature (Lundblad et al., 2006; Erdey-Heydorn, 2008; Wienberg et al., 2013), were adapted to meet the requirements of the morphology of this tropical continental shelf. For fine-scale BPI, an internal radius of 10m and an external radius of 25 m were used. For the broad-scale, an internal radius of 10 m and an external radius of 100 m were chosen.

In the BTM, slope and the BPI grids were computed from the bathymetry raster. To avoid the influence of spatial autocorrelation in the broad-scale and fine-scale BPIs, the BPIs were standardized to 1 standard deviation, as proposed by Weiss (2001). For the geomorphological classification of the seafloor, the slope was used in the decision table (**Table 1**) to distinguish the thresholds between Flat Plains (ID 01) (up to 1 degree inclination), Gentle Slopes (ID 03) (1 to 5 degrees inclination), Steep slopes (greater than 5 degrees inclination) and Local Pinnacles on Broad Flats (ID 08) (up to 1 degree inclination). Previous studies conducted in areas with a large variation in depth have also used bathymetry (depth values) in the decision table to define benthic structures (Erdey-Heydorn, 2008). As the seafloor in our study site is delimited to 20 m isobath, the seafloor classes were not differentiated based on depth.

Sedimentological Characterization of Seafloor Classes

The relationships between morphology and the deposition of surface sediments were also investigated. The benthic structures,

TABLE 1 | Decision table summarizing the factors used for the definition of benthic structures in the study area.

ID	Benthic structures	Broad-scale BPI		Fine scale BPI		Slope	
		Lower	Upper	Lower	Upper	Lower	Upper
01	Flat Plains	−100	100	−100	100		1
02	Depressions	−100	100		−100		
03	Gentle Slopes	−100	100	−100	100	1	5
04	Steep Slopes	−100	100	−100	100	5	
05	Flat Ridge Tops	100		−100	100		
06	Rock Outcrop Highs	100		100			
07	Local Pinnacles in Depressions	100			−100		
08	Local Pinnacles on Broad Flats	−100	100	100			1

derived from the BTM analysis, were also analyzed in conjunction with the spatial variability of (gravel, sand and mud) fractions of the surface sediment samples.

Sedimentological characteristics were derived from 29 surficial grab samples (locations on **Figure 1**). The sedimentological analysis followed the methodology proposed by Suguio (1973) with wet and dry sieving. The resulting, sediment grain size (McLane, 1995) were analyzed using SysGran software and classified according to Folk (1954) into three classes: Gravel (>2 mm); Sand (2–0.062 mm); and Mud (<0.062 mm). In order to correlate the seafloor classes/benthic structures with the sedimentary surface composition, the percentages of mud (silt + clay), sand and gravel content of all the samples were also calculated.

RESULTS

Benthic Structures

Based on the grids of bathymetry, slope, BPIs broad-scale and fine-scale, and the decision table (**Table 1**), eight classes of benthic structures were differentiated by the BTM (**Figure 3**). In relation to bathymetry, the DBM (**Figure 3**) revealed the identification of the heterogeneity of the geomorphological features, both in size and location, mainly due to the occurrence of bank reefs and channels. In the northern part of the study area, the bank reef is closed (i.e., attached) to the coast. However, in the central part it is possible to identify the presence of two elongated bank reefs, not attached to the coast, with channels between them.

In the transition to the southern part of the area, the presence of the reef banks is not as distinctive, occurring only as discontinuous features (small patches). The bank reefs are once again present in the southern region of the study site, but not as distinguished as in the central part of the area. The most pronounced changes in the slope are related to the heterogeneity of the depth gradient, delineating the occurrence of the positive and negative reliefs.

Broad-scale BPI demonstrates the major features of the marine landscape (e.g., reefs and channels), while the fine-scale BPI captures the subtler differences in the study area (e.g., outer edges of reefs). According to the broad-scale BPI, the reef and channel demarcation is observed where the mathematically higher differences (7) coincide with the reefs, while the lower (−7) coincide with the channels. The Fine-scale BPI highlight the subtle differences in the study area. This BPI grid shows the surrounding sectors of the large features (e.g. reefs and channels), marking the boundaries between these features and the flat regions of the seafloor.

Finally, eight classes of benthic structures (**Figure 3** and **Table 2**) were recognized, occupying different percentages of surface on the explored area: Flat Plains (49.22%), Depressions (16.10%), Gentle Slopes (8.56%), Steep Slopes (5.03%), Flat Ridge Tops (5.80%), Rock Outcrop Highs (9.98%), Local Pinnacles in Depressions (>1%), and Local Pinnacles on Broad Flats (5.28%).

The Flat Plain (ID 01), was the most predominant class in the study area (49.22%), and was defined as the flat regions of the seafloor with BPI values close to zero. They are within the standard deviation of the mean (0) and have a soft slope (up to 1 degree inclination). Moreover, these areas have few changes in fine-scale BPI. Depressions (ID 02) were defined as low points on the ground, with BPIs values greater than one standard deviation from the mean in the negative direction (−1), occurring in 16.10% of the area.

Gentle Slopes (ID 03) were simpler relief zones, with no alternating of concave and convex areas. They have BPI close to zero, within the standard deviation of the mean (0), with slope varying between 1 and 5 degrees. In contrast, Steep Slopes (ID 04) were extensive regions of sloping seafloor, of BPI close to zero, within the standard deviation of the mean (0), with slope values greater than 5 degrees.

Flat Ridge Tops (ID 05) were areas where flat, broad-scale seafloor features are higher than the surrounding seafloor, and primarily comprising the top of narrow, linear structures running parallel to the coastline and without any slope. Rock Outcrop Highs (ID 06) were bathymetric high points in the field, with positive BPI values greater than one standard deviation of the mean in the positive direction (1). In these zones, the fine-scale and broad-scale features were less deep than the surroundings.

The Local Pinnacles in Depressions (ID 07) were narrow ridges within a sunken terrain, represented by the fine-scale BPI. They can be considered as high points in the field with positive BPI values greater than one standard deviation of the mean in the positive direction (1). Similarly, Local Pinnacles on Broad Flats (ID 08), correspond to narrow crests within a broader flat region of the seafloor highlighted by the fine-scale BPI. Like Local Pinnacles in Depressions (ID 07), they are considered as high points on the ground with positive BPI values greater than one standard deviation of the mean in the positive direction (1).

Association of Benthic Structures and Grain Size of the Surface Sediment

The analysis of the samples collected along the area also revealed the variety of sediment composition (**Figure 4** and **Table 3**), according to the final classification shown in

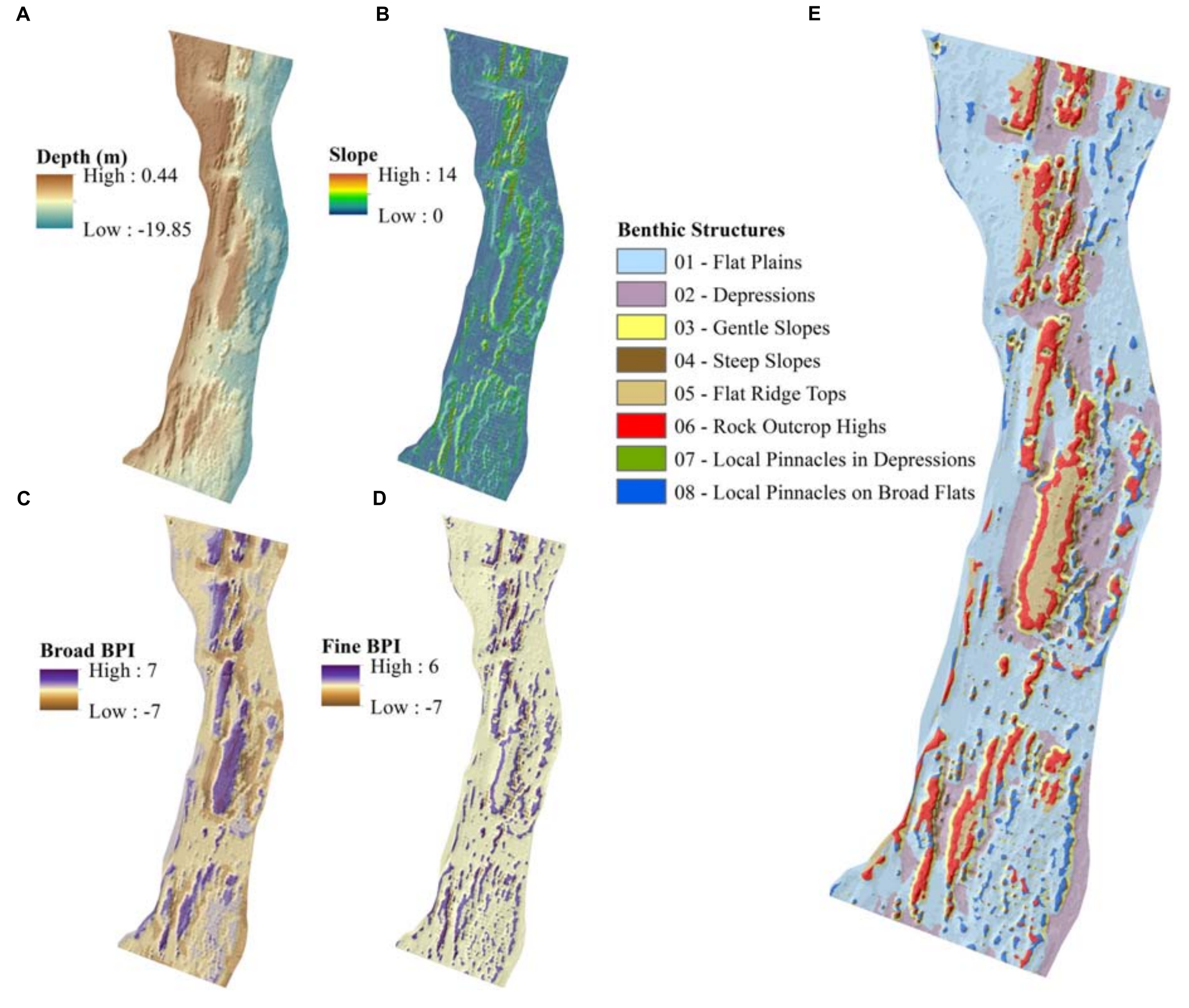

FIGURE 3 | Bathymetry database and its derivatives: **(A)** Digital Bathymetric Model (DBM); **(B)** Slope; **(C)** Broad-scale Bathymetric Position Index (Broad-BPI); **(C)** Fine-scale Bathymetric Position Index (Fine–BPI); **(E)** Geomorphological classification of the study area.

TABLE 2 | Depth-related description of the geomorphological classification and the percentage of occurrence.

Structures				Depth				
ID		**Area (km^2)**	**Area (%)**	**Min. (m)**	**Max. (m)**	**Mean (m)**	**Range**	**STD**
01	Flat Plains	44.78	49.22	−19.31	0.33	−8.48	19.64	5.63
02	Depressions	14.65	16.10	−19.86	−2.64	−12.07	17.21	4.29
03	Gentle Slopes	7.79	8.56	−19.26	0.23	−9.06	19.48	4.13
04	Steep Slopes	4.58	5.03	−19.28	0.32	−9.30	19.60	3.91
05	Flat Ridge Tops	5.28	5.80	−14.88	0.29	−3.39	15.17	2.87
06	Rock Outcrop Highs	9.08	9.98	−16.34	0.43	−4.79	16.78	3.69
07	Local Pinnacles in Depressions	0.01	0.01	−8.74	−2.80	−3.57	5.94	1.05
08	Local Pinnacles on Broad Flat	4.81	5.29	−18.23	0.44	−9.81	18.67	4.66

Figure 3E. In relation to the sedimentological composition (gravel, sand, and mud), it is observed that in the Depressions (ID 02) there is a predominance of sand, while in the Gentle Slopes (ID 03) there is an alternation between the dominance of the percentages of gravel and sand.

In Local Pinnacles on Broad Flats, there is a predominance of gravel, and in the Flat Plains (ID 01), there is a substantial variation among the percentages of the sediment components; however, it is in this structure that the highest percentages of mud are found. Flat Ridge Tops (ID 05) are represented by a

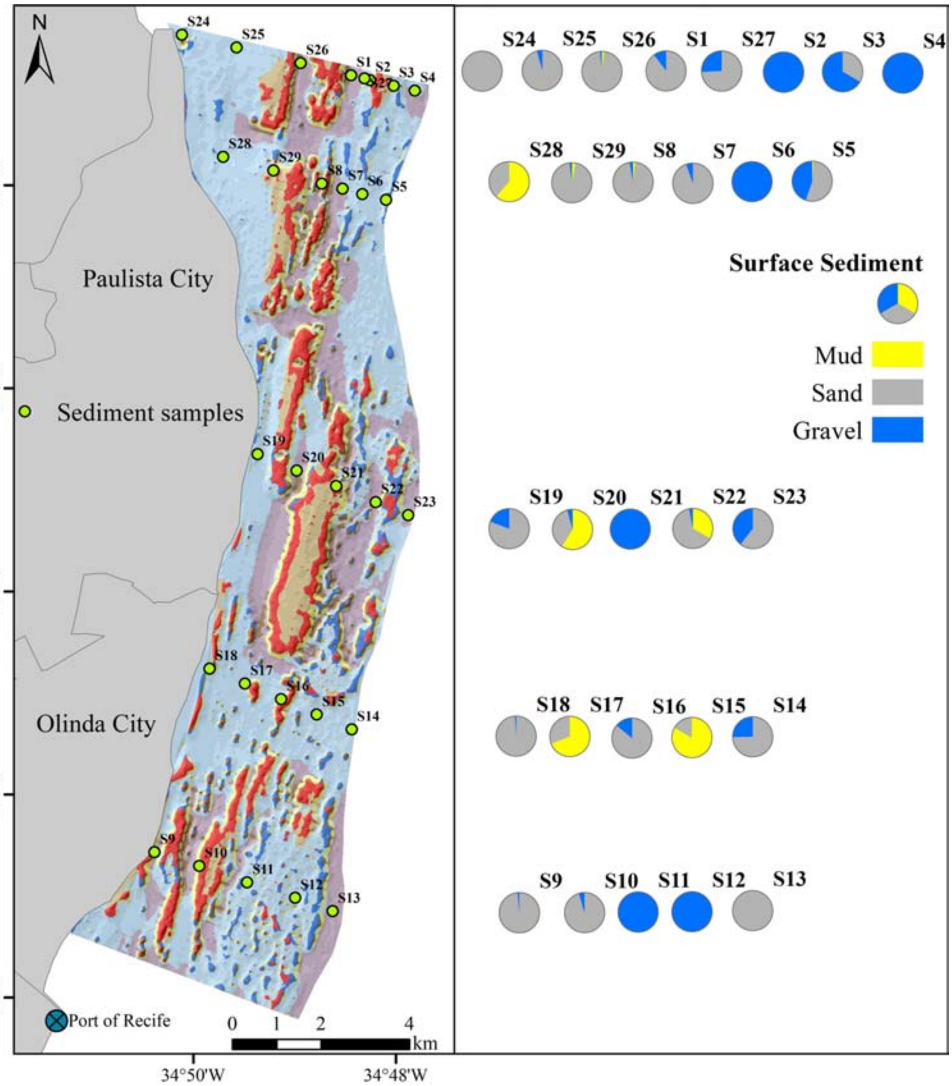

FIGURE 4 | Spatial variability in the percentages of mud, sand and gravel contents in surface sediment.

higher percentage of sand while in Rock Outcrop Highs (ID 06) an alternation of larger values between gravel and sand was observed.

DISCUSSION

In the study area, eight geomorphological classes are defined by the BTM, recognized as benthic structures (**Figure 5**). The benthic structures that occur in this tropical area highlight the heterogeneity and diversity of the seafloor of the study area. The results of the methodological process used in this study provide an unprecedented recognition of the relief patterns for the study area, not described in any previous study. The final classification can be considered a "potential habitat map" (Greene et al., 2007) and adds to the knowledge and understanding of the environmental characteristics of this area, but does not provide a complete description of benthic habitats for the study area due to the limited amount of ground validation data. However, particularly for ecosystem studies, can be considered that the morphology affects the distribution of benthic communities, influencing environmental factors (e.g. substrate, erosion or sediment deposition, currents and available nutrients) (Lundblad et al., 2006; Jerosch et al., 2015). On the other hand, according to Dartnell and Gardner (2004), a basic data set that describes the surficial characteristics of the seafloor is the baseline used for a habitat study, therefore important for ecological studies.

Although multibeam echosounder have emerged as the tool of choice for seafloor habitat modeling, because of their ability to collect both bathymetry and backscatter information simultaneously (Mumm, 2015), the use of single beam echosounder also demonstrates reasonable accuracy in seafloor habitat mapping (Parnum et al., 2009). In this sense, the proposed methodology, through the use of the BTM extension,

TABLE 3 | Mean grain size, percentages of gravel, sand, and mud of surface sediment.

ID	Benthic structures	Samples	Mean (mm)	% Gravel	% Sand	%Mud	Textural classification
01	Flat Plains	S2	–	100.00	0.00	0.00	Gravel
01	Flat Plains	S3	1.9924	66.60	33.30	0.10	Sand
01	Flat Plains	S11	–	100.00	0.00	0.00	Gravel
01	Flat Plains	S14	0.8536	25.17	74.64	0.18	Sand
01	Flat Plains	S15	0.0198	0.14	16.85	83.02	Mud
01	Flat Plains	S17	0.0410	0.28	30.80	68.92	Mud
01	Flat Plains	S18	0.4222	1.05	98.20	0.75	Sand
01	Flat Plains	S19	1.1237	19.08	80.67	0.25	Sand
01	Flat Plains	S25	0.6018	4.36	94.94	0.70	Sand
01	Flat Plains	S27	1.1340	25.69	74.11	0.20	Sand
01	Flat Plains	S28	0.0243	0.1256	38.64	61.24	Mud
02	Depressions	S7	0.9991	5.586	94.24	0.17	Sand
02	Depressions	S13	0.5719	0.27	99.47	0.27	Sand
02	Depressions	S20	0.0561	4.386	36.69	58.93	Mud
02	Depressions	S22	0.1436	3.15	63.64	33.21	Sand
02	Depressions	S23	1.4803	39.45	60.41	0.14	Sand
03	Gentle Slopes	S1	1.0529	10.32	89.51	0.17	Sand
03	Gentle Slopes	S8	0.6851	2.931	95.32	1.74	Sand
03	Gentle Slopes	S10	0.9095	4.66	95.27	0.07	Sand
03	Gentle Slopes	S12	–	100.00	0.00	0.00	Gravel
03	Gentle Slopes	S24	0.2050	0	99.66	0.34	Sand
03	Gentle Slopes	S26	0.4494	1.397	97	1.61	Sand
05	Flat Ridge Tops	S29	0.2270	1.939	95.29	2.77	Sand
06	Rock Outcrop Highs	S9	0.3025	1.417	97.84	0.74	Sand
06	Rock Outcrop Highs	S16	1.0254	14.01	85.79	0.20	Sand
06	Rock Outcrop Highs	S21	–	100.00	0.00	0.00	Gravel
08	Local Pinnacles on Broad Flats	S4	–	100.00	0.00	0.00	Gravel
08	Local Pinnacles on Broad Flats	S5	1.1252	44.82	54.11	1.07	Sand
08	Local Pinnacles on Broad Flats	S6	–	100.00	0.00	0.00	Gravel

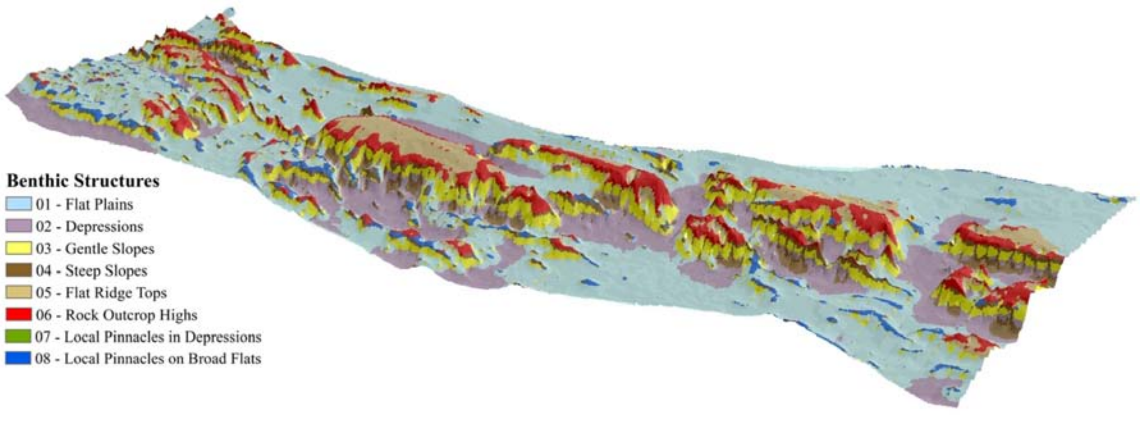

FIGURE 5 | Geomorphological classification/benthic structures of the study area.

functions as a first step for mapping the ocean floor, especially considering the widely spaced nature of available single beam surveys and the scarcity of multibeam survey data for this area. Wide spacing of survey lines creates anisotropic features in the spatial interpolation and may therefore influence the benthic habitat classification. However, in this location, the anisotropy is considered to be strongly offset by the geological structure, with long rocky ridges running almost parallel to shore. Residual effects of the interpolation include limited ability to identify slopes except along the survey lines, and large horizontal uncertainty in the alongshore scale and position of discontinuities, such as gaps between rock ridges. The constraints of survey coverage should be considered in conjunction with known characteristics of the local morphology when applying BTM to develop a potential benthic habitat model.

Pereira and Bonetti Filho (2018) presented an analysis of the background relief of three Brazilian conservation units, also from the BTM extension. National Marine Park of Fernando de Noronha (PARNAMAR Noronha), National Marine Park of Abrolhos (PARNAMAR Abrolhos), and the Biological Marine Reserve of Arvoredo (REBIOMAR Arvoredo). The analysis concluded that these areas have great morphological complexity of the seafloor. They suggested that the high biodiversity indexes, to a certain degree, may be associated with the high seafloor morphological complexity of the respective benthic structures (Pereira and Bonetti Filho, 2018).

Analysis of the sediment grain size samples in our study indicated that the highest percentage of mud was found in the Flat Plains (ID 01), while the Rock Outcrop Highs (ID 06) are marked by high levels of gravel. Likewise, in the northern region of the area, samples collected on structures classified as Local Pinnacles on Broad Flats (ID 08) were characterized by high gravel content. This configuration is observed in analyses conducted in the Weddell Sea, where coarser grain sizes appear in more exposed geomorphic features, such as crests and outcrops (Jerosch et al., 2015).

Such variation of the surficial sediment characteristics may indicate that this area has a greater variation in the communities that are associated to the sector, whereas different organisms suit the area depending on their particularities (Post, 2008; Verfaillie et al., 2009; McArthur et al., 2010). These patterns indicate possible heterogeneity in the potential distribution of benthic habitats, since changes in depth and mud contents are strongly correlated, and reflect distinct processes of association of benthic communities (Post et al., 2011).

Prominent structures on the seafloor in the study area may serve as useful proxies for estimating areas of higher biodiversity (Bouchet et al., 2015). Furthermore, the complexity of the rock forms itself presents both a greater surficial area for colonization and a greater variety of niche habitats than would a flat rock surface (Diesing et al., 2009).

The peculiar characteristics of coral reef and beachrocks feature parallel to the main shoreline axis (Laborel, 1965; Dominguez et al., 1990; Maida and Ferreira, 1997; Costa et al., 2016; Leão et al., 2016) is remarkable in this study area. These features are represented by the alternation of positive and negative BPIs, in addition to a relatively large slope.

It is concluded that approximately 40% of the area is formed by Gentle Slopes (ID 03), Steep Slopes (ID 04), Rock Outcrop Highs (ID 06), and Depressions (ID 02). These areas, which present greater morphological complexity, probably indicate regions supporting high biodiversity, given that geometrically complex surfaces are known to provide an abundance of stable, niche habitats exploited by a wide diversity of species (Kostylev et al., 2003; McArthur et al., 2010; Zawada et al., 2010; Darling et al., 2017). For this reason, they constitute a key ecological factor often positively linked to biodiversity and carry capacity of habitats (Yanovski et al., 2017; Rees et al., 2018). In contrast, 49.22% of the area is formed by Flat Plains (ID 01). These areas with low morphological complexity can be considered areas of lower biodiversity, as already observed in other studies (e.g., Kostylev et al., 2003; McArthur et al., 2010; Zawada et al., 2010; Darling et al., 2017).

The habitat heterogeneity, offered by this seafloor complexity, such as beachrocks features, is often associated with high biodiversity (Gladstone, 2007; Guevara-Fletcher et al., 2011). Studies have shown that features on the Australian shelf provide three-dimensional structures supporting benthic communities that contrast with the adjacent seabed, which is often flat (Brooke et al., 2017). Therefore, the importance of the recognition of the structural patterns present in the study area for marine environmental conservation and management plans is emphasized (Riegl and Piller, 2003).

Recently, Rinne et al. (2014) used large-scale bathymetric data to designate geographically complex areas of reef occurrences through the geomorphological analysis of the benthoscape on the northern Baltic Sea, with subsequent validation of the prediction ground-truthing. The results from our study may therefore assist in selecting priority areas to investigate, supporting improved marine spatial planning in the region, and, in the future, collaborate to determine biodiversity patterns. Furthermore, the results obtained in this work contribute to the achievement of the Aich Targets 2011–2020, regarding the improvement of the knowledge, scientific base and technologies related to the biodiversity in the Brazilian continental waters, besides the diffusion of generated knowledge (Ministério do Meio Ambiente [MMA], 2017).

Finally, this study has generated the first model of potential benthic habitats for this tropical area, which is particularly important for ecosystem studies. Over wider spatial scales or with coarser data resolutions (such as GEBCO data for example), the geomorphic classification algorithm needs to be adjusted for the scale and resolution of the underlying data.

AUTHOR CONTRIBUTIONS

EG analyzed the data and prepared the manuscript. CB assisted in the preparation of the manuscript. TA secured funds, participated in field work, and assisted in the preparation of the manuscript. All authors have read and contributed to the final version of the text.

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POLICY AND PRACTICE REVIEWS
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Lost Floodplain Wetland Environments and Efforts to Restore Connectivity, Habitat, and Water Quality Settings on the Great Barrier Reef

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Managers are moving toward implementing large-scale coastal ecosystem restoration projects, however, many fail to achieve desired outcomes. Among the key reasons for this is the lack of integration with a whole-of-catchment approach, the scale of the project (temporal, spatial), the requirement for on-going costs for maintenance, the lack of clear objectives, a focus on threats rather than services/values, funding cycles, engagement or change in stakeholders, and prioritization of project sites. Here we critically assess the outcomes of activities in three coastal wetland complexes positioned along the catchments of the Great Barrier Reef (GBR) lagoon, Australia, that have been subjected to restoration investment over a number of decades. Each floodplain has been modified by intensive agricultural production, heavy industry and mining infrastructure, urban/peri urban expansion, aquaculture development and infrastructure expansion. Most development has occurred in low-lying coastal floodplains, resulting in major hydrological modifications to the landscape. This has left the floodplain wetlands in a degraded and hydrologically modified state, with poor water quality (hypoxic, eutrophication, sedimentation, and persistent turbidity), loss of habitat, and disconnected because of flow hydraulic barriers, excessive aquatic plant growth, or establishment of invasive species. Successful GBR wetland ecosystem restoration and management first requires an understanding of what constitutes "success" and must be underpinned by an understanding of complex cause and effect pathways, with a focus on management of services and values. This approach should recognize that these wetlands are still assets in a modified landscape. Suitable, long term, scientific knowledge is necessary to provide government and private companies with the confidence and comfort that their investment delivers dividend (environmental) returns.

Keywords: estuaries, floodplains, restoration, fisheries, water quality, connectivity

INTRODUCTION

Connectivity of wetlands and drainage channels crossing coastal floodplains provides an essential habitat for a range of flora and fauna that hold cultural, social and economic values that deliver diverse amenity and ecosystem services (Baran et al., 2001; Amoros and Bornette, 2002; Buijse et al., 2002; King et al., 2003; Elliott and Whitfield, 2011; Elliott et al., 2016; Waltham and Fixler, 2017). Because of their low-lying positions, these ecosystems are the receiving environment for runoff from urban, agricultural and industrial sites (Bulleri and Chapman, 2010; Sheaves et al., 2010; Barbier, 2013), as well as being the first line of exposure to climate change and sea level rise (Kelleway et al., 2017; Pettit et al., 2018). They have also been extensively impacted by drainage and reclamation, with global floodplain wetland loss estimated at 95 km^2/years (Coleman et al., 2008), that is not likely to slow (Davidson, 2014). There is an increasing global movement by managers and community to halt this loss and degradation, and to commence large-scale programs to repair and restore coastal wetland ecosystem habitat and connectivity (Barbier, 2013).

Large-scale restoration has a long history in north America (e.g., Repair America's Estuaries[1]), and plans for extensive restoration efforts are advanced in many other parts of the world. For instance, China plans to invest $1 billion on more than 50 large programs by 2030 – with the aim of restoring and recreating wetland connectivity to mitigate poor water quality and lost habitat for local wildlife species (Dobson et al., 2007). While restoration efforts are vital (Creighton et al., 2016), access to relevant and appropriate scientific data demonstrating biodiversity and ecosystem service return for the investment are lacking (Zedler, 2016; Waltham et al., 2017).

In planning restoration projects, it is important to recognize that stakeholders (beneficiaries) have different and sometimes conflicting views or priorities when determining coastal wetland ecosystem services (Harris and Heathwaite, 2012). For example, placing high value on services such as the freshwater extraction for agriculture from floodplains can directly undermine cultural ecosystem service values related to aquatic biodiversity (Boulton et al., 2016), not to mention reduce duration and frequency of water connection across floodplains, which has biological consequences (Baran et al., 2001; Rayner et al., 2009). Ecosystem repair strategies seem to be most effective when values of all stakeholders are incorporated, a process best facilitated through discussions to set objectives early in the project lifecycle (Sheaves et al., 2014; Zedler, 2016; Guerrero et al., 2017). Scale is another important aspect, e.g., local-scale improvement of fish habitat vs. catchment-scale amelioration of agricultural fertilizer loads exported to coastal waters. Focusing at an appropriate scale is important not only for informing technical aspects of the restoration management activities, but also ensures appropriate management bodies are involved (Butler et al., 2013).

Great Barrier Reef World Heritage Area – Lost Coastal Floodplain Wetlands

Australia faces a legacy of degraded coastal wetland habitats despite a small population and a relatively short 200 years of urban/industrial development and agricultural intensification (Creighton et al., 2016). The Great Barrier Reef (GBR) lagoon (**Figure 1**), a World Heritage Area and National Marine Park, protected under an assortment of international agreements, and national, and state legislation/policies is suffering on-going poor water quality from catchment agricultural runoff and intensification (Bainbridge et al., 2009; Brodie and Waterhouse, 2012; Waterhouse et al., 2016; Dubuc et al., 2017). A causative factor is loss of coastal wetland habitats associated with agricultural and urban development expansion (Sheaves and Johnston, 2010; Sheaves et al., 2014; Waltham and Sheaves, 2015), which is reducing the GBR's resilience to future development and climate change pressures (Department of Environment Heritage and Protection [DEHP], 2016). Conservation and repair of the GBR coastal wetland ecosystems' and connectivity has only recently come into focus due to the threat of ongoing decline of the GBR, particularly around major agricultural regions (Department of Environment Heritage and Protection [DEHP], 2016; Waterhouse et al., 2016). In response, ecosystem protection and restoration has been recognized as key to reef resilience, and is now reflected in long-term strategic planning policies (e.g., Reef 2050 Plan). Reef 2050 Plan recognizes that freshwater floodplain wetlands form an important biological component of the GBR seascape and are part of the broader coral reef system that it is most famous for (**Figure 2**). However, there is still a lack of data to quantify the change that has occurred from "natural" floodplain wetland areas to the current state (Sheaves, 2016). Here the objectives are to review and assess the learnings from floodplain connectivity repair projects from the GBR catchments. In doing so, we evaluate current and developing institutional settings, in addition to funding opportunities that enable effective coastal wetland connectivity repair.

Reef 2050 Plan and Seeking the Outcomes

Numerous Australian and Queensland Government laws and policies contain provisions related to coastal habitat management in the GBR, notably the Australian Government's *Environment Protection and Biodiversity Conservation Act 1999* and the Queensland Government's *Environmental Protection Act 1994*, *Fisheries Act 1994*, *Marine Parks Act 2004*, *Planning Act 2016*, *Vegetation Management Act 1999*, and *Water Act 2000*. These generally regulate development or disturbance of coastal habitats. Offset laws and associated policies provide a mechanism to support restoration of coastal habitats. The *Queensland Environmental Offsets Act 2014* provides a framework to facilitate environmental offsets that may lead to restoration of degraded habitats, as well as point-source water quality offsets policies that may also support investment into constructing wetlands or other systems with demonstrable water quality benefits. Proposed changes to reef protection regulations would include a water quality offset framework, which may trigger coastal habitat

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[1] www.estuaries.org

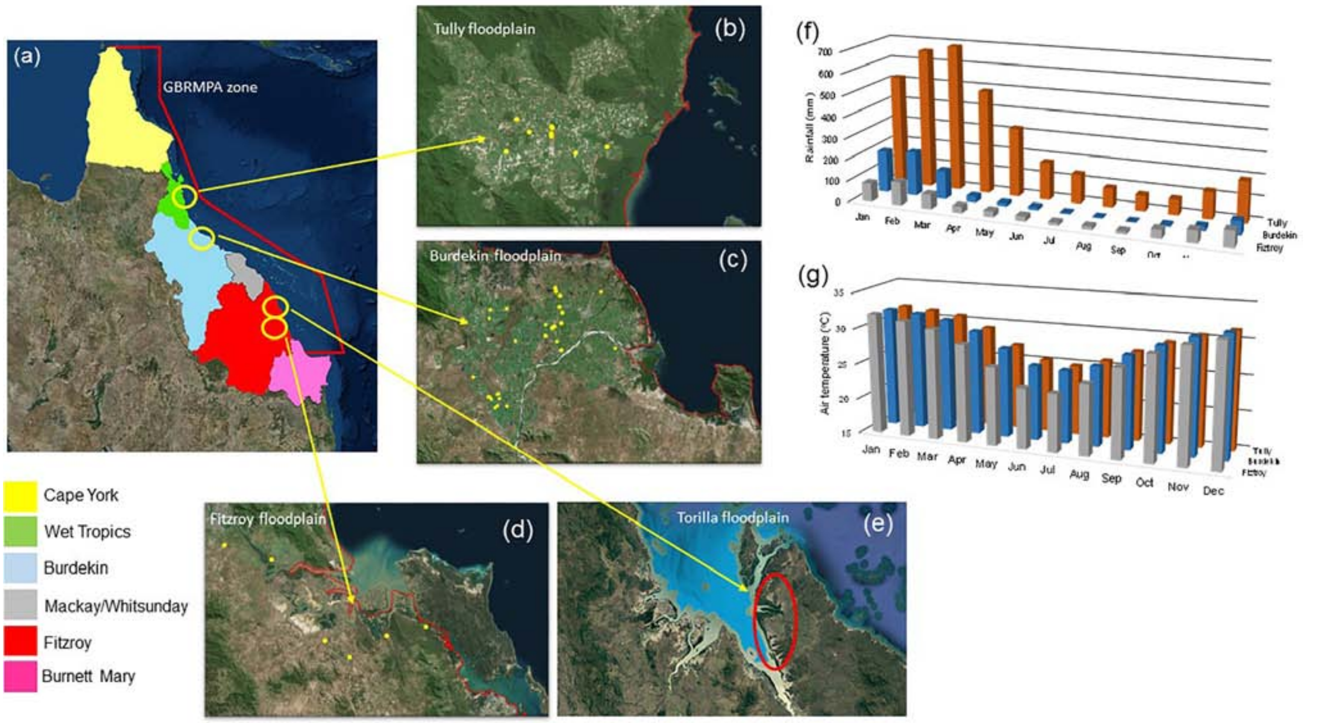
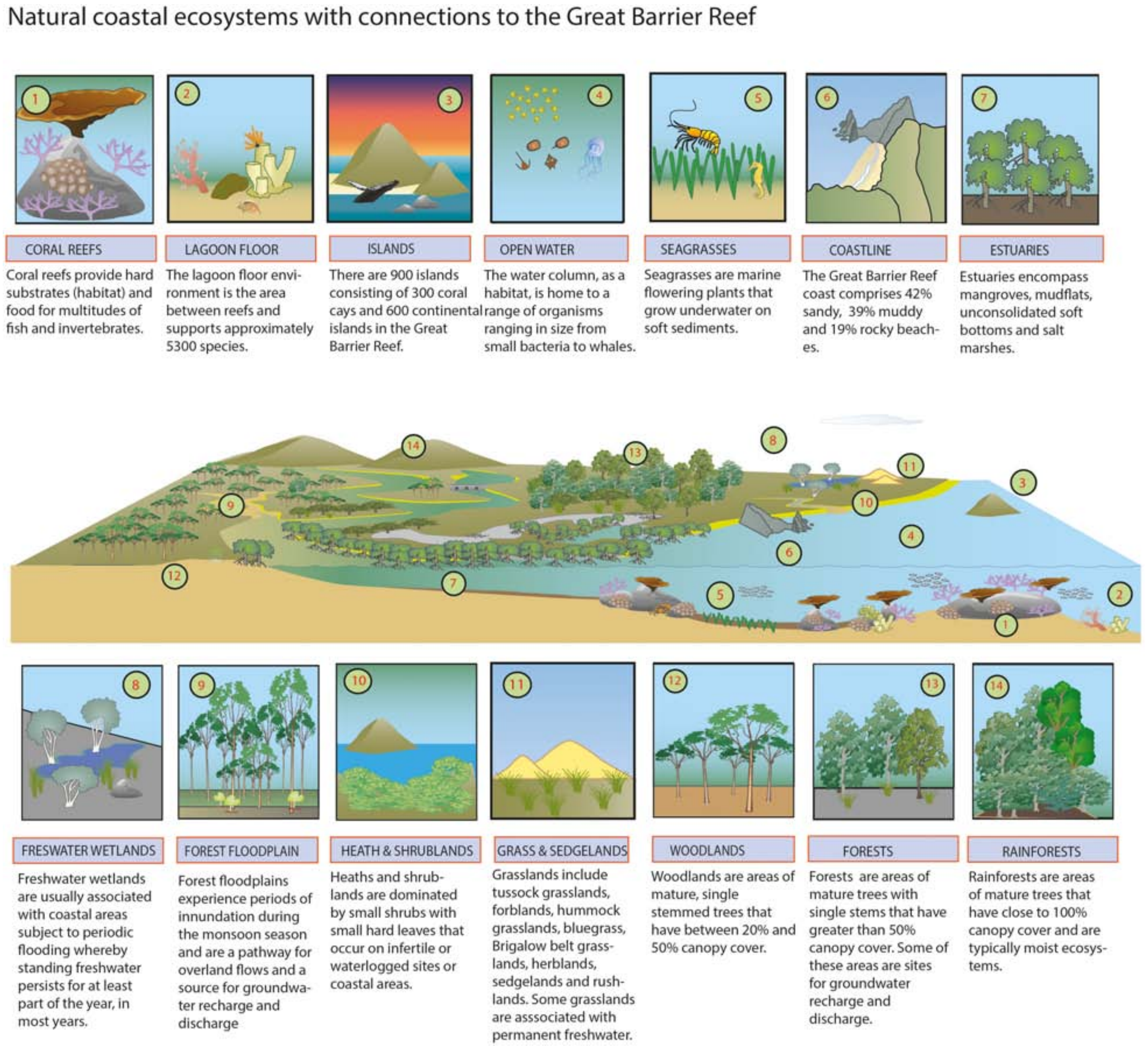


FIGURE 1 | (a) Location map of the Great Barrier Reef World Heritage Area (GBRMPA) along the Queensland coastline, including NRM regional bodies (see **Figure 3**). **(b)** Tully floodplain; **(c)** Burdekin floodplain; **(d)** Fitzroy floodplain along with field fish sampling completed in previous surveys; **(e)** Torilla floodplain in Broad Sound catchment. **(f)** Monthly average rainfall totals at gauging stations in each floodplain area [Tully gauging station 32042 (1925–2018); Burdekin station 33001 (1887–2018); Fitzroy station 39083 (1939–2018)]; and **(g)** monthly ambient air temperature records at BOM recording stations [Tully station 032004 (1871–2018); Burdekin station 33002 (1951–2018); and Fitzroy station 39083 (1939–2018)].

restoration for water quality improvement purposes (State of Queensland, 2017). In addition, landholders and government will also need to take care to fully consider tidal boundary laws and amendments when considering ponded pasture reconversion projects (Bell-James and Lovelock, in press).

The overarching framework for managing the GBR is the Reef 2050 Long-term Sustainability Plan (Reef 2050 Plan hereafter) (Great Barrier Reef Marine Park Authority [GBRMPA], 2015). In the Reef 2050 Plan, "*coastal habitat*" is recognized as supporting the ecological and biological processes of the Reef, providing habitat for biodiversity, community and economic benefits and increasing resilience to climate change. Reef 2050 Plan has a target for 2020 that "*There is no net loss of the extent, and a net improvement in the condition, of natural wetlands and riparian vegetation that contribute to Reef resilience and ecosystem health.*" An important and necessary action has been to implement the *Wetlands in the Great Barrier Reef Catchments Management Strategy 2016–2021* that outlines on-ground actions, education, and scientific research necessary to improve management and repair of wetlands in the GBR catchment. The Reef 2050 Water Quality Improvement Plan 2017–2022 (Reef WQ Plan) is nested under the water quality theme in the Reef 2050 Plan and is charged with the role to address all land-based sources of water pollution. The Reef WQ Plan identifies the need for targeted catchment repair projects, which is best achieved via a whole-of-system catchment management approach (State of Queensland, 2018b).

A key challenge to achieving these outcomes is that, since European settlement, the GBR catchment has continued to be modified (**Figure 3**), with estimates around 64% of the catchment area cleared of the predominant native vegetation, most occurring south of Cooktown (QLUMP data 2009, Queensland Government), though the rate of clearing has slowed and in some places has changed very little in the past few decades. The remaining undeveloped areas are predominately used for grazing, with around 10% of the catchment area within Protected Areas. The impacts of grazing on remnant natural areas include increased erosion, weed transfer, nutrient enrichment and loss of riparian understory (Brodie and Waterhouse, 2012). Feral pigs and cattle are also impacting Protected Areas (Waltham and Schaffer, 2018). Noticeably a major limitation in the success of repair efforts is the ongoing competing land uses (e.g., sugar cane production), and that so much of the GBR floodplain wetland and connectivity loss is not readily reversable. Investment is needed in order to understand these complex landscapes, aquatic floodplain connectivity, and how to restore function and achieve solutions that balance the environment with the desires of the community. With further investment for implementation, we could then be in a position to scale up efforts in order to work toward achieving the objectives set in the Reef 2050 Plan.



Natural coastal ecosystems with connections to the Great Barrier Reef

CORAL REEFS Coral reefs provide hard substrates (habitat) and food for multitudes of fish and invertebrates.

LAGOON FLOOR The lagoon floor environment is the area between reefs and supports approximately 5300 species.

ISLANDS There are 900 islands consisting of 300 coral cays and 600 continental islands in the Great Barrier Reef.

OPEN WATER The water column, as a habitat, is home to a range of organisms ranging in size from small bacteria to whales.

SEAGRASSES Seagrasses are marine flowering plants that grow underwater on soft sediments.

COASTLINE The Great Barrier Reef coast comprises 42% sandy, 39% muddy and 19% rocky beaches.

ESTUARIES Estuaries encompass mangroves, mudflats, unconsolidated soft bottoms and salt marshes.

FRESWATER WETLANDS Freshwater wetlands are usually associated with coastal areas subject to periodic flooding whereby standing freshwater persists for at least part of the year, in most years.

FOREST FLOODPLAIN Forest floodplains experience periods of innundation during the monsoon season and are a pathway for overland flows and a source for groundwater recharge and discharge

HEATH & SHRUBLANDS Heaths and shrublands are dominated by small shrubs with small hard leaves that occur on infertile or waterlogged sites or coastal areas.

GRASS & SEDGELANDS Grasslands include tussock grasslands, forblands, hummock grasslands, bluegrass, Brigalow belt grasslands, herblands, sedgelands and rushlands. Some grasslands are asssociated with permanent freshwater.

WOODLANDS Woodlands are areas of mature, single stemmed trees that have between 20% and 50% canopy cover.

FORESTS Forests are areas of mature trees with single stems that have greater than 50% canopy cover. Some of these areas are sites for groundwater recharge and discharge.

RAINFORESTS Rainforests are areas of mature trees that have close to 100% canopy cover and are typically moist ecosystems.

FIGURE 2 | The range of different coastal floodplain wetland habitats within the GBR lagoon, and a description for each habitat.

CRITICAL REVIEW AND SYSTEM REPAIR ATTEMPTS

In this perspective, we draw attention to three major wetland complexes subjected to years of intensive land use change in the GBR catchment: (1) Tully/Murray floodplain; (2) Burdekin floodplain, and (3) Broad Sound floodplain (**Figure 1**). These regions represent different climate conditions, land uses and different pressures on wetland systems, and restoration approaches. A review of available published scientific reports and government reports reveal that GBR floodplain wetlands (note that there are no fish data for the Torillia floodplain, which is evaluated below) provide habitat for nearly 80 fish species, across the types of wetland areas in this review (**Table 1**). Many species have a diadromous life history, requiring migration to freshwater or estuarine habitat areas at critical life stages, and as such a migration barrier or delay could avert future reproduction success (Sheaves, 2009). An example is the mangrove jack (*Lutjanus argentimaculatus*), which spawns on offshore coral reef areas (Russell and McDougall, 2005), with larvae drifting into nearshore waters and estuaries where new recruits then use estuaries for feeding and shelter, while continuing further upstream to floodplain wetlands (**Figure 4**). Mature fish eventually migrate to sea again to complete their lifecycle. This complex pattern of life-history connectivity between coral reefs and low-land freshwater wetlands (Sheaves, 2009) emphasizes the obligate requirement for a connected seascape in GBR catchments (Russell and McDougall, 2005).

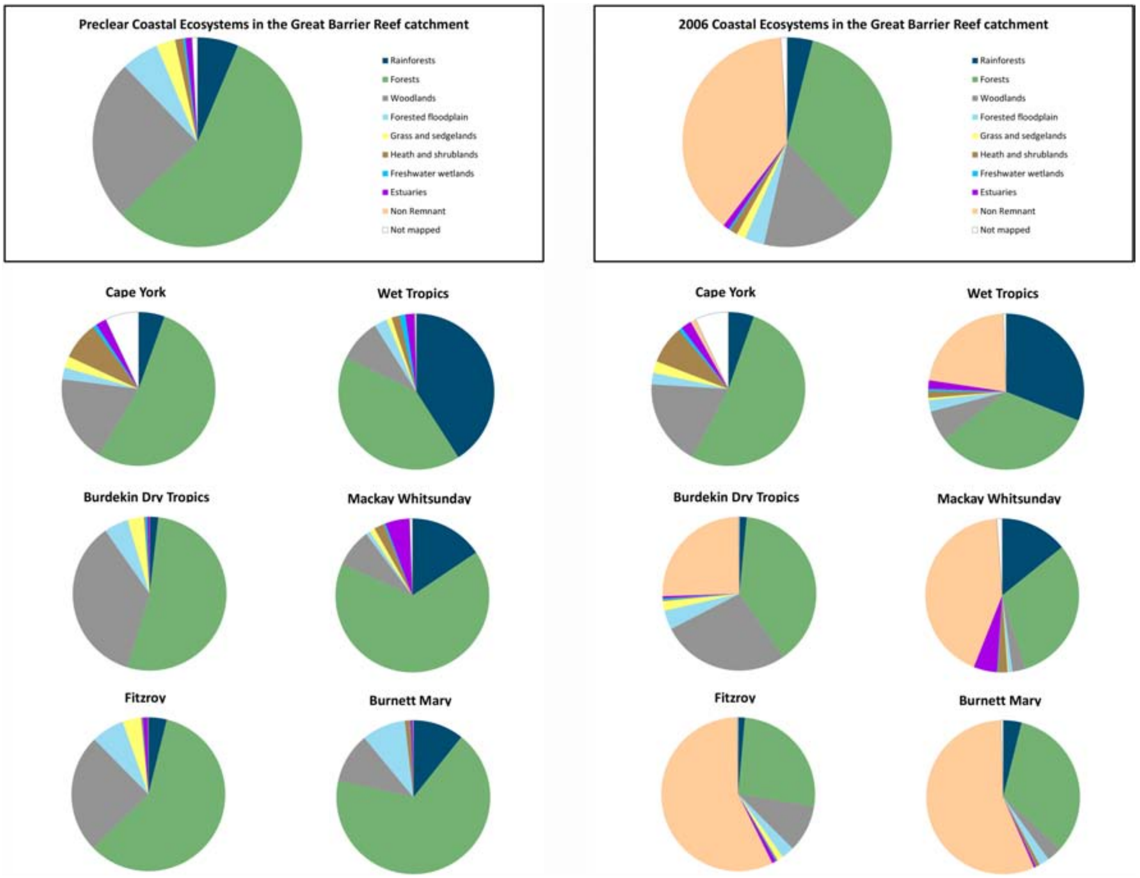


FIGURE 3 | Mapped land use change between preclear and 2009 coastal ecosystems in the GBR. Natural Resource Management areas mapped in **Figure 1**.

Restoration Case Study 1: Ponded Pastures in the Torilla Plain, Broad Sound Catchment

The Torilla Plain (**Figure 1d**), which is listed under the Directory of Important Wetlands in Australia (DIWA), has been identified as high value wetland through state-wide Aquatic Conservation Assessment (Inglis and Howell, 2009), and provides multiple ecosystem services including: cattle grazing, fisheries nursery habitat, high bird biodiversity, and threatened-species habitat (**Table 2** and **Figure 5A**). The coastal wetland complex is an intricate and dense network of small ponds and channels, and small earth-walls (~20 m wide) which were constructed by graziers to preclude tidal flow, as well as improve and extend ponded pasture opportunities for cattle during the late dry season (WetlandInfo, 2016).

Although saltmarsh is a protected habitat in Queensland (*Fisheries Act 1994*) and establishment of new ponded pastures is subsequently precluded, landholders are allowed to maintain existing earth walls. This infrastructure benefits Yellow Chats (*Epthianura crocea macgregori*) – a threatened species that require freshwater wetland vegetation for breeding and foraging purposes (Houston et al., 2004). However, ponded pastures may reduce overall productivity of the wetlands by restricting saltwater flow. This can negatively impact fish by impairing connectivity to nursery areas, particularly for diadromous species [such as Barramundi (*Lates calcarifer* which are known in the region more broadly, **Table 1**)], and by diminishing water quality (in particular high temperatures and pH, and low dissolved oxygen which occur in pond pasture areas elsewhere; Waltham and Fixler, 2017).

In 2015, the Torilla floodplain was identified as a priority wetland for local National Resource Management (NRM) investment, due in part due to its diverse stakeholder values (i.e., cattle grazing, threatened species habitat, biodiversity, and fisheries stocks), and the wetland's national importance (DIWA listed) (Jaensch et al., 2015). To restore and maintain ecological function of the Torilla wetland plain complex, while also sustaining cattle production services, landholders and local NRM groups are working to deliver a coordinated management strategy (WetlandInfo, 2016). Sustainable grazing practices (i.e., correct rotation between upland forest and floodplain, and low to moderate stocking densities; Houston et al., 2006, 2013), as well as fish passage infrastructure in earth walls are actions to improve cattle production, threatened-species habitat and connectivity for diadromous fish species. Earth walls installed at the correct

TABLE 1 | Fish species recorded from GBR coastal floodplain wetlands in the three study regions.

Family	Fish species	Tully	Burdekin	Fitzroy
Apogonidae	*Glossamia aprion*	✓	✓	✓
Ambassidae	*Ambassis agassizii*	✓	✓	
	Ambassis agrammus		✓	
	Ambassis spp.			✓
	Denariusa bandata	✓	✓	
Anguillidae	*Anguilla obscura*	✓	✓	
	Anguilla reinhardtii	✓	✓	✓
Ariidae	*Neoarius graeffei*			✓
Atherinidae	*Craterocephalus stercusmuscarum*	✓	✓	✓
Belonidae	*Strongylura krefftii*		✓	
Carangidae	*Scomberoides commersonianus*			✓
Chanidae	*Chanos chanos*		✓	
Cichlidae	*Oreochromis mossambicus**		✓	
Clupeidae	*Herklotsichthys castelnaui*			✓
	Nematalosa come			✓
	Nematalosa erebi	✓	✓	✓
Cyprinidae	*Carassius auratus*			✓
Eleotridae	*Hypseleotris compressa*	✓	✓	
	Hypseleotris galii		✓	
	Hypseleotris klunzingeri		✓	
	Hypseleotris sp. 1	✓	✓	✓
	Giuris margaritacea	✓	✓	
	Mogurnda adspersa	✓	✓	
	Oxyeleotris lineolatus		✓	
	Unidentified Eleotrid			✓
Elopidae	*Elops hawaiensis*		✓	
Engraulidae	*Thryssa hamiltonii*			✓
	Thryssa scratchleyi		✓	
Gerreidae	*Gerres erythrourus*			✓
	Gerres filamentosus			✓
Gobiidae	*Gobid* sp. A			✓
	Redigobius bikolanus	✓	✓	
Hemiramphidae	*Arrhamphus sclerolepis*			✓
Kuhliidae	*Kuhlia rupestris*		✓	
Latidae	*Lates calcarifer*	✓	✓	✓
Lutjanidae	*Leiognathus decorus*			✓
	Leiognathus equulus			✓
	Lutjanus argentimaculatus		✓	
	Lutjanus russellii			✓
Megalopidae	*Megalops cyprinoides*		✓	
Melanotaeniidae	*Melanotaenia maccullochi*	✓	✓	
	Melanotaenia splendida	✓	✓	✓
Monodactylidae	*Monodactylus argenteus*			✓
Mugilidae	*Mugil cephalus*			✓
	Liza subviridus			✓
	Unidentified *Valamugil* sp.			✓
	Valamugil seheli			✓
	Rhinomugil nasutus			✓
Osphronemidae	*Trichogaster trichopterus**		✓	
Plotosidae	*Neosilurus ater*	✓	✓	
	Neosilurus hyrtlii	✓	✓	✓
	Porochilus rendahli		✓	
Poeciliidae	*Gambusia holbrooki**		✓	
	*Xiphophorus maculatus**	✓	✓	
Pseudomugilidae	*Pseudomugil gertrudae*	✓	✓	
	Pseudomugil signifer			✓
Scatophagidae	*Selenotoca multifasciata*		✓	
	Scatophagus argus		✓	
Siganidae	*Siganus lineatus*			✓
Sillaginidae	*Sillago sihama*			✓
Sparidae	*Acanthopagrus australis*			✓
	Acanthopagrus berda			✓
Synbranchidae	*Ophisternon* ef. *gutturale*	✓	✓	
Terapontidae	*Amniataba percoides*		✓	
	Bidyanus bidyanus			✓
	Hephaestus fuliginosus	✓	✓	
	Leiopotherapon unicolor		✓	
	Scortum parviceps		✓	
	Terapon jarbua			✓
Tetrarogidae	*Notesthes robusta*	✓	✓	
Toxotidae	*Toxotes chatareus*		✓	
Zenarchopteridae	*Zenarchopterus buffonis*			✓
	Species richness	**22**	**43**	**36**

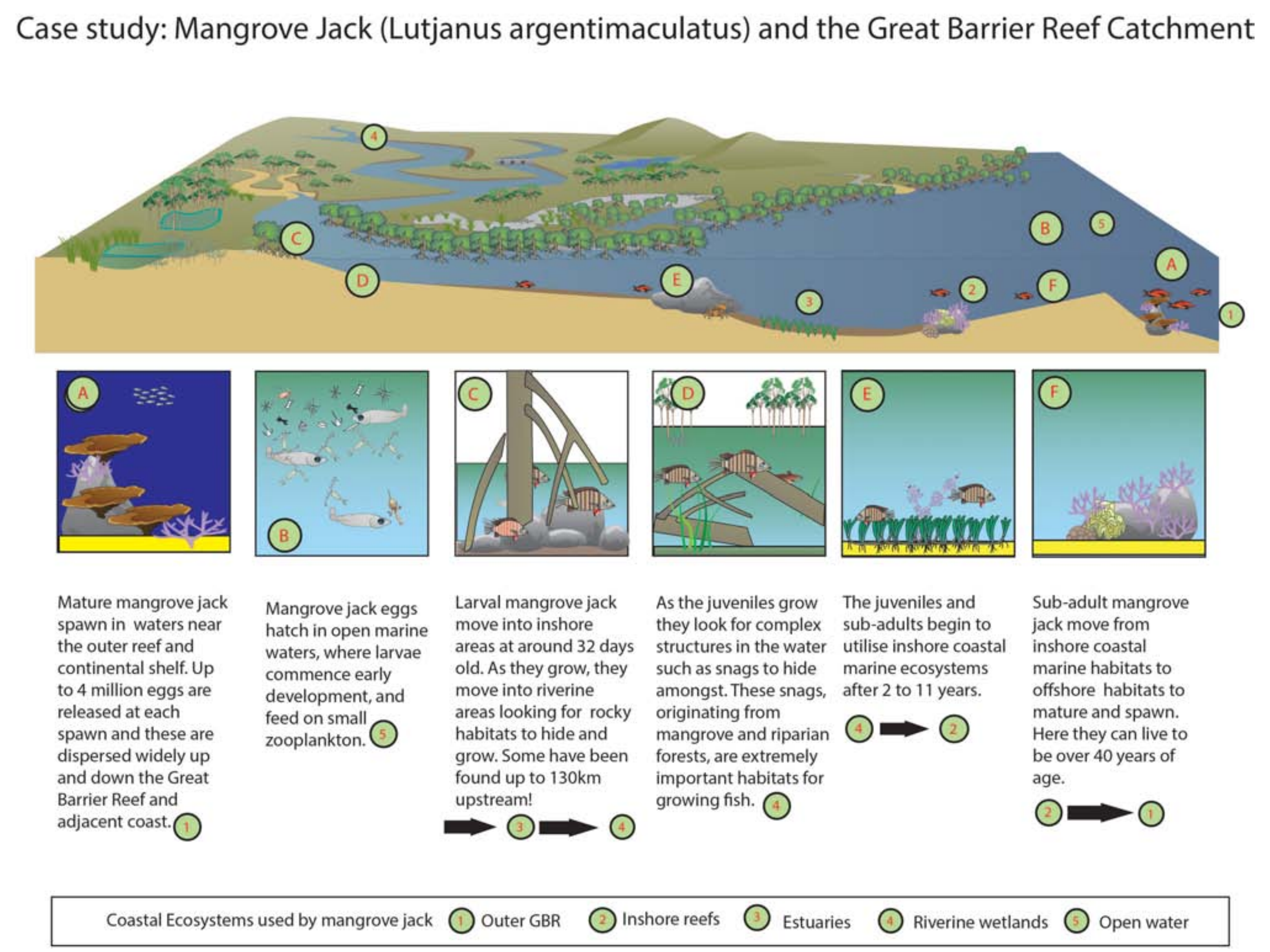
(Continued)

TABLE 1 | Continued

**Declared invasive species. The Fitzroy data here doesn't include a field site from Torilla floodplain; the data here present a case of the types of fish species found on GBR coastal floodplains.*

height could simultaneously promote the extension of the area of freshwater vegetation, while also allowing tidal connection aims to maintain high productivity in the Torilla floodplain. Creation of deep-water refuges in ponded pastures to ensure water quality (particularly water temperature) is suitable for fish (for example, avoiding acute thermal risks; Wallace et al., 2015) could also be considered as an additional engineering solution for maintaining high quality habitat (Hyland, 2002).

Whether this restoration case study constitutes success is dependent on which of the many ecosystem functions and services provided are most highly valued by the community (e.g., bird habitat, water quality, or fish habitat). Furthermore, whether this and similar local-scale management efforts contribute in any real way to broader wetland restoration priorities of the Reef 2050 Plan has not been evaluated. A more pressing question is: Which stakeholder values should take priority? The *Wetlands in the Great Barrier Reef Catchments Management Strategy 2016–2021* recognizes this issue and suggests that a balanced approach is needed to effectively manage for multiple and conflicting values (Department of Environment Heritage and Protection [DEHP], 2016). However, as is the case in the Torilla Plains, management effort and outcomes will be determined by which stakeholders are engaged in the restoration area/activity, and the scale at which they have capacity or will to manage. Management of these ponded pastures here, and indeed elsewhere in the GBR catchments will also require careful legislative consideration around the tidal boundary laws (Bell-James and Lovelock, in press).



Case study: Mangrove Jack (Lutjanus argentimaculatus) and the Great Barrier Reef Catchment

Mature mangrove jack spawn in waters near the outer reef and continental shelf. Up to 4 million eggs are released at each spawn and these are dispersed widely up and down the Great Barrier Reef and adjacent coast. ①

Mangrove jack eggs hatch in open marine waters, where larvae commence early development, and feed on small zooplankton. ⑤

Larval mangrove jack move into inshore areas at around 32 days old. As they grow, they move into riverine areas looking for rocky habitats to hide and grow. Some have been found up to 130km upstream!

As the juveniles grow they look for complex structures in the water such as snags to hide amongst. These snags, originating from mangrove and riparian forests, are extremely important habitats for growing fish. ④

The juveniles and sub-adults begin to utilise inshore coastal marine ecosystems after 2 to 11 years.

Sub-adult mangrove jack move from inshore coastal marine habitats to offshore habitats to mature and spawn. Here they can live to be over 40 years of age.

Coastal Ecosystems used by mangrove jack ① Outer GBR ② Inshore reefs ③ Estuaries ④ Riverine wetlands ⑤ Open water

FIGURE 4 | Lifecycle of the mangrove jack (*Lutjanus argentimaculatus*) outlining critical need for access to freshwater and marine coastal wetland areas to complete lifecycle stages. This lifecycle outlines that any disturbance in the seascape, that prevents access to habitats may implicate successful reproduction success for this diadromous species.

Restoration Case Study 2: Modified Hydrology and Aquatic Weed Infestation, Burdekin Floodplain

The Burdekin floodplain (**Figure 1c**) is one of the largest sugar cane production regions in northern Australia (Davis et al., 2014), placing high value on agricultural ecosystem service provisioning for the nation's economy. The Bowling Green Bay Ramsar site is within the northern part of the Burdekin floodplain and supports rich and abundant birdlife, with more than 20,000 waterbirds occurring seasonally, including some of the largest colonies of fish-feeding birds in eastern Queensland (Queensland Wetlands Program, 2013). The area also supports commercial, recreational, and Indigenous fisheries (Davis et al., 2014).

Since the 1800's extensive hydrological changes have occurred to the Burdekin floodplain due to infrastructure development for the purpose of irrigating agricultural land (Davis et al., 2014). Extreme hydrological changes have resulted in the loss of wetland ephemerality (wet and dry seasonality), and in doing so, have increased aquatic weed infestation (Perna and Burrows, 2005; Burrows and Butler, 2007; Connolly et al., 2012; Waltham and Fixler, 2017). Changes in hydrology, increased prevalence of natural weed barriers to fish movement, and high levels of nutrient pollution from agriculture have had negative consequences for water quality (increased turbidity and decreased dissolved oxygen) and fish accessing the floodplain (Perna and Burrows, 2005; Waltham and Fixler, 2017). Management intervention has been necessary to restore ecological function, and connectivity, in degraded areas of the Burdekin floodplain, and continues to be a priority (Great Barrier Reef Marine Park Authority [GBRMPA], 2015).

Restoring natural hydrological processes of the Burdekin floodplain requires significant investment and may not, indeed, be a feasible course of action because of the scale and severity of floodplain modification (Davis et al., 2014). Approximately a decade ago, the Burdekin Shire Council and the Burdekin Bowen Integrated Floodplain Management Advisory Committee

TABLE 2 | Overview of stakeholder values and management bodies involved in three coastal wetland restoration case studies across catchments of the Great Barrier Reef.

Case study				**Management bodies involved in restoration case study**				**Case study restoration recommendations**
Location	**Region**	**Management issue**	**Stakeholder values**	**NRM**	**Governance**			
					Government	**Scale**	**Role in case study**	
Torilla floodplain	Fitzroy	Ponded pastures	Food provisioning ecosystem service value – pasture for cattle graziers, nursery for commercial fisheries stocks	Fitzroy Basin Association	Queensland Wetlands Program – Queensland Government Department of the Environment and Energy	State	DSS – Decision Support System used to identify Torilla floodplain for management investment	Fish passage structures in ponded pasture earth walls, regulated cattle grazing, maintaining correct height of ponded pasture earth walls
			Regulating ecosystem service value – Water quality: ponded pastures can retain sediments, filter water		Fisheries Act (1994) – Queensland Government Department of Agriculture and Fisheries	State	Statutory protection of saltmarsh	
			Biodiversity value: high diversity and abundance of shorebirds, waterbirds, fish		DIWA – Australian Government Department of the Environment and Energy	National	No statutory regulation	
			Conservation value, threatened species habitat: Yellow Chat (Capricorn subspecies, *Epthianura crocea macgregori*), Australian Painted Snipe (*Rostratula australis*)					
Burdekin Floodplain	Burdekin	Modified hydrology and aquatic weed infestation	Food provisioning ecosystem service value – water extraction for agricultural production, nursery for commercial fisheries stocks	NQ Dry Tropics NRM	Burdekin Shire Council	Local	Catchment management strategy: improve water quality and fish habitat in degraded lagoons (BBIFMAC), Council acquired mechanical weed harvester	Mechanical weed removal shows immediate positive response (weeks) in water quality conditions and fish abundance (months) (Perna et al., 2012). On-going weed maintenance is required
Tully Murray Floodplain	Tully Murray	Riparian habitat loss and degraded water quality	Food provisioning ecosystem service value – riparian forest clearing for agricultural production, nursery for commercial fisheries stocks	Terrain NRM	DIWA – Australian Government Department of the Environment and Energy	National	No statutory regulation	Riparian vegetation restoration and constructed wetlands
			Regulating ecosystem services value – Water quality: riparian vegetation filters groundwater flows, provides temperature and aquatic weed regulation		Reef Water Quality Protection Plan – Australian and Queensland Government	National and State	Provide funding to develop Wet Tropics Water Quality Improvement Program (WQIP)	

(Continued)

TABLE 2 | Continued

Case study				Management bodies involved in restoration case study				Case study restoration recommendations
Location	Region	Management issue	Stakeholder values	NRM	Governance			
					Government	Scale	Role in case study	
			Biodiversity value: high aquatic biodiversity		Wet Tropics Major Integrated Project (MIP) – Queensland Government (2017–2020)	State	Foster collaborative land-holder and community-based restoration initiatives	
			Cultural ecosystem service value: recreational fishing, particularly Barramundi (*Lates calcarifer*), and tourism					

Restoration recommendations from each case study are also provided.

prioritized local management actions to repair degraded water quality and to improve hydrologic connectivity associated with natural weed barriers (**Table 2**). Mechanical weed removal was identified as the best strategy (**Figure 5B**), and via a community-based initiative/partnership (i.e., local council, industry, and landholders) aquatic weeds were excavated, water quality improved, native vegetation returned, and fish diversity and abundance was restored (Perna and Burrows, 2005; Butler et al., 2007; Perna et al., 2012). Increases in the abundance and diversity of freshwater fish species is partly attributed to the return of native freshwater plants, which provide a suitable micro-habitat for dependent freshwater fish species (e.g., *Melanotaenia splendida*, *Glossamia aprion*, *Ambassis agrammus*; **Table 1**; Perna et al., 2012). However, it is important to note that for diadromous fish (in particular *Lates calcarifer*, *Chanos chanos*, *Scatophagus argus*; **Table 1**) to successfully recolonize upstream areas following weed removal, it would require a flood event to permit connection to a downstream recruitment source, or major investment to construct fish ladders over barriers across the floodplain (Perna et al., 2012).

Although restoration efforts are localized here, broader investment and restoration action is necessary across the floodplain. An important lesson is that even local-scale restoration efforts require on-going maintenance. To begin upscaling restoration, this would require a coordinated effort including funding and resources for long-term maintenance (Waltham and Fixler, 2017). Further research is necessary to examine the sustainability of restoration by active, expensive, mechanical aquatic weed removal against alternative passive restoration that requires minimal on-going maintenance, such as the reinstatement of natural tidal flows in the floodplain – using saltwater ingress as a means of controlling invasive freshwater aquatic plants (Reid et al., 2018).

Restoration Case Study 3: Riparian Habitat Loss and Reduced Water Quality, Tully Murray Floodplain

The Tully Murray floodplain (**Figure 1a**),located in the Wet Tropics bioregion, hosts a broader diversity of agricultural land-uses than the preceding case studies, primarily sugar cane, bananas, and grazing. Intense agricultural activity has resulted in the classification of the Tully Murray floodplain as a "pollutant hotspot," and degraded water quality, in particular low dissolved oxygen, has reduced aquatic biodiversity in the region (**Figure 5C**) (Pert et al., 2010; Pearson et al., 2013). Additionally, most native riparian vegetation has been cleared and fragmented, contributing to degradation of the coastal wetland complex as a whole (Pert et al., 2010). Riparian vegetation is tightly linked to coastal wetland ecosystem function, particularly through regulation of sunlight, thereby limiting aquatic weed growth and stabilizing temperature and dissolved oxygen levels (Bunn et al., 1998; Pert et al., 2010). Available data outlines that restoration of riparian vegetation provides additional benefits for aquatic macrophyte, macroinvertebrate, and fish assemblages on this floodplain (Arthington et al., 2007; Pearson et al., 2013; Arthington et al., 2015).

Given its status as a "pollutant hotspot" and high biodiversity and cultural ecosystem service values (**Table 2**), the Tully Murray floodplain has received management attention through the Tully Water Quality Improvement Program (Tully WQIP), with objectives to restore water quality and aquatic biodiversity (Kroon et al., 2009). Restoration of riparian vegetation was a key directive of the Tully WQIP for its potential to deliver supporting and regulating water quality ecosystem services (Kroon et al., 2009). In addition to shade for temperature and aquatic weed regulation, riparian vegetation may also filter groundwater nitrate, trap sediments, and reduce erosion

FIGURE 5 | Photographs illustrating restoration case studies: **(A)** bird habitat and cattle grazing in the Torilla floodplain (Photo credits: R. Jaensch); **(B)** aquatic weed removal in the Burdekin floodplain (Photo credits: P. Groves); and **(C)** Tully Murray floodplain constructing wetlands (Photo credits: R. Digman).

(Rassam and Pagendam, 2009; Pert et al., 2010). To locate target areas for restoration that would provide the best return on investment, riparian ecosystem services in the Tully Murray floodplain have been mapped (Pert et al., 2010), including riparian areas with high denitrification ability near agricultural land with elevated nutrient loads (Rassam and Pagendam, 2009).

An evaluation of riparian restoration across catchments of the GBR shows that overall water quality improvements are dependent upon: the length of time since restoration initiation and the width and connectivity of riparian re-vegetation sites (Paul et al., 2018). In addition to water quality improvements, riparian re-vegetation projects also provide biodiversity and bio sequestration co-benefits (Paul et al., 2018). However, to achieve meaningful outcomes for the Reef 2050 Plan, a whole-of-ecosystem approach to coastal wetland restoration is required to effectively "scale-up" improvements in water quality. Riparian re-vegetation projects could be coordinated by means of other restoration activities such as: weed or pollutant removal; reinstatement of tidal connectivity, and the construction of wetlands in marginal cane land (Waltham et al., 2017). Constructed wetlands can improve water quality by reducing nutrient and suspended sediment levels (Jia et al., 2016). Additionally, transitioning low-lying, marginal cane land to constructed wetlands has received recent interest as a cost-effective water quality improvement solution in the Tully Murray floodplain (Waltham et al., 2017). This interest extends beyond water quality benefits, with potential to provide an economic benefit to landholders through public/private market schemes investing in restoration "green" projects (Waltham et al., 2017). Additional water quality co-benefits could be gained by planting riparian buffers around constructed wetlands, enhancing filtration capacity of the low-lying land through denitrification by riparian vegetation (Rassam and Pagendam, 2009).

PLAN OF ACTION

Framework for Assessing Rehabilitation Activities

The three case studies highlight that coastal floodplain restoration projects are underway, however, there is a major risk if they continue to occur in a "stakeholder silo." A coordinated restoration strategy matching local capacity, land holder willingness, with regional incentives is needed. When assigning or making management decisions about a wetland, it is important that these consider the full range of floodplain ecological, economic, and social values (Maes et al., 2012). Wetland management decisions can favor either conversion or management for a single ecosystem service, such as water supply or food production (Villamagna et al., 2013; Broszeit et al., 2017). As wetlands become scarce and under more pressure (Finlayson, 2013; Mitsch et al., 2013), and as we develop a better understanding of the full range of values provided by them, the best options will increasingly involve managing wetlands for a broader array of services (stacked services; Waltham et al., 2017), in addition to aligning with the wise use principles of the Ramsar Convention.

Numerous prioritization or decision support tools are available[2]. A wetland prioritization decision support system (WDSS) was developed specifically for the GBR catchment to strategically prioritize wetlands for rehabilitation. It uses biophysical, socio-economic, community capacity, and threat data, as well as expert input to identify high priority wetlands for strategic investment (Francis and Tait, 2006). Although the WDSS is an effective tool for prioritizing project sites, it does not adequately represent the interplay between the terrestrial and aquatic environment, and the influence of processes happening in the broader catchment – the WDSS wasn't available or used as part of the three case studies examined here. There is a need to take a whole-of-catchment approach to planning activities, consistent with the Queensland Government's *Wetlands in the Great Barrier Reef Catchment Management Strategy 2016–2021*. A decision support framework is needed that firstly establishes what stakeholders value and want (e.g., through a structured decision making process; Kozak and Piazza, 2015; Guerrero et al., 2017), the biophysical components, processes and drivers at the site and broader catchment, and relevant policy drivers or constraints that might pose a barrier to success. The framework then would need to consider a range of possible management interventions (e.g., on-ground restoration, education, research) at different scales (site, catchment, or regional), the spatial thresholds of interventions to achieve the desired objective, the synergistic or aggregative effects (i.e., the cumulative benefit of several interventions), and the time frame in which the objectives will be met (Guerrero et al., 2017). We need to revisit objectives and ensure that the selected intervention/s achieve the objectives, ensure probity of the knowledge underpinning the restoration decision, clearly define what constitutes success and the limits of predictability of outcomes in uncertain floodplain systems (this is also the case for the three case studies examined here, to determine whether further improvements and restoration outcomes are possible or necessary). We also need to ensure restoration efforts conform to budgetary constraints (Creighton et al., 2015), and what, if any, trade-offs there may be to other services, such as biodiversity, water quality or carbon (Waltham et al., 2017). A recent framework developed for climate change adaption in the coastal zone (Sheaves et al., 2016) could be adopted here for the floodplain wetland restoration situation in the GBR.

Government and Market-Based Investment Mechanisms to Facilitate Restoration

The Reef 2050 Plan and Reef WQ Plan guides Australian and Queensland Government investment into initiatives to manage and protect the values of the Reef, including investment into coastal habitat restoration. To value-add to government investment, the Australian and Queensland Governments' are seeking private industry and philanthropic co-investment (Commonwealth of Australia, 2016). The Reef Trust Partnership outlines opportunities for co-investment, including riparian rehabilitation, fish habitat repair, connectivity, and improving coastal ecosystem functioning through weed and pest control (examples of which are provided in the case studies). The first project involving matched co-investment through the Reef Trust commenced in 2016 with Greening Australia, in partnership with Birdlife Australia, Conservation Volunteers Australia, and Wetland Care Australia. This arrangement includes a \$4 million project to restore 200 hectares of wetlands in priority areas along the GBR coast (Commonwealth of Australia, 2015). Based on the success of that partnership model, the Australian Government's Reef Trust committed another \$5 million to Greening Australia, who will match this investment dollar-for-dollar through its Reef Aid program for a total investment of \$10 million to restore an additional 500 hectares of priority coastal wetland habitat (State of Queensland, 2018b). A Reef Credits Initiative will also be rolled out to provide a market based incentive approach to achieve water quality improvement through agronomic practice change or habitat restoration, including constructing wetlands (State of Queensland, 2018b). The Australian and Queensland Governments also invest in habitat "system repair" through the Australian Government's Reef Trust and Queensland Government's natural resource management program and Reef Water Quality Program (Commonwealth of Australia, 2016).

Long-Term Investment and Maintenance

Government funding is usually project based, it is short-term (1–5 years) and generally does not invest public funds for necessary long-term maintenance. Restoration projects usually require maintenance beyond the life of the initial funding (Moore and Rutherfurd, 2017). Those projects involving revegetation or weed control can (and mostly do) rapidly revert to a degraded state without planned and funded ongoing maintenance support. Therefore, there is a need for careful consideration of the value, and particularly so when considering longer-term funding for maintenance and new mechanisms to ensure project sites are maintained. One option could be funding through local government environment levees, and maintenance by landholders or Landcare groups (as outlined in Restoration Case Study 2). Payments for ecosystem services, to value the fisheries and other services provided by coastal habitats, will require better quantification of fisheries values of coastal habitats (Wegscheidl et al., 2017), and support tools such as benefit calculators

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[2] https://wetlandinfo.ehp.qld.gov.au/wetlands/resources/tools/assessment-search-tool/

and capacity building (Waltham et al., 2017). Recognition of the multiple benefits that may be accrued, resulting in new and emerging investment opportunities are emerging. These include carbon additionally programs, such as the Australian Government's Clean Energy Finance Corporations Reef Funding Program and the Queensland Government's $500 million Land Restoration Fund, that support carbon projects that can also leverage co-benefits such as enhancing wetlands for fisheries and restoring ecosystems and degraded land (State of Queensland, 2018a).

CONCLUSION

There has been considerable investment in coastal wetlands and floodplains along the GBR coastline, tackling catchment water quality runoff, floodplain aquatic habitat connectivity, and land use practice changes to improve water quality – more projects are on the horizon as interest from private investor groups grows. All these wetlands are valued for their role in ameliorating pollution entering the GBR lagoon. However, they form part of the broader GBR ecosystem, and indeed, require a similar level of ecosystem protection and restoration necessary under the objective of GBR ecosystem protection. Some data are emerging around the ecosystem value of GBR coastal wetlands, but more is needed particularly when considering the connected seascape (reef to freshwater wetlands). Exciting opportunities to access philanthropic and corporate investment that supports social responsibility toward environmental management and protection are on the horizon, which require careful planning and assessment. Repairing and protecting the GBR coastal wetland ecosystems and connection with offshore coral reef ecosystems is challenging, but the social, environmental, and economic returns for this investment outweighs not doing anything.

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All authors contributed to the discussion. NW, CW, and CB wrote the manuscript. DB, CC, MR, DM-A, PG, and MS edited the manuscript. DA and PG prepared the figures.

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frontiers in Marine Science

ORIGINAL RESEARCH
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Elemental Inventory in Fish Otoliths Reflects Natal Origin of Atlantic Herring (*Clupea harengus*) From Baltic Sea Juvenile Areas

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Despite centuries of human exploitation and research on Atlantic herring (*Clupea harengus*) in Europe, there is still much uncertainty on where major nursery areas are located. However, understanding the quantitative contribution of particular coastal systems to adult fish populations is of utmost importance to secure sustainable fish resources. Routinely, marker elements indicating certain hydrological conditions, which are incorporated into calcified structures, the so-called otoliths, are used to trace the origin of fish. However, as in the Baltic Sea, small and large scale salinity gradients potentially masking specific salinity signals. Based on the entire elemental inventory of the otolith core region, indicating the chemical signature of the spawning area, we developed a unique elemental fingerprinting index (*EFI*), allowing comparisons of multi-elemental chemical signatures from within and between herring juvenile areas. Our results show significantly distinct chemical "fingerprints" on the scale of particular bays and estuaries, which were not detectable with the usual marker elements. We further demonstrate that heavy metals levels drive the potential to distinguish natal origin of herring. These findings provide an essential baseline for further studies on the impact of small scale productivity for exploited fish resources and central components of marine food webs.

Keywords: *Clupea harengus*, Western Baltic Sea, inshore spawning areas, age-0 herring, otolith chemistry, elemental fingerprinting, LA-ICP-MS

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INTRODUCTION

Coastal ecosystems are highly productive, serving as crucial spawning and juvenile habitats for many fish species worldwide (Blaber and Blaber, 1980; Orth et al., 1984; Shulman, 1985). At the same time, coastal systems are under increasing anthropogenic pressure, resulting in global losses of species biodiversity and habitat degradation (Lotze et al., 2006; Worm et al., 2006; Waycott et al., 2009). However, management of natural fish resources is widely limited to fishery regulations for adult stocks. Regional coastal zone management rarely includes a certain focus on important fish nursery areas although impacts can have drastic consequences on resilience and recruitment strength of a fish population. The definition after Beck et al. (2001) emphasizes the concept of a nursery area, revealing the importance to identify the quantitative contribution of particular areas to the adult population of fish or invertebrates. Accordingly, a nursery area is not just one of multiple areas inhabited by juveniles of a population, but is defined as an area, which contributes a greater than average number of individuals to the adult population (Beck et al., 2001; Dahlgren et al., 2006). According to these quantitative aspects, research is nowadays increasingly focused on studies on juvenile-adult habitat connectivity and dependency of fish species on certain habitats (Thorrold et al., 2001; Forrester and Swearer, 2002; Gillanders, 2002a). This connectivity and dependency aspect is highly relevant to evaluate the relation between habitat availability and fish population dynamics and at the same time exposed a great lack of knowledge on general life history and migratory patterns of economic important fish species with a great uncertainty of obligate or facultative habitat use (Able, 2005).

Otoliths are the calcified ear stones in teleost fish and were formerly used for annual age and growth estimations (Beamish, 1979; Hoyer et al., 1985). During the last decades the scope of otolith research further expanded and resulted in new scientific applications, such as otolith microstructure analyses for age estimates of early life stages on a daily scale (Nishimura and Yamada, 1984; Campana and Moksness, 1991), otolith shape analyses for stock identification (Campana and Casselman, 1993; Tracey et al., 2006) and chemical analyses of the otolith core region to investigate elemental signals and spatial differences in juvenile fish otoliths (De Pontual et al., 1999; Gillanders and Kingsford, 2003; Hamer et al., 2003). This otolith chemistry approach takes advantage of specific fish otolith characteristics, being metabolically inert, growing continuously without resorption and incorporating elements into their growing surface. Hence, these calcified structures reflect the physical and chemical characteristics of the ambient water, where the fish is residing during the early ontogeny (Campana, 1999). With the implementation of otolith microchemistry, a new age of fishery research was established, resulting in studies concerning stock discrimination analyses (Geffen et al., 2011; Heidemann et al., 2012) and fish migration patterns (Limburg, 1995; Barnett-Johnson et al., 2008), mainly based on elements indicating hydrologic conditions like strontium and barium, which are known as markers for salinity gradients (Kennedy et al., 2002; Elsdon and Gillanders, 2005). Further approaches to investigate habitat connectivity were predominately based on a few selected elements in tropic and sub-tropic fishes (Milton et al., 1997; Thorrold et al., 2001). Studies concerning the elemental inventory of fish otoliths and habitat connectivity of economically important fish species in the North Atlantic region, such as flatfishes, cod and herring, are rather scarce (but see Brophy et al., 2003; Vasconcelos et al., 2008; Thorisson et al., 2011).

The Atlantic herring (*Clupea harengus*, L. 1958) is one of the most economically important marine fishery target species in the world (FAO, 2016). Moreover, this small pelagic fish is of high ecological relevance, linking different trophic levels in the marine food web (Casini et al., 2004; Möllmann et al., 2004). In the Baltic Sea, *C. harengus* is a highly migratory fish, accomplishing annual migrations between their feeding grounds in the Kattegat-Skagerrak and their coastal spawning grounds located in bays, estuaries and lagoons along the coastal Western Baltic Sea during spring, showing a distinct homing behavior (Wheeler and Winters, 1984; McQuinn, 1997). This herring population is of high economic value for the Western Baltic Sea region. Herring reproduction success is affected by multiple abiotic and biotic parameters (Holliday and Blaxter, 1960; Laine and Rajasilta, 1999; Peck et al., 2012; Kotterba et al., 2017), as well as by human-induced stressors, such as pollution (Dethlefsen et al., 1996; Incardona et al., 2012) or eutrophication (Aneer, 1987; Rahikainen et al., 2017; von Nordheim et al., 2018). Eutrophication processes in the past decades led to severe habitat degradation of important spawning areas in Baltic coastal waters (Kääriä et al., 1988; Kanstinger et al., 2016). Western Baltic herring recruitment decreased during the past two decades and remained on a low level ever since, reaching the lowest value of the time-series in 2017 (ICES, 2018). The reasons for this decline are still unclear, but evidence mounts for a synergy of eutrophication, climate change and resulting ecological cascades negatively affecting the survival of early life stages (Moll et al., 2018). However, quantitative studies on the contribution of single coastal juvenile habitats to the adult herring population are lacking, but are of vital importance to understand the impact of local hazards to fish population dynamics and to establish adequate coastal zone management strategies.

The objectives of this study are to identify differences in the elemental composition of age-0 herring otoliths from different inshore spawning areas along the Western Baltic coastline. Hypothesizing that herring otoliths from different juvenile areas differ in their elemental composition, we created an elemental fingerprinting index (*EFI*) based on a multi-element approach.

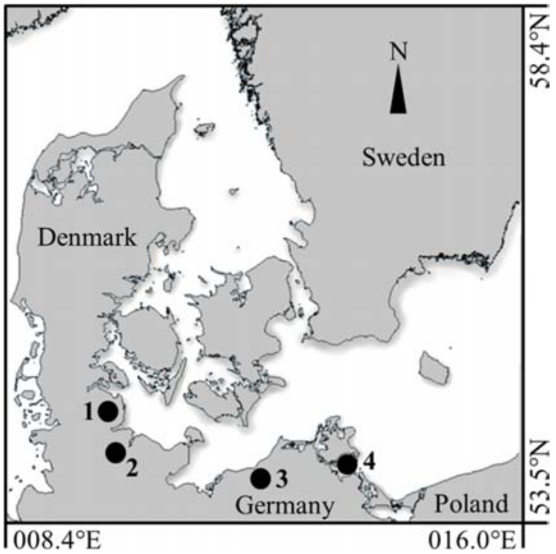

FIGURE 1 | Inshore sampling locations along the German coastline of the Western Baltic Sea. The four inshore spawning sites, sampled in summer 2016, are indicated by black circles **(1)** Schlei Fjord (SF), **(2)** Kiel Canal (KC), **(3)** Warnow Estuary (WE) and **(4)** Greifswald Bay (GB).

MATERIALS AND METHODS

Age-0 Herring Sampling

All four inner coastal sampling sites are anthropogenic-influenced spawning areas for the Western Baltic spring spawning herring population, located along the German coastline of the Western Baltic Sea. In June 2016, sampling was conducted in the eutrophic Schlei Fjord (SF: ∼54.62°N, 09.09°E) and in Kiel Canal (KC; ∼54.33°N, 09.72°E), an artificial waterway with heavy ship traffic, connecting the Baltic Sea and the North Sea. Furthermore, young-of-the-year (YOY) herring was sampled in the Warnow Estuary (WE; ∼54.12°N, 12.10°E), with its dockyard and landing pier for cruise liners and ferries, and the eutrophic Greifswald Bay (GB; ∼54.25°N, 13.50°E) (see **Figure 1**). YOY herring was caught by beach seine (7 m opening, 5 mm mesh size, wing height 1.5 m) in the SF sampling area and by purse seine (40 m length, 4 mm mesh size, 3 m height) in KC, both nets were pulled by two people. Sampling areas WE and GB were sampled with a ring trawl of 1 m diameter (1550 μm mesh size) onboard a research vessel. Hydrological parameters [sea surface temperatures (SST) and salinity] were either recorded with a hand held field probe (YSI Professional Plus) or a remotely operated CTD. The characteristics of each sampling site, including abiotic parameters during sampling, mean total length (TL mm) of YOY herring, as well as numbers of individuals per sampling site are summarized in **Table 1**. Herring were frozen immediately after the catch and were transported to the laboratory for otolith dissection.

Young-of-the-year herring sampling was conducted under current licenses for wild fish sampling according to Mecklenburg-Western Pomeranian (Germany) fishery law (§11 LFischG, Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei, Mecklenburg-Vorpommern).

Sample Processing

Prior to otolith dissection, microscope slides were washed in 2% nitric acid (Rotipuran Supra 69%, Carl Roth), were rinsed with ultrapure water and were dried under a flow cabin to keep them free from dust particles. Double-sided adhesive transparent pads, placed on the cleaned glass slides, were used as otolith fixing material (for further information, see **Supplementary Figure 1**). Herring otoliths were dissected under a microscope (Olympus SD 30) and sagittal otoliths were removed with non-metallic equipment to minimize potential contamination. After dissection, each otolith (either left or right sagittal otolith) was rinsed in ultrapure water several times to remove any adhesive tissue and 30 otoliths per sampling area were used for chemical analysis of habitat-specific signatures, except for GB ($n = 15$). The chosen sample size was above the commonly accepted standard for this kind of analysis (Gillanders, 2002a; Hamer et al., 2003) and was assumed to be adequate to test our hypotheses. Otoliths were transferred and placed on the fixing material. Microscope slides with attached otoliths were stored in a plastic vials for further processing in the laboratory.

Analytical Methods

Elemental composition of herring otolith core regions were analyzed with the laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) technique, using a ThermoFinnigan ELEMENT2 ICP-MS with a Nd:YAG UP213 laser ablation system at the Max Planck Institute of Chemistry in Mainz, Germany. The certified reference material NIST612 (National Institute of Standards and Technology) and the micro analytical reference material MACS3 (United States Geological Survey) were used for calibration (Jochum et al., 2007; Jochum et al., 2011) and were analyzed prior to sample measurement and reference material measurements were constantly repeated to ensure quality. Otolith core regions were ablated with 80 μm laser spot size at 60% power with a pulse repetition rate of 10 Hz and energy densities of ∼10.2 J cm^{-2}. Dwell durations of otoliths were operated manually, due to individual otolith size and thickness. Further technical information of the New Wave laser ablation system and the operating parameters for the ELEMENT2 ICP-MS (further information is given in **Supplementary Table 1**).

Data Analysis

Values near detection limits were excluded and only elements with no more than two missing values were considered for the analysis. In total, the following 17 elements were used: lithium (Li), boron (B), sodium (Na), magnesium (Mg), silicon

TABLE 1 | Description of each inshore sampling area [Schlei Fjord (SF), Kiel Canal (KC), Warnow Estuary (WE), Greifswald Bay (GB)] with respective water body type, prevailing salinity ranges in PSU (Messner and von Oertzen, 1990; Feibicke, 1997; Kafemann et al., 2000), abiotic parameters at sampling location (SST and salinity), number of analyzed individuals and mean total length TL [mm] of caught age-0 herring with standard deviation.

Location	Water body type	Salinity range PSU	SST °C	Salinity PSU	No. of individuals	Mean TL mm
SF	Fjord 42 km	Mesohalin 3–18	20.8	4.03	30	37.2 (±2.9)
KC	Artificial water way 97 km	Mesohalin 2.5–15	20.0	7.05	30	38.0 (±1.8)
WE	Estuary 12.6 km^2	Mesohalin 5–18	20.1	10.7	30	23.2 (±3.5)
GB	Lagoon 514 km^2	Mesohalin 5–10	Ø18.3	Ø7.8	15	22.7 (±2.2)

The SST and salinity for GB are averaged due to different pooled stations.

(Si), manganese (Mn), iron (Fe), cobalt (Co), copper (Cu), zinc (Zn), rubidium (Rb), strontium (Sr), tin (Sn), barium (Ba), lead (Pb), thallium (Tl) and uranium (U). Potential chemical differences between different sampling locations were visualized by multidimensional scaling (MDS-plot), using the PRIMER Software (Version 6.1.13) and the dissimilarity matrix of calculating the Euclidean distances. Elemental concentrations were $\log(x+1)$-transformed for standardization. Statistical tests were performed with the software SPSS, statistical significance (significance level of $p < 0.05$) was tested by using one-way analysis of variance (ANOVA). Data sets were tested for variance homoscedasticity by Levene's test. Due to variance heteroscedasticity and unequal sample sizes, statistical significances were tested with ANOVA including Welch correction (Welch, 1938) which also compensates for non-normal distributions and *post-hoc* test for inhomogeneous variances and sample sizes (Games Howell test). *EFI* values were tested for significant differences within and between sampling areas using Welch Test and Games Howell *post-hoc* test to investigate significant differences between the four sampling sites.

Elemental Fingerprinting Index (*EFI*)

We visualized chemical otolith signatures for each spawning area by radar plots, based on the relative mean proportion of each element to the highest concentration found among the total of 105 individuals included in this study. We modified a well-established ecological overlap index (Schoener index, Schoener, 1974) to create the *EFI*, a novel measure of similarity between 2 fish individuals considering numerous chemical signatures in their otoliths. The $EFI_{i,j}$ describes the comparison of two fish individuals that includes 17 elements and was calculated according to the following equation:

$$EFI_{i,j} = \frac{2 \times \sum_{x=1}^{17} \min\,(conc\_x_i;\ \ conc\_x_j)}{\sum_{x=1}^{17} (conc\_x_i +\ \ conc\_x_j)}.$$

Where $conc\_x_i$ and $conc\_x_j$ represent the concentrations of element x in fish i and fish j, respectively, while min ($conc\_x_i$; $conc\_x_j$) represents the lower value of these two concentrations (for detailed information, see **Supplementary Figures 2**, **3**). The *EFI* ranges from 0 to 1, where a value of 0 indicates that two compared individuals are most different in otolith elemental composition, whereas a value of 1 indicating the highest similarity in elemental composition of two comparing individuals. We conducted elemental concentration comparisons for all individuals within one sampling area resulting in $\binom{30}{2} = 435$ pairs for each sampling area (except for GB: $\binom{15}{2} = 105$ pairs).

And comparisons of all individuals between the different sampling areas: $\binom{60}{2} - 2 \times \binom{30}{2} = 900$ pairs for each comparison (GB: $\binom{45}{2} - \left(\binom{30}{2} + \binom{15}{2}\right) = 450$).

Subsequently, we tested whether the variance among the *EFI*s derived from comparisons within the areas differed significantly from the *EFI*s obtained from comparisons of individuals from differing areas.

RESULTS

Chemical Signatures in Herring Otoliths

In total, 39 elements could be determined in young-of-the-year otolith samples from different inshore spawning areas. Altogether, 17 elements were used to distinguish the chemical otolith signatures from different sampling sites. The mean elemental concentrations are given in **Supplementary Table 2**. The element concentrations found in all 105 individuals were included in an MDS-plot for visualizing the differences in chemical signatures for each sampling area (**Figure 2**). Otolith signals from the western sampling areas Schlei Fjord (SF) and Kiel Canal (KC) are more similar in their elemental concentrations compared to the eastern sampling areas Warnow Estuary (WE) and Greifswald Bay (GB) with some intermingling signals from KC, GB and WE. Elemental otolith compositions from WE showed a higher variability in individual element concentration. However, a clear separation between the western and eastern spawning areas is discernible (**Figure 2**).

Significant Differences in Elemental Compositions

We found continuously high significant differences ($p \leq 0.001$) in element concentrations between all four sampling areas and significant differences ($p = 0.008$) for tin (Sn) (**Table 2**). Based on these results we performed *post-hoc* tests for single elements to identify habitat-specific significant differences between single sampling areas. Detailed information on the results for each element is given in **Table 3**. We found 13 elements to be significantly different between SF-WE comparison. The comparisons SF-KC and SF-GB revealed significant differences of 11 elements with uranium (U), being significantly different between SF-GB. Ten elements were significantly different within the KC-WE comparison. Furthermore, 7 elements were significantly different between KC-GB. The comparison WE-GB revealed significant differences in 6 elements (**Table 3**).

Elemental Fingerprinting Indices (*EFI*)

The entire chemical otolith inventory for each inshore coastal spawning area revealed 4 habitat-specific fingerprint plots with similarities in the generally dominance of single elements, but clear differences in their relative element ratio (**Figure 3**). We conducted multi-elemental concentration pairwise comparisons for individuals within one sampling site and pairwise comparisons of individuals between different sampling

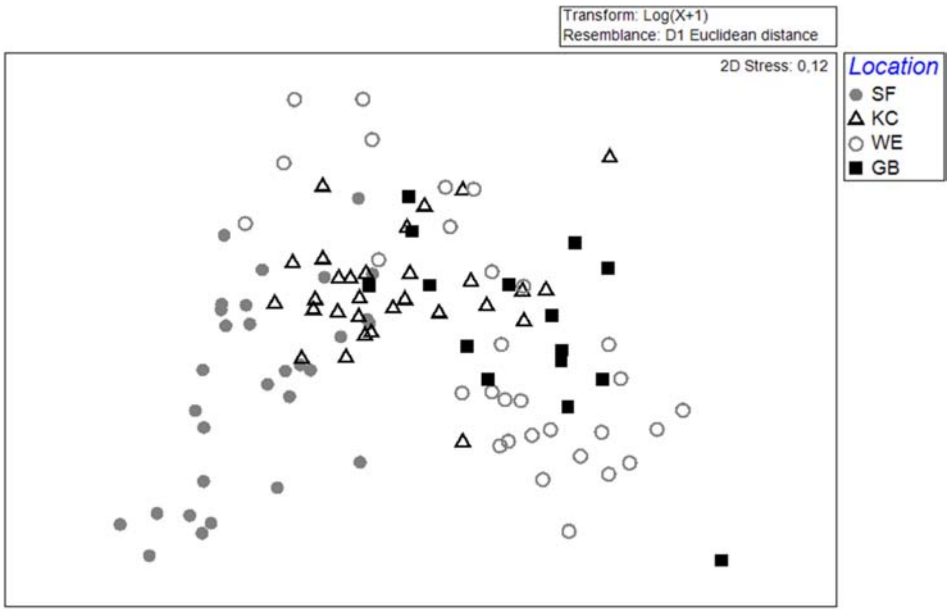

FIGURE 2 | MDS-Plot, using the Euclidean distance to classify groups of age-0 herring otoliths (based on 17 elements). Data were log(x+1)-transformed for standardization. The Schlei Fjord (SF, gray circles) and Kiel Canal (KC, black open triangles) are located along the western German coastline. The Warnow Estuary (WE, gray open circles) and Greifswald Bay (GB, black squares) represented samples from the eastern spawning areas. Each data point represents a single otolith and individual fish (n = 105).

sites, using *EFI* to identify similarities in element concentrations within one group and differences between groups. Elemental concentrations of individuals within each of the SF, KC and GB sample groups were rather stable, whereas WE samples were slightly more variable in their multi-element composition (lower mean *EFI*). Comparisons of individual fingerprints between two sampling groups revealed clear differences between WE and SF, whereas comparisons between SF-KC and KC-GB were more similar in their element signatures (**Table 4**). *EFI* values for comparisons of SF-GB, WE-KC and WE-GB were smaller than *EFI* values of within-group comparisons, indicating that elemental concentrations between all four groups are more different than within groups (**Table 4**). Regarding statistical differences between two group comparisons, the *EFI* values showed highly significant differences for all comparisons (GB-KC: $F_{(2,288.7)} = 253.2$, $p < 0.001$; GB-WE: $F_{(2,345.1)} = 144.8$, $p < 0.001$; GB-SF: $F_{(2,289.1)} = 410.8$, $p < 0.001$; WE-KC: $F_{(2,1767)} = 959.5$, $p < 0.001$; WE-SF: $F_{(2,1013.4)} = 1413.6$, $p < 0.001$; SF-KC: $F_{(2,975.5)} = 563.2$, $p < 0.001$). *Post-hoc* test results are shown in **Supplementary Table 3**.

TABLE 2 | Results of ANOVA with Welch correction to identify statistical differences in age-0 herring otolith element concentration between the four juvenile inshore areas [Schlei Fjord, Kiel Canal, Warnow Estuary (n = 30) and Greifswald Bay (n = 15)], with degrees of freedom (*df1* and *df2*), *F*-value and significance level (*p*) for each single element.

	df1	*df2*	*F*	*p*
Li	3	41.22	18.92	<0.001
B	3	43.43	70.19	<0.001
Na	3	43.66	27.65	<0.001
Mg	3	40.56	41.25	<0.001
Si	3	44.82	26.65	<0.001
Mn	3	43.29	7.77	<0.001
Fe	3	43.47	61.25	<0.001
Co	3	45.00	19.41	<0.001
Cu	3	39.31	14.91	<0.001
Zn	3	37.42	12.62	<0.001
Rb	3	39.57	16.79	<0.001
Sr	3	45.61	12.98	<0.001
Sn	3	37.89	4.59	0.008
Ba	3	46.95	12.98	<0.001
Pb	3	35.28	10.93	<0.001
Tl	3	52.02	61.11	<0.001
U	3	35.36	6.87	0.001

DISCUSSION

The successful outcome of otolith microchemistry studies strongly depends on spatial variability of elemental concentrations between investigated habitats. There is abundant evidence that fish otoliths from different basins and even sites within basins show spatial variability in their elemental composition (De Pontual et al., 1999; Rooker et al., 2001; Yamane et al., 2010). Our approach included the entire inventory of otolith-core elements summarized by a unique *EFI*, based on 17 elements. To our best knowledge, this approach allows comparing multi-elemental chemical composition of otoliths

TABLE 3 | Results of Games Howell *post-hoc* test to identify site-specific significant differences for each element with respective significant levels ($p \leq 0.05$), including sample sizes of $n = 30$ for Schlei Fjord (SF), Kiel Canal (KC) and Warnow Estuary (WE) and $n = 15$ for Greifswald Bay (GB).

	Site comparisons					
Element	**SF-KC**	**SF-WE**	**SF-GB**	**KC-WE**	**KC-GB**	**WE-GB**
Li	**0.001**	**<0.001**	**0.006**	**<0.001**	0.107	0.110
B	**<0.001**	**<0.001**	0.070	**<0.001**	**<0.001**	**<0.001**
Na	**<0.001**	**<0.001**	**<0.001**	**0.011**	0.419	0.523
Mg	**0.003**	**<0.001**	**<0.001**	**0.001**	0.486	**0.028**
Si	0.634	**0.002**	**<0.001**	**0.038**	**<0.001**	**0.002**
Mn	**0.001**	**0.006**	**0.001**	0.108	0.873	0.083
Fe	**<0.001**	0.202	0.547	0.207	**<0.001**	0.337
Co	**<0.001**	**0.045**	0.990	0.824	**<0.001**	**0.040**
Cu	0.118	**0.001**	**0.001**	**0.003**	**0.005**	0.536
Zn	**0.023**	**<0.001**	0.077	**0.003**	0.132	0.691
Rb	**<0.001**	**0.046**	**0.012**	0.632	0.968	0.810
Sr	0.938	**<0.001**	**0.038**	**<0.001**	0.088	0.095
Sn	0.736	**0.005**	1.000	0.907	0.738	**0.007**
Ba	**<0.001**	0.898	0.203	**<0.001**	**0.017**	0.052
Pb	0.234	**<0.001**	**0.047**	**0.001**	0.370	**0.009**
Tl	**<0.001**	0.152	**<0.001**	0.645	**<0.001**	0.282
U	0.158	0.175	**0.016**	0.189	0.051	0.280

Significant p-values are given in bold type.

within and between herring juvenile areas for the first time. Our results show significantly distinct chemical "fingerprints" on the scale of particular bays and estuaries providing a chemical "birth certificate" of their natal origin.

Environmental Factors

The incorporation of elements into the growing surface of fish otoliths is related to environmental variables, such as water temperatures, salinity and the availability of specific elements in the water (Tzeng et al., 1997; Elsdon and Gillanders, 2003). In addition, endogenous factors (such as physiology, genetics and growth effects) control incorporation processes (Fowler et al., 1995; Martin and Thorrold, 2005; Barnes and Gillanders, 2013). Elemental uptake by prey digestion might be marginal, at least for some species (Farrell and Campana, 1996; Milton and Chenery, 2001; Buckel et al., 2004). The impact of environmental variables on element incorporation is sufficiently studied, but results are rather contradictory (Kalish, 1989; Radtke et al., 1990; Townsend et al., 1992; Hoff and Fuiman, 1995), indicating that interactions between environmental and endogenous factors might be species-specific. However, it is stated that non-physiologically regulated elements (such as Sr, Ba, Mn) are usable for life history studies (Elsdon and Gillanders, 2003). Woodcock et al. (2012) indicated that Mg, an element often used in microchemistry studies, might also be physiologically regulated in fish otoliths. Hence, validation experiments for the species of interest are highly recommended to verify interpretations (Kalish, 1989).

Whereas studies on the elemental uptake are almost entirely focused on single elements (see review in Elsdon and Gillanders, 2003), multi-element investigations are rather scarce (Fowler et al., 1995; Elsdon and Gillanders, 2002). With our multi-element approach, including also heavy metals, we assume that observed chemical patterns are more related to habitat-specific differences than affected by endogenous factors. However, more research is required to understand the impact and interaction of different factors on elemental incorporation in herring otoliths.

Potential temporal variability of element concentrations is one important aspect to be considered in future connectivity studies (Milton et al., 1997; Hamer et al., 2003; Swearer et al., 2003; Arkhipkin et al., 2009). Although some studies showed high temporal variability in elemental concentrations, other studies revealed inter-annual consistency of elements (Patterson et al., 1999; Rooker et al., 2001), indicating that variability might be habitat-specific. Gillanders (2002b) stated to build up a library of elemental fingerprints over several years for each study area to increase the interpretation success of fingerprint patterns from juvenile fish, regarding contribution estimates of single reproduction areas to the overall fish population. A multi-year sampling should be considered in the future to investigate temporal consistency of the found habitat-specific signals.

Element Concentrations in Herring Otoliths

The concentrations levels found in YOY herring otoliths corresponded to levels for single elements (Mg, Zn, Sr, Ba, Pb) from a study by Brophy et al. (2003), except for the two elements Sr and Ba. Those in particular are marker elements for an origin relative to certain salinity conditions, with higher Sr concentrations in marine habitats and higher Ba concentrations in freshwater habitats (Tzeng and Tsai, 1994; Elsdon and Gillanders, 2005). The concentrations found in otolith samples from inshore juvenile areas were generally

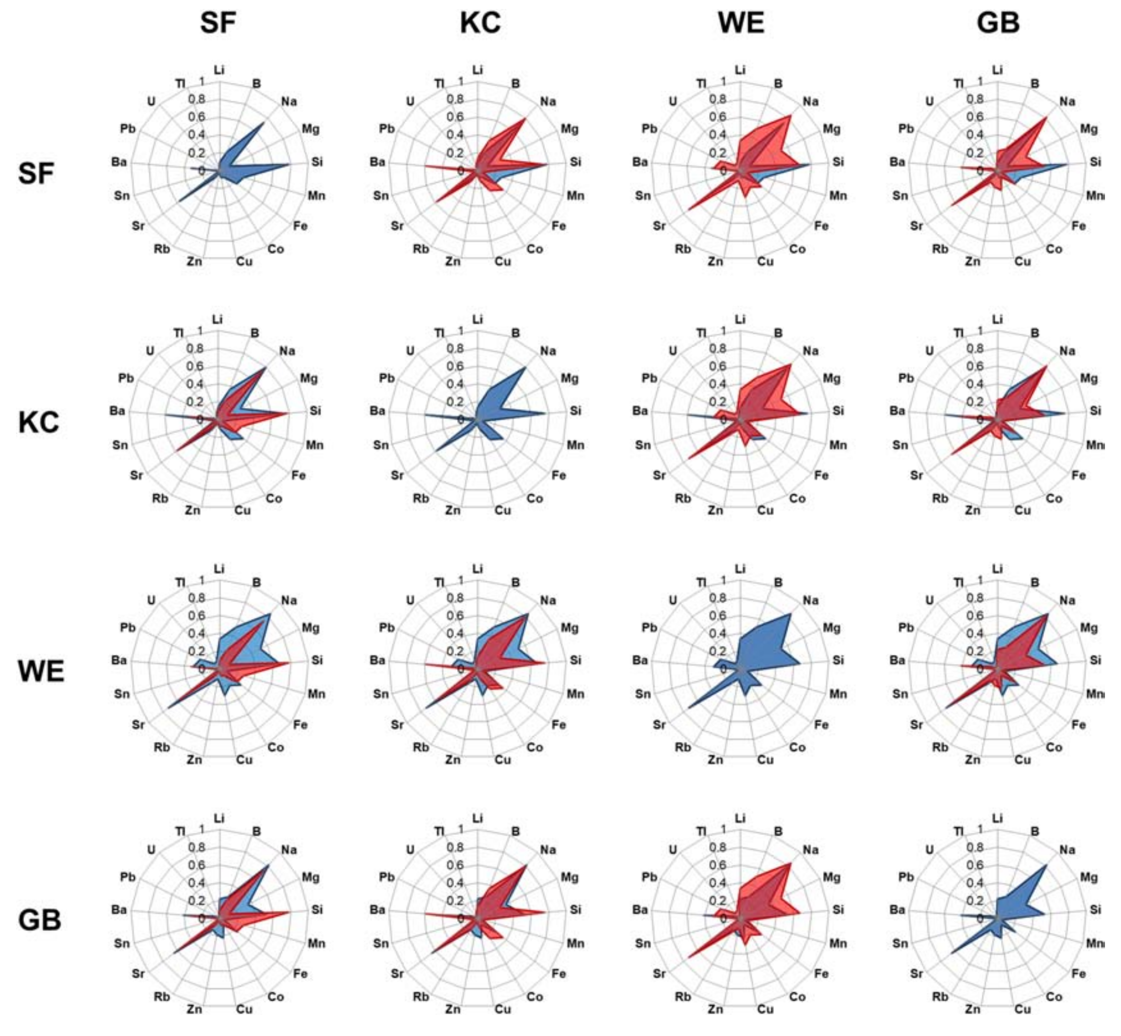

FIGURE 3 | Mean standardized concentrations of each single element for each sampling area are shown in a defined order, revealing radar plots with site-specific elemental fingerprints (blue radar plots in horizontal rows). Data were standardized to deal with different concentration units. Each site-specific radar plot was compared with the respective other three site-specific radar plots (shown by column in red) to visualize similarity or differences in elemental concentrations of western locations [Schlei Fjord (SF), Kiel Canal (KC)] and eastern locations [Warnow Estuary (WE) and Greifswald Bay (GB)].

lower in Sr and higher in Ba, compared to herring otoliths from the North Sea (Brophy et al., 2003), reflecting the brackish Baltic Sea ecosystem, with high salinity gradients (from rather marine salinities of ∼30 PSU) in adult herring feeding areas up North in the Kattegat and Skagerrak to more brackish conditions within the Western Baltic Sea. In addition to the overall Baltic Sea salinity gradient from Southwest to Northeast, there are multiple local inshore-offshore salinity gradients composed by river estuaries or other transitional waters, making it difficult to interpret results solely based on these salinity signatures. Hence, we focused on the multiple-element approach to find differences in elemental composition of herring otolith from different coastal spawning grounds.

Sampling in four historically known juvenile areas was performed in summer 2016. Due to sampling site-specific time of spawning and larval growth, we were not able to sample YOY herring otoliths of the same size. However, high concentration variations between different otolith sizes could not be observed during our measurements. Using the LA-ICP-MS approach for unpolished herring otoliths within a specific size-range was applicable, at least for the Western Baltic Sea, since all herring samples were collected within their inshore coastal reproduction areas. Moreover, the approach of solution-based ICP-MS is an approved method, where whole otoliths are dissolved in nitric acid to analyze chemical signatures and habitat-specific patterns (Patterson et al., 1999; Rooker et al., 2003). However, the choice of sample processing and analytical methods is depending on single fish species and their particular habitat utilization.

Multi-Element Approach

Although we were able to detect concentration values of 39 elements in total with the LA-ICP-MS approach, we had to exclude all rare earth metals and some heavy metals

TABLE 4 | Elemental fingerprinting indices {mean *EFI* [with standard deviation (±SD)] and median *EFI*} with number of comparisons for each sampling area (upper table) and results of comparisons between respective groups (lower table) with number of comparisons.

	Comparisons within one group			
Area 1		**No. comparisons**	**Mean *EFI* (±SD)**	**Median *EFI***
SF		435	0.877 (±0.039)	0.879
KC		435	0.858 (±0.043)	0.861
WE		435	0.755 (±0.074)	0.762
GB		105	0.845 (±0.048)	0.850
	Comparisons between two groups			
Area 1	**Area 2**	**No. comparisons**	**Mean *EFI* (±SD)**	**Median *EFI***
SF	KC	900	0.799 (±0.048)	0.802
SF	WE	900	0.705 (±0.086)	0.703
SF	GB	450	0.777 (±0.062)	0.784
KC	GB	450	0.792 (±0.046)	0.795
WE	KC	900	0.737 (±0.059)	0.739
WE	GB	450	0.759 (±0.067)	0.764

The EFI ranges from 0 to 1, where a value of 0 indicates that two compared individuals are most different in otolith elemental composition, whereas a value of 1 indicating the highest similarity in elemental composition of two comparing individuals.

(such as Cd and Hg), due to concentration levels below the instrument detection threshold. All together 17 elements could be used for data analysis, which is still an appreciable element number. In most studies, differences in elemental compositions were mainly based on a few established elements (e.g., Ba, Mg, Mn, Sr) (see Thorrold et al., 1998; Campana et al., 2000) with some exceptions, focusing also on multiple elements (Edmonds et al., 1991; Leakey et al., 2009). For our interdisciplinary multiple-element approach, we created a unique and innovative *EFI* to describe differences and similarities of the otolith chemical inventory. The *EFI*s were more similar within one group/sampling area than between different sampling areas, indicating that habitat-specific chemical signatures were more stable within a particular area and more variable between different sampling areas, except for the comparison GB-WE, due to higher variability in chemical composition of WE samples. Our results show a clear separation between the western and eastern spawning areas, based on site-specific water chemistry, including salinity and pollutant signals. We can only speculate, if these patterns reflect the historical pollutant signals of different water management strategies, caused by the boundary of the "German Wall," since pollutants are known to accumulate into the sediment over decades (Deely and Fergusson, 1994; Ruiz, 2001; Buccolieri et al., 2006) or if different elemental signals are based on site-specific alterations (ship traffic, industrial and agricultural discharge).

The lack of knowledge on the quantitative contribution of single reproduction areas to the overall herring population is problematic, since herring show a distinct homing behavior to their traditional spawning areas. If important nursery areas are affected by human-induced habitat degradation and environmental conditions of important nurseries become unfavorable for successful herring reproduction, but herring continue their migrations to these specific anthropogenic-stressed habitats, this might have severe impacts for the population persistence. This unknown habitat dependency demonstrates the relevance of our results, which set the baseline for future estimates on habitat productivity, which could lead to a more directed coastal zone management of important spawning grounds and coastal nursery areas in the future.

AUTHOR CONTRIBUTIONS

DM, PK, LvN, and PP conceptualized the study. DM wrote the manuscript, performed the sampling and was responsible for laboratory processing and sample preparation. KJ and DM performed the measurements with the LA-ICP-MS. DM and PK analyzed the data. PK contributed the *EFI* calculations and *EFI* statistical analyses. PK, LvN, PP, and KJ revised the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00191/full#supplementary-material

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Systematic Review of Fish Ecology and Anthropogenic Impacts in South American Estuaries: Setting Priorities for Ecosystem Conservation

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Research on estuarine ecology in South America (SA) increased quali-quantitatively since the early 1980 in search of consistent recommendations for estuarine conservation. The most important ecological theory achieved is that the seasonal fluctuation of the salinity gradient creates an ecocline influenced by gradual changes between river-dominated to marine-like waters. Estuarine fish fauna adapts to these changeable abiotic characteristics, including the spatial, and seasonal bioavailability of dissolved oxygen and numerous pollutants. However, studies on the influence of the estuarine ecocline are still missing for key estuarine systems. This study provides an overview of fish ecology and anthropogenic impacts within estuarine systems of SA and discusses priorities for environmental conservation. Research on fish reached important conclusions regarding essential habitats and fish interaction with other biological and abiotic compartments over spatio-temporal settings, including conditions of severe anthropogenic impacts. These impacts are related to unplanned urban settlements, industrial estates, ports, damming of major rivers, dredging activities, and deforestation for extensive farming. Changes in estuarine morphology alter natural flows and lead to habitat losses, disrupting the ecocline and impairing fishes from moving among formerly connected habitats, especially earlier ontogenetic phases. In addition, industrial, urban, and farming activities often result in high loads of metals and persistent organic pollutants, organic enrichment and oxygen depletion. Moreover, plastic debris, a ubiquitous contaminant with sources on every human activity, including fishing, when fragmented into microplastics, become preferably concentrated in semi-enclosed environments, as estuaries. Metals, POPs and microplastics are actually asserted to be persistent. When in high concentrations, they become bioavailable to the estuarine trophic web through bioaccumulation, being biomagnified or biotransfered toward higher trophic level organisms, such as top predator fishes. Therefore, research on environmental quality and fish ecology must be based on robust sampling designs along the whole ecocline using long-term approaches. In addition, basic sanitation, co-management, an improved

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licensing system and scientifically-based risk assessments/monitoring for all sorts of enterprise are also urgent. These conservation priorities need to be in place before human-driven changes surpass the ecosystem's capacity to produce resources and maintain services.

Keywords: estuarine ecocline, estuarine conservation, human modification, contamination of aquatic habitats, fish ecology, environmental quality

INTRODUCTION

Estuaries are characterized by gradual changes between freshwater inputs and marine waters intrusion (Barletta et al., 2017a). The encounter of these two water masses creates zones of mixing and vertical stratification of various strengths. Such stratification results in a variety of abiotic habitats that function as boundaries defining different faunal communities, which are influenced mainly by the seasonal fluctuation of the salinity gradient as induced by diel tidal variation and river runoff. Thus, an ecocline can be defined as a "gradation from one ecosystem to another when there is no sharp boundary between the two" (Attrill and Rundle, 2002). Usually, these boundaries are freshwater-oligohaline/upper, mesohaline-mixoeuhaline/middle, and euhaline-hyperhaline/lower reaches (Day et al., 2012). Each of these reaches can actually move horizontally, advancing seawards according to increased rainfall patterns or upstream under tidal influence (Barletta et al., 2005). Moreover, the seasonal balance of dissolved oxygen, suspended solids, pollutants, and microbiological contaminants are also ruled by the estuarine ecocline and temperature variability (Barletta et al., 2017a). Not surprisingly, this ecocline is the strongest forcing structuring physico-chemical conditions and fish communities within any estuarine ecosystems (Barletta et al., 2008).

Human interventions, such as damming of major rivers and dredging of channels along the estuarine course, might weakens and even disrupt the ecocline, reducing the original ecological functions, impairing the sustainable use of estuarine resources and services (Blaber and Barletta, 2016). These modifications are also responsible for disrupting sediment flows, change bottom composition and impair freshwater flow seawards, leading to changes in habitat availability, biodiversity damages, and shifts in biogeochemical cycles of several chemicals and pollutants (Barletta et al., 2016, 2019). Moreover, entire river basins, estuarine courses, and adjacent coastal waters are subjected to the influence of industrial, urban and farming activities, which are responsible for high loads of wastewaters and solid wastes (Huang et al., 2014; Pereira et al., 2015). Thereby, plastic debris, metals, nutrients, POPs and emerging pollutants present high concentrations closer to their sources, usually urban settlements, industrial estaes, and farms. Their chemical behavior and bioavailability for fishes along the way to the sea are also influenced by the major annual water quality shifts. The solubilisation, speciation, sorption, precipitation, diffusion, advection, sinking toward sediments, complexation, and absorption by the estuarine food web is the result of the seasonal fluctuation of the estuarine ecocline. Overall, pollutants are entraped in estuaries when saline intrusion is great and flushed out to the sea when river runoff increases (Barletta et al., 2012, 2019; Lima et al., 2014). Metals, POPs and microplastics are all persistent in the environment. The bioaccumulation and biomagnification of metals and POPs (Lanfranchi et al., 2006; Cappelletti et al., 2015), as well as the trophic transfer of microplastics (Galloway et al., 2017) are common in estuarine trophic webs. In addition to habitat loss by water quality/volume changes and damming of major rivers, fishes are also subjected to fishing pressure and to compete for resources with introduced species, often resulting in decreased native fish biomass within estuaries (Neuhaus et al., 2016; Barletta et al., 2017b). Currently, it is asserted that if human-driven changes remain uncontrolled, estuaries may become increasingly vulnerable to co-working global changes (Costa and Barletta, 2016; Ríos-Pulgarín et al., 2016). However, despite these impacts, changes in local climate and hydrodynamic variability might contribute to reduce pollution through biodilution and transport of contaminants out of the system, especially during the rainy season, when river flow increases, in a process known as environmental homeostasis (Elliott and Quintino, 2007). On the other hand, systems that suffer with severe droughts may not be able to recover and will face long and lasting antropogenic modifications.

This work is an overview of estuarine fish research and anthropogenic influences on estuarine fishes and estuarine ecosystems of SA located in tropical, subtropical and warm temperate provinces (**Figure 1** and **Table 1**; study areas are described as **Supplementary Material**). Whereas, the current knowledge of estuarine fish fauna are poorly understood in this continent, this review focused in the description of the available information on fish ecology and how human-driven contamination and modifications have affected several estuarine systems and fishes of commercial and subsistence importance. To gather and interpret all the relevant literature aiming at generating managerial information was a daunting task, but a unique opportunity to promote well-informed decision-making, especially considering the transition among environments from equatorial to temperate regimes (Costa and Barletta, 2016). However, the ecocline theory is hardly ever attempeted in most studies. Therefore, the review also discusses on how to work in favor of the seasonal fluctuation of the ecocline is important to understand the distribution pattern of dominant fish species and major contaminants along estuarine systems and food webs.

METHODS

To address fish ecology and environmental quality of SA estuaries into a single manuscript, we performed a vast scientific search aiming at collect the greatest amount of studies in estuarine systems of every coastal country sourrunding the continent. We compiled information of nearly 420 articles found in the databases Web of Science, Scopus, and Google Scholar.

RESULTS

Western Atlantic Estuaries

Tropical Northwestern Atlantic

Ciénaga Grande de Santa Marta Lagoon: Colombian Caribbean Coast

A complete description on the influence of the seasonal fluctuation of the estuarine ecocline on fish assemblages is available encompassing two annual cycles of 1993–1994 and 1997 within the Ciénaga Grande de Santa Marta Lagoon (Rueda and Defeo, 2003; **Figure S1**). The most contrasting seasons (major rainy and major dry), were used as temporal factors to reveal a strong relation between salinity variability and fish density ruled by seasonal shifts. Three distinct assemblages were determined by the salinity gradient, changing from freshwater to marine-estuarine and marine assemblages (Rueda and Defeo, 2003). *Eugerres plumieri*, *Diapterus rhombeus* (Gerreidae), *Micropogonias furnieri* (Sciaenidae), *Mugil incilis* (Mugilidae), *Cathorops spixii* (Ariidae), *Elops saurus* (Elopidae), and *Anchovia clupeoides* (Engraulidae) were the most frequent species. *Anchovia clupeoides* typified the rainy season of 1997; *Cathorops spixii* and *E. saurus* typified the dry season; and *M. incilis* and *M. furnieri* the rainy season in both annual cycles. *D. rhombeus* and *E. plumieri* typified the dry and rainy seasons of 1993–1994 (Rueda and Santos-Martínez, 1999; Rueda and Defeo, 2003). The highest densities of *E. plumieri* and *M. incilis*; and a peak of *C. spixii* occurred during the rainy season, near the opening of the lagoon (Rueda, 2001).

Regarding biological studies, the feeding ecology of *A. clupeoides* (Duque and Acero, 2003) and *Oligoplites* spp. (Carangidae) (Duque-Nivia et al., 1996) were described using spatio-temporal patterns along the salinity ecocline. The reproduction of *Bairdiella ronchus* (Sciaenidae) was also described according to the relationship between monthly gonadosomatic index and salinity variability, however no relationship was identified (Castro et al., 1999).

North Brazil Shelf

Amazon Estuarine Complex: North Brazil/Amazonia

In the Amazon Estuarine Complex (**Figure S2**), ecological guilds and fish diversity were assessed according to spatial and sesonal structures within the main channel and tidal creeks of the Pará River estuary (Mourão et al., 2014, 2015). Fish composition, abundance, and the use of estuarine habitats as nursery and reproduction grounds were mainly structured by salinity. The highest diversity and abundance of fishes occurred during the dry season in the main channel, while tidal creeks were used for reproduction. Migrants and freshwater stragglers were dominant in the lower estuary (Guamá River and Guajará Bay), while estuarine, marine stragglers and migrants predominated along the main channel (Mourão et al., 2014). Piscivorous and zoobenthivorous were the dominant feeding groups in all studied areas. Most species were occasional, characterizing the estuary as a transition zone (Mourão et al., 2015).

Starting from this estuary and traveling all the way to the Andes foothills, Amazonian catfishes (*Brachyplatystoma* spp.) perform one of the longest fish migrations in the world. They are commercially important and utilize the entire Amazon Basin to complete their life cycles. Populations are declining due to overfishing and to the presence of dams in the upper reaches of the migration range, which impairs spawning (Barthem et al., 1991). Otolith microchemistry revealed that larvae migrate downstream from the Andean piedmont to the lower Amazon (Duponchelle et al., 2016), while juveniles exhibit diverse strategies, rearing upstream, or downstream (Hegg et al., 2015).

Studies on the ecology of Amazonian freshwater stingrays (Potamotrygonidae) were performed within the Amazon complex. *Potamotrygon motoro* is a predominant species in Marajó Island (between the Amazon and Pará estuaries) showing preference for intermediate salinities and being resistant to critical conditions of pH, dissolved oxygen and temperature (Almeida et al., 2009). *Paratrygon aiereba* was studied according to cytogenetic approaches. The results revealed that their populations are structured within each one of the five rivers of the Amazon Basin, with no gene flow. Thus, the species is acknowledged as three distinct biological species, emphasizing that the management of their exploitation needs to focus on each river, rather than the entire river basin (Frederico et al., 2012).

In the Pará River Estuary, length–weight relationships of fish species (Loureiro et al., 2017), as well as the reproductive biology of commercial sciaenids are available (Santos et al., 2010; Barbosa et al., 2012). *Plagioscion squamosissimus* (sciaenidae) reproduces primarily in February/March and August/September (Barbosa et al., 2012), while *Plagioscion magdalenae* (Sciaenidae) spawns mainly from August to February (Santos et al., 2010).

Curuçá Estuary: North Brazil/Eastern Amazon

In Curuçá Estuary (**Figure S3**), forty intertidal fish species had their weight-length relationship studied by Giarrizzo et al. (2006). Moreover, the ontogenetic and seasonal diet shifts of *Sciades herzbergii* (Ariidae) (Giarrizzo and Saint-Paul, 2008), *Lutjanus jocu* (Lutjanidae) (Monteiro et al., 2009), and *Colomesus psittacus* (Tetraodontidae) (Giarrizzo et al., 2010) were also assessed for tidal creeks. The seasonal availability of food was more important than ontogenetic diet shifts; and stable isotope approaches revealed different types of food webs within the same ecosystem (Giarrizzo et al., 2011; Schwamborn and Giarrizzo, 2015).

The seasonal changes in the composition of intertidal fish assemblages inhabiting four creeks of the same salinity zone in the upper and middle reaches were investigated (Giarrizzo and Krumme, 2007). Fish composition changed seasonally, while density and biomass differed spatially, suggesting that spatial composition within habitats of homogenous salinity are dependent on landscape features.

Caeté River Estuary: North Brazil/Eastern Amazon

In the Caeté Estuary (**Figure S4**), fluctuations of the salinity gradient were the main forcing structuring fish assemblages over the annual cycle of 1996–1997 (Barletta et al., 2005).

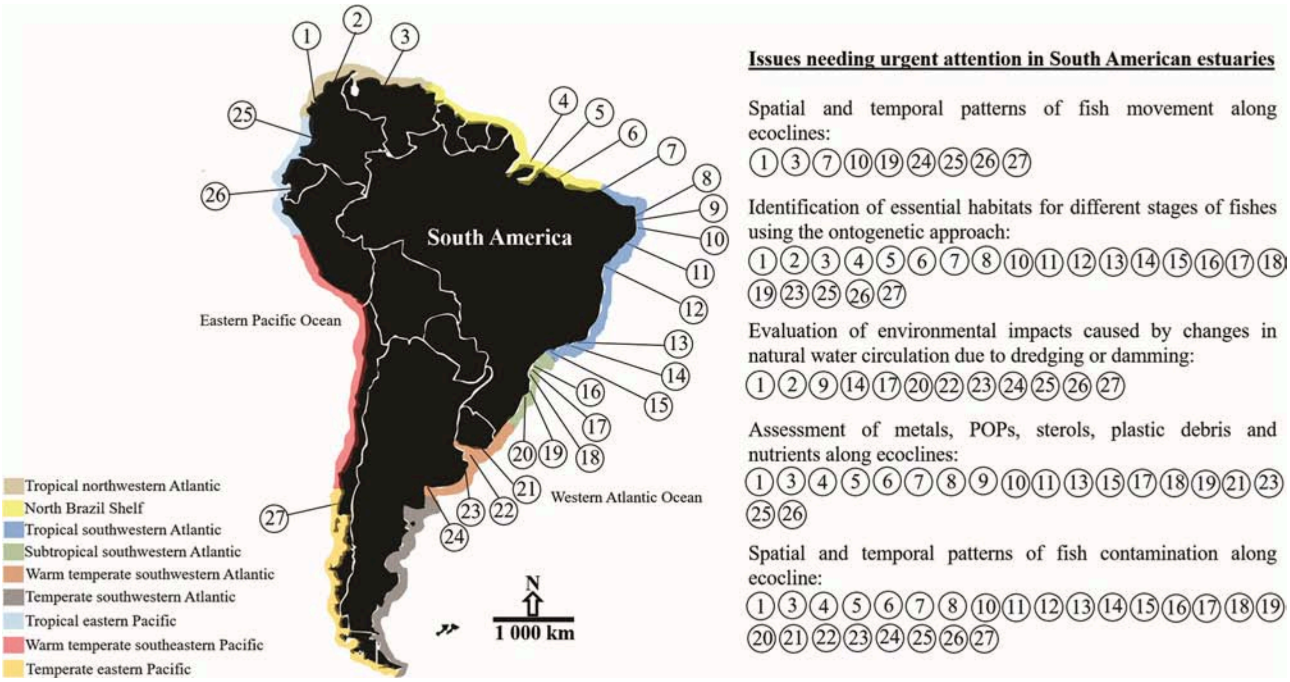

FIGURE 1 | Location and main conservation issues identified in South American estuaries. Tropical northwestern Atlantic [(1) Atrato River Delta; (2) Ciénaga Grande de Santa Marta Lagoon; (3) Orinoco River Delta]. North Brazil Shelf [(4) Amazon Estuarine Complex; (5) Curuçá Estuary; (6) Caeté Estuary]. Tropical southwestern Atlantic [(7) Parnaiba River Delta; (8) Potengi Estuary; (9) Goiana Estuary; (10) Itamaracá Estuarine System; (11) São Francisco River Estuary; (12) Paraguaçu Estuary; (13) Guanabara Bay; (14) Sepetiba Bay; (15) Santos Estuary]. Subtropical southwestern Atlantic [(16) Paranaguá Estuarine Complex; (17) Guaratuba Bay; (18) Babitonga Bay; (19) Laguna Estuarine Complex; (20) Patos Lagoon Estuary]. Warm temperate southwestern Atlantic [(21) Pando Sub-Estuary; (22) Río de La Plata Estuary; (23) Mar Chiquita Coastal Lagoon; (24) Bahía Blanca Estuary]. Tropical eastern Pacific [(25) Bahía Málaga Estuary; (26) Rio Palmar and Rio Javita Estuaries]. Temperate eastern Pacific [(27) Valdivia Estuary]. Source: Google Earth.

Stellifer rastrifer, *Stellifer microps* (Sciaenidae), *C. spixii*, and *Aspredo aspredo* (Aspredinidae) were the most abundant species. The species *S. rastrifer* was found along the entire main channel, regardless seasons; *S. microps* and *A. aspredo* were abundant in the upper estuary over the year, while *C. spixii* peaked in the middle and lower reaches in the early-rainy season. Larval phases of these four frequent species were also found in the main channel (Barletta-Bergan et al., 2002a). In addition, larvae of *Stellifer* and *Cathorops* genera were also found in mangrove creeks, emphasizing the importance of the system for the life cycle of subsistence species (Barletta-Bergan et al., 2002b).

Larval *A. Clupeoides* and *S. microps* were abundant in the main channel, peaking in the upper estuary in the dry season (Barletta-Bergan et al., 2002a). *Guavina guavina* (Eleotridae) and *A. clupeoides* were also frequent in the creeks, peaking in August (Barletta-Bergan et al., 2002b). Larval *Cynoscion acoupa* (Sciaenidae) was the most abundant commercial species in terms of density in both main channel and creeks. However, later stages were not frequent in the main channel (Barletta et al., 2005) or even in creeks (Barletta et al., 2003), placing this species as marine-estuarine dependent. Moreover, in a mangrove lake at the middle estuary, *Achirus achirus* (Achiridae), and the commercial taxa *Centropomus pectinatus*, *Centropomus undecimalis* (Centropomidae) and *M. curema*, accounted for 82% of the total catch in weight along 24 h sampling-cycles in wet and dry months, reinforcing the importance of the connectivity among estuarine habitats for fishes (Goch et al., 2005).

Tropical Southwestern Atlantic

Goiana River Estuary: Northeast Brazil

The main channel of the Goiana Estuary (**Figure S5**) was year-round characterized along its ecocline. In a rare effort, the influence of the ecocline on the movement patterns of fishes have been assessed throughout their ontogeny, from larval to adult phases along the annual cycles of 2005–2006 and 2012–2013. Fluctuations of the salinity ecocline and levels of dissolved oxygen structured the ariids *C. spixii* and *Cathorops agassizii* (Dantas et al., 2012). Juveniles peaked in the middle estuary in the early-rainy season (March–May), characterizing their nursery ground. For *C. spixii*, the nursery shifted to the lower estuary during the late-rainy season (June–August), while for *C. agassizii* it remained in the middle estuary. Sub-adults and adults peaked in the upper estuary in the rainy season. High densities of mouth-brooder males, free embryos and young juveniles were observed in the upper estuary during the late-dry season (December–February), characterizing their reproductive grounds. Mangrove creeks are important grounds only for later phases of these species, since earliest phases receive parental care (Ramos et al., 2011; Lima et al., 2012, 2013).

Salinity and water temperature shifts structured the patterns of estuarine use by *Stellifer brasiliensis* and *Stellifer stellifer*

TABLE 1 | Ecoregions, geographical regions, and total area of key estuarine systems in South America based on available published data.

Ecoregions	Estuarine systems	Total areas	Geographical regions	References
WESTERN ATLANTIC				
Tropical Northwestern Atlantic	Atrato River Delta	Unavailable	Colombia/Panamá Bight	Correa-Herrera et al., 2017
	Ciénaga Grande de Santa Marta Lagoon	45,000 ha	Colombia/Caribbean	Rueda and Defeo, 2003
	Orinoco River Delta	2,250,000 ha	Colombia/Guianan/Caribbean	Blaber and Barletta, 2016
	Amazon Estuarine Complex	700,000,000 ha	Northern Brazil/Amazonia	Borba and Rollnic, 2016
North Brazil Shelf	Curuçá Estuary	20,000 ha	Northern Brazil/Amazonia	Giarrizzo and Krumme, 2007
	Caeté Estuary	22,000 ha	Northern Brazil/Amazonia	Barletta et al., 2005
Tropical Southwestern Atlantic	Parnaiba River Delta	275,000 ha	Northeastern Brazil/Amazonia	Barletta et al., 2017b
	Potengi Estuary	Unavailable	Northeastern Brazil	Oliveira et al., 2011
	Goiana Estuary	4,700 ha	Northeastern Brazil	Ferreira et al., 2016
	Itamaracá Estuarine System	82,400 ha	Northeastern Brazil	Vasconcelos Filho et al., 2003
	São Francisco River Estuary	Unavailable	Northeastern Brazil	Barletta et al., 2017b
	Paraguaçu Estuary	12,800 ha	Northeastern Brazil	Reis-Filho and Santos, 2014
	Guanabara Bay	40,000 ha	Southeastern Brazil	Rodrigues-Barreto et al., 2017
	Sepetiba Bay	30,500 ha	Southeastern Brazil	Araújo et al., 2017
	Santos Estuary	4.41 ha	Southeastern Brazil	Santos J. A. P. et al., 2015
Subtropical Southwestern Atlantic	Paranaguá Estuarine Complex	61,200 ha	Southern Brazil	Barletta et al., 2008
	Guaratuba Bay	4,500 ha	Southern Brazil	Vendel et al., 2010
	Babitonga Bay	13,000 ha	Southern Brazil	Vilar et al., 2011
	Laguna Estuarine Complex	21,500 ha	Southern Brazil	Barletta et al., 2017b
	Patos Lagoon Estuary	1,036,000 ha	Southern Brazil	Garcia et al., 2001
Warm Temperate Southwestern Atlantic	Pando Estuary	17 ha	Uruguay	Acuña-Plavan et al., 2010
	Río de La Plata Estuary	3,800,000 ha	Uruguay-Argentina	Jaureguizar et al., 2004
	Mar Chiquita Lagoon	4,600 ha	Argentina	Bruno et al., 2013
	Bahía Blanca Estuary	190,000 ha	Argentina	Sardiña and Lopez Cazorla, 2005a
EASTERN PACIFIC				
Tropical Eastern Pacific	Bahía Málaga Estuary	13,00 ha	Colombia/Panamá Bight	Cordoba and Giraldo, 2014
	Rio Palmar and Rio Jovita Estuaries	Unavailable	Ecuador/Guayaquil	Shervette et al., 2007
Temperate Eastern Pacific	Valdivia and Corral Bay Estuaries	Unavailable	Chile/Araucanian/Chiloense	Fierro et al., 2014

(Sciaenidae) along the system (Dantas et al., 2015). The middle estuary was an important nursery ground for juveniles and a feeding ground for sub-adults and adults of both species in the late-rainy season (June–August), except for adult *S. stellifer*, which peaked in the early-dry season (September–November). Later phases and larval *S. brasiliensis* were also found in mangrove creeks (Ramos et al., 2011; Lima et al., 2016), but were absent in the main channel, while larval *S. stellifer* were only recorded in the main channel (Lima et al., 2015). The species *C. acoupa* uses the upper estuary as a nursery in the early-rainy season (Ferreira et al., 2016). Sub-adults peak in the upper estuary during the entire annual cycle and migrate to the middle estuary in the late-rainy season, while adults inhabit adjacent coastal waters. Larval *C. acoupa* peaks in the lower estuary over the entire year (Lima et al., 2015), suggesting that spawning occurs in coastal waters; and later, larval and sub-adult phases inhabit the estuary (Ramos et al., 2011; Ferreira et al., 2016; Lima et al., 2016).

The patterns of estuarine use by Gerreidae species were influenced by changes in salinity gradient and dissolved oxygen (Ramos et al., 2016). Juvenile *Eugerres brasilianus* uses the upper estuary and the middle estuary as nursery grounds during the late-dry and early-rainy seasons, respectively. Sub-adults peaked in the upper estuary in the early-dry season, while adults were abundant over the entire year. On the other hand, juvenile *Eucinostomus melanopterus* uses estuarine beaches as nursery in the early-rainy and dry seasons. Independent of seasons, the abundance of sub-adults and adults at beaches toward the north of the estuarine mouth points to a degree of competition for estuarine resources, since both phases rely on the same food items (Ramos et al., 2016). Both species were found in tidal creeks (Ramos et al., 2011), but the larval phase of *E. brasilianus* was recorded in the main channel (Lima et al., 2015).

São Francisco River Estuary: Northeast Brazil

Flood pulses and river flow dynamics structured fish movement in the São Francisco River basin (Nestler et al., 2012). However, the estuarine portion is severely affected by eight upstream hydroelectric power dams that control flood pulses and alternative fish habitats (Coimbra et al., 2017; **Figure S6**). Alterations in flow regime facilitated the establishment of the non-native *Metynnis lippincottianus* (Serrasalmidae), while some endemic fishes disappeared (Assis et al., 2017). Restocking programs for the endemic *Prochilodus argenteus* (Prochilodontidae) were successful, but are no further recommended because the low allelic richness of the hatchery stock can minimize genetic diversity and increase the divergence from ancestral generations (Coimbra et al., 2017). Restocking programs were also tried for *Brycon orthotaenia* (Bryconidae), and now, after 40 years, they are recorded in the system (Brito et al., 2016).

The estuary, however, still maintains important ecological functions regarding connectivity. Its mouth is an important ground for the gonadal maturation of *E. brasilianus* (Rodrigues et al., 2017). Moreover, coastal demersal fishes are also influence by changes in abiotic conditions. The freshwater flux during the rainy months increases the functional diversity of fishes at shallower depths along the coast and estuarine-adapted fishes invade shallow coastal regions in a process known as estuarization of the coast (Passos et al., 2016).

Paraguaçu River Estuary: Northeast Brazil

Fish assemblages and functional guilds in the Paraguaçu Estuary are distributed according to differences in the salinity gradient (Reis-Filho et al., 2010; **Figure S7**). The middle estuary was dominated by *S. rastrifer* and *Cynoscion microlepdotus* (Sciaenidae). *Eucinostomus argenteus* (Gerreidae), *Pellona harroweri* (Pristigasteridae), and *D. rhombeus* were frequent in the middle and lower estuaries, while *Sphoeroides greeleyi* (Tetraodontidae) was frequent over the main channel. Deep-water and estuarine-resident fishes were abundant in the middle estuary, while shallow-water fishes were common in more saline areas. Marine-migrants were found in all sectors, while marine-stragglers were common from the middle to the mouth of the estuary (Reis-Filho et al., 2010). Organic matter and salinity were the main factors influencing overall fish distribution. Dissolved oxygen and organic matter structured the distribution of *Eleotris pisonis* (Eleotridae), *Trinectes paulistanus*, *Achirus declives* (Achiridae), *Sphoeroides testudineus* (Tetraodontidae), *D. rhombeus*, *Citharichthys spilopterus* (Paralichthyidae), *Ctenogobius stomatus* and *Ctenogobius stigmaticus* (Gobiidae) in habitats unaffected by aggardation, and *Dormitator maculatus* (Eleotridae), *E. argenteus* and *Atherinella brasiliensis* (Atherinopsidae) in affected habitats of the upper estuary.

Guanabara Bay: Southeast Brazil

In Guanabara Bay, the influence of the seasonal variability of local environmental factors on spatial patterns of demersal fishes was assessed in a fortnightly survey among 2005–2007 (Silva et al., 2016; **Figure S8**). Salinity, dissolved oxygen, ammonium, and phosphorus were responsible for quali-quantitative changes in spatio-temporal estuarine use. *Chilomycterus spinosus* (Diodontidae), *G. genidens*, *E. argenteus*, and *M. furnieri* were abundant species. The species *C. spinosus* were concentrated in the middle bay exhibiting high tolerance to eutrophic conditions and variations in salinity and temperature (Santos S. R. et al., 2015). A rise in the abundance of small specimens were observed when rainfall increased. The species *G. genidens* had strong association with the upper bay, where ammonium, total phosphorus and temperatures were higher (Silva et al., 2016).

The species *M. furnieri* (Mulato et al., 2015) and *E. Argenteus* (Corrêa and Vianna, 2016) were also frequent throughout the year. Juveniles had higher frequency in the upper and middle bays, while larger fishes were frequent in the lower bay. Recruitment of *M. furnieri* is observed in late fall, winter and spring (Mulato et al., 2015), and *E. argenteus* recruits in the first semester of each year (Corrêa and Vianna, 2016).

At the seawards end of the bay, Haemulidae, Pomacentridae and Labrisomidae were the richest families, and *Diplodus argenteus* (Sparidae), *Haemulon aurolineatum* (Haemulidae), *Stephanolepis hispidus* (Monacanthidae), and *Abudefduf saxatilis* (Pomacentridae) were the abundant species inhabiting an exposed estuarine beach located in a marine-estuarine transitional zone (Vermelha beach) (Rodrigues-Barreto et al., 2017). For a sheltered estuarine beach (Flamengo beach), richness and abundance were higher during spring (September to November) and lower during winter (June to August), while the relative abundance of fishes varied according to seasonal shifts in day length (Vasconcellos et al., 2010). *Harengula clupeola* (Clupeidae) peaked in spring, *A. brasiliensis* in austral summer/autumn, and *Trachinotus carolinus* (Carangidae), *Umbrina coroides* (Sciaenidae), and *M. liza* in winter.

At the entrance of the Bay, fish larvae peaked with highest temperatures and lowest salinities (March) (Castro et al., 2005). Abundance was higher at night, and lower during the day.

Larval *Cetrengraulis edentulus*, *Anchoa lyolepis* (Engraulidae), and *Harengula jaguana* (Cupeidae) were dominant during both ebb and flood tides.

The species *C. edentulus* is the main commercially exploited species in this environment, and spawns from late winter to spring with a peak in November (Franco et al., 2014). *Genidens genidens* (Ariidae) is a potential sentinel species due to its abundance and non-migratory habits; and southern and southeastern Brazil populations of this species exhibit similar reproductive season and length-weight relationship (Silva et al., 2013).

Sepetiba Bay Estuary: Southeast Brazil

Salinity, depth, and transparency are the main variables influencing fish assemblages along the Sepetiba Bay and sandy beaches in the inner and outer bay areas (Araújo et al., 2002; Pessanha and Araújo, 2003; **Figure S9**). The species *D. rhombeus*, *C. spixii,* and *G. genidens* dominated the system and preferred shallow, less saline and less transparent waters of the inner bay, where the lowest diversity and highest abundance were also observed. In the outer bay, it was observed the opposite situation (highest diversity and lowest abundance), and *Cynoscion leiarchus* (Sciaenidae), *Diplectrum radiale* (Serranidae), and *G. aprion* were frequent species. The middle bay is inhabited by fishes that prefer average salinities, or with no clear preference [e.g., *G. genidens, G. aprion,* and *Eucinostomus gula* (Gerreidae)] (Araújo et al., 2002).‘

In a long-term survey, the salinity gradient influenced spatial changes in fish communities (Araújo et al., 2017). The inner bay was characterized by *Chloroscombrus chrysurus* (Carangidae), *G. genidens,* and *M. furnieri*. In the middle bay, *Prionotus punctatus* (Triglidae), *G. genidens*, and *M. furnieri* were frequent species, while in the outer bay *P. punctatus* and *D. radiale* were typical species. Fish richness and abundance decreased over the last three decades (1990–2010s) and sharpest changes were observed in the inner and middle bays since they are the most impacted areas due to high loads of metal and to the enlargement of the Sepetiba Port (Araújo et al., 2017).

Santos Estuary: Southeast Brazil

In the Santos Estuary, *D. rhombeus*, *A. brasiliensis*, *B. ronchus*, *G. genidens*, and *H. clupeola* were the most abundant species in the upper estuary during a short-term survey of one rainy (March) and one dry month (August) (Santos J. A. P. et al., 2015; **Figure S10**). The dry period was dominated by *H. clupeola* and *A. brasiliensis*, while the rainy period was dominated by *D. rhombeus*, *G. genidens* and *B. ronchus*. Fish diversity peaked during the rainy month and it was associated to the appearance of a species with affinities for lower salinities (Santos J. A. P. et al., 2015).

Environmental Impacts in Tropical Western Atlantic Estuaries

Habitat Changes

In the Amazon Estuarine Complex, the replacement of culture of sugar cane to permanent agroforests, timber logging (including a shipping terminal), and an industrial estate at Pará River Estuary resulted in habitat loss and critical alterations of fish communities (Barros and Uhl, 1995; Viana and Lucena Frédou, 2014). For the Goiana Estuary, sugarcane plantations, milling, aquaculture, limestone mining, dredging, and urban development are among the landscape modifications (Barletta et al., 2017b).

Alterations in river flow patterns and volume due to damming and dredging, as well as water quality changes due to wastewater disposal, building, and operation of artisanal fishing harbors are severely degrading the São Francisco River Estuary (Barletta et al., 2017b). The decreased river flow reduced dissolved inorganic nitrogen and silicate seawards, and the estuary became oligotrophic (Martins et al., 2011; Medeiros et al., 2011; Genz and Luz, 2012).

Urbanization and pipeline routes for oil and gas industry have caused coastal erosion problems in Guanabara Bay (Araruna et al., 2014), and fish diversity became low in estuarine sandy beaches exposed to wave action with unlimited human access (Franco et al., 2016). In Sepetiba Bay, human modification include the enlargement of Sepetiba Port, dredging activities, construction of a steel factory and a terminal for building submarines (Araújo et al., 2016).

Environmental and Fish Contamination With Plastic Debris

Contamination by microplastics is a concern in the main channel and mangrove creeks of the Goiana Estuary and exibits complex patterns (Lima et al., 2014, 2016). Microplastics are found in every habitat throughout the entire year, sharing the same habitats as fishes and their prey (Lima et al., 2014, 2015, 2016). When precipitation increases, the freshwater flow seawards is a powerful exporter of this contaminant from the upper estuary to the marine environment. Total density of microplastics present the same order of magnitude as total fish larvae and fish eggs in the main channel. Simultaneous comparable amounts of microplastics and fish increase the chances of interactions of these two compartments (Lima et al., 2015). The ingestion of plastic debris by demersal fishes was recorded in ariid catfishes (Possatto et al., 2011), gerreids (Ramos et al., 2012), sciaenids (Dantas et al., 2012; Ferreira et al., 2016), and centropomids (Ferreira et al., 2019).

Sediments in beaches within Guanabara Bay are also polluted with plastic debris, especially microplastics (Carvalho and Baptista Neto, 2016). Microplastics peaked in the warm-rainy season (January-February), but also presented high concentration during the cold-dry season (June–July). Sources are associated to local rivers and streams, fishing and harbor activities, domestic effluents, maritime terminals, and mussel farming (Carvalho and Baptista Neto, 2016; Castro et al., 2016).

Sewage Contamination and Eutrophication

In Santos (Braga et al., 2000; Aguiar and Braga, 2007) and Curuça Estuarine Systems (Venekey and de Melo, 2016), fecal sterols, fecal coliforms, and high loads of nutrients are higher near industrial estates, farms, and cities, revealing a strong sewage contamination. High levels of eutrophication and thermotolerant coliforms are observed in the upper reaches of the Caeté Estuary during the dry season, however, water quality might improve during the rainy season (Monteiro et al., 2016a,b). Water in shallow areas of the inner Guanabara Bay have the poorest quality, being hypertrophic, and sometimes hypoxic (Ribeiro and Kjerfve, 2002; Aguiar et al., 2011). There, fecal sterols in sediments indicate areas of severe and historical sewage contamination (Paranhos et al., 1998; Santos et al., 2008). Poor water quality represents a risk to the biota due to low dissolved oxygen (Braga et al., 2000) and pathogens.

Environmental and Fish Contamination With Petroleum Hidrocarbons and Persistent Organic Pollutants

A pipeline leak following an accident in 2000 was responsible for ∼340,000 gallons of oil spilled into Guanabara Bay, severely polluting the upper reaches of the bay with polycyclic aromatic hydrocarbons (PAHs) (Gabardo et al., 2000; Farias et al., 2008; Massone et al., 2013). After two years, sediments in the inner bay were highly contaminated with PAHs, while water samples no longer showed toxicity effects (Silva et al., 2007a). After four years, PAHs decreased by 70%, showing that climatic variations over time can be efficient in hydrocarbons degradation (Farias et al., 2008) and that water circulation was somehow effective in the spill area. Another Diesel oil spill (60,000 L) accident occurred in 2005, and PAHs in tissues of *C. parallelus*, *M. liza*, *G. genidens*, *Brevoortia aurea* (Clupeidae), and *M. furnieri* peaked when rainfall inuced the runoff of adjacent streams and left the bay exposed to oil from other sources (Silva et al., 2007b; Soares-Gomes et al., 2010).

In Guanabara Bay, *M. furnieri* and *M. liza* presented relatively high levels of polychlorinated biphenyls (PCB) and low levels of polybrominated diphenyl ethers (PBDE) when compared to other ecosystems around the world (Gonçalves da Silva et al., 2013). Croakers presented the highest PCB and PBDE levels, while mullets showed intermediary levels. For *C. parallelus*, *M. liza*, *T. lepturus*, and *Sardinella brasiliensis* (Clupeidae) the levels of PCBs and organochlorine pesticides (OCs) are below the maximum limit established by the Food and Drug Administration (U.S. Environmental Protection Agency-EPA) and, apparently, pose low risk to human consumption (Silva et al., 2003).

Environmental and Fish Contamination With Metals

According to ^{210}Pb dating, increases in heavy metal flux started at the beginning of the last century in Guanabara Bay (Baptista Neto et al., 2013). Sediments are affected by Cr, Pb, and Zn, being the northwestern bay and the Rio de Janeiro harbor the most polluted sectors (Abreu et al., 2016). Sources of metals are related to urban emissions, continental sources, biogeochemical processes, and a chlor-alkali plant at the western portion of the estuary that was responsible for mercury-contaminated effluents entering the bay (Wasserman et al., 2000; Cordeiro et al., 2015; Aguiar et al., 2016). Hg peaks in the western bay, while the northwestern bay is not severely contaminated (Machado et al., 2008). Dredging can pose additional risk of Hg contamination (Silveira et al., 2017), however mangrove forests are biogeochemical barriers accumulating metals and promoting the reduction of metal transport by tidal currents (Kehrig et al., 2003; Borges et al., 2007).

Metal contamination in waters and sediments were also assessed in the Amazon Complex (Lima et al., 2017), Sepetiba Bay (Fonseca et al., 2013), Paraguaçu Estuary (Hatje and Barros, 2012), and Santos Estuarine System (Kim et al., 2016). Sources are associated with mining, industry, natural igneous rock decomposition, reduced freshwater flow, farming, and non-treated sewage (Braga et al., 2000; Paraquetti et al., 2004; Genz et al., 2008).

Bagre spp., *M. liza*, *M. furnieri*, *C. undecimalis* (Kehrig et al., 1998, 2002; Baêta et al., 2006) and *T. lepturus* (Seixas et al., 2012) are still not severely contaminated with heavy metals in Guanabara Bay. Livers of *M. furnieri*, *Bagre* spp. and *M. liza* accumulates higher loads of Hg and methil-Hg, showing relationship with total length (Kehrig et al., 2002, 2009; Baêta et al., 2006). In Sepetiba Bay, *M. liza*, *C. leiarchus*, *M. furnieri*, and *G. genidens* had their muscles, gonads, and livers contaminated with heavy metal above maximum permissible levels established by the Brazilian Ministry of Health for human consumption (Lima Junior et al., 2002). Hg in Guanabara and Sepetiba Bays presented positive relationship with trophic levels, suggesting that Hg is being biomagnified through the food webs (Kehrig et al., 2002; Baêta et al., 2006; Bisi et al., 2012).

In the Goiana Estuary, Hg levels in muscles of *T. lepturus* increased with body size and weight. Hg levels decreased when rainfall increased, through biodilution (Costa M. F. et al., 2009; Barletta et al., 2012). Such seasonal pattern was also observed in Ciénaga Grande de Santa Marta Lagoon for *E. plumieri* and *M. incilis* (Alonso et al., 2000). However, Cd, Zn, and Cu in muscle of *Ariopsis bonillai* (Ariidae) were highest when salinity was lower (Campos, 1992). In the Santos Estuarine System, high levels of Hg in muscle of *C. spixii* (Azevedo et al., 2009, 2011) and above-limits for Cu and Zn in liver of *M. curema* (Fernandez et al., 2014) confirmed a high anthropogenic influence.

Subtropical Southwestern Atlantic

Paranaguá Estuarine Complex: South Brazil Tropical-Subtropical Transition

The interaction between seasons and estuarine habitat shifts (ecocline) structured fish movement in the Paranaguá Estuarine Complex (Barletta et al., 2008) (**Figure S11**). Seasonal variations in temperature and salinity influenced the spatio-temporal use of intertidal habitats for *A. brasiliensis* (Carvalho and Spach, 2015). Batoids are also distributed according to seasonal variation in the salinity gradient (Possatto et al., 2016). The species *C. spixii*, *S. stellifer*, *Anchoa parva* (Engraulidae), *Achirus lineatus* (Achiridae), and *G. genidens* were the most abundant taxa (Barletta et al., 2008). These species preferred the upper and middle estuaries during most of the year, except *A. parva*, which peaked in the lower estuary during the dry season. During the late-rainy season, when rainfall increases, fishes move seawards to the middle estuary.

Strong influence of the salinity ecocline on fish distribution was also observed in a multiple sampling survey (1993–2011) in the same estuary (Passos et al., 2013). *Anchoa januaria*, *Anchoa tricolor* (Engraulidae) *A. brasiliensis* and *H. clupeola* were the most abundant species in this system. The upper estuary was inhabited by the estuarine *A. januaria*, while marine fishes as *A. brasiliensis*, *H. clupeola*, and *A. tricolor* dominated the middle and lower estuaries.

The feeding ecology of *Rhinobatos percellens* (Rhinobatidae) (Carmo et al., 2015), *Ctenogobius shufeldti* (Gobidae) (Contente et al., 2012), and *A. brasiliensis* (Contente et al., 2011); the reproduction and recruitment of *Etropus crossotus* (Paralichthyidae) (Oliveira and Favaro, 2011); and the importance of the system as nursery for *Epinephelus itajara* (Serranidae) (Félix-Hackradt and Hackradt, 2008) and *Manta birostris* (Myliobatidae) (Medeiros et al., 2015) are other information available for this estuarine complex.

Guaratuba Bay Estuary: South Brazil/Tropical-Subtropical Transition

Salinity fluctuations, hydrodynamic variability, and geomorphology of the channel structured fish assemblages in Guaratuba Bay (Vendel et al., 2010; **Figure S12**). Salinity, transparency, and organic matter were the most important factors distinguishing habitats. *A. januaria*, *A. lepidentostole*, *O. oglinum*, *A. brasiliensis*, *S. greeleyi*, and *A. lyolepis* were all abundant species. The upper-inner estuary was characterized by *A. januaria*, while the lower-outer estuary was characterized by *O. oglinum*, *A. lyolepis*, *A. lepidentostole*, *S. greeleyi*, and *A. brasiliensis*.

In mangrove areas, *Haemulopsis corvinaeformis* (Haemulidae), and *S. rastrifer* were the most representative species (Chaves and Vendel, 1997; Chaves and Bouchereau, 1999; Chaves and Corrêa, 2000) and, *E. argenteus*, *E. melanopterus*, *B. ronchus*, and *Citharichthys arenaceus* (Paralichthydae) were common species (Chaves and Corrêa, 1998). High catches were recorded for winter months, when temperature decreased and salinity increased (Chaves and Bouchereau, 1999). However, mangroves are spawning areas for ∼40% of fishes species, especially in summer and spring months, when maturation and spawning become evident (Chaves and Vendel, 1997; Chaves and Bouchereau, 2000). However, for other species as *C. parallelus*, spawning and hatching are associated to stronger marine influence, while juvenile recruitment associates to salinity declines during the rainy season, when river runoff increases (Chaves and Nogueira, 2013). Mangroves, salt marshes (Chaves and Vendel, 1996, 2008) and adjacent rivers (Costa P. V. et al., 2009) are also feeding grounds for several taxa.

Babitonga Bay Estuary: South Brazil/Subtropical

Depth and salinity structured the spatio-temporal variability of dominant species in Babitonga Bay (**Figure S13**). Engraulidae, *Eucinostomus* spp. and *Mugil* spp. dominated shallow fish assemblages in abundance, followed by *A. brasiliensis*, *A. januaria*, *A. tricolor*, *H. clupeola*, and *Oligoplites saliens* (Carangidae) (Vilar et al., 2011). The marine species *H. clupeola*, *O. saliens*, *A. tricolor*, and *T. carolinus* were characteristic of the outer bay, while estuarine-residents and marine-migrants (*A. brasiliensis*, *A. januaria*, *S. greeleyi*, *C. spilopterus* and *D. rhombeus*) were characteristic of the inner bay. Thespecies *T. carolinus* peaked in the warm rainy season; *M. furnieri* in the transition season; and *O. saliens* in the cold dry season.

The first occurrence of larval *Microdesmus longipinnis* (Microdesmidae) (Souza-Conceição et al., 2013) and the distribution of larvae of the invasive species *Omobranchus punctatus* (Blennidae) were assessed in Babitonga Bay (Costa et al., 2011). Sciaenidae larvae (*B. ronchus*, *Cynoscion* sp., *M. furnieri*) are abundant and distributed along the entire bay, and peak in abundance in spring and summer months (Costa et al., 2012). Larval *Lycengraulis grossidens* (Engraulidae) also exhibit spatio-temporal patterns within the Bay (Costa and Souza-Conceição, 2009).

Patos Lagoon Estuary: South Brazil/Subtropical

Salinity and temperature explained most of the variability in a long-term assessment of shallow-water estuarine-dependent fishes in the Patos Lagoon Estuary (Garcia et al., 2012; **Figure S14**). The westerly wind belt movement, or Southern Annular Mode, influenced variations occurring at a scale of 2 years, while rainfall anomalies due to ENSO events influenced inter-annual variability at scales of 3–7 years. *Mugil liza*, *Brevoortia pectinata* (Clupeidae), and *M. furnieri* occurred year-round. *Mugil gaimardianus* (Mugilidae), *M. curema,* and *B. pectinata* were associated with higher salinities and temperatures. *Mugil liza* and *M. furnieri* associated with lower salinities and temperatures.

Shallow-water marine fishes peaked in the 1995/1996 *La Niña* due to low precipitation rates and freshwater runoff; decreasing in the 1997/1998 *El Niño* when precipitation and river discharge increased (Garcia et al., 2001, 2004). *Anchoa marinii* (Engraulidae), *A. brasiliensis*, *M. liza*, *M. platanus*, *M. curema,* and *Jenynsia multidentata* (Anablepidae) were frequent species. Estuarine-resident fishes increased upstream in *La Ninã* situation, and showed opposite patterns in *El Niño*. Estuarine-dependent fishes also showed contrasting patterns (Garcia et al., 2001). The species *A. brasiliensis* and *M. platanus* peaked in shallow waters. *Mugil liza* peaked in *La Niña* and lowered in *El Niño*. During *El Niño*, sub-adults and adults of *A. brasiliensis* were absent from upstream shallow waters due to the high freshwater discharge (Garcia et al., 2001), while the freshwater fishes *Astyanax eigenmaniorum*, *Oligosarcus jenynsii* (Characidae), and *Parapimelodus nigribarbis* (Pimelodidae) dominated the upstream reaches (Garcia et al., 2001, 2003).

Age, growth, and reproductive aspects of *Mycteroperca marginata* (Epinephelidae) (Seyboth et al., 2011), *Odontesthes argentinensis* (Atherinopsidae) (Moresco and Bemvenuti, 2006), *M. liza* (Garbin et al., 2014), and *Jenynsia multidentata* (Anablepidae) (Garcia et al., 2004) were also studied for this system. New species belonging to the families Loricariidae (Carvalho et al., 2008; Rodriguez and Reis, 2008) and Gobiidae (Burns et al., 2010; Cheffe et al., 2010), and reports on the occurrence range and competition of the invasive *Acestrorhynchus pantaneiro* (Acetrorhynchidae) (Neuhaus et al., 2016) are also available for the lagoon. Long-term assessments of ichthyoplankton are also available and must be incorporated into conservation planning (Martins et al., 2007; Costa et al., 2016; Costa and Muelbert, 2017).

Population genetics revealed that many species in the lagoon and adjacent systems are in process of speciation, suggesting that managerial actions must consider different sub-populations (Beheregaray and Levy, 2000; Da Silva Cortinhas et al., 2016).

The ariid white sea catfish *Genidens barbus* was once an important fishery resource in the estuary, where the species had the most abundant population known in the past (Velasco et al., 2007). Therefore, studies on this species became important for the region. Description of growth parameters using length and age data (Velasco et al., 2007) and the use of estuarine carbon sources revealed by isotope analyses (Pereyra et al., 2016) report biological aspects for the species. Ecological aspects were revealed by otolith microchemistry and patterns of estuarine uses (Avigliano et al., 2015), inter-annual variability (Avigliano et al., 2017a), freshwater residence times (Avigliano et al., 2017b), nursery grounds and connectivity (Avigliano et al., 2016) are available for the species.

Micropogonis furnieri is a common species in the Patos Lagoon and represents an economically important fish for the artisanal fishery (Costa et al., 2015). Several aspects of the biology and ecology of this species is also available regarding the system. Feeding ecology studies using different aspects, as daily consumption (Figueiredo and Vieira, 2005), feeding strategies (Mendoza-Carranza and Vieira, 2008), and stable isotope inferences are available (Mont'Alverne et al., 2016). Otolith microchemistry was used to reveal aspects of growth and age of young individuals (Cavole and Haimovici, 2015). In addition, studies have emphasized the importance of ontogenetic approaches while studying fish movement, since early life stages of *M. furnieri* have multiple and complex habitat preferences, suggesting that essential fish habitats must be explored for species with complex life cycles to improve management and conservation planning (Costa et al., 2014, 2015).

Environmental Impacts in Subtropical West Atlantic Estuaries

Habitat Changes

The largest Latin America maritime terminal for agro-industrial products (e.g., soy beans) is located in the Paranaguá Estuarine Complex and Pontal do Felix port is a recent additional structure built in the upper estuary. Dredging operations for maintenance of the shipping channel have altered its geomorphology resulting in upstream intrusion of coastal waters and changes in fish communities (Barletta et al., 2016). During the dredging process, total mean density and biomass of *C. spixii*, *Aspistor luniscutis* (Ariidae) and *G. genidens* increased, while *Menticirrhus americanus* (Sciaenidae), *S. rastrifer* and *C. leiarchus* decreased significantly in the dredged channel. Ariid catfishes were favored by the damage of the benthic fauna, while other species as sciaenids disappeared. Future dredging operations must be avoided during reproductive (October to December) and recruitment (April to June) seasons of fishes, which occurs in the late-rainy season. Therefore, dredging in the Paranaguá Estuary should be performed during the dry season (July to September) to promote sustainable fishery practices (Barletta et al., 2016).

The expansion of the Rio Grande Port and jetties at the entrance of the Patos Lagoon Estuary has changed sediment deposition patterns (texture and distribution) in the estuarine and coastal regions (Cunha and Calliari, 2009; Silva et al., 2015). Moreover, the construction of a dam between the estuary and the Patos-Mirim lagoon to prevent the entrance of salt water resulted in the absence of estuarine and marine species upstream (Burns et al., 2006).

Sewage Contamination and Eutrophication

In Paranaguá Bay (Martins et al., 2010; Cunha et al., 2011; Brauko et al., 2016), Babitonga Bay (Martins et al., 2014) and Patos Lagoon (Martins et al., 2007), fecal steroids are higher close to ports and urban areas pointing to a significant sewage contamination of waters and sediments. In Guaratuba Bay, signs of eutrophication due to organic and inorganic matter inputs are still partially controlled by precipitation and tidal currents (Mizerkowski et al., 2012; Rodrigues et al., 2013). Phosphorus is higher in sediments from the upper estuary and in the transition between the upper and middle estuary (Cotovicz Junior et al., 2014). Increases in nutrient inputs, water temperature and salinity induce blooms of harmful diatoms in the bay, poisoning the biota and causing human intoxication (Tibiriçá et al., 2015).

Plastic Contamination

Contamination with plastic debris was assessed only in the Paranaguá Estuarine Complex, being more significant near urbanized areas in the upper and middle reaches. It is affected by local hydrological processes, with no seasonal or spatial trends along the salinity gradient (Possatto et al., 2015).

Environmental and Fish Contamination With Persistent Organic Pollutants

In November 2004, an oil tanker spilled methanol and bunker oil in front of Paranaguá harbor and the osmoregulation of *A. brasiliensis* was affected until seven months after the accident (Souza-Bastos and Freire, 2011). Tributyltin (TBT) and organic contaminants of antifouling paints in liver were reported for *C. spixii*, with higher levels closer to Paranaguá harbor (Santos et al., 2014). Furthermore, a model revealed that PAHs adsorbed in sediments and solubilized in water can be possibly transferred to fishes and biomagnified along the trophic chain of the estuarine complex (Froehner et al., 2011).

In Guanabara Bay, aliphatic hydrocarbons and linear alkylbenzenes inputs are related with geochemical processes. Higher loads were observed during summer months due to increased summer holidays (Dauner and Martins, 2015). OCs and PCBs had low concentrations due to low inputs from the Germany rivers discharging in the bay (Combi et al., 2013). In Babitonga Bay, PCBs and diclorodifeniltricloroetano (DDT) also presented high concentration at specific sites close to anthropogenic impacted areas of São Francisco harbor (Rizzi et al., 2017).

For the Patos Lagoon Estuary, hydrocarbon pollution is related to combustion of fossil fuels, release of oil, industrial and domestic effluents. Higher concentrations in sediments are observed near refineries and oil terminals, shipping lanes and sewage discharges (Medeiros et al., 2005; Garcia et al., 2010).

Environmental and Fish Contamination With Metals

Sediments in Paranaguá (Anjos et al., 2012) and Guaratuba Bays (Sanders et al., 2008) are contaminated with metals, sometimes above World Health Organization (WHO) critical limits. Metal contamination in water is widely reported for the Patos Lagoon Estuary (Windom et al., 1999; Mirlean et al., 2001; Costa and Wallner-Kersanach, 2013). Metals presented higher concentrations close to urban and industrial areas, being human inputs and geochemical anomalies the main identified sources of these pollutants (Niencheski et al., 1994; Sá et al., 2006; Anjos et al., 2012; Costa et al., 2013).

In the Paranaguá Estuarine Complex, muscles of *C. spixii* and *G. genidens* are contaminated by metals, with levels of Cr and As exceeding the permissible limits for seafood consumption (U.S. EPA) (Angeli et al., 2013). In Babitonga Bay, levels of Zn and Cr in muscles of *E. brasilianus*, *C. paralellus,* and *M. platanus* are still acceptable for human consumption (Bonatti et al., 2004). However, in the Patos Lagoon Estuary, Hg levels in *M. furnieri*, *N. barba*, *G. genidens,* and *Odontesthes bonariensis* (Atherinopsidae) were above background levels, but below critical levels for human consumption (U.S. EPA) (Niencheski et al., 2001; Kutter et al., 2009).

Warm Temperate Southwestern Atlantic

Río de La Plata Estuary: Subtropical/Temperate Transition

A comprehensive overview of fish diversity and the environmental influence on fish distribution and composition is available for the Río de La Plata Estuary (Jaureguizar et al., 2016; **Figure S15**). Salinity structured spatial patterns of larval fishes during austral late spring (December 1999) and summer (February 2000) (Berasategui et al., 2004). The horizontal salinity gradient, bottom salinity and water temperature are the main factors structuring species composition across seasons (Jaureguizar et al., 2003b, 2004; Lorenzo et al., 2011). *Micropogonias furnieri*, *C. guatucupa*, *B. aurea*, *M. schmitti,* and *M. ancylodon* are abundant species. The freshwater and shallow upper estuary was typified by *P. valenciennesi* and *N. barbus* (Jaureguizar et al., 2004). The middle estuary contained the highest densities of *M. furnieri*, *B. aurea*, *M. ancylodon*, where depths and salinities had intermediate values (Jaureguizar et al., 2004). Density of *M. furnieri* and *M. ancylodon* were higher in summer, while density of *B. aurea* increased during winter and autumn. The saltier and deeper lower estuary was dominated by *C. guatucupa*, *M. schmitti*. Larger catches of *C. guatucupa* were observed in autumn, while *M. schmitti* during winter and spring (Jaureguizar et al., 2004).

Studies regarding ontogenetic diet shifts in *Urophycis brasiliensis* (Phycidae) (Acuña-Plavan et al., 2007), first records of larval *Elops smithi* (Elopidae) (Machado et al., 2012) and adult *E. melanopterus* (Gerreidae) (Solari et al., 2010), phylogenetic approaches for the endemic *Pimelodus albicans* (Pimelodidae) (Vergara et al., 2008) and aspects of reproduction in *B. aurea* (Macchi and Acha, 2000) are available. However, most studies have focused on Sciaenidae species, especially the most abundant and commercially interesting ones (*M. furnieri*, *C. guatucupa*, *Pogonias cromis*, and *Macrodon ancylodon*).

The species *P. cromis* spawn between October and January (Macchi et al., 2002), *M. ancylodon* between October and March (Militelli and Macchi, 2006), *C. guatucupa* in March and December (Militelli and Macchi, 2006), and *M. furnieri* between November and March (Macchi et al., 2003). Young age-classes of *C. guatucupa* decreases seawards, with a reverse pattern in spring, while older age-classes inhabit marine coastal areas (Jaureguizar et al., 2006). Short-term changes in oceanographic conditions have greater influence structuring *C. guatucupa* populations than long-term variability (Jaureguizar and Raúl, 2009). During 1998 *El Niño* and 1999 *La Niña*, adults were associated with high salinities, when the area was dominated by wind driven inflow of seawater. During typical years (1994 and 2003), juveniles correlated with low salinities, when winds forced freshwater to flow seawards (Jaureguizar and Raúl, 2009).

Selective processes differentiate populations of *M. furnieri* between the estuary and adjacent coastal locations, and the influence of salinity and temperature in phenotypic cohesion can structure these populations (D'Anatro et al., 2011; D'Anatro, 2017). Larvae of *M. furnieri* are abundant during the warmest months, showing high predominance in the river-estuarine transition and positive correlation with bottom salinity horizontal gradient (Braverman et al., 2009). Ontogenetic approaches revealed a complex use of the estuary by *M. furnieri*, based on the bottom salinity gradient (Jaureguizar et al., 2003a, 2008). Spawning occurs in the innermost areas, near the upstream edge of the salinity wedge (Acha et al., 1999).

Pando Estuary: A Sub-estuary of Río de La Plata

For the Pando Sub-Estuary (**Figure S16**), *M. furnieri*, *M. liza*, *P. orbignyanus*, *B. aurea*, and *Parapimelodus valenciennis* (Pimelodidae) are the most abundant species (Acuña-Plavan et al., 2010; Gurdek and Acuña-Plavan, 2016). Marine migrants were correlated with higher salinity, while freshwater species peaked at lower salinity and estuarine species correlated with higher temperature. Significant correlations between abundance and temperature are related to synchronized events during species life cycles.

Length-weight relationship of 12 species, including the abundant ones, are available for this sub-estuary (Gurdek and Acuña-Plavan, 2014). For the most abundant species *M. furnieri*, the length-weight relationship was assessed along its ontogeny over an intra-annual cycle (Gurdek and Acuña-Plavan, 2016). This species produces the seasonal courtship/spawning sounds from November to March (spawning season), with a strong seasonal variability, appearing in October, peaking in January-March, and disappearing in April (Tellechea et al., 2011).

Mar Chiquita Coastal Lagoon: Temperate Southwest Atlantic, Argentina

In Mar Chiquita Lagoon (**Figure S17**)., *B. aurea*, *O. argentinensis*, *M. liza*, and *M. furnieri* are abundant species, especially in summer months (Bruno et al., 2013). Juveniles of *Platanichthys platina* and *Ramnogaster arcuata* (Clupeidae) are also frequent (González Castro et al., 2009). Marine fishes peaked in the lower estuary when temperature increased in summer and autumn. *Brevoortia aurea* was the most abundant species in the southern-lower portion, and *O. argentinensis* in the middle and northern-upper portion of this estuary (Bruno et al., 2013). Juvenile recruitment is ruled by seasonal onshore winds (Bruno et al., 2015). However, salinity and temperature structured fish assemblages (González Castro et al., 2009). *Brevortia aurea* peaks in higher salinity and temperatures. The species *M. liza* and *O. argentinensis* correlated with low salinities. Peaks of *O. argentinensis* occurr at lower temperatures, while *M. furnieri* peaks at higher temperatures. The occurrence of *M. curema* (González Castro et al., 2006) and *T. carolinus* (Díaz de Astarloa et al., 2000), both with tropical-subtropical affinities, in the temperate lagoon is related to the presence of warm neritic waters from the continental shelf originated in subantarctic waters of the Malvinas Current.

Anchoa marinii (Engraulidae) reproduces between December and April when temperature increases and mature females aggregates in adjacent coastal areas (López et al., 2015). The species *M. liza* migrates seawards in April-May and November-December to spawn (González Castro et al., 2011). Aggregations of mature females of *B. aurea* can be observed in October-November in the lower estuary (Lajud et al., 2016).

Bahía Blanca Estuary: Temperate Southwest Atlantic, Argentina

For the Bahía Blanca Estuary (**Figure S18**), the reproductive aspects of *Sympterygia acuta* (Rajidae) (Díaz-Andrade et al., 2009) and the feeding ecology of *R. arcuata* (Lopez Cazorla et al., 2011) are described. In addition, the influence of biotic and environmental factors on seasonal patterns of juvenile fishes in *Spartina alterniflora* saltmarsh and a contiguous tidal flat in the Bahía Blanca Estuary was also evaluated (Valiñas et al., 2012). However, fish research is focused on three economically important species: *M. furnieri*, *C. guatucupa* and *P. orbignyanus* (Blaber and Barletta, 2016).

The age structure of the population of *C. guatucupa* was revealed by otolith analyses (Lopez Cazorla, 2000), while for *P. orbignyanus*, age structure was revealed by scales reading and growth parameters (Lopez Cazorla, 2005). Seasonal diet shifts and ontogenetic changes in the feeding ecology of the three species (Lopez Cazorla and Forte, 2005; Sardiña and Lopez Cazorla, 2005a,b), as well as dietary overlaps between the two co-occurring sciaenid species (Sardiña and Lopez Cazorla, 2005c) were assessed within the system. Foraging activities of *M. furnieri* have direct and indirect effects on the granulometric composition and stability of bottom sediment of salt marshes (Molina et al., 2017).

Environmental Impacts in Warm Temperate Western Atlantic Estuaries

Habitat Changes

Habitat modifications in Río de La Plata Estuary include shoreline retreats due to deforestation, tourism activities, and land development (Cellone et al., 2016). Urban beach erosion and accretion have strong relationships with climate changes, sea level rise, and increased storminess (Gutiérrez et al., 2016).

Various ports, cities, livestock, agriculture and oil, chemical, and plastic industries are located in Bahía Blanca Estuary (Spetter et al., 2015). The estuary has one of the largest deep water ports in the country (Ingeniero White port), which is regularly dredged (Zilio et al., 2013). A project to deepening a navigation channel in the inner estuary to a depth of 13.5 m related to a natural gas provision have been pointed to cause physical and social consequences to the system. The loss of nursery services and of the jobs associated with fishing activities, cease of recreational activities during the dredging process, the loss of the coastal landscape, water pollution derived from sediment removing and the effects on groundwater are imminent possibilities (Zilio et al., 2013). Increased erosion of coastal terraces in response to rising sea level, increased land use in the harbor area and aggradation due to dredged spoils deposition are also observed in Bahía Blanca (Pratolongo et al., 2013).

Sewage Contamination and Eutrophication

The Río de La Plata Estuary is moderately eutrophic. Increases in freshwater runoff and nutrient loads, associated to a low potential to dilute and flush nutrients, suggest that the system is prone to worsening eutrophication conditions generating further dissolved oxygen stress and harmful algal blooms (Nagy et al., 2002). Sewage effluents pose a potential ecotoxicological risk to aquatic biota due to inputs of estrogens (Valdés et al., 2015). In the Bahía Blanca Estuary, sewage and industrial discharges receive poor or no treatment before reaching the system (Pierini et al., 2012). Microbiological contamination was revealed by the presence of *Escherichia coli* and *Samonella* spp. in water and sediments close to sewage discharges in the Rosales Harbor and tributaries discharging into the estuary (Spetter et al., 2015; Streitenberger and Baldini, 2016).

Environmental Contamination With Plastic

Plastic contamination has been assessed since 1999 by the National Direction of Aquatic Resources in the Río de La Plata Estuary and by the Ocean Conservancy's International Coastal Cleanup Day in Uruguayan aquatic systems. Most plastic debris comes from urban wastes, waterways, and marine traffic in Uruguayan waters (Lozoya et al., 2015). The bottom salinity front of the salt-wedge is the main barrier accumulating plastic debris upstream (Acha et al., 2003). In the southern coast of the system, 100% of freshwater fishes belonging to eleven species were contaminated with microplastics in their gut contents, especially fibers, with higher numbers near sewage discharges, where they varied from 30 to 89 fibers per stomach (Pazos et al., 2017).

Environmental and Fish Contamination With Petroleum Hidrocarbons Persistent Organic Pollutants

High levels of aliphatic and aromatic hydrocarbons in waters, sediments, soils and biota were observed after ∼1,000 tons of oil spilled in coastal waters of Río de La Plata (Colombo et al., 2005a,b). Petroleum direct inputs and combustion, harbor activities, and vehicular emissions are the main sources of hydrocarbons to this system (Venturini et al., 2015). PCBs have highest concentrations near industrialized areas close to Buenos Aires, and transformers oil containing Aroclor 1,254–1,260 are the probable sources (Colombo et al., 2005c).

PAHs, PCBs, and PBDEs in sediments of the Bahía Blanca Estuary had higher concentrations near urban and industrial areas (Arias et al., 2010; Oliva et al., 2015; Tombesi et al., 2017). TBT and dibutyltin (DBT) concentrations were higher in sediments near Puerto Belgrano harbor (Argentina's Army), where there are intense shipyard activities (Delucchi et al., 2007). Levels of OCs were moderate, when compared to worldwide ranges, and showed a high correlation with precipitation in sites near agricultural fields (Arias et al., 2011).

In Río de La Plata, *Cyprinus carpio* (Cyprinidae), *Mugil cephalus* (Mugilidae), *O. bonariensis*, and *Prochilodus lineatus* (Prochilodontidae) showed moderate to high levels of aliphatic hydrocarbons and PCBs in their muscles with signs of bioaccumulation (Colombo et al., 2000, 2007a,b; Menone et al., 2000; Cappelletti et al., 2015). The highest concentrations were recorded in *P. lineatus*, especially near the urban center, exceeding guidelines for human consumption (U.S. EPA) (Colombo et al., 2000; Speranza et al., 2016). In the Bahía Blanca Estuary OCs contaminated *C. guatucupa* with a size-related bioaccumulation pattern (Lanfranchi et al., 2006). PAHs were reported to contaminate *Odontesthes* sp. in the system; and the global average for this pollutant indicated that Bahía Blanca is chronicaly polluted (Arias et al., 2009, 2010).

Environmental and Fish Contamination With Metals

Metal contamination in sediments and water were assessed in Río de La Plata Estuary (Tatone et al., 2013, 2015), Mar Chiquita Lagoon (Marcovecchio et al., 2001; Beltrame et al., 2009), and Bahía Blanca Estuary (Botté et al., 2007; Grecco et al., 2011). Sources and highs levels of metals are related to polluted discharges from agricultural, urban and industrial sources (Camilión et al., 2003; Marcovecchio et al., 2016; Santucci et al., 2017).

In Río de La Plata, *Pterodoras granulosus* (Doradidae), *P. lineatus* (Villar et al., 2001), *M. platanus*, and *M. furnieri* are contaminated with metals with signs of bioaccumulation. Hg is the most important contaminant for *M. furnieri*, however values are still below the international standards (U.S. EPA) recommended for suspending human consumption (Corrales et al., 2016). Hg levels in edible muscle of fishes from Mar Chiquita Lagoon are also safely below recommendation standards (Marcovecchio et al., 2001; Marco et al., 2006). In the Bahía Blanca Estuary, low levels of Cd and Zn were observed in top predators *M. schmitti* and *Halaelurus bivius* (elasmobranchii), however Hg levels exceeded the international standards (Marcovecchio et al., 1986, 1988a,b, 1991) and also showed signs of bioaccumulation. Livers of *Brevortia aurea*, *O. argentinensis*, *M. furnieri*, *C. guatucupa*, *M. schmitti*, and *P. orbignyanus* are also contaminated with metals. At least one sample of each species presented concentrations of Mn and Cr hazardous to humans (La Colla et al., 2017).

Eastern Pacific Estuaries

Tropical Eastern Pacific

Bahía málaga estuary: Colombia/Panamá Bight Ecoregion

At least 237 species inhabit the Bahía Málaga Estuary (**Figure S19**) (Artunduaga, 1978; Rubio, 1984a,b; Castillo, 1986; Castellanos-Galindo et al., 2006). The combination of tidal and dial cycles explained shifts in fish communities, but a biomass decrease was notable when rainfall increased at the end of the annual cycle (Castellanos-Galindo and Krumme, 2013). Spatial and temporal patterns of larval fish community along the main channel of the estuary was also assessed during an annual cycle (Medina-Contreras et al., 2014). *Seriola* sp. (Carangidae) and *Cetengraulis mysticetus* (Engraulidae) were the most abundant larvae. Salinity or temperature were not correlated with larval density, but larvae varied greatly among months, suggesting a strong influence of seasonality in the bay (Medina-Contreras et al., 2014).

The composition and diversity of intertidal fishes were assessed in Isla Palma, in the lower estuary (Castellanos-Galindo et al., 2005). Freshwater fishes are known to reach Isla Palma due to high rainfall rates influenced by the Intertropical Convergence Zone (Cordoba and Giraldo, 2014). Clupeidae were the most abundant family, in terms of numbers, inhabiting intertidal mangrove habitats in the innermost portion of the estuary, however Lutjanidae, Tetraodontidae and Ariidae dominated in weight (Castellanos-Galindo and Krumme, 2013).

Studies on the feeding ecology of *Centropomus unionensis* (Centropomidae) (Mancilla and Rubio, 1992), and diet, growth and reproduction of *Lutjanus guttatus* (Lutjanidae) (Suárez and Rubio, 1992a,b) are also available. According to a trophic flow model performed in the inner portion of the bay, the very low salinity throughout the year is responsible for the low number of primary and secondary consumers (e.g., zooplankton, crustaceans and some fishes) in the mangrove system. Therefore, zoobenthivorous (snappers, catfishes) and detritivorous (mullets) fishes dominate in biomass, when compared to piscivorous and zooplanktivorous fishes (Castellanos-Galindo et al., 2017).

Rio palmar and rio javita estuaries: Ecuador/Guayaquil Ecoregion

Fish communities were compared between the dry and the wet season in mangrove creeks and main channel of Palmar and Javita rivers (Shervette et al., 2007; **Figure S20**). The diversity of species belonging to the families Gobiidae, Gerreidae and Engraulidae is high in the mangrove system of Palmar Estuary, while species of Carangidae, Engrauliae, and Gerreidae are diverse in the Javita main channel. Significant differences were detected among areas and seasons for both systems, and the percent of mangroves and mean depth influenced fish communities. Although these estuaries present low species diversity compared with other tropical estuarine systems (Blaber, 2000), they still provide important nursery habitats for many fishes of commercial and ecological importance (Shervette et al., 2007).

Environmental Impacts in Tropical Eastern Pacific Estuaries

Habitat Changes

Not more than 4,000 people, distributed in small villages, live in Bahía Málaga (Castellanos-Galindo and Krumme, 2013). However, over the last 25 years, Bahía Málaga has faced anthropogenic changes relative to the construction of a naval base in the mid 1980's and an increased tourism activity nearby

(Castellanos-Galindo et al., 2011). This resulted in mangrove loss, but no specific estimates are available. Governmental agencies plan to construct a deep-water commercial harbor, what might be an important threat to marine and estuarine fish diversity. Nevertheless, La Plata (∼6,791 ha) and La Sierpe (∼25,178 ha) areas have recently been declared protected areas by local environmental agencies.

Sewage Contamination and Eutrophication

Water quality assessments asserted that Bahía Málaga is still in good conditions with no signs of eutrophication or changes in physic-chemical parameters (Betancourt Portela et al., 2011). However, further chemical pollution assessments are necessary for the region, including their fate for the local biota.

Temperate Eastern Pacific

Valdivia River Estuarine System: Chile/Araucanian/Chiloense Ecoregion

A study on the migratory patterns of *Galaxias maculatus* (Galaxiidae) from larval to adult stage revealed a strong association with seasonal changes in salinity along the Valdivia estuary (Hugo, 1973; **Figure S21**). Another study in Corral Bay detected that higher densities of larvae were observed near the tidal front, and differences were related to tidal intrusion of salt water (Vargas et al., 2003). According to patterns of circulation, Corral bay is a source of young fish larvae. *Strangomera bentincki* (Clupeidae), *Odontesthes regia laticlavia* (Atherinopsidae), *Gobiesox marmoratus* (Gobiesocidae), and *Hypsoblennius sordidus* (Blenniidae) were the most abundant larval species.

The seasonal influence on diatery ontogenetic shifts of the Chilean silverside *O. regia* was assessed in the Valdivia Estuarine System and this species is acknowledged as a selective omnivorous predator (Fierro et al., 2014). In the Corral bay, the feeding ecology of *Myxodes viridis* (Clinidae) was also assessed in different depths and tidal cycles (Ochoa-Muñoz et al., 2013).

Environmental Impacts in Temperate Eastern Pacific Estuaries

Environmental Contamination With Persistent Organic Pollutants

PAHs in sediments of Corral Bay showed a medium pollution rate with a temporal variation, with a substantial increase observed from March to September during 2000 (Palma-Fleming et al., 2004). Aliphatic hydrocarbons were at low to medium contamination rate with no temporal variation, and inputs are relative to the petroleum hydrocarbon-diesel fraction and biogenic hydrocarbons (Palma-Fleming et al., 2012). Such impacts are related to control of prague, fluvial wood transportation, wood and paper industries, shipyards, fishing industries, and salmon conditioning jails.

Environmental Contamination With Metals

Dramatic changes in the Valdivia River Estuarine System are related to wastewater and solid emissions from industrial or domestic activities, aerial emissions, farming/agriculture, and oil spills (Palma-Fleming et al., 2012). Cd level within the Corral Bay was lower than in other Pacific coastal areas, but increased upstream rivers as salinity decreased (Pinochet et al., 1995). Cu and As in sediments were above standards of the Sediment Quality Guidelines (U.S. EPA) in all sampling points of Corral Bay, being an indicative of toxicological effects for the biota (Palma-Fleming et al., 2012).

DISCUSSION

The Importance of the Ecocline and Seasonality Concepts to Study Fish Movement and Environmental Quality Assessments

Estuaries were long poorly understood because of their complex natural processes and only recently, over the past four decades, fully recognized as a key coastal ecosystem (Elliot and Whitefield, 2011). Therefore, studies regarding the estuarine ecocline concept and the influence of environmental variability on fish movement and environmental changes are still missing even in large and important systems of the Western Atlantic and along all eastern Pacific coast of SA (Blaber and Barletta, 2016). The influence of the estuarine ecocline on fish movement were discussed in the Amazon, Caeté, Guanabara, Santos, Guaratuba, Babitonga, Pando and Mar Chiquita systems. In Ciénaga Grande, Goiana, Paraguaçu, Sepetiba, Paranaguá and Patos Lagoon systems, not only fishes, but also environmental quality (water and sediments) were assessed regarding the influence of the ecocline. However, the main concern is that in most surveys, fishes and environmental quality were short-term assessed, and/or across limited spatial scales, regardless the annual variability of the salinity gradient, as in Cienaga Grande Lagoon (Rueda and Defeo, 2003), Paraguaçu Estuary (Hatje and Barros, 2012), Guaratuba Bay (Vendel et al., 2010), and Río de La Plata (Jaureguizar et al., 2003b). Therefore, ecological patterns, biological behavior and physico-chemical processes might still be obfuscated by the lack of annual cycles, long-term, and full lenght approaches. Thus, efforts for conservation, recovery and sustainable use of estuarine resources were lead by poorly informed managerial actions (Barletta et al., 2010).

Systems in the tropical Northwestern Atlantic have recently gained attention. Lists of species are available for the Atrato River Delta (Correa-Herrera et al., 2016, 2017) and Orinoco River Delta, on the Caribbean coast (Cervigón, 1985; Blaber, 2000; Blaber and Barletta, 2016) (**Figure 1**, **Table 1**). In the Atrato Delta, spatio-temporal patterns of fish larvae and their densities, comparable to microplastics available in the water, were also assessed (Correa-Herrera et al., 2017). In Northeast Brazil, few fish and human impacts studies are available for the Parnaíba River Delta (Oliveira, 1974; Watanabe L. A. et al., 2014; Ribeiro et al., 2017), Potengi River Estuary (Oliveira et al., 2011; Buruaem et al., 2013; Souza et al., 2016) and Itamaracá Estuarine System (Ekau et al., 2001; Vasconcelos Filho et al., 2003, 2010). In Southern Brazil, the Laguna Estuarine Complex has intense artisanal fisheries activities and an industrial fleet focused on mullets for most of the year (Barletta et al., 2017b).

However, fish research and human impacts along the ecocline were never evaluated.

"An ecocline represents a boundary of progressive change between two systems, representing the response to the gradual difference in one major environmental factor acting at a different scales and influencing the total differences within the gradient" (Attrill and Rundle, 2002). Within any estuarine system, the salinity is the major environmental factor referred in the ecocline concept (Barletta and Dantas, 2016). Hence, researchers have proposed that the proper management of estuaries are dependent upon reliable biological and abiotic data encompassing multiple aspects of space and seasonality along the estuarine gradient (Machado et al., 2016; Barletta et al., 2017a; Underwood et al., 2017).

Regarding fish research, accurate sampling design using monthly surveys replicated along different reaches and encompassing several aspects of seasonality are available for the Caeté Estuary (Barletta et al., 2005), Goiana Estuary (Dantas et al., 2013) and Paranaguá Estuarine Complex (Barletta et al., 2008, 2016). These provided reliable data on fish movement over annual cycles on which managerial reccomendations must be build. In European Atlantic estuaries (Vetemaa et al., 2006; Martinho et al., 2007), as well as in North-American Atlantic estuaries (Love and May, 2007; Granados-Dieseldorff and Baltz, 2008), accurate sampling designs for fish research are also available as reference to be replicated in any estuarine system.

In addition, the spatio-temporal variability of the estuarine ecocline influences patterns of use of essential habitats by the different ontogenetic phases of a fish species. Therefore, the ontogenetic approach is another important point of view while studying fish movement (Acuña-Plavan et al., 2007; Ferreira et al., 2019). Very few studies worldwide address ontogeny, such as in estuaries from Australia (Taylor et al., 2006), North America (Stehlik and Meise, 2000), South Africa (Harris et al., 1999), and Asia (Lin et al., 2007). In SA, fish ontogeny was assessed in Río de La Plata (Acuña-Plavan et al., 2007), Pando (Gurdek and Acuña-Plavan, 2016), Bahía Blanca (Lopez Cazorla and Forte, 2005; Sardiña and Lopez Cazorla, 2005a,b), and Goiana (Dantas et al., 2010, 2015; Ramos et al., 2016) estuaries. These studies asserted that the ecological unit is not the species in their own, but their different ontogenetic phases. Costa et al. (2014) and Ferreira et al. (2016, 2019) emphasized that the different phases of a species can have multiple and complex habitat preferences over spatio-temporal scales, and essential habitats must be explored to improve management and conservation planning.

Regarding environmental and fish contamination, accurate samplings are available for microplastics in the Goiana Estuary (Lima et al., 2014; Ferreira et al., 2016, 2019; Silva et al., 2018), for metals in Guanabara Bay (Baêta et al., 2006; Cordeiro et al., 2015) and for POPs in Río de La Plata (Colombo et al., 2000; Venturini et al., 2015). However, for most SA systems, the bioavailability and contamination of fishes with POPs, metals and microplastics were never assessed along the ecocline. Rainfall variability is a strong controller of metal and POP levels in fish tissues, since drought periods can enhance contamination and high precipitation rates diminishes the contaminants through biodilution (Costa M. F. et al., 2009; Barletta et al., 2012; Bisi et al., 2012). Fish contamination is higher near urban, industrial or rural areas and, sometimes, values exceeded the permissible limits for human consumption (U.S. EPA) (Marcovecchio et al., 2001; Delucchi et al., 2007; Fernandez et al., 2014). Moreover, the bioaccumulation and biomagnification of metals and POPs are occurring in the trophic web of most estuaries (Marcovecchio et al., 1986; Cappelletti et al., 2015). In the Negombo Estuary (Sri Lanka), for example, metal contamination of *M. cephalus* was year-round categorized along spatial locations and seasons providing a reliable design that can be replicated worldwide using different pollutants (Mendis et al., 2015).

Moreover, metals and POPs are somewhat controlled by other abiotic factors and their proper assessment are indeed also needed. The biogeochemistry and bioavailability of metals and POPs in estuaries are controlled by suspended particulate matter loads and dissolved oxygen levels, which in turn are strongly controlled by the salinity gradient (Janeiro et al., 2008; Bayen, 2012; Costa et al., 2012). Freshwater inputs from rivers and streams; effluents from the agriculture fields; untreated domestic and industrial sewages; oil spill and release; and combustion of fossil fuel are probable sources of metals and POPs contamination for fishes, but are hardly ever assessed (Costa M. F. et al., 2009; Barletta et al., 2012; Venturini et al., 2015). For this reason, all these sources still need further attention in SA coastal systems.

On the other hand, the inadequate disposal practices and fishery activities along river basins and coastal areas are the most obvious source of plastic pollution (Lima et al., 2014). This problem become worse when large plastics fragment into smaller particles (<5 mm), increasing the chances of interactions even during the earliest phases of a fish life cycle (Lima et al., 2015, 2016). Microplastics present higher concentrations within semi-enclosed environments and the river basin is recognized as one of the main source of microplastic inputs into estuaries, where they become ubiquitous over the year (Lima et al., 2014; Cheung et al., 2016; Lebreton et al., 2017); Vendel et al., 2017.

The problems regarding the interaction of microplastics and fishes are available for the Goiana (Ferreira et al., 2016, 2019; Silva et al., 2018) and Río de La Plata (Pazos et al., 2017) estuaries. The most complete scenario is reported for the Goiana Estuary, where the distribution patterns of microplastics were first reported (Lima et al., 2014). The estuarine ecocline acts as a control of microplastics in drier months and exporter of microplastics to the marine environment in rainy months, when runoff increases seawards (Lima et al., 2014; Lebreton et al., 2017). Microplastics have comparable densities with ichthyoplankton, emphasizing a high concentration in the main channel (Lima et al., 2015). Ingestion of plastic filaments is widespread and affect different ontogenetic phases of demersal fishes (Possatto et al., 2011; Dantas et al., 2012; Ramos et al., 2012; Ferreira et al., 2016, 2019; Silva et al., 2018). Every estuarine system in SA is experiencing this same problem of contamination due to generalized poor disposal practices (Costa and Barletta, 2015). However, "*there have been very few papers describing* *multivariate tests of spatial or temporal patterns of microplastics*" (Underwood et al., 2017).

Disruption of Estuarine Ecoclines Caused by Human Modifications in Estuarine Morphology

Human interventions in estuarine geomorphology lead to alterations in the natural inflow of salt water, and disrupt the ecocline along the whole system. Such problem is worse under the influence of industrial activities due to several months of dredging to the maintenance of waterways and artificial channels or the damming of major rivers, which increase saline intrusion, changing fish communities (Barletta et al., 2016, 2017b; Prestrelo and Monteiro-Neto, 2016). Impacts of dredging has been widely discussed worldwide (Wilber and Clarke, 2001; Nayar et al., 2003; Güt and Curran, 2017). The loss of nursery services and of the jobs associated with fishing activities are the main consequences of dredging or damming. Wasserman et al. (2016) asserted that the main concern for the interpretation of such impacts is the absence of studies using local hydrodynamics.

In SA, dredging activities were discussed in Sepetiba Bay (Araújo et al., 2016), Guanabara Bay (Silveira et al., 2017), Bahía Blanca Estuary (Zilio et al., 2013), and Paranaguá Estuarine Complex (Barletta et al., 2016). The damming of the São Francisco Estuary, for example, decreased the magnitude of its flow from 2,846 $m^3 s^{-1}$ to 800 $m^3 s^{-1}$, leading to increased saline intrusion (Barletta et al., 2017b). Water transposition from the river basin to the adjacent semi-arid region to serve rural populations, industrial, and tourism activities during severe droughts has been widely criticized for its potential impacts (Barletta et al., 2017b). In the Rhine-Meuse estuary, for example, it is suggested that the restoration of tidal and river dynamics in polders are the best options for the ecological rehabilitation of one of the most important wetlands in the Netherlands (Storm et al., 2005; Slater, 2016). However, possibilities for a natural recovery of the São Francisco Estuary are far from any perspective, since background and novel information on human-driven changes are absent. Further investigations are needed since the saline intrusion in the current stagnant estuary has increased, changing ecological functions for fishes. Fortunately, larger systems have shown the capacity to withstand human modifications. However, "*the full recovery of coastal marine and estuarine ecosystems from over a century of degradation can take a minimum of 15–20 years for attainment of the original biotic composition and diversity may lag far beyond that period*" (Borja et al., 2010).

Estuarine Conservation and Recommendations

The avoidance of governmental institutions in using the basic estuarine concepts has been debated for decades (Dauvin and Ruellet, 2009). Researches using ecocline concepts are increasing in quantity and quality (Blaber, 2000; Barletta et al., 2016; Reis et al., 2016). However, the time elapsed to compile scientific information and the establishment of plans is the main challenge. Despite the variety of coastal ecosystems in SA, the number of effective Marine Protected Areas is still insufficient, and conservation measures are not implemented outside these areas to guarantee the conservation of connected habitats.

The lack of basic sanitation is the worst concern in SA (Costa and Barletta, 2016). In riverside settlements, uncontrolled sewage discharges along the whole course of rivers only increases at estuaries. Several nano- and biotechnologies are alternatives to reduce contaminants in effluents and offer a potential treatment of surface water, groundwater and wastewater contaminated by toxic metal ions, organic and inorganic solutes, and microorganisms (Wang et al., 2010; Qu et al., 2013; Martínez-Huitle and Ferro, 2016).

Plans aiming at estuarine conservation must consider year-rounded cycles of retention and flush of environmental contaminants along ecoclines, as well as their interactions with fishes (Barletta et al., 2016). However, the majority of studies consider only limited spatial patterns based on the distance to point-sources of impacts. The lack of temporal assessments also leads to misinterpretation of whether estuaries are able to withstand human modifications and when (and if) estuaries will recover from unpredictable climatic events. Withal, environmental quality assessment have evolved when biological measures in fishes were integrated to ecological relevance, providing a new support for management, and monitoring schemes (Duarte et al., 2017).

An example of successful monitoring of is through the use of the Integrated Biomarker Response index (IBR), which can indicate different sources of anthropogenic contamination in aquatic environments using fish as bioindicator. Larger biomarker responses are often found in the most contaminated sites (Duarte et al., 2017). In the Estuarine-Lagoon Complex of Iguape-Cananéia (Southeast Brazil), the spatio-temporal changes in parameters such as oxidative stress, biotransformation, genotoxicity, and histopathological alterations in *Atherinella brasiliensis* correlated to sediment pollution with metals, PAHs and pharmaceuticals and personal hygiene products (PPCPs) in areas of greater human presence (Salgado et al., 2018). The IBR corroborated with these results, indicating that the Cananéia City has the worst environmental quality (Salgado et al., 2018). The metabolic enzyme activities, protein content and lipid peroxidation were analyzed in muscle and liver of *Ramnogaster arcuata* (Clupeidae) to assess the correlation with PAHs levels in tissues. IBR was significant to assess PAH toxicity and highlighted *R. arcuata* as a good bioindicator in the Bahía Blanca Estuary (Ronda et al., 2018). These multi-biomarker approaches help in the comprehension of ecosystem health aiming at a more comprehensive assessment of environmental quality (Duarte et al., 2017). Moreover, comparative measures of IBR before and after any type of managerial or conservative action can help to assure the success or failure of such actions. Therefore, further studies regarding fish indices should be performed as a tool to assess environmental quality in SA estuaries.

Another problem faced in SA is the overexploitation of estuarine fishery resoruces. Along the Amazon River basin, multispecies fishery follows a clear seasonal pattern of river hydrological cycles (Isaac et al., 2016). However, hydrological alterations due to the construction of dams, in addition to deforestation and climate change affect the seasonal and annual dynamics of these fisheries (Isaac et al., 2016; Pinaya et al., 2016). Overexploitation of fishery resources is known since the early 80's, when traditional communities shift from labor in multiple resources (agriculture, fishing, and small-scale stock raising) to concentrate in commercial fishing (McGrath et al., 1993). Although captures per unit effort remained stable over time, body lengths of most-caught species were below length at first maturation (Castello et al., 2011). Fishery was characterized as moderately exploited, with few profitable species being overexploited. For the region, management of fisheries can lead to increased yields through the enforcement of minimum size of capture and closed seasons of catches (Castello et al., 2011).

Landings at Guanabara Bay, accounted to ∼19,000 tons (US$ 4.8 million) between 2001 and 2002 (Jablonski et al., 2006). Small pelagic fishes (Atlantic anchoveta and Brazilian sardinella) and demersal fishes (croakers, mullets and catfishes) comprised the main catches, with densities compatible with commercial fisheries (Jablonski et al., 2006). However, fishermen associations have complained that fish abundance and fishery income has decreased since the oil spill in January 2000 (Jablonski et al., 2006). Unless regional industries implement regulations to avoid environmental degradation and measures to treat effluents, pollution will continue to threaten the development of artisanal fishing (Bessa et al., 2004).

State of poverty and lack of power of the artisanal fishermen are pointed as the main factor making this group invisible in the formulation of public policies, which favors industrial fishing (Galli et al., 2007). In the Rio de LA Plata Estuary, for example, the overexploitation of *M. furnieri* was attributed to improvements of the industrial fleet (Horta and Defeo, 2012). In Bahia Blanca Estuary, *Cynoscion guatucupa* is the most important resource captured by the artisanal fishery fleet. However, overexploitation and collapses in stocks are also related to increasing industrial operations in open waters adjacent to the estuary (Lopez Cazorla et al., 2014). Thus, the recognition of the socio-economic importance of artisanal fishing through the participation in decisions to the sustainability of their activities, improvement of the fishermen income through fish processing and selling at the landing points are frames needed to change this situation (Jablonski et al., 2006; Galli et al., 2007).

The conservation of coastal ecosystems and traditional livelihoods are ruled by different policies to preserve natural resources through the co-management perspective (ICMbio, 2012; Barletta et al., 2017b). Limited mesh sizes, closed periods, establishment of fishing seasons; no-take-zones, quotas for common resources; efforts to reduce/eliminate wastewater disposal, control uptake of freshwater by damming and control salinity intrusion by dredging can be highlighted as priorities for SA estuaries.

Re-establish operation licenses and accurately analyse risk assessments of activities next to river basins and sourround estuaries are important steps to prevent habitat loss (Lotze et al., 2006; Huang et al., 2014). Mangrove deforestation, for example, is of major concern in most estuarine systems along the Ecuadorian coast, especially due to aquaculture, and construction of shrimp ponds (Shervette et al., 2007; Hamilton and Stankwitz, 2012). It is asserted that shrimp aquaculture is responsible for 80% of carbon lost due to mangrove deforestation (Hamilton and Lovette, 2015). From an estimated 362,000 ha of mangrove forest, almost 50% had been lost, being the Muisne region the most impacted area (Zhengyun et al., 2003). In the Chone Estuary, for example, the establishment of shrimp farms, covering 51,919,128 m^2 was responsible to reduce mangrove area from 42,377,182 m^2 in 1968 to 14,654,255 m^2 in 2006 (Hamilton and Stankwitz, 2012). In the Grande Estuary, most estuarine area is dedicated to shrimp farms, accounting for a mangrove loss of 47%. On the other hand, in Rio Hondo and Cayapas-Mataje, only 16 and 10% of mangrove loss due to shrimp farming was recorded by 2008 (Hamilton and Stankwitz, 2012). The maintenance of shrimp ponds needs to be managed and integrated to mangrove functioning, as an example of using mangroves as nutrient filter of pond effluents prior to the return of water back to the estuary (Twilley et al., 1998). Moreover, successful actions aiming at the recovery of deforested and degraded mangrove has been presented for some systems in SA. Replanting of mangroves in the Acaraú River (Paula et al., 2016) and Paraiba do Sul River estuaries (Rezende et al., 2015); and salt marshes in the Patos Lagoon (Tagliani et al., 2007) are acknowledged as a good approach to recover degraded wetlands and restablish biodiversity (Rezende et al., 2015).

Biodiversity is also threatened due to invasive species, which in turn are introduced by water ballast and aquaculture escaping. Estuaries and coasts are susceptible to introductions of non-native species since they are centers for the vessel activities. The introduction of these species may cause niche overlaps, when the invasive species uses the same resources as native species (Neuhaus et al., 2016). Although this sharing of resources may not affect the survival of the species, introductions and invasions of piscivorous predators, for example, can impact not only the species richness of native fish community but may also cause changes over all trophic levels, altering the equilibrium of the system (Neuhaus et al., 2016). This might also lead to impacts on native fishery resources, diseases, and parasites occurrences (Tomás et al., 2012). In Brazil, several case studies relate the introduction of non-native carnivorous fish to a decrease in local diversity. Examples are the introduction of *O. beta* in the Santos Estuary (Tomás et al., 2012), *A. pantaneiro* in the Patos Lagoon Estuary (Neuhaus et al., 2016) and *O. punctatus* in Babitonga Bay (Costa et al., 2011). Thus, studies assessing the overlapping food niches and, consequently, the degree of competition in the presence of invasive species, are important for the conservation of native species.

The estuarine ecocline has a great influence in the connectivity among river basins and coastal waters, and estuaries are recognized as important ecosystems for providing biological and geochemical demands to both these systems (Able, 2005; Barletta et al., 2010; Watanabe K. et al., 2014). Conservation issues aiming to improve resilience must onset before the ecosystem modifications overpass their capacity to maintain its natural resources and services (Williams and Crutzen, 2013). This is the case of the environmental tragedy at Doce River basin (southeast Brazil), on November 2015, where the disruption of a containment dam of mining tailings (Fundão/Samarco) contaminated the river with 50 million.m^{-3} of mud flood

(Barletta et al., 2017b). It caused an immeasurable impact along hundreds of km of river bed toward the coasts of more than one Brazilian state. Lives and livelihood losses, kill of tons of fishes (Barletta et al., 2017b), contamination of sediments, potable and surface waters with metals (Segura et al., 2016; Gomes et al., 2017) are among the many accounted impacts. This is just one case of environmental accident affecting a SA coastal system, where co-management, practices of emergency and risk assessment protocols have traditionally less and less attention. Therefore, potentially, every system can share the fate of Doce River.

All these issues are of major concern for the South Eastern Pacific estuaries, since the lack of estuarine research lead to a poor understand of what is the real status of the systems. This might be attributed to socio-economic problems. Most countries have a lower development indicator and the percentage of gross domestic product destined to research and development is lowest in countries such as Peru, Colombia, Ecuador and Chile, when compared to Brazil and Argentine, for example (Cociocca and Delgado, 2017). In addition, problems such as guerrillas, narco-traffickers, decaying economy due to populism, inequality, and educational options has been of major concern for these contries. Therefore, financial support is hardly ever destined to research and development (Cociocca and Delgado, 2017). Moreover, the commoditization of shrimp farmings in Ecuador has destroyed thousands of hectares of mangroves (Zhengyun et al., 2003), but concomitantly has generated $ 1 billion annually, leading to government negligencies (Hamilton, 2012). In Peru, a research Agenda of priorities for coastal systems has only recently gained attention due to the workshop "Advancing Green Growth in Peru" in 2016 (McKinley et al., 2018). Nevertheless, Brazil and Argentina has been also suffering due to economic instability, corruption, crime and narco-traffickers and the future of research is an imminent concern (Cociocca and Delgado, 2017).

According to all recorded damages, SA estuaries have almost never recovered to background situations, despite time and efforts. The constant habitat modifications that were relatively slow for nearly 400 years, have increased since after Second World War and industrialization (and urbanization) in the continent, worsening environmental quality and reducing fish yields for coastal zones. If anthropogenic interferences keep with their course and speed, regardless all reported environmental concerns, natural resources and services provided by estuaries will face the most severe degradation in the near future. Further research to support managerial planning and action should, therefore, not only be scientific-based on the continent-wide natural diversity, but also need to consider the social importance of estuaries for traditional fishers and other populations, whose dependence upon these systems goes beyond livelihoods.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00237/full#supplementary-material

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The Effect of Hydrological Connectivity on Fish Assemblages in a Floodplain System From the South-East Gulf of California, Mexico

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The effect of hydrological connectivity of the fish assemblages was assessed on a floodplain in the SE Gulf of California, Mexico using a before–after control-impact (BACI) design. Community structure attributes of species abundance, biomass, richness, diversity, and differences in the structure of fish assemblages were compared between two periods (January to June in 2011 and 2015) and two flood plains, one designated as the control zone which was divided by a road, and another one designated as the treatment zone which from January to June 2011 was divided by a road, and then sampled from January to June 2015, as the site was rehabilitated by removing the road in the year 2012. Fish were sampled at monthly intervals using a seine net at different stations in both floodplains. A total of 7024 organisms, comprising of 14 species belonging to 11 families, were analyzed. In the control zone during both periods and in the treatment zone before removal of the road *Poecilia butleri* was the most abundant species and two exotic species (Tilapia) accounted for more than 95% of the total biomass. After the removal of the road in the treatment zone *Poeciliopsis latidens* was the most abundant species and the relative biomass of both species of tilapia decreased to 85%, but was still the most important in terms of biomass. However, richness and diversity were higher and the structure of the fish assemblages was different in the treatment zone after the road was removed, due to the presence of species with estuarine and marine affinity in this zone and period. Our results indicate that hydrological connectivity proved to be a key factor influencing the fish composition and abundance in the floodplain system in the region. Hence, a better hydrological connectivity implied higher abundance and diversity, likely related to an increase in the habitat complexity. The priority in the management of the ecological functioning of the floodplain system should be set on minimizing the modifications of the natural flow and thus avoiding the changes on the fish biota.

Keywords: floodplain restoration, fish assemblages, estuarine fish, freshwater fish, multivariate analyses, BACI design

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INTRODUCTION

Seasonal coastal floodplains along tropical latitudes are amongst the most biologically productive and diverse ecosystems on earth (Tockner and Stanford, 2002; Junk et al., 2006) and are an important component of rivers and wetlands, acting as a nursery habitat and refuge for fish (Junk and Wantzen, 2004). These dynamic systems are seasonally flooded during flow and ebb currents resulting on water level variations. Particularly, wetlands on estuary floodplains are dynamic entities, driven by connections of tidal habitats and freshwater flooding which can have positive consequences for the fish inhabiting these systems, and from the ecological point of view, these ecosystems play an important role in improving the water quality by filtering and recycling nutrients, storing sediments, and supporting high biodiversity (Junk et al., 1989; Bayley, 1995). Also, considering that tropical floodplain systems are home to diverse fish species representing an important source of protein for human populations (Welcomme, 2001), these sites also possess an economic importance, which is altered seasonally depending on the wet and dry seasons. The response of the fish to these variations is expressed in particular adaptations across the seasonal floodplain (Bayley, 1995). During the wet season the inundation covers large areas and thereby increases the availability of food and shelter for fishes and other organisms (Welcomme, 2001). Contrary, during the dry season the floodplains are prone to an alteration of the hydrological connectivity (Jardine et al., 2012), which limits the fish movement and certainly provokes the mortality of many organisms trapped in dried habitats.

The estuarine complex of Marismas Nacionales is located in the alluvial plain of the States of Nayarit and southern Sinaloa on the North-Central Pacific coast of Mexico. This large complex comprises approximately 175,300 ha of mangrove wetlands, saltwort (*Salicomia* spp. and *Balis maritima*), vegetated and un-vegetated extensive seasonal flood plains, including some saltpans, coastal lagoons, and tidal channels (Ramírez Zavala et al., 2012). It is estimated that this region alone accounts for 50–70% of Mexico's annual small-scale fisheries production (Spalding et al., 2007). However a high percentage of its ecosystems are under threat (Tockner et al., 2008) and despite its low population density there is still increasing pressure on the floodplains and wetlands in this region due to human activities. The continued decline of floodplain and wetland ecosystems is mainly caused by habitat alteration (Taylor et al., 2007), transforming these areas into agriculture or aquaculture fields, and tourism developments (Páez-Osuna et al., 1999; Glenn et al., 2006). Additionally, hydrological modifications such as construction of marinas, channels, coastal erosion, dam infrastructure, and urban development are also an important threat for these coastal ecosystems (Giri et al., 2011). As a consequence habitat diversity patterns are strongly affected (Bunn and Arthington, 2002) because the construction of these structures often changes the rate of the flow (Sparks et al., 1998). At present different floodplains in this area have their flooding seasonality altered and get less water than in the past (Kingsford, 2000). This anthropogenic activity may lead to the ecosystem fragmentation, which could potentially cause the isolation of some populations by limiting the migrations and/or species movements, but on the other hand exotic species can benefit from the stabilization of the habitat and invade the system (Bunn and Arthington, 2002). As a result of these modifications many ecological benefits of the floodplains may be restricted.

The awareness of the value of seasonal floodplains has gradually increased (Ratti et al., 2001) and there is a need to integrate the sustainable management of seasonal floodplains and their associated fishes. Firstly, it is important to understand the relationship between the habitats and fishes, not only for sustainable fisheries but for the overall management of these ecosystems. One of the strategies of how to conserve and preserve these systems is through habitat restoration (Ormerod, 2003). Restoration has been suggested as a mechanism for enhancing the fisheries/higher biodiversity in degraded areas (Levings, 1991). In order to implement successful restoration strategies it has been agreed that hydrology is key (Wolanski et al., 1992). The enhancement of the hydrological connectivity is one of the techniques for the ecosystem rehabilitation which aims to restore the natural component of the flow (Arthington et al., 2010). Most of these enhancement projects are focused on wildlife and are rarely designed to benefit fish communities, therefore there are gaps in the understanding of the use of seasonal floodplains by fishes. However, in general, higher spatial connectivity contributes to the creation of better conditions for fish, shrimps, and other fishing resources (Rozas et al., 2013). Several studies have investigated the relation between hydrological connectivity, wetland characteristics, and the fish community with the conclusion that connectivity is a key factor determining the diversity and structure of fish assemblages (e.g., Lasne et al., 2007; Pearson et al., 2011). Likewise, it has been proven that a better hydrologic connectivity increases the diversity of native fish species, whilst the number of exotic species increases with isolation (Lasne et al., 2007). Isolation could alter the aquatic environment, thereby increasing hypoxia and indirectly affecting the structure of fish assemblages (Rozas et al., 2013). However, even though the rehabilitation process has been widely used over the broad range of riverine and wetland ecosystems resulting in a positive outcome, within the field of conservation biology hydrologic connectivity remains a largely neglected dimension.

The present study assessed the influence of attributes of hydrological connectivity based on a road removal performed in October 2012 on the fish assemblages in a subtropical seasonal floodplain. Rural communities in the studied region, such as fishing villages, constructed many roads through the floodplains during the dry season in order to access suitable locations for their small fishing boats. These dirt roads were usually built at 50 to 80 cm above the maximum local tidal amplitude in order to avoid flooding during the spring tides. The specific dirt road in this study consisted of a pathway for off-road vehicles that was abandoned for unknown reasons. The hypothesis is that the lack of hydrological communication created a less suitable environment for the fish community, and thus local fishermen abandoned this seasonal floodplain in order to find a more suitable location. Consequently, it was decided to remove this abandoned dirt road in order to assess the diversity of fish species by enhancing tidal hydrological connectivity. The fish response was measured as the abundance, diversity, and structure of the fish assemblages before and after the road was removed. The working hypothesis was that opening of the channel through the removal of the road would increase the hydrologic connectivity in the system, therefore increasing the fish abundance and diversity, and altering the structure of the fish assemblage. In order to do this a before–after control-impact (BACI) design was employed.

MATERIALS AND METHODS

Study Area

The study was conducted in the salt marsh of Las Cabras (**Figure 1**), located on an alluvial plain in the State of Sinaloa, within the Marismas Nacionales complex. The study area presents a hot semiarid-climate (BSh) (García, 1998). Mean annual air temperature ranges from 24 to 28°C and the annual total precipitation, which occurs between the months of July and September, ranges between 900 and 1,300 mm (INEGI and Gobierno del Estado de Sinaloa, 1999). The salt marsh Las Cabras is a seasonal floodplain of approximately 60 km^2, with no direct connection to the adjacent Pacific Ocean. The underground salt wedge that passes through the coastal sand barrier depends on the local tide, which presents a semi-diurnal pattern with maximum amplitude of 1.8 m in spring tides during the summer months of June to September. This subtropical semiarid saltmarsh includes multiple tidal creeks, seasonal flood plains, and an extensive saltpan area with hypersaline conditions (Flores-Verdugo et al., 1993).

Black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*) are commonly found where topographic profile is regular, and flood and ebb currents occur regularly without retaining standing water. Conversely, a depression is commonly found where there is a more complex geomorphology, such as the Easter section of this area, where tidal influence is minimal, creating a less frequent inundation zone with an extensive community of *Batis* sp. and *Salicornia* sp. Consequently, these saltmarshes have hypersaline pore-water conditions for much of the year (Flores Verdugo et al., 2007). The remaining terrestrial vegetation consists of dry deciduous forest and palm trees at relatively higher elevations.

Sampling Design

In order to perform an assessment of the effect of the road removal on the fish assemblage's diversity and structure a BACI design was employed. This design consists of measurements taken at the treatment (impacted) site and at a control site both before and after the impact occurs (Smokorowski and Randall, 2017). Thus, there are a total of N observations with multiple observations over time or space, and the resulting data can be analyzed with a factorial ANOVA (Green and Green, 1979). Usually this design is used to evaluate environmental impacts due to anthropogenic induced changes. However, in this case, it was used to evaluate a restoration effort.

The region of our study went through degradation and now it is in the process of restoration through hydrological rehabilitation. In the analyzed flood plain (i.e., the impacted area) rehabilitation was initiated in 2012 when a road was removed, connecting habitats and enhancing the water circulation in this ecosystem. Further rehabilitation includes planting of mangrove seedlings and construction of new channels at other sites nearby. However, due to its recent progress and locations these factors were not considered in the present study.

In the same region there is a flood plain which is divided by a dirt road which has remained there since it was constructed during the 1990s (i.e., control area).

As the area where this flood plain is located consists of private lands, with very limited access, it was only possible to conduct the study at two different time intervals; monthly from January to June 2011, before the road was removed, and monthly from January to June 2015, after the road was removed. A total of 27 stations were sampled each month along the impacted/restored seasonal floodplain, and 10 stations were sampled each month in the control area (**Figure 1**). In the impacted area there was limited water circulation before the road was removed, and the only connection was through a passage with a diameter of approximately 1 m. In the control area the connection to the main body of the floodplain was also through a channel located under the road with a diameter of about 1 m.

Environmental Measurements

The environmental factors of dissolved oxygen (mg/l), salinity (ppm), depth (m), and temperature (°C) were recorded at each station in each sampling month using a YSI multiparameter.

Fish Sampling and Laboratory Processing

The fish were sampled with seine nets (70 m in length, 3.4 m in height, and 1 cm mesh size) hauled by four people at each station in each sampling month. After each fishing operation fish were kept on ice and transported to the laboratory. In the laboratory, fish were taxonomically identified to species, counted, weighted to the nearest 0.01 g, and measured (total length in cm).

Data Analysis

The initial and end positions were recorded with a GPS in order to estimate the mean catch per unit effort (CPUE). This was computed for every station and was used for all analyses. This index was obtained according to the method proposed by Viana et al. (2010) by estimating the number of individuals (n) according to the equation: $y = 100\, n(A)^{-1}$, where A is area swept.

A randomized cumulative species curve was constructed for every year and every location sampled to determine if sample sizes were sufficient to describe the total number of species from our modeled samples (Flather, 1996). The order in which samples were analyzed was randomized 1000 times, for each new cumulative species sample using Chao's estimator of the absolute number of species in an assemblage. It is based upon the

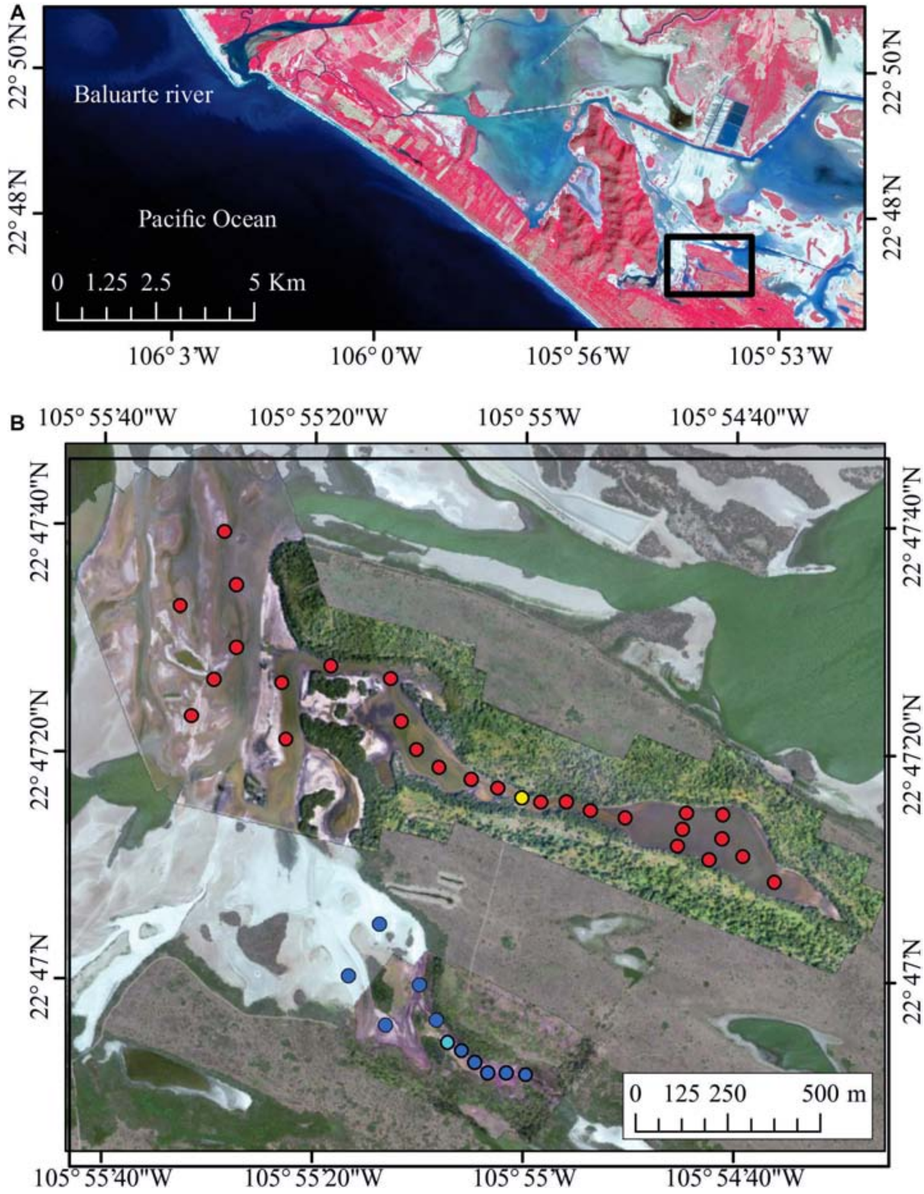

FIGURE 1 | (A) Study site (Las Cabras floodplain), in the southeast Gulf of California (enhanced near infrared, red, and green composition from a Sentinel-2 image). **(B)** Detailed digital image of the sampling sites. Red dots indicate the zones where the fish were collected, and yellow point indicates the place where the road was placed in the treatment area. Dark blue dots indicate the zones where the fish were collected, and light blue dot point indicates the place where the road is still placed in the control area.

number of rare classes found in a sample (Chao, 1984), and the notation is:

$$S_{\text{est}} = S_{\text{obs}} + \left(\frac{f_1^2}{2f_2}\right)$$

Where S_{est} is the estimated number of species, S_{obs} is the observed number of species in the sample, f_1 is the number of singleton taxa (taxa represented by a single occurrence in the assemblage), and f_2 is the number of doubleton taxa (two or more occurrences in the assemblage). Further details of this method can be found in Magurran (2004).

Each station was treated as a replica; therefore, fish species diversity was estimated for every sampling station at every month, year, and location using the Shannon index of diversity (H′). The form of the index is:

$$H' = -\sum p_1 \; lnp_1$$

Where p_i is the proportion of individuals found in the i^{th} species (Magurran, 2004).

The diversity values were used to perform a simple BACI – 1 year before/after; one site impact; one site control, design, although in this case the time after the event was more

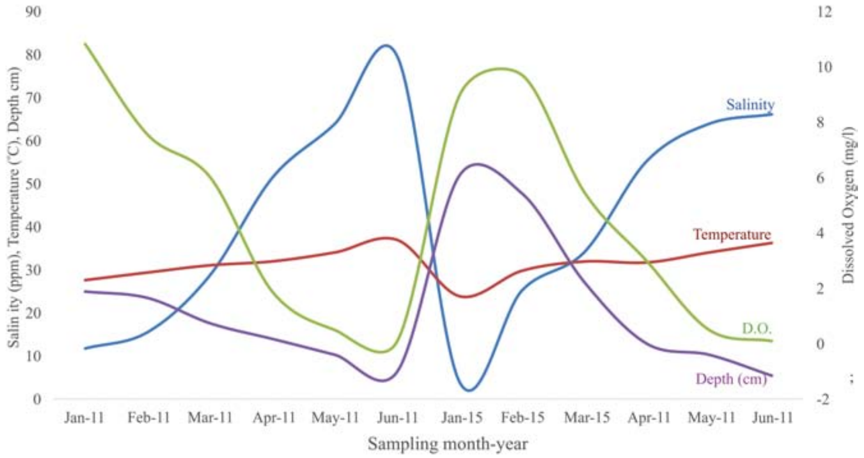

FIGURE 2 | Temporal variation of the abiotic parameters in the study site.

than 2 years long. The analysis was performed with a three-factor completely randomized design (three-way ANOVA). According to Magurran (2004), this diversity index follows a normal distribution; therefore, a parametric test can be performed. The factors were location (control and impact floodplain), year (before: 2011, after: 2015), and month (January to June). Homoscedasticity of variances was tested with Cochran's C test, and a Tukey test was performed in case statistical differences were found to do pairwise comparisons.

Multivariate analyses were also used to test the same BACI design, comparing the fish assemblages between the different locations, months, and years. A matrix containing the sampling month and locality per year as columns, and fish species as rows was created and from this a Bray–Curtis similarity matrix was generated. The factors assigned to this matrix were month, year, and location. To test the H_0 that the fish assemblages did not differ according to these factors, a PERMANOVA was employed using the same three-way design as it was used with the ANOVA. If significant results were found the data were graphically represented using a distance based redundancy analysis (dbRDA) (McArdle and Anderson, 2001). This analysis predicts the multivariate variation of the fish assemblages in the months and years in multivariate space. Multivariate analyses and the estimation of the diversity index were completed using the PRIMER 6 statistical package with the PERMANOVA+ add-on (PRIMER-E, Plymouth Marine Laboratory, United Kingdom). All parametric statistical analyses were performed on STATISTICA 13 (TIBCO Software, Inc.).

RESULTS

Environmental Patterns

All the sampling stations were shallow, with a highest water level of 75.2 cm during January 2015, and lowest of 18.5 cm in the restored area during May 2011, and 15.0 cm in the control site during May 2015. During June 2015 at the restored area the depth was of 26.0 cm. During June 2011 in the control and restored area, as well as June 2015 in the control site, the systems were completely dry. In both periods and sites, the temperature behaved similarly with a variation through the sampling months (**Figure 2**), ranging between 27.7 and 36.9°C during 2011, and lower during 2015, with a range of 24.2–36.2°C. Salinity increased gradually as months passed. Before the opening of the road, and in both periods at the control site the salinity increased from 11.85 ppt in January to 79.3 ppt at the end of June. After the road was removed in the rehabilitation site, salinity ranged from 4 ppt in January to 66.2 ppt in May. Dissolved oxygen (mg/l) decreased as months passed in all sites, from 10.8 in January, to 0.1 mg/1 in June 2011, and from 9.7 in January 2015 to 0.1 mg/1 in June 2015.

Fish Assemblages

A total of 7024 individuals were captured over the course of this study, from 11 families, representing 12 native and 2 exotic species (Tilapia, Cichlidae). The sampled fish collected on the floodplain were represented by both small and large bodied species; however, small-bodied species were dominant. The size range of all fish species was 1.2–33.5 cm (mean = 3.75 cm) before the road was removed, and 1.2 to 43 cm (mean = 4.5 cm) after the road was removed. In both periods and locations, the majority of species in the system were found according to Chao's model when fitting the species accumulation curve; an asymptote was reached in both periods and both locations (**Figure 3**).

The number and composition of species in the restored system varied before and after the road was removed. Before the removal of the road six species were captured from four families. *Poecilia butleri* (48.2%) was the dominating species in terms of numeric abundance, followed by *Poeciliopsis latidens* (23.9%), *Orechromis aureus* (22.9%), *Orechromis* sp. (2.8%), *Lile stolifera* (0.8%), and *Atherinella crystallina* (0.03%). However, in terms of total biomass, both species of tilapia were the most important species and accounted for more than 95% of the total biomass (*Orechromis aureus*: 54.9%, *Orechromis* sp.: 40.4%).

After the road was removed 14 species from 11 families were recorded. These included the six species found during the previous sampling period plus another eight. The top five in

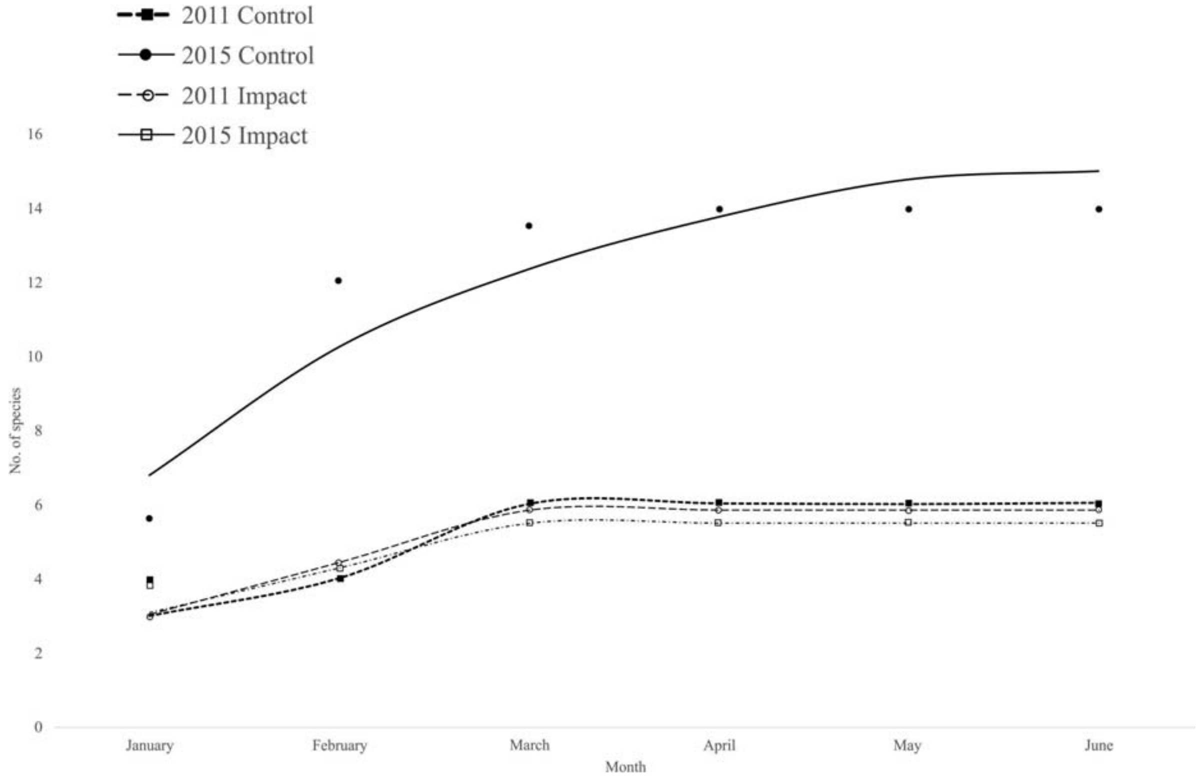

FIGURE 3 | Fish species accumulation model for the two different sampling periods. The model used was Chao.

terms of numeric abundance were *Poeciliopsis latidens* (42.4%), *Oreochromis aureus* (30.0%), *Poecilia butleri* (22.1%), *Atherinella crystalina* (1.5%), and *Lile stolifera* (1.1%), which accounted for more than 97% of the total abundance. In terms of biomass, both tilapia species remained dominant, but in this period their importance decreased from more than 95% before the road was removed, to approximately 80% after the removal of the road (*Orechromis aureus*: 44.8%, *Orechromis* sp.: 35.6%). In 2015 4 other species accounted for 95% of the biomass; these were *Poecilia butleri* (5.3%), *Dormitator latifrons* (3.6%), *Chanos chanos* 3.2%, and *Poeciliopsis latidens* (2.6%).

In the control site the number of species found during 2011 and 2015 were the same (i.e., 5), and these included the identical ones as found in the restored site during 2011, with the exception of *Atherinella crystalina*, which was not found in the control site. During 2011, *Poecilia butleri* was the most numerically abundant (61.4%), followed by *Poeciliopsis latidens* (22.7%), and *Orechromis aureus* (14.9%). These three species accounted for 99% of the total relative numeric abundance. In terms of relative weight, both Tilapia species accounted for more than 97% of biomass (*Orechromis aureus* 51.1%, *O.* sp. 46.3%), followed by *Poeciliopsis latidens* (1.4%). Between these three they accounted for almost 99% of the relative biomass during that period of time.

During 2015 at the control site *Poecilia butleri* was also the most numeric abundant species, but the relative numeric abundance was smaller (45.7%), followed also by *Poeciliopsis latidens* although during this period, the relative numeric abundance of this species increased to 28.7%. *Orechromis aureus* showed a relative numeric abundance similar to the previous period (13.8%), but in this year, *O.* sp. showed a much higher numeric abundance that during 2011 (10.3%). These four species accounted for 98.5% in terms of biomass, both species of Tilapia were also the ones accounting for the higher relative biomass with 98.5% (*Oreochromis aureus* 61.4%, *O.* sp. 37.1%). The total number of species found together with their relative numeric abundances and biomasses can be observed in **Table 1**.

Upon examination of fish diversity among both sites, periods, and sampled months, statistical differences were found according to year ($F_{(1,46)} = 131.5$, $p < 0.05$), month ($F_{(5,46)} = 19.64$, $p < 0.05$), site ($F_{(1,46)} = 136.4$, $p < 0.05$), interaction year/month ($F_{(5,46)} = 2.5$, $p < 0.05$), interaction year/site ($F_{(1,46)} = 18.6$, $p < 0.05$), interaction month/site ($F_{(5,46)} = 13.0$, $p < 0.05$), and interaction year/month/site ($F_{(5,46)} = 3.2$, $p < 0.05$).

The mean diversity was higher in the restored site in both years; however, it showed a statistically significant increment after the road was removed. In the control site, although the mean diversity was higher for all months during 2015, these differences were not statistically significant (**Figure 4**, Tukey HSD test $p > 0.05$). In both sites and years diversity decreased as time passed, always being higher in January, and decreasing toward May and June. The control site was completely dried up in June in both years; therefore, the fish diversity was 0 at that time. The restored site was also dried up in June 2011, and during June 2015 it was very shallow, but there were a few individuals of

TABLE 1 | Relative numeric abundance and biomass of the fish species found in the system at each period.

	Control				Impact			
	Abundance		Biomass		Abundance		Biomass	
Species	**2011**	**2015**	**2011**	**2015**	**2011**	**2015**	**2011**	**2015**
Atherinella crystallina	–	–	–	–	0.4	1.5	0.1	1.1
Centropo musarmatus	–	–	–	–	–	0.2	–	0.2
Chanos chanos	–	–	–	–	–	0.1	–	3.2
Diapterus peruvianus	–	–	–	–	–	0.2	–	0.2
Dormitator latifrons	–	–	–	–	–	0.7	–	3.6
Elops affinis	–	–	–	–	–	0.1	–	1.2
Etropu scrossotus	–	–	–	–	–	0.1	–	0.1
Gerres cinereus	–	–	–	–	–	0.2	–	0.3
Liles tolifera	0.5	1.5	0.4	0.5	0.8	1.2	0.4	0.8
Mugil curema	–	–	–	–	–	0.1	–	1.1
Orechromis aureus	15.0	13.8	61.4	51.1	22.9	30.0	54.9	35.6
Orechromis sp.	0.5	10.3	37.0	46.2	2.8	1.2	40.4	44.7
Poecilia butleri	61.4	45.7	0.7	0.9	48.2	22.1	3.6	5.3
Poeciliopsis latidens	22.7	28.7	0.5	1.4	23.9	42.4	0.6	2.6

both Tilapia species inhabiting the system, therefore the diversity index was low, but not 0 (**Figure 4**).

General PERMANOVA results were similar to those obtained with the three-way ANOVA, as significant results were also found in the fish assemblages according to year (pseudo-$F_{(1,46)}$ = 16.8, $p < 0.05$), month (pseudo-$F_{(5,46)}$ = 13.7, $p < 0.05$), site (pseudo-$F_{(1,46)}$ = 226.3, $p < 0.05$), interaction year/month (pseudo-$F_{(5,46)}$ = 5.7, $p < 0.05$), interaction year/site (pseudo-$F_{(1,46)}$ = 21.8, $p < 0.05$), interaction month/site (pseudo-$F_{(5,46)}$ = 11.2, $p < 0.05$), and interaction year/month/site (pseudo-$F_{(5,46)}$ = 5.5, $p < 0.05$).

The dbRDA plot (**Figure 5**) shows that the fish assemblages were very similar in the control site in both analyzed years, as no clear separation was distinguished from 1 year to another, and no statistical differences were found according to the PERMANOVA test, when testing for differences between years in the control site (Year pseudo-$F_{(1,13)}$ = 2.84, $p > 0.05$; Month pseudo-$F_{(5,13)}$ = 2.64, $p < 0.05$; interaction Year-Month pseudo-$F_{(5,13)}$ = 0.65, $p > 0.05$). These results indicate monthly differences, as previously indicated, but no differences between the analyzed years.

The assemblages found in both years in the control site, were also similar to the fish assemblage found in the restored area prior to the road being removed. However, the fish assemblage in the area to be rehabilitated was different to the fish assemblages found in the control site in both years (Site pseudo-$F_{(1,46)}$ = 4.21, $p < 0.05$).

A clear-cut group containing the fish assemblages in the rehabilitation site after the removal of the road is observed in the lower part of the graph. The fish assemblages were changing chronologically through the sampling months, as a pattern can be seen from January to May or June during 2015 in the rehabilitated zone.

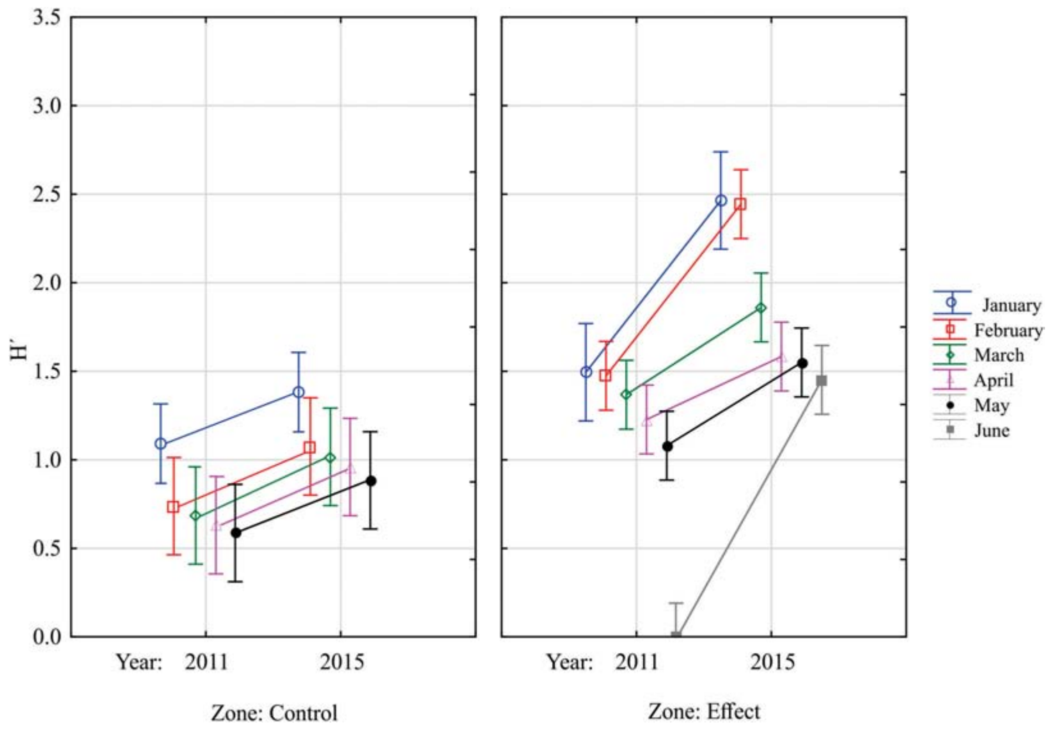

FIGURE 4 | Mean values of the Shannon diversity index in both analyzed sites during the sampled years and months. Vertical bars denote 95% confidence intervals.

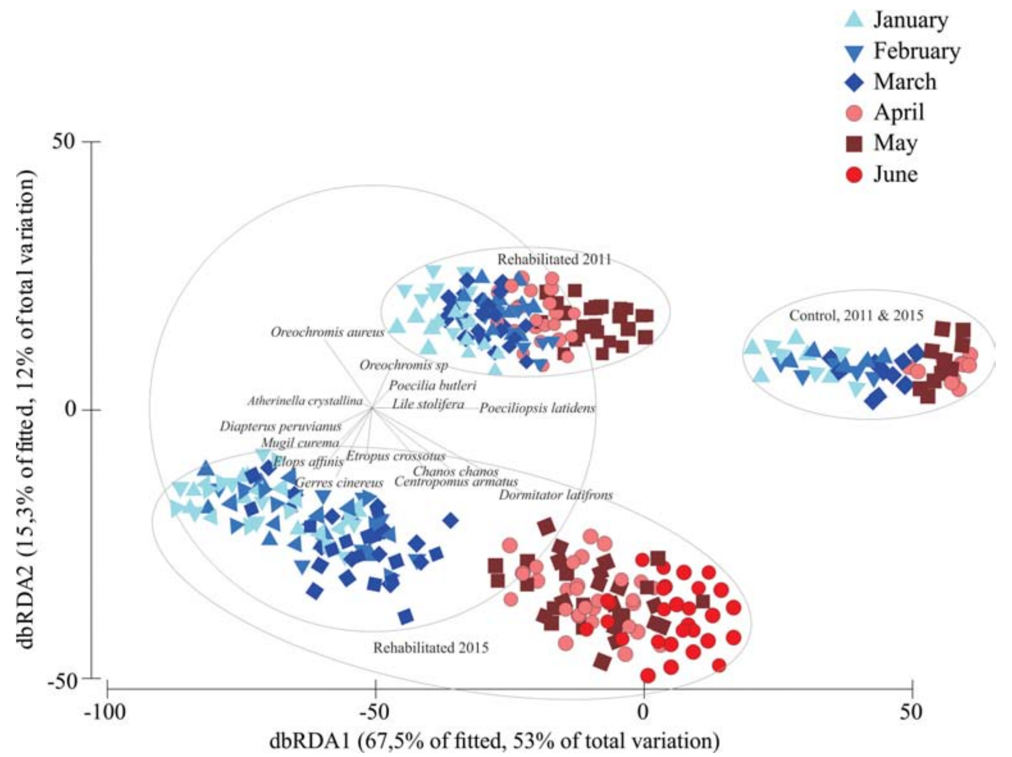

FIGURE 5 | Distance based redundancy analysis (dbRDA) describing the patterns in the fish assemblages in both sampling periods.

The dbRDA vectors indicate that *Poecilia butleri, Poeciliopsis latidens, Lile stolifera,* and both Tilapia species were the characteristic species in the control site in both years and during 2011 in the rehabilitated site, prior to the removal of the road. After the road was removed more species appeared in the rehabilitated zone only, and their importance seems to relate to seasonal changes. For example, the species *Dormitator latifrons*, *Chanos chanos,* and *C. armatus* seemed to be characteristic during the warmest months of 2015. These species are known for their tolerance to high salinities and high-water temperatures.

DISCUSSION

Environmental Patterns and Their Effect on Fish Assemblages

Shallow aquatic environments, such as floodplains, are strongly influenced by local driving factors (Thomaz et al., 2007). Therefore, the adaptations and life history of the biota might reflect the temporal environmental changes determined by the seasonal flooding (Cucherousset et al., 2007). In spatially heterogeneous environments such as floodplain mangrove systems, the variability of the accessibility and environmental conditions influence the fish assemblages. The importance of the environmental variables in fish assemblages has been recognized by Jackson et al. (2001). This same pattern was observed in the present study, as abiotic factors seem to meaningfully define changes in fish composition through time. Regardless of road removal, the water temperature and salinity increased gradually from January to June, and the depth and dissolved oxygen decreased, and at some points, the system became completely dry. The floodplains analyzed were brackish at the beginning of the year, and in general had good water quality, but as time passed they became hypersaline and hypoxic, until the control zone in both studied periods, and the rehabilitated zone during 2011, dried up by June. In this area the dry season runs from mid-November to mid-June (Amezcua et al., 2019), so all the sampled months occurred during the dry season, and as time passed, the temperature increased, causing evaporation, and therefore a reduction in the depth of the system, an increase in the salinity and temperature of the water, and also a decrease in the dissolved oxygen. These results are likely influencing the changes in the fish assemblages observed throughout the course of this study; regardless of the rehabilitation. In both periods and in both systems, the fish assemblages changed according to a clear monthly pattern that is likely associated with the changes in these abiotic factors. However, different fish species were found in the sites even in very harsh conditions. Inland aquatic environments are subject to drying periods with the highest variations in concentrations of dissolved oxygen (Okada et al., 2003). Most of the fish species found exhibited tolerance to shifts in the salinity and dissolved oxygen which demonstrates their morphological and physiological abilities to maximize survival and adapt to changing conditions in the environment such as variations in hydrological regime. Most of the sampled fish were freshwater species with higher environmental tolerances, inhabiting shallow, warm, brackish waters.

Fish Assemblages Before and After the Rehabilitation

Considering that we were able to obtain samples in the rehabilitated and control floodplains before and after the road was removed, the use of a BACI designed seemed to be optimal, as this design is one of the best models for environmental effects monitoring programs (Smokorowski and Randall, 2017). However it has been discussed that a proper BACI design would require about 3 to 5 years of sampling prior to and after the impact, as this is the period of time in which most of the fish species would reach their maximum age, and also when most species would complete one generation. It is necessary to consider that those studies were undertaken in temperate and cold zones where the water bodies are permanent and the fish species have longer fish spans (Smokorowski and Randall, 2017). This is opposite to what we have in our study: ephemeral water bodies that last less than a year, because at some point the system dries up, or the conditions become too harsh to support any living organisms, and also the life spans of some of the analyzed fish species are very short, as is the case of the guppies that have a life span of less than 2 years (Reznick et al., 2005), or the fringed flounder, whose life span is 1 year (Reichert, 1998), and although the biology of most of the fish species found in the present study is not known, it is very likely that some of the other fish species have similar short life spans.

Also, as previously stated, access to the study site was very limited, and only during the months when the samplings took place, therefore the pre and post -treatment periods were limited to only the months analyzed. However, we were able to use the months as replicas in the study, and considering that the studied sites are ephemeral, as previously stated, we consider that the results of the present work can be considered as valid.

Results indicate significant changes in richness, diversity, and structure of the fish assemblages in the treatment zone before and after the road was removed, and with the control zone. Prior to the removal of the road, the number of fish species and the structure of fish assemblages was very similar between the control and the treatment zones. After the road was removed, the diversity, richness, and the structure of the fish assemblage changed in the treatment zone.

During 2011 both zones were dominated by three species in terms of abundance, and two in terms of biomass. Two poeciliids *Poecilia butleri* and *Poeciliopsis latidens*, and the exotic species of tilapia (*Orechromis aureus*), were the most abundant, and in terms of biomass, both tilapia species found accounted for more than 95% of the biomass. In the control site during 2015, the tilapia (*O.* sp.) increased its abundance, and was also dominant in similar numbers to *Oreochromis aureus*, but in terms of biomass, both species of tilapia accounted for more than 97%. It is necessary to consider that the conditions in these sites were harsh. Finding these species is likely related to the adaptations that these present to tolerate such conditions. It is known that the members of the family Poecilidae have a tolerance for such environmental conditions, especially thermal and wide range of salinity (0–135 ppt), which explains its high abundances and presence at all sampling sites (Meffe and Sheldon, 1988). These shallow, sheltered environments with soft sediment bottoms in the floodplain wetland appear to provide an ideal habitat for the formation of a breeding area for poecilids. Their diet mostly consists of detritus, zooplankton, and insects. For the case of the tilapia species, severe conditions, such as the ones found in this area, permit the high presence of exotic species. They have become the dominant species in many of their introduced ranges. It is known that *Oreochromis aureus* is a freshwater fish with a high tolerance for brackish water and to a wide range of the water quality and habitat conditions (McKaye et al., 1995). This ability explains its presence during all the sampled months, as this species is capable of withstanding severe conditions and poor water quality. This species is considered a competitor with the native species for food and space (Buntz and ManoochIII, 1969). *Atherinella crystalina* and *Lile stolifera* were not very abundant species during 2011 in the treatment area, and in the control area *Atherinella crystallina* was never collected. However, these species were found in some stations, from January to March, when the water quality was acceptable. *Atherinella crystallina* is restricted to freshwater areas of Sinaloa state and northern Nayarit, and is prone to declines due to habitat degradation, especially coastal development and pollution, and very little is known about its biology and habits (González-Díaz et al., 2015). *Lile stolifera* is known to enter and be very common in estuarine systems in the region, and is also an abundant species (Amezcua et al., 2006).

In the treatment zone after the road was removed the system was still dominated by the same three species in terms of abundance, and the two species of tilapia were still the dominant species in terms of biomass, although during this time its biomass accounted for 80%, 15% less than prior to the removal of the road, and other species appeared with some importance, and the diversity and richness of species increased in a significant manner. The species found during 2011 were also present in 2015, but additional species that are typical inhabitants of estuarine systems were also found, such as *Dormitator latifrons*, mojarras (Gerreidae), milk fish (*Chanos chanos*), snooks (Centropomidae), and the machete (*Elops affinis*). The studied area is close to the sea (approximately 3 km), and two estuarine systems (Huizache-Caimanero and Teacapan). Although there is no direct connection to these during the flooded period there are indirect connections. The closest is approximately 13 km to the north (Huizache-Caimanero), and the other is 20 km to the south (Teacapan), so there is the potential of estuarine species to find its way to the studied system, which occurred after the road was removed, as the number of species as well as the diversity increased, and the relative presence of both tilapias species decreased.

Nevertheless, the richness and diversity were low in both zones and both periods when compared with values observed in nearby systems [Huizache-Caimanero: species richness 61, Shannon diversity 4.0; Teacapan: species richness 51, Shannon diversity 3.8; (Amezcua et al., 2019)]. Previous studies indicate that a lower richness and diversity in similar sites is associated with the physiological limits of the species by salinity and dissolved oxygen (Okada et al., 2003). Although the conditions of the water improved with the removal of the road the water quality was still not optimal.

After the removal of the road however, there was an increment in diversity and richness. This increase might be related to rise in the volume of the water due to new hydrological connectivity, which is also related to the diversity and richness (Amezcua et al., 2019). Bayley (1995) pointed out the importance of the influence of the hydrological connectivity in the floodplain for the maintenance of biological and physical diversity. Furthermore, with the floods, there is a higher inundation which brings a greater amount of food and shelter for the fish (Welcomme, 2001).

Biodiversity is often used for assessing the success of the hydrological connectivity. However a single metric for quantifying the connectivity might be not enough, as there are more complex interactions occurring in the floodplains (Amoros and Bornette, 2002). Other factors such as connection frequency or the water body permanency, the intensity, degree, and duration of hydrological connectivity, etc., can strongly affect the biological characteristics of the aquatic environment (de Macedo-Soares et al., 2010), therefore analyzing the structure of the fish assemblage and its spatiotemporal changes might better reflect the success of an increase in hydrological connectivity. To do this assessment, a multivariate analysis was performed, and the results clearly reflected significant differences between sites, years, and months. The distance-based redundancy analysis clearly shows these changes, as clear-cut groups were formed depending on the site and year, and a change is observed regarding the sampling month. Before and after the road was removed seasonal changes occurred in both sites. This is likely related to the decrease in water quality as the time passed, because the temperature and salinity increased, whilst the depth and dissolved oxygen decreased, therefore, at the end of the sampling regime, only species that were able to withstand these harsh conditions were able to remain there. However, these changes might also be related to the specific biological rhythm, foraging ecology, and behavior of each species, besides the variability in hydrological terms (Dantas et al., 2012). The removal of the road had a significant influence in the fish assemblages in the treatment area, because, as pointed out before, species able to withstand these harsh conditions, such as *Dormitator latifrons*, were not recorded before the road was removed. Before the road was opened the low degree of hydrological connection in the environment probably promoted spatial heterogeneity and environmental gradients that shaped the structure of the fish assemblages according to tolerances of individual species (de Macedo-Soares et al., 2010). This would explain why during 2011, and in both periods in the control zone, there were fewer species, and the fish assemblage was dominated by poecilids and cichlids (tilapias), with an important presence of exotic species. On the other hand, enhanced hydrological connectivity which was based on the road removal implied a higher number of species, because the opportunity of movements within the system was enhanced, and they could easily move through the system. A larger area of the wetlands flooded implies more time that the fish can spend in the system and benefit from the wetland's services. Previous studies in similar environments have also documented that an increase in the connectivity also increases the number of fish species (Petry et al., 2003; Lasne et al., 2007; Sheaves et al., 2007).

Hydrological connectivity can also influence the trophic structure. Based on the food web theory, larger ecosystems support longer food chains because they have a higher species diversity and habitat availability (Post et al., 2007). Hydrological connectivity after the road was removed made the patches in the aquatic habitat more frequently connected, which may contribute to longer food chains, as opposed to habitats which are infrequently connected. This enhanced the higher species richness and diversity, which might explain the absence of species such as *Dormitator latifrons* prior to the road being removed; being able to withstand harsh conditions might not be the only factor that determines the presence of certain species, but aspects such as the availability of food are also important. This also might be the reason why different fish species appeared after the road was removed, as the connection and the general habitat complexity might have increased as a consequence of the removal of the road.

Floodplains are today amongst the most threatened ecosystems, and for the preservation and the enhancement of native fishes it is essential to recognize the factors that influence the ecological functions of this ecosystem. The key for the conservation of the floodplain system and its biota is the understanding and maintenance of connectivity pathways. Our results show that limited hydrological connectivity and flow is a factor which relates to a diminishing of the abundance and diversity of the aquatic biota, the distribution of native fish, and favors the presence of exotic species such as tilapia, as previous studies have highlighted (Lasne et al., 2007). The fish assemblages have seasonal variations, and it is likely that in similar conditions the fish species composition is prone to variation among years; therefore there is a need to focus on the drivers of diversity of assemblages to understand the habitat function and improve the conservation and the management. It has been suggested that the alteration of the flow in the system could lead to the loss of the floodplain habitat and a decrease of the taxonomic and functional diversity (White et al., 2012). Our results precisely indicate that poor connectivity is associated with lower diversity, which also implies a more reduced and simple trophic structure, while an increase in habitat connectivity incrementally increases the abundance of a diversity of fish, and also seems an important factor to help the presence of native species.

AUTHOR CONTRIBUTIONS

FA, leading author, responsible for the whole project, organized the contributions of all the authors, and put everything together, in charge of the final edition of the manuscript, the collection and analysis of fish in 2015, all statistical analysis, and the conception and design of the final objective of the work on its present form.

JR, M.Sc. student, elaborated her M.Sc. thesis with the results of this project, in charge of all sampling during 2015, and contributed to the design of the work. FF-d-S contributed to the conception of this work by linking the connectivity with the increase in diversity, in charge of all the abiotic factors, the description of the studied area, and the elaboration of the maps, and helped with the BACI design. FF-V contributed to the idea, in charge of the restoration trough the road removal, established a control and a treatment area, and helped to link the connectivity with the fish assemblages. FA-L in charge of the design, sampling and analysis of all the fish samples collected during 2011, and helped with the final redaction of the manuscript.

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Long-Term Spatiotemporal Variation in the Juvenile Fish Assemblage of the Tramandaí River Estuary (29°S) and Adjacent Coast in Southern Brazil

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We evaluated connectivity, resiliency, and spatiotemporal variation in fish associations between the Tramandal River estuary (TRE) and the adjacent coast (AC). This was based on intermittent and seasonal data covering a discontinuous 21-year period (1995 to 2016) obtained using a standard beach seine with replicate samples collected at several points. In the TRE (405 samples; 42,987 individuals) 55 species were captured. In the AC (297 samples; 54,295 individuals) 41 species were captured. After data standardization the expected richness of the TRE [$E(S) = 18.2$] was significantly greater ($P < 0.05$) than that of the AC [$E(S) = 14.4$]. The fish association structure and distribution patterns in TRE and AC were dynamic and interconnected but quite different in terms of species composition, especially due to the influence of local salinity. The TRE association was richer in a number of species but numerically dominated by marine estuarine-dependent juveniles. The AC association was represented by a few typical marine species in addition to a couple of estuarine-related transient species who used the surf-zone as a passageway to enter the estuary. Even if there was a higher percentage of common species reported (30 out of 66), the monthly average Jaccard index of similarity ($I_J = 28\%$) and the monthly average percent similarity index ($I_{PS} = 30\%$) were low, suggesting that the shallow water functional connectivity between AC and TRE was represented by few species that occur equally in abundance in both environments. *Trachinotus marginatus* and *Mugil liza* numerically dominated in the AC and *M. liza*, *Mugil curema,* and *Atherinella brasiliensis* at TRE. Juvenile *M liza* and *M curema* added up to >70% of the total individuals sampled in both environments. General linearized models (GLM) revealed that diversity was not influenced by interannual variations, evidencing that juvenile fish assemblage of AC and TRE are resilient through the years. Standardized beach samples are able to reveal long-term fluctuation in shallow estuarine fish communities but without an apparent loss in species composition, richness, and relative total abundance. The only observed interdecadal trend was the reduction in abundance of juvenile *M. liza* that seemed to parallel the reduction in abundance of the adult fishing stocks in southern Brazil.

Keywords: juvenile fishes, connectivity, resilience, long-term studies, mullet

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INTRODUCTION

Globally, estuaries, and coastal areas are environments with high biological productivity, and are considered important nursery areas for juvenile of many coastal fish species, including those of economic interest (Beck et al., 2001; Barletta et al., 2010). Estuaries potentially provide connectivity between marine and freshwater environments (Guimarães et al., 2014; Petry et al., 2016) and several species develop dependency on them. The natural variation of the estuarine environment and anthropogenic effects influence the dynamics of fish populations over time (Barletta et al., 2010; Martins et al., 2015).

The southern coastal plain of Brazil, especially the Rio Grande do Sul state, is composed of several aquatic ecosystems, encompassing habitats of great biological importance (Ramos and Vieira, 2001; Odebrecht et al., 2017). The Tramandaí River estuary (TRE; 29°S; estuarine area *c.*18.8 km²) is the second larger estuary after the Patos Lagoon estuary (32°S; estuarine area *c.* 1,000 km²).

Ecological studies of the Patos Lagoon estuary show that increased precipitation during *El Niño* events change the salinity regime due to increased runoff of continental water. As a consequence there is an increase in the number of freshwater fish species in the estuary (Garcia and Vieira, 2001; Garcia et al., 2004, 2017; Possamai et al., 2018). Freshwater species are much less frequent in the coastal region adjacent to estuaries (Ramos and Vieira, 2001; Monteiro-Neto et al., 2003; Lima and Vieira, 2009; Rodrigues et al., 2014), but the general abundance and diversity of the fish fauna in the marine coastal region are also affected by freshwater runoff coming from the estuary (Martins et al., 2015).

The Tramandal River estuary (TRE) is characterized as a dynamic system, ecologically complex, with high fish diversity, and having significant economic, and recreational importance (Silva, 1982, 1984; Ramos and Vieira, 2001; Guimarães et al., 2014). The system is permanently connected to the sea by an estuarine bar, which represents a transition zone (Silva, 1982) where juvenile marine-estuarine related fishes shelter and feed in shallow estuarine waters (Ramos and Vieira, 2001). Artisanal fishing is of social and economic importance for a large part of the local population, and the TRE attracts tourists during the summer vacation (Silva, 1982; Malabarba and Isaia, 1992; Santos et al., 2018). Other anthropogenic activities in the TRE, such as the petroleum industry, agriculture, forestry, rice cultivation, and sand extraction, have increased considerably in recent decades (Loitzenbauer and Mendes, 2012) and could adversely affect the functional and ecological execution of the system.

Long-term studies are key to determine changes in ecological processes in coastal environments (James et al., 2013; Barceló et al., 2016). In some cases, long-term records are used as the basis for environmental quality or restoration program targets (Tonn et al., 1990). Long-term studies, such as the Brazilian Long Term Ecological Program (PELD) in the Patos Lagoon estuary, provide a unique perspective on the complex dynamics of organisms and ecosystems (Odebrecht et al., 2017). Long-term studies have provided answers concerning spatial and temporal patterns of fish abundance and diversity. They have also explained relationships between environmental variables, anthropic activities and especially natural phenomena (for example, *El Niño* events) in the Patos Lagoon estuarine region (Garcia and Vieira, 2001; Garcia et al., 2004, 2012; Vieira et al., 2010). These studies enhance the capacity to predict biodiversity responses to global change, specifically responses to both anthropogenic pressures and large-scale climatic events, and

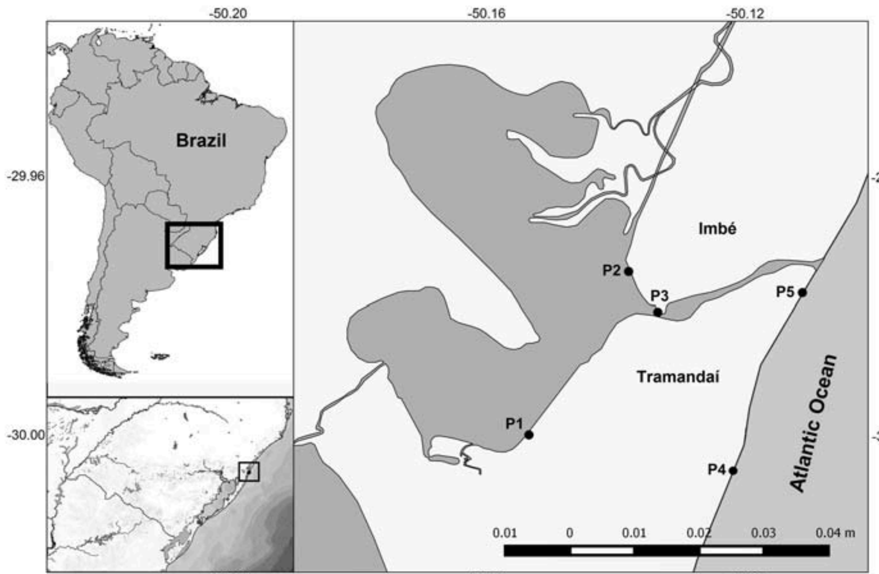

FIGURE 1 | South America, Brazil, Rio Grande do Sul State, and study area with the location of collection points in the Tramandaí River estuary (TRE; P1, P2, and P3) and adjacent coast (AC; P4 and P5).

can lead to proposals for the conservation and sustainability of local areas (Odebrecht et al., 2017).

Currently, limited information has been compiled about the TRE and the adjacent coast (AC—Ramos and Vieira, 2001; Malabarba et al., 2013; Garcia et al., 2018b; Santos et al., 2018). However, the Laboratory of Ichthyology at the Federal University of Rio Grande (FURG) has a series of unpublished long-term data on the TRE.

Based on a set of intermittent and seasonal data collections, covering a period of 21 years (1995 to 2016), the present study investigated the connectivity between the shallow water of the TRE and the AC. The study specifically examined and compared the structure of shallow water fish associations and local species diversity of TRE and AC throughout the study period of three decades. The seasonal influence of local abiotic variables (salinity, temperature, and water transparency) and connectivity between both environments was scrutinized.

MATERIALS AND METHODS

Study Area

Sampling was conducted over the estuarine system of the Tramandaí-Armazém lagoons (TRE with an area of 18.8 km²) and at the surf-zone of the AC (29° 55′ to 30° 00′ S; 50° 06′21″ to 50° 11′20″ W; **Figure 1**). The TRE is located on the northern coast of the state of Rio Grande do Sul, Brazil, and is part of the Tramandaí-Mampituba ecoregion (Abell et al., 2008). The Tramandaí River basin (2,500 km²) is connected to the Atlantic Ocean by a permanent channel (1.5 km long and 100 m wide) (Würdig, 1988) (**Figure 1**).

We used a historical intermittent seasonal database (1995–2003) and recent samples (2015–2016) clustered in 15 seasonal sample periods called "visits." The first 11 intermittent seasonal visits correspond to the summer of 1995, winter of 1996, summer of 1997, spring of 2001, autumn of 2002, winter of 2002, spring of 2002, summer of 2003, autumn of 2003, winter of 2003, and spring of 2003. The four recent visits were during the period autumn 2015 to summer 2016. At each visit at least five sampling points were systematically collected (**Figure 1**): three points in the estuarine system (P1, P2, and P3) and two in the adjacent marine surf-zone region (P4 and P5). At each visit to the sampling points, environmental variables such as salinity (optical refractometer), temperature (thermometer), and transparency of the water column (Secchi disk) were recorded.

Shallow-water fishes were collected using a "picaré" beach seine (9 m long and 1.5 m high, with a 13 mm mesh in the 3 m wings, and 5 mm mesh in the central part). The minimum sampling effort corresponded to five beach seine hauls at each sampling point per visit. All fishes captured were fixed with 10% formalin solution and processed at the Laboratory of Ichthyology

TABLE 1 | List of species caught per season per year in the marine adjacent coastal area (AC) and number of samples, number of species, total catch per unit effort (CPUE), mean temperature (°C), mean salinity and mean transparency (cm).

AC	Su-95	Wi-96	Su-97	Sp-01	Au-02	Wi-02	Sp-02	Su-03	Au-03	Wi-03	Sp-03	Au-15	Wi-15	Sp-15	Su-16
Species															
Mugil liza	0.8	421.9	2.1	12.7	28.0	3.9	1.8	3.7	1.5	1.5	1.9	7.6	1.3	0.9	0.1
Mugil curema	307.0	0.4	705.8	0.2	4.5		<0.1	0.1				31.2	0.1		1.2
Trachinotus marginatus	3.6	<0.1	23.6	1.3	35.7	3.7	83.2	62.8	7.6	6.8	1.1	127.2	13.7		28.3
Odontesthes argentinensis		0.6	2.3	21.2	1.5	0.7	6.0	0.6	3.5	1.0	2.8		0.1	0.4	
Micropogonias furnieri	0.4	0.4	95.9			3.3	0.1					0.5			
Stellifer rastrifer				34.4											
Mugil sp.1	0.1		5.7		8.8			0.6		0.1		4.3	0.3		0.6
Umbrina canosai							6.9	0.1			1.1				
Platanichthys platana	0.1		0.1	0.2							6.8				
Trachinotus carolinus	3.6						<0.1					5.4	0.5	0.1	6.6
Brevoortia pectinata	7.6		0.2		1.0	0.3	<0.1	1.6			0.3	18.1			0.8
Atherinella brasiliensis	8.9	3.2	6.8		0.6	<0.1						0.1	0.1		0.5
Menticirrhus littoralis	0.1	<0.1	1.4	1.1	0.7	0.4	1.3	1.8	0.1	<0.1	0.3	3.0			0.2
Pomatomus saltatrix			4.8		<0.1								0.2		
Caranx latus			0.8									0.2			0.3
Oncopterus darwinii				0.6		<0.1			0.1	<0.1	<0.1			0.4	
Samples	20	27	29	10	23	29	36	14	10	30	29	10	10	10	10
Number of species	16	11	22	10	12	8	15	11	5	11	11	17	8	4	9
CPUE total	334.2	426.7	866.2	71.9	81.0	12.3	100.4	71.9	12.8	9.8	14.7	199.4	16.3	1.8	38.6
Temperature (°C)	27	15	25	24	18	15	23	22	19	17	24	25	17	21	28
Salinity	30	33	29	33	34	31	34	32	36	33	34	37	33	28	23
Transparency (cm)	9	34	8	42	26	20	20	8	5	15	29	30	20	17	40

Based on the species frequency of occurrence (%FO) and relative abundance (CPUE%) the species were classified as: abundant and frequent (black shading), frequent and not abundant (light gray shading), abundant and infrequent (dark gray shading), infrequent and not abundant (no shading) or absent (–).

at FURG. All specimens were identified at the lowest possible taxonomic level, counted and weighed (g) using an analytical balance. Changes in nomenclature of the species over the years, including synonyms, have been adjusted. Type specimens were stored in the collection of the Laboratory of Ichthyology at FURG.

Data Analysis

Data collections were compared with each other in terms of space (sampling points along the gradient sea/estuary) and time (seasonal visits). The abundance of each species was determined by means of the catch per unit effort (CPUE), obtained using the ratio *N*:*f*, where *N* is the total number of fishes caught in a specific sampling points and *f* is the number of beach seine hauls (effort).

For each sample point and visit, the numerical relative abundance (%CPUE) was determined from the ratio of the CPUE for a given species, divided by the sum of the CPUEs of the set of collected species (×100). Frequency of occurrence (%FO) of individual species was calculated using the ratio between the number of occurrences of a given species, divided by the total number of samples (×100) at each point and visit.

Based on Garcia and Vieira (2001), and modified by Artioli et al. (2009), the dominance pattern of each species at each collection point was determined using a combination of %CPUE and %FO. Values of %CPUE and %FO were compared with their respective means (μ%CPUE and μ%FO), and the species classified as follows: abundant and frequent (%CPUE ≥ μ%CPUE, FO% ≥ μFO%); abundant and non-frequent (%CPUE ≥ μ %CPUE, FO% < μ FO%); non-abundant and frequent (%CPUE < μ %CPUE, FO% ≥ μ FO%); or present (%CPUE < μ %CPUE, FO% < μ FO%). The species identified as abundant and frequent were considered as dominant (Artioli et al., 2009; Ceni and Vieira, 2013).

Principal co-ordinates analysis (PCO), from a dissimilarity matrix (coefficient of Bray-Curtis), based on the dominant species was used to evaluate the patterns of spatial distribution of species. PERMANOVA was used to test significant differences between the centroid distances of each group (Anderson and Willis, 2003). Canonic co-ordinate analysis principal (CAP) was used to describe which of the environmental variables analyzed explained the patterns of spatial distribution (in TRE and AC) of fish associations in the best way. The influence of environmental variables (temperature, transparency and salinity) on the association of fishes in the TRE and AC was evaluated by canonical correspondence analysis (CCA). The analyses were performed using software R (https://www.r-project.org).

TABLE 2 | List of species caught per season per year in Tramandaí River estuary (TRE) and number of samples, number of species, total catch per unit effort (CPUE), mean temperature (°C), mean salinity, and mean transparency (cm).

TRE	Su-95	Wi-96	Su-97	Sp-01	Au-02	Wi-02	Sp-02	Su-03	Au-03	Wi-03	Sp-03	Au-15	Wi-15	Sp-15	Su-16
Species															
Mugil liza	2.3	83.4	43.2	78.7	25.8	174.8	90.3	5.0	30.2	27.1	5.8	19.0	22.1	0.7	5.4
Mugil curema	3.8	1.9	137.9		11.4	1.7	8.3	35.7		0.7	8.7	378.7	0.1		21.4
Atherinella brasiliensis	6.5	7.7	5.8		12.4	10.1	1.5	1.5	0.9	0.2	4.6	42.5	1.5	0.2	11.5
Jenynsia multidentata	9.3	0.5	1.2	4.7	4.0	0.1	1.6		0.6		1.8			0.1	
Ctenogobius schufeldti	0.1	0.1	0.4	1.7	0.5	0.1	0.6	0.1	0.2	0.2	1.0			0.9	
Odontesthes argentinensis				1.9	4.2	0.2		0.9	0.1	1.7	1.2	0.3	0.2		
Eucinostomus melanopterus	2.3				<0.1	2.9	0.2	0.1	0.6	1.0		1.7	0.5		
Lycengraulis grossidens			0.4	0.1	0.8	5.7	0.4	0.1		<0.1	<0.1	0.9			
Eucinostomus argenteus	4.6					0.8	0.4				0.8	0.1			
Eucinostomus lefroyi	29.6		16.7		0.7	0.2	<0.1		0.2	0.3	0.4				
Brevoortia pectinata			0.1	0.1	1.0	<0.1		3.6	<0.1	<0.1	<0.1	8.7			58.9
Micropogonias furnieri	0.1		6.9	0.1	0.4	0.3	2.0				0.2	3.2			
Mugil sp.1			0.6		0.5	<0.1					0.1	21.3		0.1	
Astyanax lacustris	1.7	0.1		0.6			0.1			<0.1					0.5
Astyanax eigenmanniorum				0.1		<0.1	0.1							0.1	4.3
Platanichthys platana		0.1	0.1	0.4		0.2	0.1				14.2	0.1		0.1	
Umbrina canosai					<0.1						0.7				
Caranx latus			0.2					0.1	<0.1						0.7
Samples	20	19	18	14	46	59	61	20	34	25	29	15	15	15	15
Number of species	14	7	18	17	22	20	29	12	9	10	17	20	7	12	13
CPUE total	60.3	93.7	232.2	93.6	66.5	197.5	107.5	47.1	32.9	32.6	39.7	478.4	24.6	3.5	108.4
Temperature (°C)	32	15	27	24	21	16	24	22	19	17	25	24	15	23	32
Salinity	1	6	0	6	14	5	4	16	9	13	14	4	0	1	12
Transparency (cm)	41	80	39	13	29	17	28	35	10	22	14	47	59	62	62

Based on the species frequency of occurrence (%FO) and relative abundance (CPUE%), the species were classified as: abundant and frequent (black shading), frequent and not abundant (light gray shading), abundant and infrequent (dark gray shading), infrequent and not abundant (no shading) or absent (–).

The faunal similarity analysis, based on the species presence/absence relationship between samples, was calculated using the Jaccard index (JI). The faunal similarity, based on species relative abundance, was obtained by calculating the percent similarity index (PSI) (Krebs, 1989; Magurran, 2004; Ceni and Vieira, 2013).

In order to compare the richness of species between the points sampled (in TRE and AC), the cumulative curves of number of species per sample and the cumulative curves of number of individuals per species collected were constructed (Magurran, 2004; Ceni and Vieira, 2013). To calculate the species richness per zone (in TRE and AC) at each visit, independent of the total number of individuals sampled (N), the rarefaction technique (E[S]) was performed (Sanders, 1968; Hurlbert, 1971; Krebs, 1989) using the PAST software (https://folk.uio.no/ohammer/past/).

Generalized linear models (GLMs) were used to investigate the variation of fish species richness (gamma distribution) and the probability of the presence of four dominant species (binomial distribution), considering the two environments (TRE and AC) as a single data set, in response to a set of predictor variables (salinity, temperature, transparency of water, season, and year). Predictive variables were tested for co-linearity using the Spearman coefficient prior to model formulation (Beger and Possingham, 2008). In the models, no highly correlated variables were included ($R^2 > 0.8$). To choose the best model, we followed the "backward stepwise" procedure by selecting the template that had the lowest Akaike information criterion (AIC) value (Anderson and Burnham, 2002). The percentage of total deviance explained, and the relative contribution of each predictor were independently verified for each model (Vasconcelos et al., 2013, 2015).

RESULTS

A total of 97,282 individuals were captured, belonging to 11 orders, 27 families, and 66 species (**Appendix 1**). The dominant group of species per visit for each environment was identified (**Tables 1**, **2**). Among the 41 species that occurred in the AC, only 10 were classified as dominant in at least one visit (**Table 1**). *Trachinotus marginatus* Cuvier 1832 and *Mugil liza* Valenciennes 1836 occurred as dominant in at least 50% of the visits in the AC. Among the 55 species that occurred in the TRE, only eight were classified as dominant in at least one visit (**Table 2**). Three species occurred as dominant in at least 50% of visits in the TRE: *M. liza*, *Mugil curema* Valenciennes 1836 and *Atherinella brasiliensis* Quoy and Gaimard, 1825.

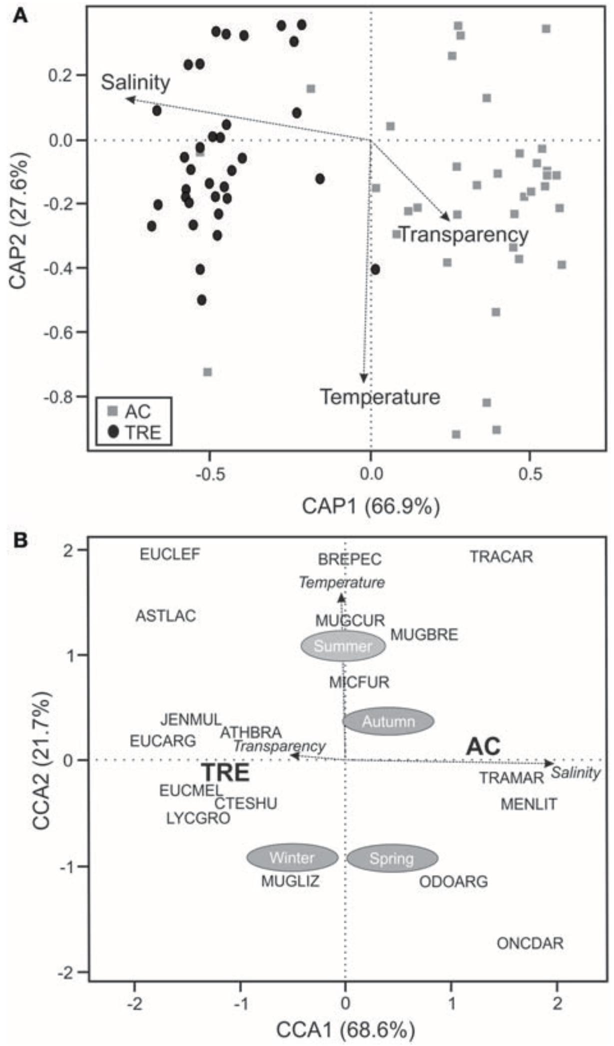

FIGURE 2 | (A) Canonic coordinate analysis principal (CAP) based on dominant species and **(B)** canonical correlation analysis (CCA) relating the dominant species to the environmental variables and seasons. TRE, Tramandaí River estuary; AC, marine adjacent coastal area.

Based on the CCA and CAP it was possible to discriminate two fish associations (**Figure 2A**): one was related to the TRE sampling points and another to the AC. Using PERMANOVA significant differences ($P < 0.05$) in the spatial variation of those associations were detected. Salinity was the variable that explained most the spatial distribution among species (**Figure 2A**). The CCA confirmed that salinity was the variable that best explained the variability in the structure of the fish fauna of TRE and AC, and that temperature explained the temporal-seasonal distribution of the species (**Figure 2B**).

In AC, 297 samples were taken capturing 41 species. In the same period at TRE, 405 samples were taken capturing 55 species (**Tables 1**, **2**). Between AC and TRE it was possible to observe a significant difference ($P < 0.05$) in the average sampling effort ($f = 19.8$ AC; $f = 27.0$ TRE) and in the average number of species caught per visit ($S = 11.3$ AC; $S = 15.1$ TRE). A greater number of individuals was collected in the AC ($n = 54.295$) than in the TRE ($n = 42.987$), although there was no significant difference ($P > 0.05$) in the mean number of individuals collected per sample (CPUE) between the areas (**Table 3**).

It is possible to observe (**Figure 3A**) that the rate of cumulative number of species per sample is greater in the TRE than in the AC. The cumulative influence of sampling effort (x-axis)

TABLE 3 | A *t*-test comparison (mean, minimum and maximum values, and S.D.) of the variables (number of samples, number of species, and catch per unit effort, CPUE) in the Tramandaí River estuary (TRE) and marine adjacent coastal area (AC).

Variable	*t*-test	Mean		S.D		MIN		MAX	
	P	**AC**	**TE**	**AC**	**TE**	**AC**	**TE**	**AC**	**TER**
Samples	0.04	19.8	27	9.61	16	10	14	36	61
Number of species	0.02	11.33	15.13	4.67	6.12	4	7	22	29
Total CPUE	0.53	150.53	107.88	235.03	120.31	1.8	3.47	866.21	478.4

and total number of individuals collected (*y*-axis) on the final number of species (size of the circles) is observed at **Figure 3B**. The largest number of samples in the TRE ($f = 405$) is the factor that best explains the greater species richness observed in the TRE as compared to the AC ($f = 297$) (**Figure 3B**). It is important also to emphasize that the lack of parity in number of sample (different efforts between TRE and AC) interferes with the comparison of observed species richness between the two habitats.

The use of GLM technique on the entire dataset (**Table 4**) shows that species richness for both the TRE or AC vary in the same way, regardless of the environment and are best explained by three variables. Temperature (**Figure 3C**) explained 14.4% of species richness and sampling effort 12.2%, which is associated with the number of individuals collected (9.5%; **Figure 3B**). This observation suggests that rarefaction techniques have to be applied in order to compare species richness independently of effort and number of individuals collected. In a simulation, where all the samples from both the TRE and AC were pooled and resampled at *c.*300 individuals, the expected richness of the TRE [E(S) = 18.2] was significantly greater ($P < 0.05$) than that of the AC [E(S) = 14.4].

Thirty out of 66 species collected were common between the TRE and AC, but the average similarity between the TRE and AC among visits was low (JI = 28%). The average similarity based on species relative abundance among visits was also low (PSI = 30%). The combination of low monthly average JI and low monthly average PSI suggests that the same species occurring equally in both environments dominate in abundance (**Tables 2**, **3**).

Both the TRE and AC were dominated by two species of mullets (*M. liza* and *M. curema*). In both environments, these two add up to >70% of individuals caught. The diversity differences between TRE and AC are due to the remaining additional species.

The GLM model (Gamma) adjusted for the $\log_{10}$ (CPUE+1) of both *M. liza* and *M. curema*, shows similar patterns (**Table 5**). For *M. liza*, the variables year (17.8%) and environment (12.8%) were the most significant predictors. For *M. curema*, seasonality (22.5%) was the variable with the best explanatory power (**Table 5**). Although both species were conspicuous in the area, *M. liza* showed a tendency to be more abundant within the TRE during the colder periods and *M. curema* more abundant in warmer months in the AC. The abundance pattern of *M. liza* presented a year-to-year downward trend during 21 years of observation, and this decrease in abundance was more obvious in the AC than in the TRE.

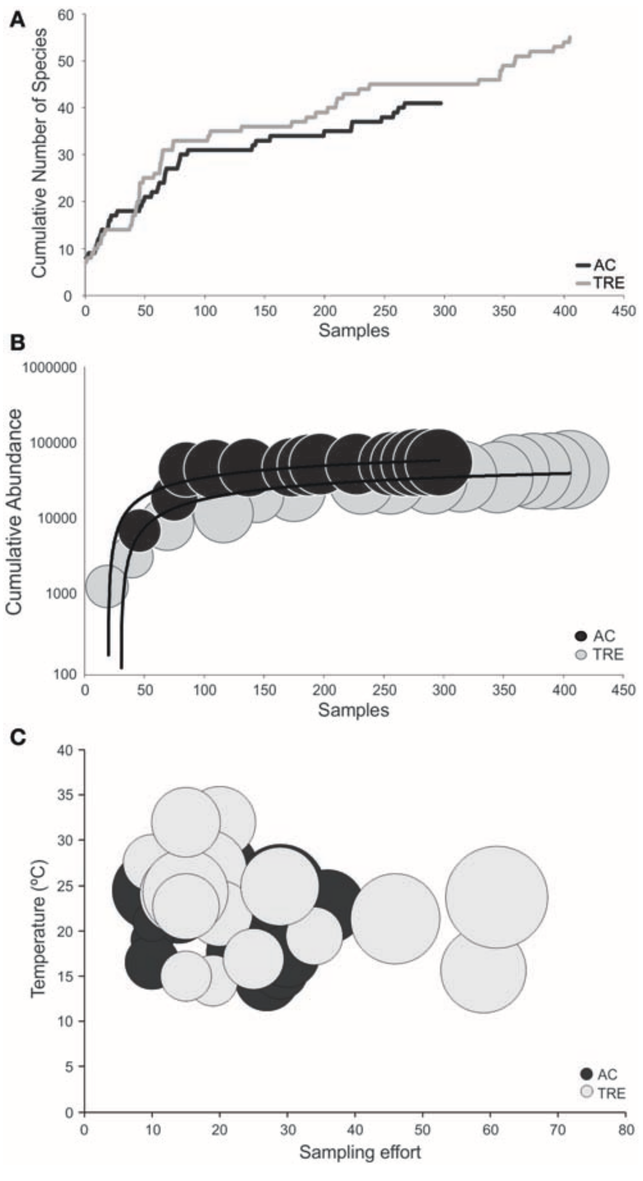

FIGURE 3 | (A) Cumulative curve of number of species per sample; **(B)** cumulative curve of number of individuals collected (*y*-axis) per samples (*x*-axis) and the relationship with number of species (circle size is proportional to species richness); and **(C)** the relationship between the variables predicted by the gamma model (effort and temperature) and species richness (circle size is proportional to species richness), separated by environment. TRE, Tramandaí River estuary; AC, marine adjacent coastal area.

TABLE 4 | Variability and adjustment for the logistic and gamma general linear models fitted to the fish richness values of the Tramandaí River estuary (TRE) and marine adjacent coastal area (AC).

Predictor	*P*	Res. dev.	Deviance	% Expl.
Richeness				
Gamma model				
NULL		22.478		
Samples	4.67e-05***	19.739	2.7389	12.18
Abundance	0.0003171***	17.596	2.1428	9.53
Temperature	9.326e-06***	14.35	3.2464	14.44
Total explained				36.2

*Significance values (P) for each factor, residual deviance (Res. Dev.), deviance, and percentage of the total deviance explained by each factor (%Expl.) are presented. *P < 0.05; **P < 0.01; ***P < 0.001.*

TABLE 5 | Variability and adjustment for the logistic and gamma general linear models fitted to the abundance values (Log10 (CPUE+1) for *Mugil liza* and *Mugil curema* in the Tramandaí River estuary (TRE) and marine adjacent coastal area (AC).

Predictor	*P*	Res. dev.	Deviance	% Expl.
Abundance (Gamma model)				
Mugil liza				
NULL		36.082		
Environment	0.00004654***	31.465	4.6166	12.79
Year	0.001601**	25.019	6.4461	17.87
Total explained				30.66
Mugil curema				
NULL		22.868		
Environment	0.926304#	22.864	0.0034	0.01
Season	0.005056**	17.713	5.1519	22.53
Transparency	0.029575*	15.809	1.9032	8.32
Total explained				30.87

*Values of significance (P) for each factor, residual deviance (Res. Dev.), deviance and percentage of the total deviance explained by each factor (%Expl.) are presented. *P < 0.05; **P < 0.01; ***P < 0.001; #P > 0.1.*

DISCUSSION

Understanding the level of connectivity between estuarine and marine environments is essential for the appropriate management of taxa associated with coastal zones. Connectivity, from a fish ecological perspective, can be described as a mechanism that facilitates the movement of fish between distinct spatio-temporal units (Dale and Sheaves, 2015) and contributes to the composition and richness of species of coastal zones environments (Petry et al., 2016).

The TRE ($S = 55$) has a greater number of juvenile species than the AC ($S = 41$). Many studies suggest that collections should be standardized to better compare community structures and monitor trends in fish abundance (Fischer and Paukert, 2009; Mourão et al., 2014). The larger species richness in the TRE compared to the AC cannot only be attributed to differences in collection effort because even after standardization (rarefaction techniques) the expected richness of the TRE [E(S) = 18.2] was significantly greater ($P < 0.05$) than that of the AC [E(S) = 14.4]. It is possible that other factors may contribute to this difference.

The estuarine regions in southern Brazil present a greater variety of habitats compared to adjacent coastal zones (Ramos and Vieira, 2001; Odebrecht et al., 2017). With regard to the TRE and AC complex, Garcia et al. (2018b) shows that fish assemblages in continental systems are sustained by a greater number of autotrophic sources than in the adjacent marine systems. Habitat heterogeneity should contribute to the greater richness of species in TRE, and also to other environments, especially coastal lagoons and other estuaries (Petry et al., 2016). These findings could be explained by the greater number of food web components (autotrophic sources, fishes trophic guilds and prey) associated with pelagic and benthic food chains within the estuary in comparison to the adjacent systems studied (Garcia et al., 2018b).

The adjacent coast (surf-zone) represent transitional areas that function as estuarine-dependent species migratory routes, indicating the connectivity between coastal zones and estuaries (Monteiro-Neto et al., 2003; Lima and Vieira, 2009; Mourão et al., 2014; Silva et al., 2016). Even if there is a good percentage of common juvenile species (30 out of 66) between the shallow water of both environments, the monthly faunal similarity based on species relative abundance (PSI = 30%), was low and similar to the average similarity based on the species presence/absence (JI = 28%). This revealed that only a few species were numerically dominant in the shallow-water fish associations. Thus, the shallow-water fish assemblages of TRE and AC have a few dominant species in common, and these common species are abundant in both environments and occur through the sampling period. These observations suggest that shallow-water estuarine and surf-zone connectivity between TRE and AC is effective for only a few species which are able to take advantage of both environments.

The surf-zone and shallow-water of estuaries of southern Brazil are mostly dominated by juveniles of Mugilidae (<50 mm total length; Vieira et al., 2010; Mont'Alverne et al., 2012). In the TRE and AC, juveniles of two species of *Mugil* represented *c.*76% of the total catch in both environments sampled. Juvenile *M. liza* showed higher abundance in the estuarine environment (54%) and *M. curema* in the marine environment (50%). Although salinity preference seems to be the main factor that segregate the juveniles of these two species, temperature is the variable that best separates them (Vieira, 1991; Garcia et al., 2018b; Mai et al., 2018). Adults of both species spawn in the marine environment and juveniles use the coastal region and estuaries as nurseries (Vieira, 1991; Mai et al., 2018). Juvenile *M. curema* abundance is associated with hot seasons, as a consequence of spawning during warmer conditions (Mai et al., 2018). It is important to note that adult *M. curema* are scarce in coastal environments located south of TRE (Patos Lagoon, for example). *Mugil liza*, however, have a high abundance of juveniles during cooler periods (Vieira, 1991; Ramos and Vieira, 2001; Lemos et al., 2014; Mai et al., 2018). They spawn during the winter and adults occur in higher numbers south of TRE (Vieira, 1991). It is possible that, in addition to the reproductive period, ecological processes related to feeding and to habitat use influence spatial patterns of juveniles of these two species (Garcia et al., 2018a).

Abiotic interactions affect ecological processes (migration, dispersion, and invasion) and also contribute to the composition and species richness of estuaries and marine areas (Desmond et al., 2002; Andrade-Tubino et al., 2008; Franco et al., 2008; Cheung et al., 2012). In south Brazilian coastal areas the seasonal variations of temperature and spatial oscillation of salinity, among other factors, provide intra- and inter-annual variability that is associated with the occurrence of larger scale climatic phenomena (Garcia et al., 2004, 2012; Moraes et al., 2012; Martins et al., 2015). Temperature plays an important role in seasonal migrations of some species, having a direct effect on the metabolic, reproductive, and abundance processes of the fish fauna (Mont'Alverne et al., 2012; Moraes et al., 2012; Cattani et al., 2016). Thus, recruitment of young fishes determines the composition and the seasonal variations in abundance of shallow-water species (Mont'Alverne et al., 2012; Moraes et al., 2012). Although temperature determines seasonal variation and enhances fish species diversity at both the TRE and AC, salinity was responsible for spatial distribution between these two environments.

Precipitation is an important factor in establishing spatial variation in salinity and the taxonomic structure of juvenile fish assemblages (Vinagre et al., 2009; Jenkins et al., 2010; Gillanders Bronwyn et al., 2011). The occurrence of the *El Niño* increases rainfall, which raises freshwater flow into the estuaries. This favors the presence of freshwater species, which increases species richness in the estuary (Garcia and Vieira, 2001; Garcia et al., 2004, 2012; Vieira et al., 2010).

During the 21-year period covered in this study, two different *El Niño* events were observed, 1997–98 and 2015–16, with the *El Niño* of 2015–16 being considered one of the most severe since 1950. The presence of freshwater species in TRE samples during this period raised species richness, masking any reduction in other estuarine and marine-related species. However, the effect of precipitation during *El Niño* events was not observed in AC.

A broad variety of sampling strategies and fishing gears has been developed to collect and record the presence and abundance of different fish species occurring in estuarine and coastal marine habitats. The beach seine, due to its robustness, rusticity, and ease of use and maintenance, is an appropriate gear for regular work in environments without catchers and entanglement (Vieira, 2006; Ceni and Vieira, 2013; Lombardi et al., 2014). The drawback of a beach seine, however, is that the catches provide low precision in estimates of abundance (Lombardi et al., 2014). However, the beach seine is a good sampling device for regular low-cost projects (Vieira, 2006; Ceni and Vieira, 2013) and we strongly recommend this gear to be used in the future so comparisons can be made with past data that have been gathered using this seine. This is illustrated in the long term studies of the Patos Lagoon estuary and adjacent area where this seine have been employed monthly since 1996 (Vieira et al., 2010; Garcia et al., 2017).

The logic behind a long-term study at TRE and AC, which analyses data from a 21-year period for two distinct but interconnected environments, is that the estuary, with a restricted topography, is subjected to more anthropic effects and greater chances of being impacted. Over the 21-year period covered by this study, local anthropic activities (fishing, tourism, and population growth), together with extreme climatic events, would be anticipated to influence the diversity and abundance of the TRE and AC fish species.

It is known that estuarine fish assemblages are highly resilient despite exposure to vast hydrodynamic variations and stress (Ching, 2015). Standardized beach samples are able to reveal long-term fluctuation in shallow estuarine fish communities but without an apparent loss in species composition, richness, and relative total abundance.

The challenge of long-term ecological studies is to understand resilience of the communities (Garcia and Vieira, 2001; Garcia et al., 2004, 2012; Vieira et al., 2010; Barceló et al., 2016). The TRE seams to be resilient especially to multiple and compounding stressors. The use of robust spatial-temporal data analysis techniques, such as GLM, was able to improve data analysis and help to show spatial and seasonal trends in the TRE and AC.

Regarding species richness, the inter-annual variations (year factor) did not appear to be significant in the GLM analysis. Therefore, this technique did not detect a reduction in species richness over the period covered by this study. The only species, during the 21-year study, in which a reduction in abundance was detected was *M. liza*, especially at surf-zone sampling points. Reported reduction of *M. liza* fishing stocks (Lemos et al., 2016; Sant'Ana et al., 2017) and juvenile abundance (Rodrigues et al., 2014; Martins et al., 2015) suggested that both adults and juveniles have shown a decrease in abundance in southern Brazil. This observation parallels the reduction in juvenile abundance of *M. liza* in AC, suggesting that this phenomenon should be better investigated in the future since mullets are among the most important fisheries resource of the TRE and adjacent coastal zones.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Brazilian Ministry of Environment (MMA) and all data collections and fish handling were endorsed by the Permanent License for Collection of Zoological Material (Number: 10125-2) granted to JV since September 2007. The fish collections analyzed in this paper occurred before the ethics committee of FURG (Comissão de Ética em Uso Animal—CEUA) was established. Nowadays the Laboratory of Ichthyology is under the CEUA license number 07/2017.

AUTHOR CONTRIBUTIONS

This paper is part of VR-R máster studies at Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais at FURG. VR-R and MdS collected data between 2015 and 2016. LR collected data from 2001 to 2003. VR-R, FR, and MdS help with data collection and analysis. JV participate in all data collection and analyses. All the authors reed part or all of this manuscript and agree with the publication of it.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

APPENDIX

TABLE A1 | Composition (total number of individuals collected) of the species registered for marine adjacent coastal area (AC) and Tramandaí River estuary (TRE) by order, family and species.

Order	Family	Species	AC	TRE
Elopiformes	Elopidae	*Elops saurus*	1	
Clupeiformes	Clupeidae	*Brevoortia pectinata*	411	1137
		Harengula clupeola	6	8
		Platanichthys platana	203	441
		Ramnogaster arcuata	13	1
		Sardinella brasiliensis	25	25
	Engraulidae	*Anchoa marinii*	4	
		Lycengraulis grossidens	26	423
Characiformes	Erythrinidae	*Hoplias* aff. *malabaricus*		4
	Curimatidae	*Cyphocharax voga*		1
		Steindachnerina biornata		1
	Characidae	*Astyanax eigenmanniorum*	5	77
		Astyanax aff. *fasciatus*		21
		Astyanax lacustris		54
		Diapoma alburnum	1	1
		Hyphessobrycon boulengeri		6
		Oligosarcus jenynsii		19
		Oligosarcus robustus		27
Siluriformes	Heptapteridae	*Pimelodella australis*		7
		Rhamdia aff. *quelen*		1
	Ariidae	*Genidens barbus*	370	
		Genidens genidens	46	317
	Callichthyidae	*Corydoras paleatus*	3	
Atheriniformes	Atherinopsidae	*Atherinella brasiliensis*	482	2672
		Odontesthes argentinensis	723	338
Cyprinodontiformes	Poeciliidae	*Phalloceros caudimaculatus*		19
		Poecilia vivipara		54
	Anablepidae	*Jenynsia multidentata*	6	641
Beloniformes	Belonidae	*Strongylura* sp.		1
Perciformes	Centropomidae	*Centropomus parallelus*		1
	Pomatomidae	*Pomatomus saltatrix*	141	15
	Carangidae	*Caranx latus*	29	15
		Chloroscombrus chrysurus	2	
		Selene vomer		1
		Trachinotus carolinus	199	
		Trachinotus falcatus	31	2
		Trachinotus marginatus	7573	66
	Gerreidae	*Diapterus rhombeus*		1
		Eucinostomus argenteus		189
		Eucinostomus gula	2	140
		Eucinostomus lefroyi	8	970
		Eucinostomus melanopterus	22	310
		Eugerres brasilianus		1
	Haemulidae	Haemulidae		66
	Sciaenidae	*Menticirrhus americanus*	12	1
		Menticirrhus littoralis	198	1
		Micropogonias furnieri	2902	341
		Paralonchurus brasiliensis	1	
		Pogonias cromis		1
		Sciaenidae	2	58
		Stellifer rastrifer	344	
		Umbrina canosai	285	23
	Mugilidae	*Mugil curema*	27052	10711
		Mugil liza	12684	23223
		Mugil sp.1	431	360
		Mugil sp.2	1	6
	Cichlidae	*Geophagus brasiliensis*		12
		Gymnogeophagus spp.		1
	Gobiidae	*Bathygobius soporator*		6
		Ctenogobius schufeldti	25	150
		Gobionellus oceanicus		2
	Stromateidae	*Peprilus paru*		1
Pleuronectiformes	Pleuronectidae	*Oncopterus darwinii*	14	
Tetraodontiformes	Monacanthidae	*Stephanolepis hispidus*	2	
Pleuronectiformes	Paralichthyidae	*Citharichthys spilopterus*	9	17
	Achiridae	*Catathyridium garmani*	1	
Total number of samples			297	405
Total number of species			41	55
Total number of individuals			54,295	42,987

Also given are total number of samples, total number of species collected, and total number of individuals caught.

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Functional Traits of Fish Species: Adjusting Resolution to Accurately Express Resource Partitioning

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One of the core challenges of functional diversity is the identification of traits that can accurately be linked to ecological processes. Trait-based metrics have been used to detect and quantify the effects of deterministic processes, such as niche filtering and co-occurrence mechanisms. However, most functional studies have simplified the measured attributes, especially for fish species. Here, we aimed to test the influence of trait resolution and surrogates on the accuracy in expressing resource partitioning among tropical fish species. We assessed pairwise species similarity between distinct ways of express resource use by species (through increasing trait resolution), and tested whether differences in resolutions are strong enough to provide different patterns in the functional structure of tropical fish assemblages. Our study shows that distinct ways of expressing resource partitioning among species may provide different ecological interpretations of this process as different resolutions or surrogates can change pairwise species, similarity.

Keywords: resolution, functional diversity, diet analysis, trophic guild, similarity

INTRODUCTION

The last decade has seen an explosion of interest in the use of functional traits in community ecology research, spurred in part by McGill et al.'s (2006) influential synthesis and repositioning of the field (Didham et al., 2016). Much of the promise of functional approaches rests on the assumption that patterns of dissimilarities among co-occurring species can provide direct insights into ecological processes (Vandewalle et al., 2010; de Bello, 2012). For instance, trait-based metrics have been used to detect and quantify the effects of deterministic processes, such as niche filtering and co-occurrence mechanisms (Siefert et al., 2013). Yet, one of the core challenges of applied functional research is the identification and discrimination of traits that can be accurately linked to direct ecological processes (McGill et al., 2006; Didham et al., 2016). More precisely, as observed by Didham et al. (2016), most functional studies have simply quantified a small number of easily measured attributes from a few "representative" sample of species within a defined taxonomic or functional group. This is potentially problematic because decisions about the chosen "resolution" (here defined as the degree of detail applied in the measurement of a particular function or process) can have a significant influence on the robustness of functional diversity estimation (Lavorel et al., 2008) and consequently in subsequent inferences about ecological processes (Poff et al., 2006).

Resource partitioning among fish species, for example, is one of the ecological process that is often inferred and expressed through different trait resolutions and/or surrogates (Albouy et al., 2011). Ideally, direct measurement of this mechanism, such as through diet analysis, would not only capture the functional structure of communities but also give a full picture of how species use available resources in ecosystems, allowing inferences about functions performed by species and their influence on ecosystem processes (Violle et al., 2012). However, such analysis typically requires considerable research effort and, thus, is rarely performed, leading researchers to often use in studies a variety of alternative methods. For example, at a smaller measurement resolution, resource partitioning within communities may be assessed by the classification of species into guilds according to the type of prey consumed, giving partial information on the trophic niche occupied by species in assemblages' organization (Albouy et al., 2011). Although widely used in studies, there are a few issues with this approach because species in the same guild will inevitably differ in some subtle aspects of resource use (Petchey and Gaston, 2002a; da Silva and Fabré, 2019), resulting in a vague understanding of the partitioning process.

In the same manner, we can also highlight other simpler and less research-intensive surrogates widely used to express resource use by species that still need further investigation on how effective they are for functional analysis (Didham et al., 2016; Soler et al., 2016; Ramírez-Ortiz et al., 2017). For instance, the use of morphological patterns and phylogenetic relationships in functional studies have always been surrounded by important issues in relation to at what extension functions and ecological processes are being assessed by these different surrogates (Hugueny and Pouilly, 1999; Cadotte et al., 2013; Gibb et al., 2015; Didham et al., 2016; Tucker et al., 2017). Ideally, traits such as mouth size, eye position and body shape are expected to indicate the types of consumed preys and/or feeding strategies adopted by species (Albouy et al., 2011; Dolbeth et al., 2016), providing information on ecological specialization of species to the use of core resources (Adite and Winemiller, 1997; Ramírez-Ortiz et al., 2017). Likewise, the evolutionary history of species should also reflect such mechanisms as the topology of a phylogenetic tree represents the differences in phenotypic, genetic and behavioral features of species (Vitt and Pianka, 2005; Grime, 2006; Diniz-Filho et al., 2010; Mouquet et al., 2012). Yet, it is still unclear how strong is the correlation between such surrogates and the direct measure of resource use in ecosystems.

Precise identification of which trait resolution and/or surrogate can be used to assess functions performed by species in ecosystems is a key factor in the advance of functional ecology studies (Villéger et al., 2017). Therefore, the present study aimed to test the influence of trait resolution on the accuracy in expressing resource partitioning among tropical fish species. Specifically, we assessed pairwise species similarity between different ways of express resource use, and tested whether differences in resolutions are strong enough to provide contrasting patterns in the functional structure of tropical fish assemblages.

MATERIALS AND METHODS

Sampling Design and Study Area

Fishes were sampled from a coastal area in the tropical Atlantic Southwest ecoregion (09°47′80′′S – 35°49′56′′W and 10°21′26′′S, 36° 05′33′′W) that is comprised of three geomorphologically distinct habitats: (i) reef habitats (hereafter named reef), characterized by sandstone reefs making up 23% of the total area; (ii) an estuary lagoon habitat (hereafter named lagoon), influenced by one of the largest lagoons of Brazil, the Mundaú-Manguaba estuarine complex (CELMM) which generates a plume of sediment that influences the surrounding coastal area; and (iii) an estuary-river habitat (hereafter named estuary), characterized by the drainage of the São Francisco River, the second largest river in Brazil (Knoppers et al., 2006), whose sediment plumes extends for 10–20 km from the river mouth.

Six sampling sites for fish collections were used in each habitat (reef, lagoon, and estuary) generating 36 sampling points per sampling trip. Samplings were carried out from January to July 2013 using ten nylon gillnets of 100 m long, 2.9 m height with different meshes which were linked by nylon cables in a random arrangement. The linked nets were set at each site, close to the bottom, for 4 h to catch demersal species (Federal Scientific Fish Sampling License 1837810). The catch was immediately placed in ice slurry to sedate the fish and to aid preservation.

Diet Analysis and Traits Characterization

In the laboratory, fish were identified to species level following Figueiredo and Menezes (1978), Lessa and Nóbrega (2000), and (Carpenter, 2002). Morphometric measurements were taken from each fish individual to obtain morphological traits, and stomachs were removed and fixed in formalin (4%) for gravimetric gut content analysis. Each food item was identified to the lowest possible taxonomic level depending on the state of preservation and then weighed to the nearest gram.

We then characterized the functional traits of species using seven different forms of measurement, all related to resource partitioning among species: five increasing levels of diet resolutions (R1 to Rmax) and two surrogates of resource use (S1 and S2). A concise summary of each form of measurement is given below:

Resolution 1 (R1)

Species were grouped in trophic guilds according to the main diet of adults, using information of published papers and online databases (e.g., FishBase[1]).

Resolution 2 (R2)

As in R1, species were also grouped in trophic guilds. However, guilds were defined by qualitative analysis of food items found in the gut content of species. A presence/absence matrix of preys found in diet composition of species was built and a hierarchical

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[1] www.fishbase.org

agglomerative clustering by Ward's Method with Euclidean distance was performed to visualize trophic similarity between species. We identified groups that had diet similarity among species greater than 50%. To test whether or not the differences in prey similarity among identified guilds were significant, we used an analysis of similarities (ANOSIM) at a significance level of $p = 0.05$. The similarity percentage (SIMPER) was later used to typify and discriminate which prey species contributed the most for dissimilarity between trophic guilds. Multivariate analyses were performed in the software PAST v.3 (Hammer et al., 2001).

Resolution 3 (R3)

We carried out a qualitative analysis (presence/absence) of food items found in the gut content without grouping species in guilds.

Resolution 4 (R4)

Quantitative data from categorized feeding index (FIiC) using an ordinal scale. We first obtained the feeding index values (FIi) for each species through the frequency of occurrence (Fi%) and total weight (Wi%) of found preys. Fi% indicates the proportion of stomachs containing a specific prey *i* in relation to all stomachs examined for the species (Hynes, 1950). The weighted index (Wi%) estimates the proportion of total weight of a specific prey taxa *i* in relation to the weight of all preys consumed by the species (Hynes, 1950). Both indexes were combined to obtain FIi for each species following Kawakami and Vazzoler (1980) adapted by Oliveira et al. (2004):

$$FIi = \frac{Fi\%^{*}\,Wi\%}{\sum(Fi\%^{*}\,Wi\%)}$$

The Feeding index was then categorized (FIiC) using an ordinal scale according to the degree of food item importance (0 = prey absence; 1 = prey with less than 20% importance; and 2 = prey with 20% or more of importance). This categorization process causes details in diet composition to be lost as the real importance of food items are not evaluated.

Maximum Resolution (Rmax)

At the highest resolution, we defined feeding habit of species using quantitative raw data from FIi values. Specifically, we took in consideration the actual importance of each food item found in the gut content analysis for each species, which provided us a more detailed and comprehensive information on how species use available resources.

Surrogate 1 (S1)

Seven morpho-functional traits were chosen based on their well-documented relationships with feeding habit and strategies (see **Table 1** for description of traits and ecological meaning). Size-related variables were taken as ratios of standard length to reduce the effects of allometry.

Surrogate 2 (S2)

A phylogenetic analysis of species was carried out based on the current taxonomy of fishes (Betancur-r et al., 2013). The phylogenetic topology was built using the software Mesquite[2]. Finally, branch length was used to estimate the dated phylogeny by the software Phylocom[3] using the function bladj.

TABLE 1 | Ecomorphological traits used as surrogates for fish diet.

Functional trait	Formula	Ecological meaning	Reference
Oral shape	$\frac{\textit{Mouth height}}{\textit{Mouth wide}}$	Capture food resources	1
Relative mouth height	$\frac{\textit{Mouth height}}{\textit{Standard length}}$	Associated with the size of prey	2
Relative mouth wide	$\frac{\textit{Mouth wide}}{\textit{Standard length}}$	Associated with the size of prey	3
Eye position	$\frac{\textit{Eye height}}{\textit{Head length}}$	Vision for feeding	1, 3, 4
Relative head height	$\frac{\textit{Head height}}{\textit{Standard length}}$	Associated with the size of prey	2
Relative head length	$\frac{\textit{Head length}}{\textit{Standard length}}$	Associated with the size of prey	3, 4
Standard length	*Standard length*	Associated with the size of prey	4

[1]*Albouy et al. (2011);* [2]*Pouilly et al. (2003);* [3]*Gatz (1979);* [4]*Hugueny and Pouilly (1999).*

A trait-species matrix was created for each diet resolution (R1, R2, R3, R4, and Rmax) and the morphological surrogate (S1) with species in rows and functional traits in columns. The number of columns (traits) varied greatly between matrices with its number increasing with higher resolutions (for the exact number of traits in each resolution see **Figure 1A**). The trait-species matrices and the phylogenetic topology were treated in two different ways which will be discussed in next sections.

Testing Similarity Pairwise Matrix

The core aim of our study was to identify how different ways of express one particular function or process may affect our perception of this process. Therefore, to test whether different trait resolutions and surrogates change pairwise species similarity, the trait-species matrices and the phylogenetic topology were all converted into distance matrices, and a Mantel test was carried out to evaluate correlations between the maximum resolution (Rmax) to the other four diet resolutions (R1, R2, R3, and R4) as well as to the two studied surrogates (S1 – morphological traits and S2 – phylogeny) (**Figure 1B**). As each resolution and surrogate presented different types of data, the distance matrix of each component was created using different measures: Jaccard distance for qualitative data (R1, R2, and R3), Bray–Curtis distance for quantitative data (R4, R5, and S1), and the Cophenetic distance for phylogeny data (S2). The pairwise similarity correlation (with 999 permutations) was performed in the software R (R Core Team, 2013) using the Vegan package at a significance level of 0.05. The threshold of 0.7 was adopted to identify which matrices were highly correlated (Dormann et al., 2013).

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[2] http://mesquiteproject.wikispaces.com/

[3] http://phylodiversity.net/phylocom/

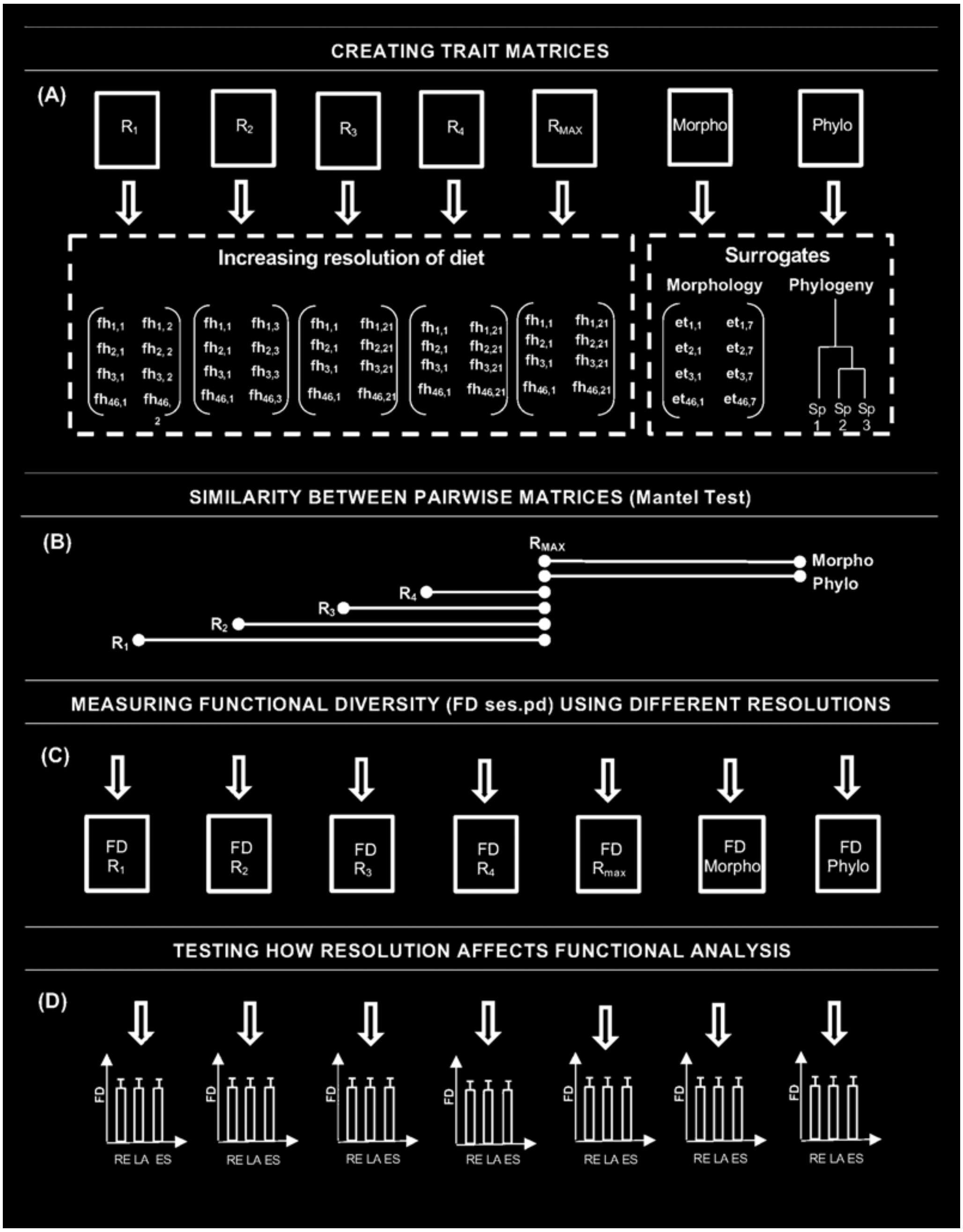

FIGURE 1 | Methodological framework. **(A)** Traits related to resource partitioning were expressed through five levels resolutions of feeding data and two surrogates of feeding strategy (ecomorphological traits and phylogeny), which were used to create six trait-species matrices and one phylogenetic topology; **(B)** a Mantel Test was carried out to test pairwise species similarity between trait matrices and the maximum level of resolution of feeding data (R_{max}); **(C)** functional diversity index (FD) was calculated using resolution and surrogate individually; **(D)** we compared observed functional patterns found for each resolution and surrogate between three habitats found in the study area to test whether differences in resolutions are strong enough to provide different patterns in the functional structure of tropical fish assemblages. (R_1 – Qualitative data grouped in guild from FishBase source; R_2 – Qualitative data grouped in guild from similar food item; R_3 – Qualitative food items data ungrouped in guild; R_4 – Quantitative data from Feeding Index Categorized (FI_iC); R_{max} – Quantitative data from FI_i not categorized; fh – feeding habitat; et – morphological trait; Morpho – ecomorphological trait; Sp – Species; Morpho and Phylo – phylogenetic topology of the species. The connotation $fh_{46,2}$ matches 46 rows and 2 columns so on; FD R_1 – Value of FD from matrix of qualitative data grouped in guild from FishBase source; FD R_2 – Value of FD from matrix qualitative data grouped in guild from similar food item; FD R_3 – Value of FD from matrix qualitative food items data ungrouped in guild; FD R_4 – Value of FD from matrix quantitative data from Feeding index Categorized (FI_iC); FD R_{max} – Value of FD from matrix quantitative data from Feeding index (FI_i) not categorized; fh: feeding habitat; et: morphological trait; (FD Morpho) Value of FD from matrix morphological trait, and FD Phylo – Value of FD from topology of phylogeny of the species. FD – Value of functional diversity; RE – reef; LA – lagoon and ES – estuary.)

TABLE 2 | Fish species collected during the study period and their respective guilds based on secondary data (R1: CARN – carnivores; OMNI – omnivores) and primary data (R2: BESI – benthivorous sedentary invertebrates; BEMI – benthivorous mobile invertebrate; and PISC – piscivores).

Family	Species	Guild	
		Secondary data (R1)	**Primary data (R2)**
Albuliformes	*Albula vulpes*	CARN	BESI
Ariidae	*Bagre bagre*	OMNI	PISC
	Bagre marinus	OMNI	PISC
	Canthorops spixii	OMNI	BESI
Bothidae	*Bothus ocellatus*	CARN	PISC
Carangidae	*Carangoides bartholomaei*	OMNI	PISC
	Caranx crysos	CARN	PISC
	Caranx hippos	CARN	PISC
	Chloroscombrus chrysurus	OMNI	PISC
	Oligoplites saurus	CARN	PISC
	Selene setapinnis	CARN	PISC
Carcharhinidae	*Rhizoprionodon lalandii*	CARN	PISC
Clupeidae	*Opisthonema oglinum*	CARN	BEMI
Dactylopteridae	*Dactylopterus volitans*	CARN	BEMI
Engraulidae Fistulariidae	*Cetengraulis edentulus*	CARN	PISC
	Lycengraulis grossidens	CARN	PISC
	Fistularia tabacaria	CARN	PISC
Gerreidae	*Diapterus rhombeus*	CARN	BESI
	Eucinostomus gula	CARN	BEMI
	Eucinostomus jonesii	CARN	BEMI
Haemulidae	*Conodon nobilis*	CARN	BESI
	Haemulom aurolineatum	CARN	PISC
	Orthopristis ruber	OMNI	BEMI
	Haemulopsis corvinaeformis	OMNI	BESI
Lutjanidae	*Lutjanus analis*	OMNI	BEMI
	Lutjanus synagris	OMNI	PISC
Mullidae	*Pseudupeneus maculatus*	OMNI	BEMI
Paralichthyidae	*Syacium micrurum*	CARN	PISC
	Syacium papillosum	CARN	BEMI
Polynemidae	*Polydactylus virginicus*	OMNI	BEMI
Rhinobatidae	*Rhinobatos percellens*	CARN	PISC
Sciaenidae	*Cynoscion jamaicensis*	CARN	PISC
	Cynoscion virescens	CARN	PISC
	Larimus breviceps	CARN	PISC
	Menticirrhus americanus	CARN	PISC
	Menticirrhus littoralis	CARN	PISC
	Micropogonias furnieri	CARN	BESI
	Stellifer brasiliensis	CARN	BEMI
	Umbrina coroides	CARN	BEMI
Scombridae	*Euthynnus alletteratus*	CARN	PISC
	Scomberomorus brasiliensis	CARN	BESI
	Scomberomorus cavalla	CARN	PISC
Sphyraenidae	*Sphyraena guachancho*	CARN	PISC
Synodontidae	*Synodus intermedius*	CARN	BEMI
Tetraodontiformes	*Aluterus monoceros*	CARN	BEMI
Triglidae	*Prionotus punctatus*	CARN	BEMI

Effect of the Trait Resolution in the Community Assemblage Patterns

Second, we tested whether studied resolutions and surrogates provide different ecological interpretations of communities. Functional diversity of fish assemblages for the three habitats found in the study area was measured by the standardized size effect of Petchey and Gaston's (2002b), using all trait-species matrices and the phylogenetic topology, individually (**Figure 1C**).

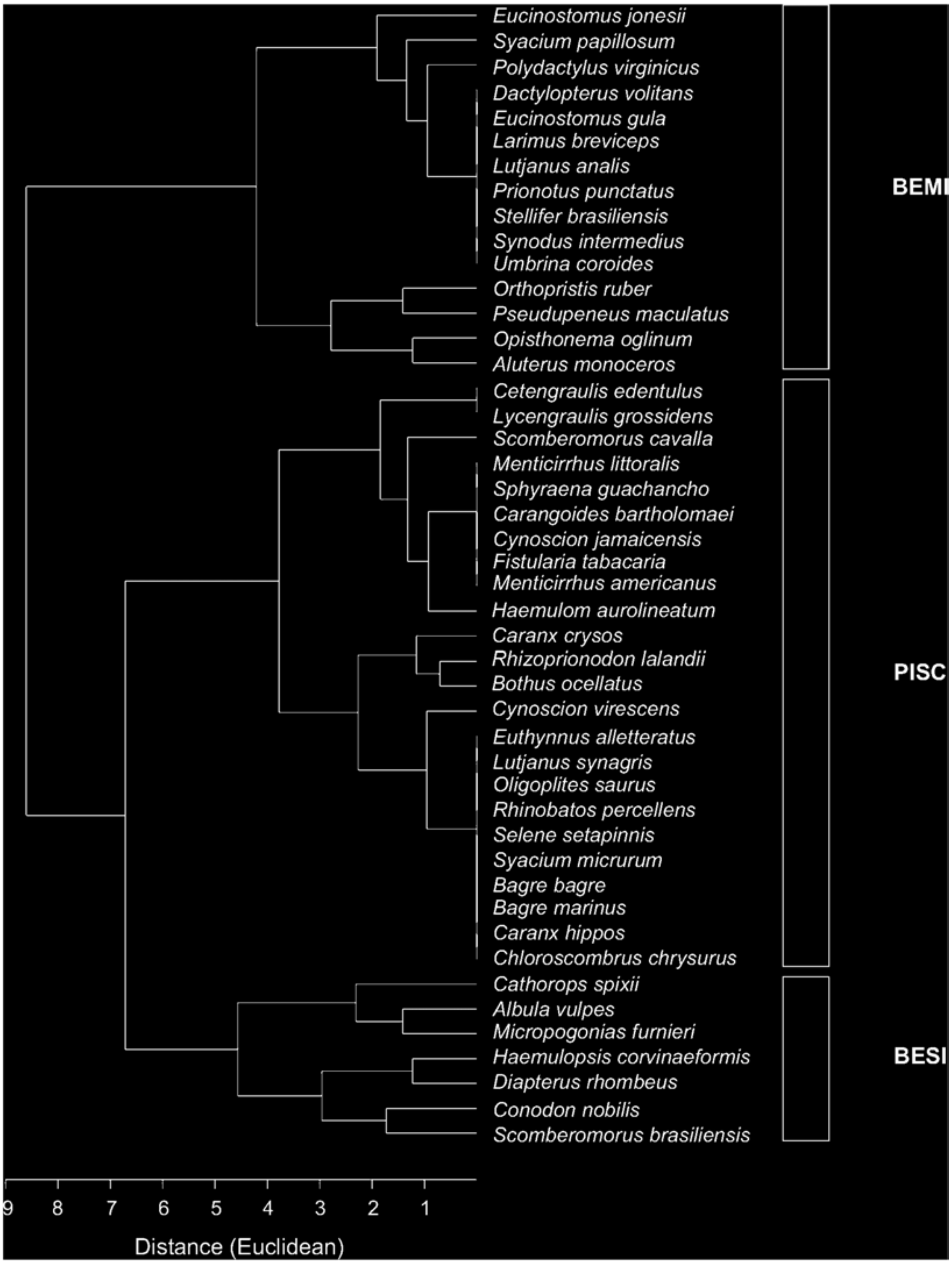

FIGURE 2 | Dendrogram of the trophic guilds of the fish assemblage using qualitative data of food item (R_2). BEMI: Benthivorous mobile invertebrates; PISC: Piscivores; and BESI: Benthivorous sedentary invertebrates.

A one-way analysis of variance (ANOVA) was then performed to test differences in FD obtained for each resolution between habitats (**Figure 1D**).

Here, FD was defined as the sum of the total branch length of the functional dendrogram connecting co-occurring species. The standardized effect size was used to control the influence of species richness in the estimation of FD (Kembel et al., 2010). Prior comparisons of FD values, normality and homoscedasticity assumptions were checked using Shapiro–Wilk and Levene's test, respectively. Whenever necessary, data was transformed – $\ln(x+1)$ or x^2 – to reduce the effect of data aggregation. All functional analyses were performed in the software R.

RESULTS

Diet Composition and Trophic Guild

The gut content of 213 individuals from 46 species was analyzed. Species classification in trophic guilds differed between applied methods (**Table 2**). For instance, in R1, according to publishing data and online database searching, species were only classified into two groups (carnivorous and omnivorous). Meanwhile, when considering the gut content in R2, three different guilds were found (benthivorous mobile invertebrates/BEMI; piscivores/PISCV and benthivorous sedentary invertebrates/BESI). The PISCV group was the most representative guild with 24 species, BEMI was comprised of 15 species, and BESI was represented by 7 species (**Figure 2**). Diet composition among the three guilds was significantly different (ANOSIM, $R = 0.538$; $p < 0.01$), supporting the results of the cluster analysis. Detritus (16%) and Decapoda (9%) contributed the most to total dissimilarity between the BESI and PISCV, while Osteichthyes (28%) and Decapoda (15%) were responsible for dissimilarity between PISCV and BEMI. Differences between BESI and BEMI were caused by detritus (11%) and Osteichthyes (10%) items. A full characterization of food items identified for species is provided in **Supplementary Material** (**Supplementary Table S1**).

Similarity Between Rmax and Resolutions and Surrogates of Diet

The correlation between Rmax and other diet measures (R1, R2, R3, and R4) increased with higher resolutions (**Figure 3**), indicating that more detailed information on diet provide a better picture of how species share resources. Although the first resolution using qualitative data from published literature (R1) did not present a significant relationship ($p > 0.05$) with the highest resolution (Rmax), from R2 onward, where we used direct analysis of gut content in different ways, correlations were statistically significant ($p < 0.05$). Surprisingly, surrogates (S1 and S2) did not present any correlation with Rmax ($p > 0.05$).

Effect of Trait Resolution on Detection of Functional Diversity Patterns

Overall, we found that observed functional patterns of fish assemblages may differ depending on trait resolution (**Figure 4**). Specifically, lower resolutions (R1 to R4) and surrogates (S1 and S2) were not able to identify significant differences in the functional structure of assemblages between studied habitats ($p > 0.05$, **Figure 4**), while the maximum resolution showed functional aggregation of species in the estuary habitat in relation to the others ($p < 0.05$).

DISCUSSION

Our results support the idea that different methods used in the measurement of a particular process can create distinct patterns in observed functional diversity. Specifically, our study shows that distinct ways of expressing resource partitioning among species may provide different ecological interpretations of this process as different resolutions or surrogates can change pairwise species similarity.

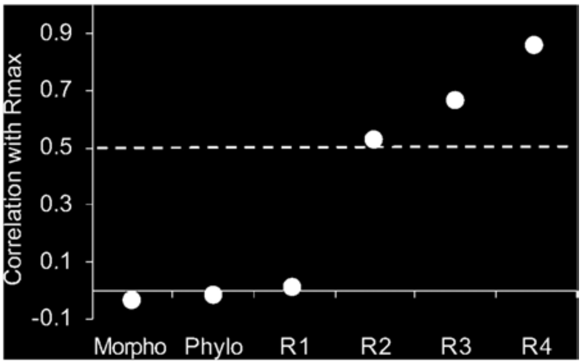

FIGURE 3 | Correlation coefficient from Mantel test performed between (Rmax) with morphological traits, phylogeny, and increasing diet resolution (R1, R2, R3, and R4). (R_1) qualitative data grouped from FishBase; (R_2) qualitative data grouped by food item; (R_3) qualitative food items data ungrouped; (R_4) quantitative data from Feeding Index Categorized (FI_iC); and (R_{max}) Quantitative data from Feeding Index (FI_i) not categorized. The dashed line represents the level of significance at $p < 0.05$.

Trait Resolution and Surrogates to Assess Resource Partitioning

Trophic interactions play an important role in maintaining the structure and functioning of ecosystems (Longo et al., 2014), thereby, it is not surprising that the trophic niche of species is one of the most studied niche dimensions in animal ecology (Winemiller et al., 2015). The description of this dimension may be accomplished through the analysis of the different mechanisms underlying this process, such as the understanding of how species use the different resources available in ecosystems.

Typically, one of the easiest ways of study resource partitioning is by categorizing species into guilds based on literature information (secondary data), as primary data for most groups of species are hard to be obtained, especially in the tropics (Nonogaki et al., 2007). However, our results indicate that data retrieved from online databases or published papers might be a poor surrogate of in locus species traits, as R1 was the only diet resolution that had no correlation with Rmax (**Figure 3**). One of the main reasons for such differences is that available data may not always translate ecological characteristics of particular species as plasticity in feeding behavior depends on many factors, such as variation in productivity levels, ontogenetic and prey availability (Bowen and Allanson, 1982; Reisinger et al., 2017). Moreover, diet shifts of single species may spatially occur due to regional differences in environmental conditions (Condini et al., 2015) which may result in the misclassification of species. Thereby, the use of published data to categorized species should be done with caution.

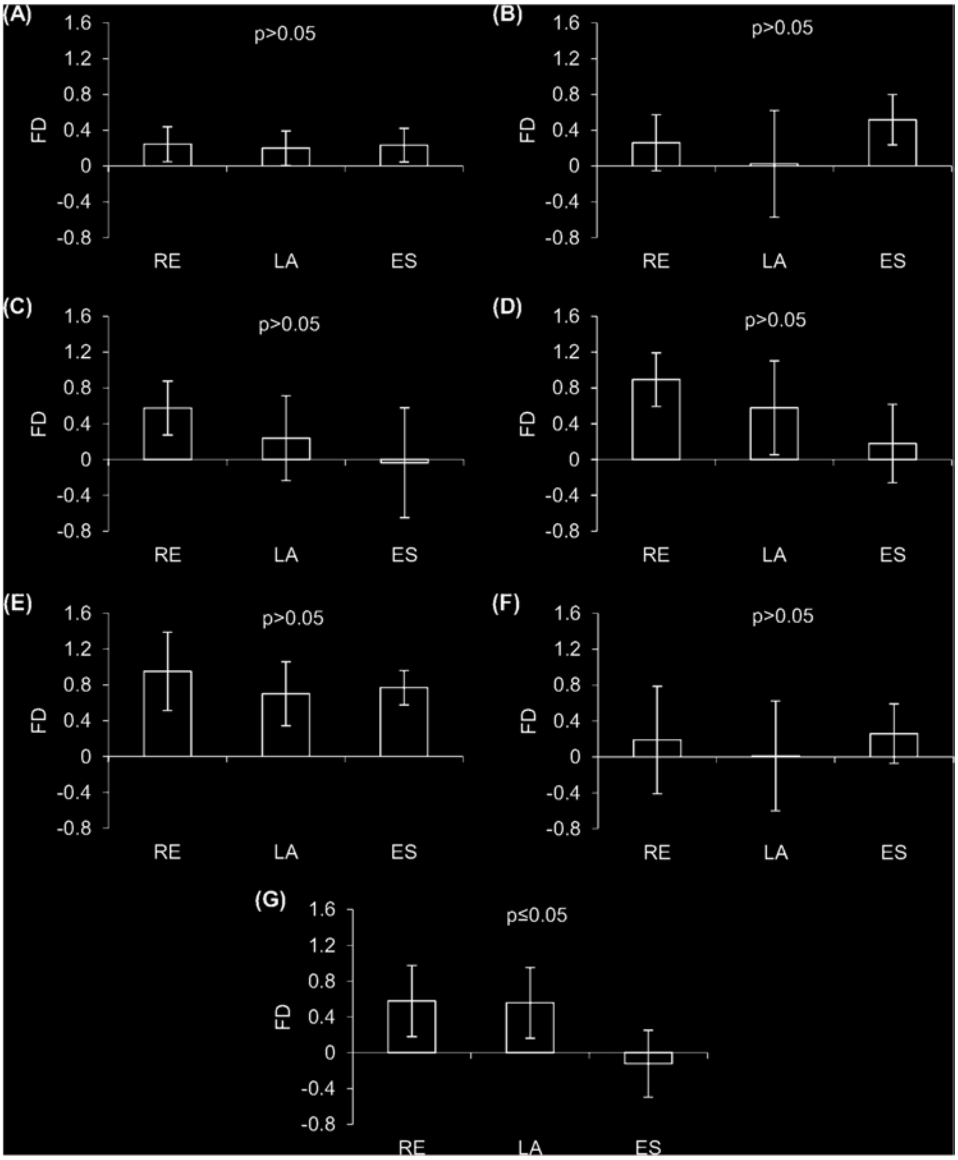

FIGURE 4 | Mean functional diversity by habitat (± standard deviation). **(A)** R$_1$ – qualitative data grouped from FishBase; **(B)** R$_2$ – qualitative data grouped by food item; **(C)** R$_3$ – qualitative food items data ungrouped; **(D)** R$_4$ – quantitative data from Feeding Index Categorized; **(E)** Morpho – morphological trait; **(F)** Phylo – topology of species phylogeny; **(G)** R$_{max}$ – quantitative data from Feeding Index (FI$_i$). FD: functional diversity index; RE: reef; LA: lagoon, and ES: estuary.

Resolutions that used data obtained from gut content analysis were all positively correlated with the maximum resolution (Rmax), with the degree of correlation increasing as more detailed information of diet were included. Many studies have acknowledged that detailed information about traits are the best choice for analyzing ecological processes and understanding ecosystem functioning (Violle et al., 2007). In fact, these "hard traits" – direct information of a particular function – are known for their highly explicative power as they take in consideration variability in many aspects of species' biology (Lavorel and Garnier, 2002), providing a better picture of the niche occupied by species (Herbert et al., 1999). For example, although species grouping in trophic guilds based on qualitative analysis of diet (R2) was correlated to the highest resolution (Rmax), this relationship was not strong (**Figure 3**), indicating that the information loss that occurs during the clustering process masks the fine-scale aspects of resource use. This is particularly problematic as new studies have shown that even redundant species may differ in the way they perform a particular function (Elmqvist et al., 2003; Nyström, 2006; Cariveau et al., 2013; da Silva and Fabré, 2019), which makes necessary the use of more detailed data to accurately assess ecological information.

Our results also suggest that both phylogeny and morphology are a poor proxy of resource partitioning among coastal marine fishes in the tropics (**Figure 3**). No relationship between morphological traits (S1) with the maximum resolution (Rmax) was found in our study, indicating that fish species with similar morphological patterns do not necessarily use the same food items available in ecosystems. Although widely used in functional ecology, many authors have addressed some important issues in relation to the use of morphology in predicting functions related to the use of resources by species, possibly due to the generalist prey selection of species as well as their high plasticity in feeding behavior (Pouilly et al., 2003; Ibañez et al., 2007; Reecht et al., 2013; Teresa and Casatti, 2017). The core challenge is that most morpho-anatomical traits are only capable of discriminate groups without assessing fine-scale aspects of fish ecology (Albouy et al., 2011), thus expressing only the potential or fundamental niche of species. This happens, in part, because species that present similar body structures may have different mechanisms for food acquisition and consumption (Konow and Bellwood, 2011), resulting in a weak relationship between body shape and the actual diet of species, as shown in our results.

The absence of correlation between the trait-phylogeny matrix with Rmax found in our study may be associated to many factors, including local environmental conditions. Even though phylogenetically related species are expected to be more similar in their functional role, trait variability may occur due to pressures from ecological divergence. For instance, in tropical areas, the high competition for resources and diet partitioning may cause trait divergence, regardless of morphology and phylogeny (Vitt and Pianka, 2005; Grime, 2006; Cadotte et al., 2013). Furthermore, the availability of preys may cause high trophic plasticity as an adaptation to current conditions, leading trait variation in the ecological time but not in the evolutionary history (Vitt and Pianka, 2005). For this reason, some studies involving phylogenetic structure and trait analysis have not been able to detect covariation (Gibb et al., 2015).

Trait Resolution and Its Impact on Functional Analysis

Our results also showed that different measures of resource partitioning may provide distinct patterns in observed functional diversity of fish assemblages. More precisely, when functional diversity between studied habitats was tested, only the direct measure of resource partitioning (expressed through the maximum diet resolution) was able to identify significant differences among habitats (**Figure 4**). These different patterns in the observed functional structure of assemblages found herein may result from the level of detailing considered in the measurement of the partitioning process. Although expensive and a research-intensive alternative, detailed information on resource use provides more reliable niche dimensions, allowing the comprehension of niche-based processes that drive assemblages' structure (Gonçalves-Souza et al., 2014; Passos et al., 2016). Moreover, hard traits, such as diet composition, have been shown as good predictors of the ecological performance of species, showing fine-scale aspects of habitat selection, physiological response to environmental conditions and shifts in behavior (Violle et al., 2007; Lozanovska et al., 2018).

AUTHOR CONTRIBUTIONS

VdS wrote the manuscript and helped with functional analysis. LS-F helped with gut content analysis and wrote the manuscript. FT helped with phylogenetic analysis and the planning of our manuscript. NF organized the project and wrote the manuscript. RL and VB supported manuscript preparation.

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SUPPLEMENTARY MATERIAL

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TABLE S1 | Trait-species matrices created to express resource partitioning among sampled fish species. Each matrix represents a different resolution (R_1 – Qualitative data grouped in guild from FishBase source; R_2 – Qualitative data grouped in guild from similar food item; R_3 - Qualitative food items data ungrouped in guild; R_4 – Quantitative data from Feeding Index Categorized (FI_iC); R_{max} – Quantitative data from FIi not categorized; S1 – ecomorphological trait).

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frontiers in Marine Science

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Connectivity Between Coastal and Oceanic Zooplankton From Rio Grande do Norte in the Tropical Western Atlantic

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The zooplankton off the coast of Rio Grande do Norte, Brazil was studied during four oceanographic campaigns from July 2002 to May 2004. A Bongo net (mesh sizes of 64, 120, and 300 μm) was used for sample collections. A total of 462 zooplankton samples was studied. These samples were classified in four areas (Coastal, Inner Shelf, Shelf Break, Slope) according to local depth and distance from coast. Most of the studied environment is oligotrophic, under the Tropical Water mass influence. We recorded 199 zooplankton taxa, and Copepoda was the most numerous with the highest number of species. There were 93 species of copepods, of which calanoids comprised 62%. The most frequent zooplankton taxa were *Undinula vulgaris*, *Nannocalanus minor*, *Oithona nana, Onychocorycaeus giesbrechti,* Crustacea nauplius, Bivalvia, and Gastropoda veligers. The species diversity varied from 0.87±0.28 bits·ind^{-1} (Coastal) to 3.96±0.12 bits·ind^{-1} (Slope). The minimum density was 11.5 ind·m^{-3} (macrozooplankton, Inner Shelf), and the maximum density was 161.6 × 10^{6} ind·m^{-3} (microzooplankton, Coastal). The biomass decreased sharply between the microzooplankton to macrozooplankton fractions. The community presented a general trend in species composition that included coastal eutrophic indicators and oceanic oligotrophic indicators, with low numerical abundance of zooplanktonic organisms. A higher density occurs in the coastal area that is near the littoral area due to the continental flux and benthic regeneration. The seasonal effect was also highlighted as an important factor responsible for the dissimilarity of zooplankton communities. Cluster analysis of the samples based on Copepoda presented differences among the four campaigns corresponding to the rainy and dry seasons. The copepod's functional traits divided the community into three groups, and

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the reproduction and the trophic strategies were the main factors in structuring the community. We found a pelagic gradient for the zooplankton community varying from a low diverse eutrophic coastal area to a high diverse oligotrophic oceanic area, located over a varied, high biomass benthic habitat, which is mostly covered by calcareous algae functioning on the shallow shelf as a large reef system.

Keywords: zooplankton, Copepoda, connectivity, functional traits, Southwestern Atlantic

INTRODUCTION

Studies on community ecology have emphasized the local processes influencing species composition and abundance. However, the effects of regional processes upon local dynamics have been shown by some researchers (Ricklefs and Schluter, 1993; Hubbell, 1997; Forbes and Chase, 2002), including those processes that connect communities. Physic-chemical processes can play an important role in the connectivity among habitats and in defining the community attributes at different size scales (Ricklefs, 1987; Cowen et al., 2006). For example, dispersal by currents in marine areas connects coastal communities to oceanic ones and *vice-versa,* thus forming species patches along interconnected environs (metacommunities) (Watson et al., 2011; Niebuhr et al., 2015).

Coastal ecosystems are of great human interest (both ecological and socioeconomic); in these ecosystems, biotic and abiotic factors vary continuously along scales that oscillate from short to long term (Walsh, 1988). In Northeastern Brazil, an arid clime, extensive beaches and high dunes characterize the littoral area in the northern region of the Rio Grande do Norte State. The continental shelf is approximately 30 km wide, and calcareous algae primarily cover the bottom; this represents the largest area covered by limestone sediments on the planet (Santos, 2010). This shelf functions as a huge "coral reef" that supports a high benthic diversity and biological production. The oligotrophic South Equatorial Current (SEC) dominates the pelagic inner shelf waters (Stramma et al., 1990); thus, like that of a coral reef area, the plankton productivity is very low, but it eventually increases due localized enrichment events (Medeiros et al., 1999). In this "coral reef"-like area, regenerated production dominates (fueled by nutrients accumulated in the benthic realm biologically recycled). The continental slope starts at a depth of 80 m and extends until 1300–3600 m (Mabesoone and Coutinho, 1970; Gomes and Vital, 2010); further, the sea floor is far beneath the photic zone, so the influence of regenerating production can be ignored when budgeting for flow in the offshore oceanic pelagic ecosystem.

This variable scenario highly influences the lively populations flourishing in the littoral area, which can cause a misunderstanding of the annual biodiversity and abundance patterns. A cooperative research program was established between the Federal University of Pernambuco (Brazil) and the Brazilian Oil Company (PETROBRAS) to develop comprehensive biotic and abiotic characterizations of the north coast of Rio Grande do Norte State and to study the plankton community; this work took place from July 2002 to May 2004. In coastal ecosystems where local processes are linked to anthropogenic impacts the biological community are threatened and can present large-scale changes (Guichard et al., 2004).

Plankton studies in this area are scarce. In relation to the zooplankton, previous investigations of tropical Southwestern Atlantic (SWA) were restricted to certain groups (Copepoda: Björnberg, 1963; Chaetognatha: Gusmão, 1986; Cnidaria: Gusmão et al., 2015) or to a few samples evaluated on a macro-scale level that were obtained by international expeditions. A zooplankton atlas (Boltovskoy, 1981, 1999) is an important reference of the SWA; however, data from the Rio Grande do Norte littoral area and the connectivity among habitats remains fragmented (e.g., Neumann-Leitão et al., 1999, 2008), and the main functional groups are still incipient (Campos et al., 2017; Neumann-Leitão et al., 2018).

Elucidation of the biotic community is important, particularly the zooplankton, and involves sampling methods capable of obtaining a representative population; as marine zooplankton comprise different size classes of organisms, they serve as a pivotal group in the transference of mass and energy from primary producers to higher trophic levels in the food web (Clark et al., 2001). The size of the zooplankton animals and their main functional traits are powerful forcing factors outlining marine systems. Also, few researches have been devoted to the comparison of the spatial-temporal variableness of micro-, meso- and macrozooplankton densities in marine systems (Smeti et al., 2015).

Thus, the goal of the present study was to produce accurate and complete information on micro-, meso-, and macrozooplankton diversity, biomass, and density distribution in different seasons along a coastal-oceanic gradient.

MATERIALS AND METHODS

Study Area

The continental shelf at the North of Rio Grande do Norte State (**Figure 1**) is divided in three sedimentary environments: the first (coastal and inner shelf) is characterized by siliciclastic sediments and huge longitudinal sandbanks with a depth around 15 m. The second (mid shelf) has a mixture of siliciclastic and carbonate sediments, and transversal sandbanks approximately on 20 m. The third (outer shelf) dominated by carbonates sediments, with a narrow shelf and depths varying from 25 to 50 m. A beachrock line at the isobath of 25 m delimits the boundary from mid- and outer shelf. The shelf extends seawards into a steep slope that spreads until 2000 m at the basin plain (Gomes and Vital, 2010). This basin has a high economic status because of the daily

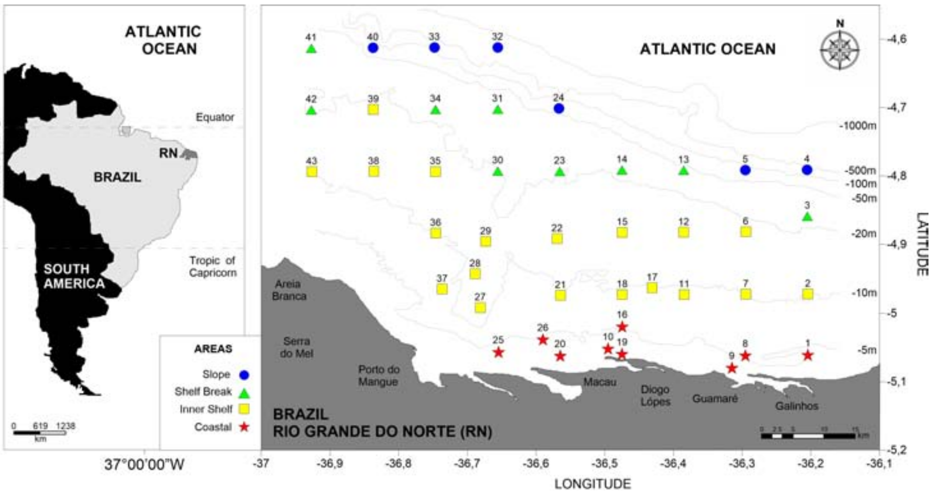

FIGURE 1 | Study area and stations located at the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic.

production of 80 thousand barrels of oil and 3 million·m^3 of gas (2003 data, production on ocean and earth), and it is the second most productive oil basin offshore in Brazil (Soares et al., 2003).

The average monthly total rainfall of North of Rio Grande do Norte (data from 1962 to 2005[1]) presents an annual average of 735.6 mm, with a higher rainfall from February to May, and a lower precipitation from September to November. The monthly average from 2001 to 2004 shows a warmer rainy season (January to May), and a dry season a bit cooler (July to November) (**Figure 2**)[1].

In the studied area the Tropical Water (TW: $\geq$ 20°C, $\geq$36.0) was present with relatively warm and salty waters, occurring from surface down to 70 m depth, and the South Atlantic Central Water (SACW: $\leq$18°C, $\leq$36.0) occurred below the TW and extended down to nearly 450 m. At depths between 70 and 150 m, there was also the Maximum Salinity Water (MSW), with temperatures varying from 18.0 to 26.0°C and salinity $\geq$37.0 (Schott et al., 1998).

The sea surface temperature average was 27.17 ± 0.7°C and ranged from 27.11°C (dry season, Slope) to 28.41°C (rainy season, Coastal). Salinity average was 36.2 ± 0.27, with a minimum of 35.90 (rainy season, Slope) and a maximum of 36.77 (dry season, Inner Shelf). Chlorophyll-*a* average was 0.52 ± 0.33 mg·m^{-3}, fluctuating from 0.23 mg·m^{-3} (dry season, Slope) to 1.13 mg·m^{-3} (dry season, Coastal) (**Figure 3**, PETROBRAS, 2005).

Sampling Strategy

The survey was performed during four campaigns from July 21 to 30, 2002 (Campaign 1, dry season), May 12 to 30, 2003 (Campaign 2, rainy season), November 14 to 23, 2003 (Campaign 3, dry season), and May 17 to 31, 2004 (Campaign 4, rainy season). The zooplankton was sampled during daytime at 43 stations, along nine transects from the coast to the offshore north of Rio Grande do Norte (latitude 4° to 5° S, longitude 36° to 37° W) (**Figure 1**). A total of 462 samples was collected; these samples were classified into four areas (Coastal: < 10 m, Inner Shelf: 10–20 m, Shelf Break: 20–50 m, and Slope: >50 m) according to local depth and distance from coast.

Field Sampling and Laboratory Analyses

The zooplankton sampling was carried out by bongo net hauls. The analyzed nets had the following mesh sizes and diameters: 64 μm/30 cm; 120 μm/30 cm; and 300 μm/60 cm. The terminology micro-, meso-, and macrozooplankton will be used throughout the text to refer to the net's mesh sizes, which were 64, 120, and 300 μm, respectively (although in the literature these sizes corresponded to micro- and mesozooplankton, see Omori and Ikeda, 1984). Oblique hauls were made at a speed of 2 to 2.5 knots from a depth of 14 m (nearshore) and 150 m (Shelf Break and Slope) to the surface. A flowmeter (Hydrobios, Kiel, Germany) was used to measure the water filtered volume. A 4% buffered formalin-seawater solution was used to preserve the samples. Seston biomass (mg·m^{-3}) was assessed by using the Omori and Ikeda (1984) wet-weight method. To identify the species, we used the Trégouboff and Rose (1957) and Boltovskoy (1981, 1999) manuals, among others. Taxa enumeration and identification considered the lowest taxonomic unit of each phylum. Taxon density was calculated from subsamples of 1 mL (for microzooplankton using a Sedgwick-Rafter chamber) and 8 mL (meso- and macrozooplankton using a Bogorov plate) taken of the whole sample (standardized to 500 mL). For each sample, three subsamples (with at least of 300 individuals) were counted and the mean calculated for abundance valuation (ind·m^{-3}).

Data Analysis

The Shannon diversity index H' was applied to Copepoda for the diversity evaluation (Shannon, 1948), as this was the most diverse

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[1] http://www.inmet.gov.br

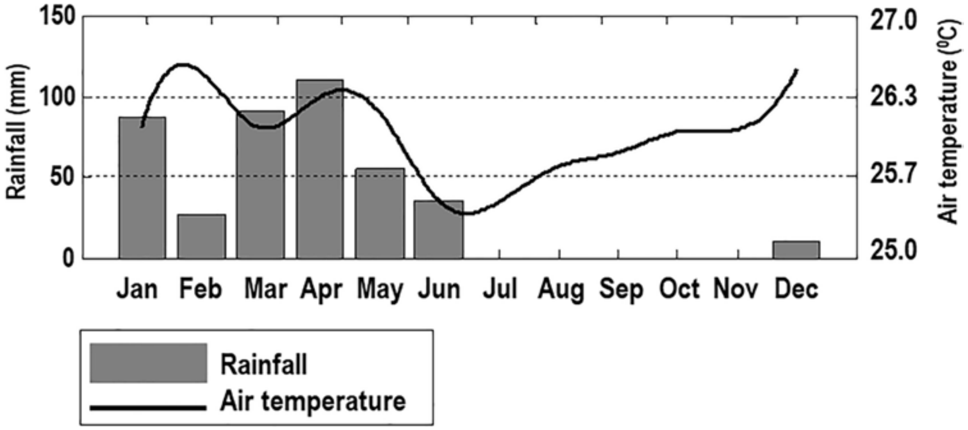

FIGURE 2 | Rainfall and air temperature from 2001 to 2004 at the coastal area of Rio Grande do Norte, Southwestern Atlantic (Source: http://www.inmet.gov.br).

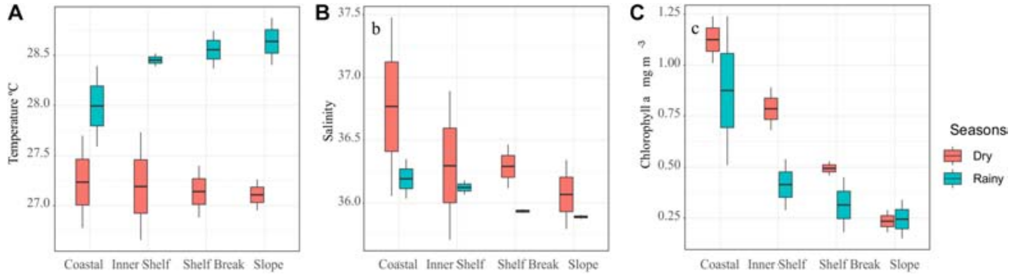

FIGURE 3 | Box-plot of the temperature **(A)**, salinity **(B)**, and chlorophyll-*a* **(C)** at the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic (Source: Petrobras, Bacia Potiguar-RN 2005).

taxon and the most identified species. Evenness was calculated according to Pielou (1977).

To investigate for trends in spatial distribution, total density ($\log_{10}$ transformed), biomass and ecological indexes (diversity and evenness) of the micro-, meso- and macrozooplankton were compared among the coastal, inner shelf, shelf break and slope areas during both dry and rainy season. As even after data transformation, the assumptions of the ANOVA model could not be satisfied for total density and evenness, we applied Kruskal–Wallis tests to compare zooplankton total density and evenness among the areas in both seasons. When significant *p* values were found, the Dunn's Multiple Comparison test was applied. Diversity was compared by means of two-way ANOVA models, after checking the validity of the assumptions of normality in distribution of the errors and homoscedasticity by means of the Shapiro-Wilk and Bartlett tests, respectively.

A Permutational multivariate analysis of variance (PERMANOVA) was used to test the micro-, meso- and macrozooplankton community structure changes in response to the factors area, season, and to investigate possible interactions among these two factors. The calculation of pseudo-*F* and *p* values was based on 999 random permutations. *Pairwise* test between different levels of significant factor(s) was performed in case of significant differences identified by the PERMANOVA. The non-metric multi-dimensional scaling (MDS) was used to represent the data in a bi-dimensional space. The PERMANOVA and the nMDS were performed with basis on a Bray–Curtis dissimilarity matrix constructed on the log $(X + 1)$ transformed abundance of species with relative abundance $>2\%$. The SIMPER (SIMilarity of PERcentages) routine was used to identify the taxa that contributed most to the Bray–Curtis dissimilarity of areas within the identified seasons. The SIMPER test was set at $\geq 50\%$ cumulative contribution.

A Redundancy Analysis (RDA) was applied to identify whether there were different size communities that could be explained by the temporal and spatial data variability. We used the total micro-, meso-, and macrozooplankton abundance and biomass data. Zooplankton groups were log $(X + 1)$ transformed and compared with an abiotic factor matrix (Temperature, Salinity, Chlorophyll *a*). The spatio-temporal factors (Coastal, Inner Shelf, Shelf Break, Slope, Dry season and Rainy season) were transformed into dummy variables, represented by 1 and 0. Non-significant variables ($p > 0.05$) were excluded from the matrix of environmental data in a step by step procedure, using Monte Carlo permutation tests with 9999 permutations to remove collinearities between variables (Ter Braak and Smilauer, 2002). The analyses were performed using the CANOCO software (version 4.5; Ter Braak and Smilauer, 2002). All analyses were conducted considering $p < 0.05$ (Zar, 1996).

Hierarchical cluster analyses in Q mode using Ward's method (Legendre and Legendre, 1998) were performed with basis on a Bray–Curtis dissimilarity matrix calculated using Copepoda density data. The goodness of fit of the data was assessed by means of the cophenetic correlation coefficient (Rohlf and Fisher, 1968).

The functional trait matrix of copepods was built using the available literature (mainly Boltovskoy, 1999 and Benedetti et al., 2016). We included seven traits with 23 trait categories: (1) Average adult female body length (0.5–1.5, 1.5–2.5, 2.5–3.5, 3.5–4.5, >4.5 mm); (2) Trophic group (herbivore, carnivore, omnivore, detritivore); (3) Feeding type (active ambush, passive ambush, filter, cruise, mixed); (4) Mode of reproduction (broadcast-spawner, sac-spawner); (5) Vertical distribution preference (epipelagic, mesopelagic, bathypelagic); (6) Diel vertical migration behavior (Yes, No); and (7) Habitat type (estuarine, neritic, oceanic). These traits are functionally important, as they relate to the life history and ecology of species and are expected to be constant through time and space (Pomerleau et al., 2015). The Sorensen index was applied to a presence/absence species-by-trait matrix, and the cluster dendrogram was formed through the average linkage method. The Calinski and Harabasz (1974) criteria were used to establish the number of functional groups. This analysis was applied only to Copepoda at the species level (see **Supplementary Table S1**).

RESULTS

Species Composition

We identified 199 taxa in the three zooplankton size fractions composed of Foraminifera, Ciliophora, Radiozoa, Cnidaria, Aschelminthes, Mollusca, Annelida, Arthropoda, Echinodermata, Chaetognatha, Bryozoa, Cephalochordata, and Chordata (**Tables 1**, **2**). A total of 88 taxa occurred in the microzooplankton fraction, 115 taxa in the mesozooplankton fraction, and 102 taxa in the macrozooplankton fraction. In the three fractions, 69 taxa cooccurred and consisted mostly of juveniles in the microzooplankton fraction and adults in the meso- and macrozooplankton fractions. Holoplankton comprised 87, 67, and 61% in the micro- meso-, and macrozooplankton fractions, respectively. Most zooplankton species (91) were oceanic indicators and were obtained mainly from the North Brazil Current. Several neritic taxa were larval stages of benthic organisms that normally occur in the continental shelf.

The most important group was Copepoda, both in richness and abundance. There were 93 copepod species, of which 62% were calanoids. In total, 54 species occurred in the microzooplankton fraction, 69 species in the mesozooplankton fraction, and 68 species in the macrozooplankton fraction. An important group found in the Coastal area was the estuarine plume indicators, which consisted of *Acartia (Odontacartia) lilljeborgi, Parvocalanus crassirostris, Oithona hebes, Oithona oswaldocruzi* and *Euterpina acutifrons*.

In the microzooplankton fraction, there was a high frequency of occurrence of Crustacea nauplius (94%), Bivalvia veliger (92%), Gastropoda veliger (82%), and *Oithona nana* (76%); furthermore, nearly 51% of the species occurred at frequencies of less than 10%. Tintinnina was observed only in the microzooplankton fraction with 18 species. The higher frequency of occurrence recorded in the mesozooplankton fraction were of Bivalvia larvae (90%), *O. nana*, and *Undinula vulgaris* (81%), as well as *Nannocalanus minor* (74%); nearly 50% of the taxa occurred at frequencies of less than 10%. In the macrozooplankton fraction, the most frequent group was composed of *Onychocorycaeus giesbrechti* (80%) and *U. vulgaris* (79%), and nearly 68% of the community occurred at a frequency of occurrence of less than 10%.

Total Density (ind·m^{-3})

At the dry season, the total microzooplankton density varied from 904 ind·m^{-3} (Slope, Campaign 3) to 161.6×10^6 ind·m^{-3} (Coastal, Campaign 1). At the rainy season, total microzooplankton densities ranged from 2,985 ind·m^{-3} (Inner Shelf, Campaign 2) to 34×10^5 ind·m^{-3} (Inner Shelf, Campaign 4). During both the dry and rainy seasons significant differences among the areas were found (Kruskal–Wallis, $p > 0.05$). During the dry season, the coastal area was different from all the other, and the inner shelf was different from the slope area (Dunn, $p < 0.05$). A decreasing pattern in total density was observed during this season. During the rainy season the coastal area was different from all other areas, presenting higher total density values, and no further differences were detected (Dunn, $p < 0.05$) (**Figure 4**).

The total mesozooplankton density varied from 275 ind·m^{-3} (Shelf Break, Campaign 1) to 39.2×10^4 ind·m^{-3} (Coastal, Campaign 1) during the dry season, and from 183 ind·m^{-3} (Inner shelf, Campaign 2) to 50.9×10^3 ind·m^{-3} (Coastal, Campaign 4) during the rainy season. During the rainy season no difference among the areas was found (Kruskal–Wallis, $p > 0.05$), but during the dry season a gradient in the distribution of the total density was detected in which the Coastal area presented densities significntly higher than all the other areas, and the Inner Shelf presented higher densities than the Shelf break and Slope (Dunn, $p < 0.05$). No difference between the Shelf break and Slope was detected (Dunn, $p > 0.05$) (**Figure 4**).

The total macrozooplankton density varied from 11.5 ind·m^{-3} (Inner shelf, Campaign 3) to 1,251 ind·m^{-3} (Coastal, Campaign 3) during the dry season, and from 14 ind·m^{-3} (Inner shelf, Campaign 4) to 613 ind·m^{-3} (Inner shelf, Campaign 4) during the rainy season. During the dry season no evidence for differences among the areas was detected (Kruskal–Wallis, $p > 0.05$). During the rainy season differences were detected (Kruskal–Wallis, $p < 0.05$), and the Slope area was different from all the other areas (Dunn, $p < 0.05$), with higher density values (**Figure 4**).

Total Copepoda density varied from 3 ind·m^{-3} (Inner Shelf, Campaign 3) to 480 ind·m^{-3} (Inner Shelf, Campaign 1) during the dry season, and from 4 ind·m^{-3} (Shelf Break, Campaign 2) to 582 ind·m^{-3} (Inner Shelf, Campaign 4) during the rainy season. The statistical results were the same as for the total macrozooplankton density, since Copepods constituted most of the organisms within the macrozooplankton size class.

TABLE 1 | List of zooplankton taxa (without Copepoda) from coastal and oceanic areas of Rio Grande do Norte, Northeastern Brazil.

- RADIOZOA
  - Spumellaria (others)
  - *Dictyocoryne profunda* Ehrenberg, 1872
  - *Rhopalastrum malleus* Haeckel, 1887
- FORAMINIFERA
  - *Globigerinoides rubra* (d'Orbigny, 1839)
  - *Trilobatus trilobus* (Reuss, 1850)
  - *Globigerinoides sacculifer* (Brady, 1879)
  - *Globigerinoides conglobatus* (Brady, 1879)
  - *Globigerinoides* sp.
  - *Globorotalia menardii* (Jones and Brady, 1865)
  - *Globorotalia* sp.
  - *Orbulina universa* d'Orbigny, 1839
  - *Tretomphalus bulloides* d'Orbigny, 1826
  - *Amphistegina* sp.*
  - *Triloculina* sp.*
  - *Textullaria* sp. *
  - *Quinqueloculina* sp *
  - *Remaneica* sp. *
  - *Spirillina* sp. *
  - *Planispirillina* sp.*
- CILIOPHORA
  - *Tintinnopsis radix* (Imhof, 1886)
  - *Tintinnopsis aperta* Brandt, 1906
  - *Tintinnopsis tocantinensis* Kofoid and Campbell, 1929
  - *Tintinnopsis nordqvisti* Brandt, 1906
  - *Tintinnopsis campanula* Ehrenberg, 1840
  - *Tintinnopsis* sp.
  - *Codonellopsis morchella* (Cleve, 1900)
  - *Codonellopsis* sp.
  - *Favella ehrenbergii* (Clapadere and Laachmann, 1858)
  - *Epiplocylis acuminata* (Daday, 1887)
  - *Epiplocylis* sp.
  - *Rhabdonella spiralis* (Fol, 1881)
  - *Rhabdonella* sp.
  - *Undella hyalina* Daday, 1887
  - *Undella claparedei (*Entz Sr., 1885)
  - *Eutintinnus lusus-undae* (Entz Sr., 1885)
  - *Amphorellopsis* sp.
  - *Xystonellopsis* sp.
- CNIDARIA
  - Hydrozoa
  - *Zanclea costata* Gegenbaur, 1856
  - *Liriope tetraphylla* (Chamisso and Eysenhardt, 1821)
  - *Aglaura hemistoma* Péron and Lesueur, 1809
  - *Bougainvillia* sp.
  - *Obelia* sp.
  - Siphonophora
  - *Lensia* sp.
  - *Bassia bassensis* (Quoy and Gaimard, 1834)
- NEMATODA (*Oncholaymus* sp.)
- MOLLUSCA
  - *Atlanta* sp.
  - *Limacina (Limacina) retroversa* (Fleming, 1823)
  - Gastropoda other (veliger/adult)
  - Bivalvia (veliger/juvenile)
  - Cephalopoda (paralarvae)
- POLYCHAETA
  - Alciopidae (larvae)
  - *Tomopteris* sp.
  - Polychaeta other larvae (different stages)
- CRUSTACEA
- Cladocera
  - *Penilia avirostris* Dana, 1849
  - *Pseudevadne tergestina* Claus, 1877
- Ostracoda
  - *Euconchoecia chierchiae* Muller, 1890
- Cirripedia
  - *Lepas* sp. (nauplius)
  - *Balanus balanoides* (Linnaeus, 1767) (nauplius and cypris)
- Stomatopoda (larvae erichthus and alima)
- Euphausiacea
  - *Euphasia* sp. (adults and furcilia, calyptopis)
- Cumacea
- Decapoda
  - *Belzebub typus* H. Milne-Edwards, 1837
  - *Belzebub faxoni* (Borradaile, 1915)
  - Luciferidae (larvae)
  - *Acetes americanus* Ortmann, 1893
  - Penaeidae (larvae)
  - Paguridae larvae (*Parapagurus* sp.)
  - Carideae (larvae)
  - Brachyura (zoeae and megalopa)
  - Palinuridae (phyllosoma)
- Porcellanideo (larvae)
- Mysida
- Isopoda (Epicaridea - larvae)
- Amphipoda
  - Gammaridea
  - Hyperiidae
- BRYOZOA (cyphonauta of *Membranipora* sp.)
- CHAETOGNATHA
  - *Ferrosagitta hispida* (Conant, 1895)
  - *Flaccisagitta enflata* (Grassi, 1881)
  - *Flaccisagitta hexaptera* (d´Orbigny, 1834)
  - *Serratosagitta serratodentata* (Krohn, 1853)
  - *Sagitta bipunctata* Quoy and Gaimard, 1827
  - *Parasagitta tenuis* (Conant, 1896)
  - *Pterosagitta draco* (Krohn, 1853)
  - *Krohnitta subtilis* (Grassi, 1881)
  - *Krohnitta pacifica* (Aida, 1897)
- ECHINODERMATA (pluteus, bipinaria, brachiolaria)
- ENTEROPNEUSTA (tornaria)
  - LARVACEA
  - *Oikopleura (Vexillaria) dioica* Fol, 1872
  - *Oikopleura (Coecaria) longicauda* (Vogt, 1854)
  - *Oikopleura* spp.
  - *Fritilaria* sp.

(Continued)

TABLE 1 | Continued

- *Limacina (Munthea) bulimoides* (d'Orbigny, 1836)
- *Limacina (Munthea) trochiformis* (d'Orbigny, 1836)
- *Heliconoides inflatus* (d'Orbigny, 1835)
- *Limacina* sp.
- *Cavolinia inflexa* (Lesueur, 1813)
- *Creseis clava* (Rang, 1828)
- *Creseis virgula* (Rang, 1828)
- *Creseis* sp.
- Gastropoda other (veliger/adult)

- THALIACEA
  - *Thalia democratica* (Forskal, 1775)
  - *Doliolum* sp.
- ASCIDIACEA (larvae)
- CEPHALOCHORDATHA
  - *Branchiostoma* sp. (larvae)
- VERTEBRATA
  - Teleostei (egg and larvae)

** = tychoplanktonic = benthic and other non-planktonic organisms that are carried into the plankton.*

Fish eggs varied from 0 (several samples) to 53 eggs·m^{-3} (Coastal, Campaign 1) during the dry season, and from 0 (several samples) to 13 larvae·m^{-3} (Inner Shelf, Campaign 4) during the rainy season. During the dry season, a decreasing pattern in total density of fish eggs m^{-3} was detected (Kruskal–Wallis, $p < 0.05$), with higher values at the coastal area, and lower values at the slope (Dunn, $p < 0.05$). No evidence for differences in fish larvae total density was detected across the areas during the dry season (Kruskal–Wallis, $p > 0.05$). During the rainy season, no difference in fish eggs density m^{-3} was observed (Kruskal–Wallis, $p > 0.05$). However, fish larvae density m^{-3} was higher at the Slope when compared to all other areas (Dunn, $p < 0.05$).

Copepods Diversity

The Shannon diversity index for copepods ranged from 0.155 bits·ind^{-1} (Coastal, Rainy season, macrozooplankton) to 4.12 bits·ind^{-1} (Shelf break, Dry season, mesozooplankton) (**Figure 4**). Although an increasing trend from coastal to offshore stations in Copepoda diversity was observed, this pattern was not statistically confirmed, nor any interaction effect among seasons and spatial areas was detected (two-way ANOVA, $p > 0.05$). The minimum evenness was 0.064 (Slope, Rainy season, macrozooplankton), and the maximum evenness was 0.953 (Inner shelf, Rainy season, mesozooplankton) (**Figure 4**). No spatial gradient was detected on evenness in any season (Kruskal–Wallis test, $p > 0.05$).

Seston Biomass (mg·m^{-3})

The total seston biomass decreased sharply from the microzooplankton to macrozooplankton fractions (**Figure 5**). Mesozooplankton biomass was significantly lower than the microzooplankton biomass (Kruskal–Wallis, $p < 0.05$), with values lower than 300 mg·m^{-3}. This pattern occurred during all campaigns, except in Campaign 2, when the macrozooplankton fraction had a higher biomass than the mesozooplankton. The biomass spatial distribution pattern varied over time, which demonstrated the importance of collecting different size classes of zooplankton. In all campaigns, microzooplankton biomass peaks were registered near coastal areas, and significant differences (Kruskal–Wallis, $p < 0.05$) were found between the Coastal and other areas. Higher macrozooplankton biomass occurred at the stations over the slope; however, the biomass was low in comparison to other fractions.

The minimum and maximum values of seston biomass for the microzooplankton community occurred in the campaign 1, varying from 16.35 mg·m^{-3} in the Shelf Break to 34,798.30 mg·m^{-3} in the Coastal region. The minimum recorded for the mesozooplankton community occurred in the Slope in the campaign 3 (18.67 mg·m^{-3}) and the maximum (17,285.5 mg·m^{-3}) in the Shelf Break in the campaign 4. The minimum and maximum biomass for the macrozooplankton community varied between 0.06 mg·m^{-3} in the Inner Shelf (Campaign 3) to 2434 mg·m^{-3} in the Slope in the campaign 2.

The spatial effect over the seston biomass of the microzooplankton community was verified in both sampled seasons (ANOVA Kruskal–Wallis, $p < 0.05$) (**Figure 5**). A decreasing trend from Coastal to Slope occurred for the microzooplankton in the dry season (**Figure 5**). From the *post hoc* test we found that the average biomass recorded during the dry season in the Coastal region (4666.9 ± 9498.9 mg·m^{-3}) was significantly higher than those recorded in the Inner Shelf (347.3 ± 776.9 mg·m^{-3}), Shelf Break (121.2 ± 98.8 mg·m^{-3}) and Slope (92.9 ± 68.4 mg·m^{-3}) (Dunn, $p < 0.05$). In the rainy season, the same pattern was observed. The coastal region (2929.5 ± 3274.5 mg·m^{-3}) recorded a significantly higher biomass than the Inner Shelf (617.1 ± 938.5 mg·m^{-3}), Shelf Break (728.2 ± 898.7 mg·m^{-3}) and the Slope (560 ± 695.2 mg·m^{-3}) (Dunn, $p < 0.05$).

The seston biomass of mesozooplankton differed among the marine areas only during the dry season (ANOVA Kruskal–Wallis, $p < 0.05$) (**Figure 5**). The Coastal area presented a biomass of 871.5 ± 1,734.6 mg·m^{-3} and this value was significantly higher than the Inner Shelf (84.3 ± 55.4 mg·m^{-3}), Shelf Break (63.3 ± 42.1 mg·m^{-3}) and Slope (67.2 ± 41.6 mg·m^{-3}) (Dunn, $p < 0.05$). During the rainy season the average values were 637.3 ± 456.6 mg·m^{-3}, 464.8 ± 728.6 mg·m^{-3}, 1,221.2 ± 3,813 mg·m^{-3} and 407 ± 411.4 mg·m^{-3}, respectively recorded to the Coastal, Inner Shelf, Shelf Break and Slope areas.

The seston biomass of the macrozooplankton community differed significantly only in the rainy season (ANOVA Kruskal–Wallis, $p < 0.05$) (**Figure 5**). During this season, an increase in biomass toward the Slope was recorded (**Figure 5**), with values in the Coastal (28.6 ± 33.3 mg·m^{-3}) significantly lower than that

TABLE 2 | List of Copepoda species from coastal and oceanic areas of Rio Grande do Norte, Northeastern Brazil.

Nannocalanus minor (Claus, 1863)^{O}
Nannocalanus sp.
Neocalanus robustior (Giesbrecht, 1888)^{O}
Undinula vulgaris (Dana, 1849)^{N}
Subeucalanus pileatus (Giesbrecht, 1888)^{O}
Subeucalanus sp.
Rhincalanus cornutus (Dana, 1849)^{O}
Paracalanus aculeatus Giesbrecht, 1888^{O}
Paracalanus quasimodo Bowman, 1971^{N}
Paracalanus indicus Wolfenden, 1905^{N}
Paracalanus spp.
Parvocalanus crassirostris (Dahl, 1894) ^{N}
Acrocalanus longicornis Giesbrecht, 1888^{O}
Acrocalanus sp.
Calocalanus pavo (Dana, 1849)^{O}
Calocalanus pavoninus Farran, 1936^{O}
Delibus sewelli (Björnberg T.K.S., 1982)^{O}
Mecynocera clausi Thompson, 1888^{O}
Clausocalanus furcatus (Brady, 1883)^{O}
Clausocalanus sp.
Ctenocalanus sp.
Euchaeta marina (Prestandrea, 1833)^{O}
Euchaeta pubera Sars, 1907 ^{O}
Phaenna spinifera Claus, 1863^{O}
Scolecithrix bradyi Giesbrecht, 1888^{O}
Scolecithrix danae (Lubbock, 1856)^{O}
Scolecithrix sp.
Haloptilus acutifrons (Giesbrecht, 1892)^{O}
Temora stylifera (Dana, 1849)^{ON}
Temora turbinata (Dana, 1849)^{ON}
Temora sp.
Pleuromamma xiphias (Giesbrecht, 1889)^{O}
Pleuromamma sp.
Centropages violaceus (Claus, 1863)^{O}
Centropages gracilis (Dana, 1849)^{ON}
Centropages velificatus (Dana, 1849)^{ON}
Pseudodiaptomus acutus (F. Dahl, 1894)^{E}
Pseudodiaptomus richardi (F. Dahl, 1894)^{E}
Lucicutia flavicornis (Claus, 1863)^{O}
Lucicutia sp.
Metridia princeps Giesbrecht, 1889^{O}
Candacia pachydactyla (Dana, 1848)^{O}
Candacia cheirura (Cleve, 1904) ^{O}
Candacia varicans (Giesbrecht, 1892)^{O}
Candacia sp.
Pontella atlantica (Milne-Edwards, 1840)^{O}
Pontella securifer Brady, 1883^{O}
Labidocera acutifrons (Dana, 1849)^{O}
Labidocera fluviatilis F. Dahl, 1894^{N}
Labidocera nerii (Kroyer, 1849)^{O}
Labidocera sp.
Pontellina plumata (Dana, 1849)^{O}
Pontellopsis sp.
Calanopia americana F. Dahl, 1894^{N}
Acartia (Odontacartia) lilljeborgi Giesbrecht, 1889^{NE}
Acartia (Acartia) danae Giesbrecht, 1889^{O}
Acartia sp.
Oithona atlantica Farran, 1908^{O}
Oithona nana Giesbrecht, 1892^{NE}
Oithona plumifera Baird, 1843^{ON}
Oithona setigera (Dana, 1849)^{ON}
Oithona hebes Giesbrecht, 1881^{NE}
Oithona oswaldocruzi Oliveira, 1945^{NE}
Oithona sp.
Oncaea media Giesbrecht, 1891^{O}
Oncaea venusta Philippi, 1843^{ON}
Oncaea sp.
Lubbockia aculeata Giesbrecht, 1891^{O}
Sapphirina nigromaculata Claus, 1863^{O}
Sapphirina angusta Dana, 1849^{O}
Sapphirina sp.
Copilia mirabilis Dana, 1849^{O}
Copilia quadrata Dana, 1849^{O}
Copilia sp.
Agetus limbatus (Brady, 1883) ^{O}
Corycaeus clausi F. Dahl, 1894 ^{O}
Corycaeus speciosus Dana, 1849 ^{O}
Ditrichocorycaeus amazonicus (F. Dahl, 1894)^{N}
Onychocorycaeus giesbrechti (F. Dahl, 1894)^{O}
Onychocorycaeus latus (Dana, 1849)^{O}
Corycaeus sp.
Farranulla gracilis (Dana, 1849)^{O}
Farranulla rostrata (Claus, 1863)^{O}
Farranula sp.
Microsetella rosea (Dana, 1847)^{O}
Microsetella norvegica (Boeck, 1864)^{ON}
Miracia efferata Dana, 1849^{O}
Macrosetella gracilis (Dana, 1847)^{O}
Euterpina acutifrons Dana, 1847^{O}
Hemicyclops thalassius Vervoort and Ramirez, 1966^{N}
Tigriopus sp.*
Caligus sp.^{P}
Longipedia sp.^{P}

*O – oceanic, N – neritic and E – estuarine (according to Björnberg, 1963, 1981; Bradford-Grieve et al., 1999), * – tychoplanktonic, P – parasite.*

observed in the Inner Shelf (259.1 ± 242.7 mg·m^{-3}), Shelf Break (307.1 ± 242.8 mg·m^{-3}) and Slope (876.8 ± 745.7 mg·m^{-3}) (Dunn, $p < 0.05$). For the dry season, the averages recorded in the Coastal, Inner Shelf, Shelf Break and Slope areas were, respectively 37.6 ± 42.5 mg·m^{-3}, 42.6 ± 40.6 mg·m^{-3}, 59.1 ± 55.2 mg·m^{-3} and 46 ± 46 mg·m^{-3}.

Zooplankton Community Structure

The nMDS analyses indicated differences in the structure of micro- (**Figure 6A**), meso- (**Figure 6B**) and macrozooplankton (**Figure 6C**) community between areas, as well as marked differences among the seasonal periods sampled (**Figures 6D–F**). The micro-, meso- and macrozooplankton community

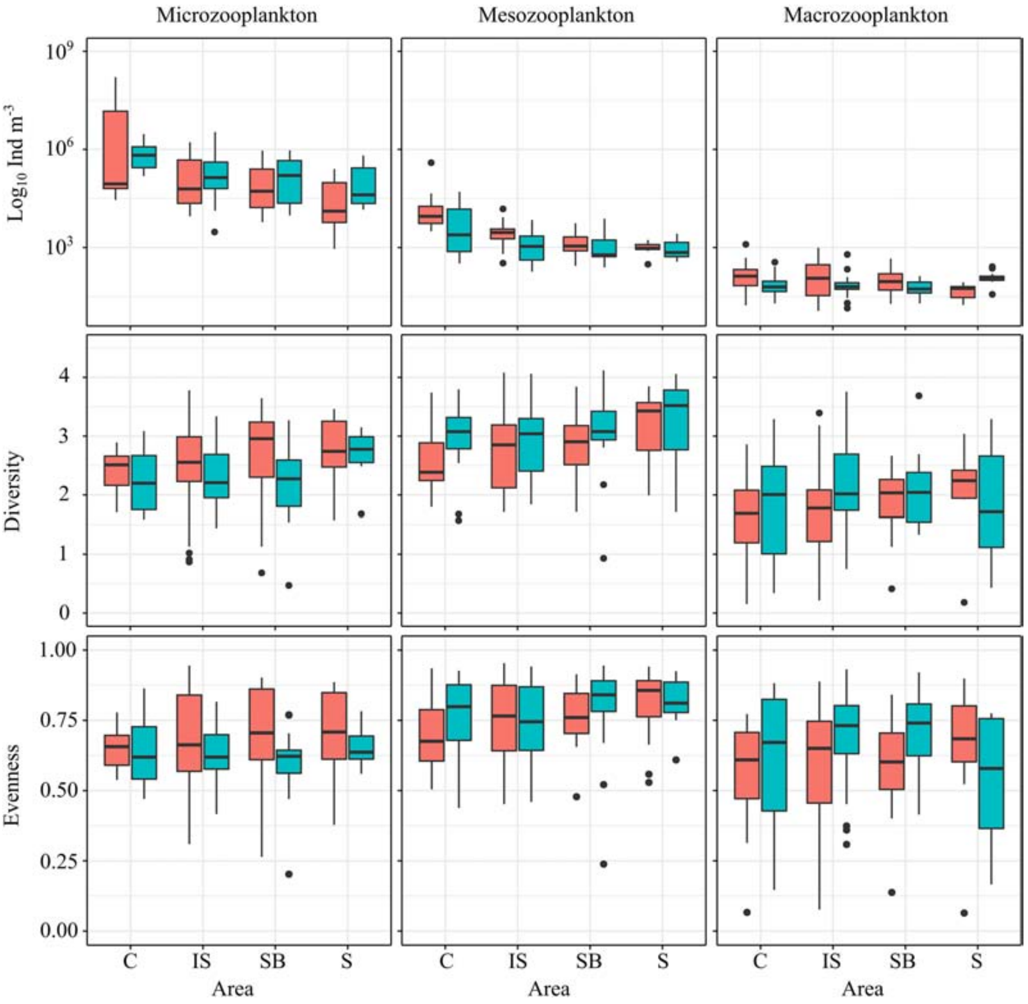

FIGURE 4 | Box-plot of zooplankton density, diversity and evenness at the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic. Dots = outliers.

differences across a coastal-oceanic gradient was verified through the PERMANOVA test (**Table 3**). The seasonal effect was also highlighted as an important factor responsible for the dissimilarity of zooplankton investigated communities (**Table 3**). We recorded a significant interaction between the tested factors (area and season) only for the macrozooplankton community (**Table 3C**).

Results of *pairwise t* tests indicate that the coastal area differs from the Inner Shelf, Shelf Break and Slope in terms of the taxonomic composition of micro-, meso- and macrozooplankton community (**Table 4**). However, the greatest difference was recorded between the coastal area and the slope for the micro- (**Table 4A**) and mesozooplankton (**Table 4B**). The significant interaction between the area and season for the macrozooplankton showed that in the dry season the greatest dissimilarity in the taxonomic composition occurred between the Coastal area and the Shelf Break (**Table 4C**), while in the rainy season occurred between Coastal area and the Slope (**Table 4D**).

The SIMPER analysis reinforced the greatest dissimilarity of the taxonomic composition of the microzooplankton occurring between the Coastal and the Slope areas (Average dissimilarity = 46.01), whose cumulative contribution of the taxa, *O. hebes*, *E. acutifrons*, *P. crassirostris*, *Oikopleura dioica*, *Oithona* (copepodite) and *Oithona* sp. corresponded to 51.86% of the dissimilarity (**Table 5A**). For the mesozooplankton the greatest dissimilarity (64.49) was also recorded between the Coastal area and the Slope (**Table 5B**). The taxa, *O. nana*, *N. minor*, *Temora turbinata*, *O. hebes*, *P. crassirostris* and *Clausocalanus furcatus* corresponded to 52.26% of the differences recorded between these areas (**Table 5B**).

For the macrozooplankton, the greatest dissimilarity (average dissimilarity = 75) of the taxonomic composition observed in the dry season between the coastal area and the Shelf Break occurred as a response of the highest contribution of the taxa, *T. turbinata*, *U. vulgaris*, *Lucifer* sp. (mysis), *Lucifer* sp. (protozoea), *Centropages furcatus*, *Oikopleura longicauda* and *Flaccisagitta enflata*. These showed a cumulative contribution of 50.94%.

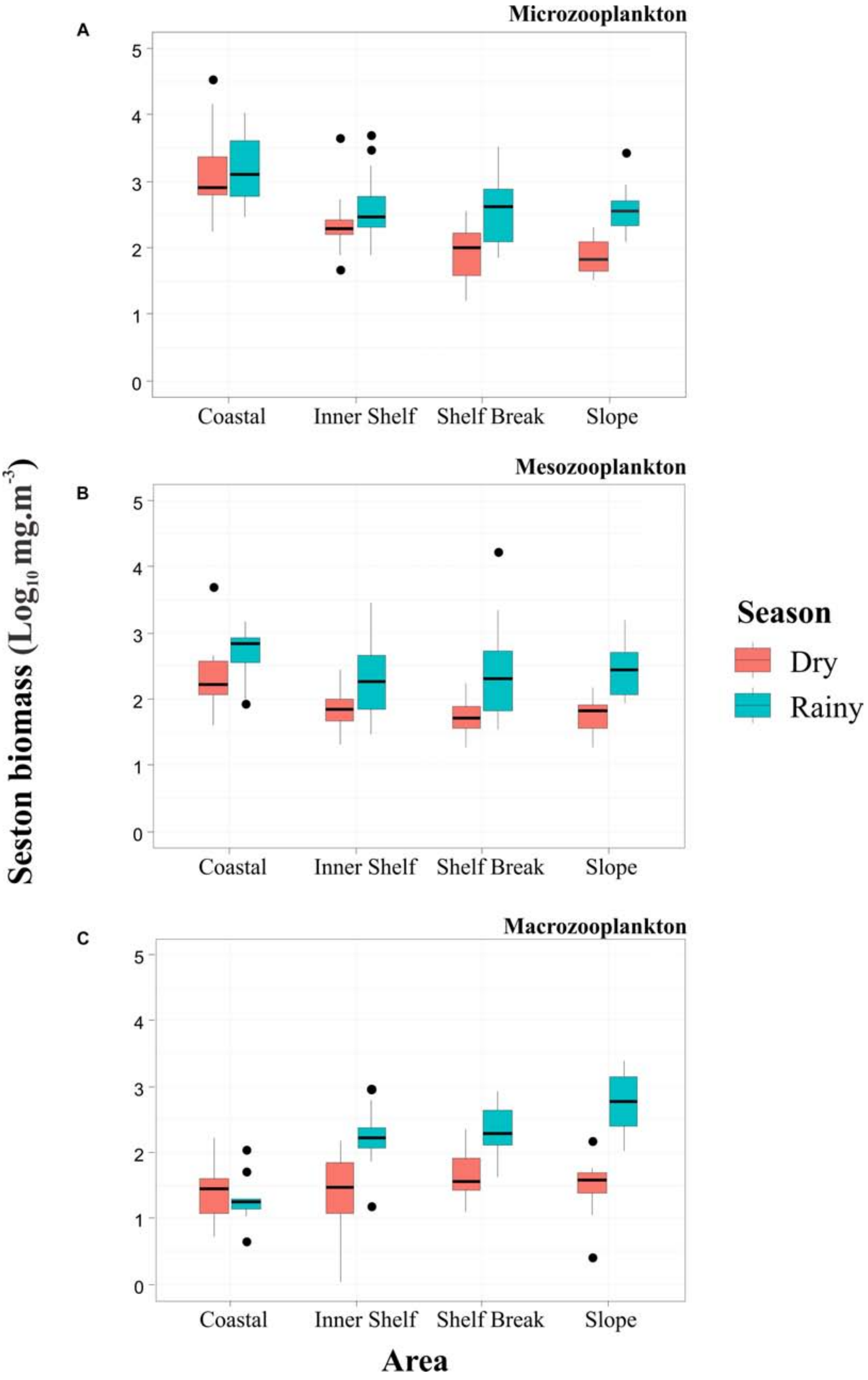

FIGURE 5 | Box-plot of seston biomass (Log_{10} mg·m^{-3}) of microzooplankton **(A)**, mesozooplankton **(B)**, and macrozooplankton **(C)** at the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic. Dots = outliers.

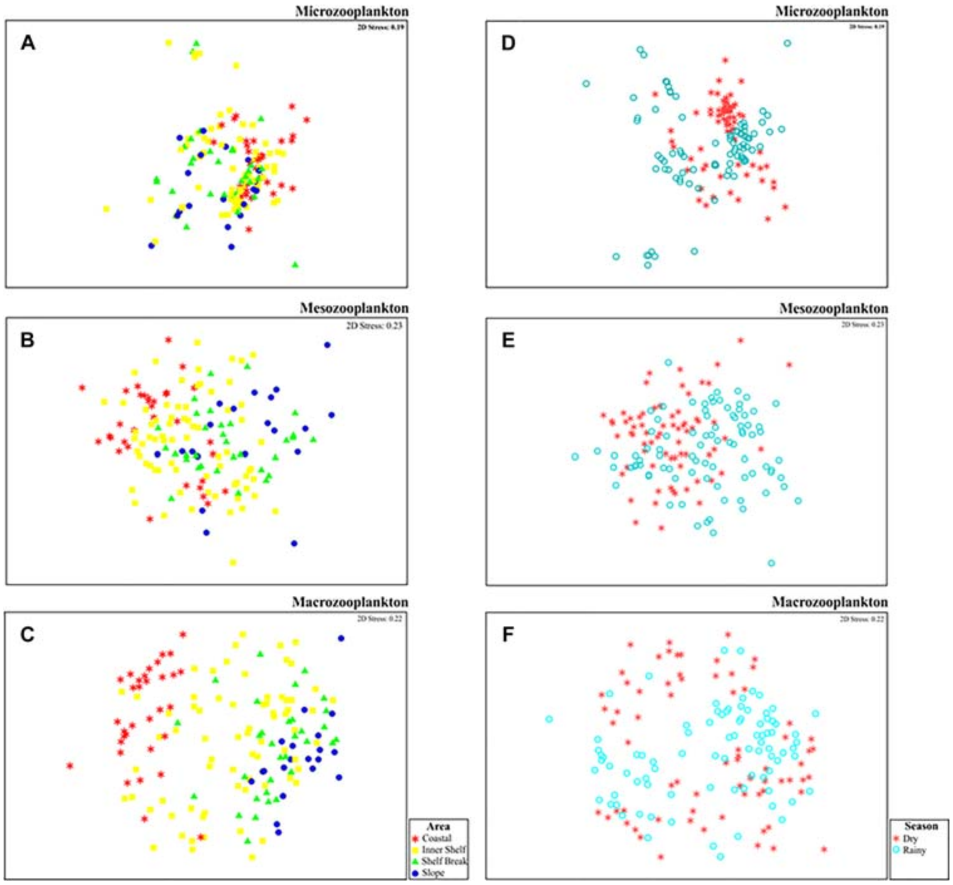

FIGURE 6 | (A–C) MDS ordination of the micro-, meso- and macrozooplankton (respectively) in response to the area (Coastal-red asterisks; Inner Shelf-Yellow squares; Shelf Break-Green triangles; and Slope-Blue circles). **(D–F)** MDS ordination of the micro-, meso- and macrozooplankton (respectively) in response to seasonality (dry season-red asterisks; and rainy season-empty blue circles).

TABLE 3 | Summary: PERMANOVA, this analysis tests differences in quantitative taxonomic composition of the micro- meso- and macrozooplankton community considering area and season as factors.

	PERMANOVA											
	(A) Microzooplankton				**(B) Mesozooplankton**				**(C) Macrozooplankton**			
Source	***Df***	**MS**	**Pseudo-*F***	***P*(perm)**	***Df***	**MS**	**Pseudo-*F***	***P*(perm)**	***Df***	**MS**	**Pseudo-*F***	***P*(perm)**
Area	3	3789.2	3.7047	**0.001**	3	10088	9.4294	**0.001**	3	20505	14.331	**0.001**
Season	1	6060	5.9249	**0.001**	1	15228	14.233	**0.001**	1	10134	7.0828	**0.001**
Area *vs.* Season	3	1183.9	1.1575	0.32	3	2484.3	2.322	0.004	3	2713.4	1.8964	**0.01**
Residual	146	1022.8			148	1069.9			148	1430.8		
Total	153				155				155			

Differences are considered significant if P (perm) = 0.01 (in bold). df = degrees of freedom; MS = average squares; P = probability associated with the Pseudo F statistic.

(**Table 5C**). In the rainy season, the high difference between the Coastal area and the Slope (Average dissimilarity = 79.66) occurred due to the greater cumulative contribution of 50.85% of the taxa *U. vulgaris*, *T. turbinata*, *Lucifer* sp. (mysis), *F. enflata*, Luciferidae (protozoea) and *C. furcatus* (**Table 5D**).

The RDA explained 68% of the variance in the zooplankton community (**Figure 7**). Two vectors with significant values (RDA, $p < 0.05$) were highlighted for the community. One vector separated the coastal from the other areas (**Figure 7**) and other associated the zooplankton to temperature. The groups most associated with the coastal area were mainly the organisms of the microozooplankton (both sestonic biomass and abundance); however, the other zooplanktonic size fractions were also associated with the coastal area. The only group associated with

TABLE 4 | Results of *pairwise t* test of the micro- meso- and macrozooplankton community structure considering area and season as factors.

***Pairwise t* test**					
(A) Microzooplankton			**(C) Macrozooplankton/Dry**		
Areas	***t***	***P*(perm)**	**Areas**	***t***	***P*(perm)**
Coastal *vs.* Inner Shelf	2.3447	0.001	Coastal *vs.* Inner Shelf	2.7176	0.001
Coastal *vs*. Shelf Break	2.6599	0.001	**Coastal *vs.* Shelf Break**	**3.4473**	**0.001**
Coastal *vs.* Slope	**2.9971**	**0.001**	Coastal *vs.* Slope	3.3509	0.001
Inner Shelf *vs.* Shelf Break	0.90931	0.559	Inner Shelf *vs.* Shelf Break	1.8362	0.011
Inner Shelf *vs.* Slope	1.5759	0.041	Inner Shelf *vs.* Slope	2.1845	0.004
Shelf Break *vs.* Slope	1.0186	0.407	Shelf Break *vs.* Slope	1.5406	0.031
(B) Mesozooplankton			**(D) Macrozooplankton/Rainy**		
Areas	***t***	***P*(perm)**	**Areas**	***t***	***P*(perm)**
Coastal *vs.* Inner Shelf	2.3447	0.001	Coastal *vs.* Inner Shelf	3.9052	0.001
Coastal *vs*. Shelf Break	2.6599	0.001	Coastal *vs.* Shelf Break	4.5206	0.001
Coastal *vs.* Slope	**2.9971**	**0.001**	**Coastal *vs.* Slope**	**5.1289**	**0.001**
Inner Shelf *vs.* Shelf Break	0.90931	0.559	Inner Shelf *vs.* Shelf Break	1.5656	0.009
Inner Shelf *vs.* Slope	1.5759	0.041	Inner Shelf *vs.* Slope	2.224	0.001
Shelf Break *vs.* Slope	1.0186	0.407	Shelf Break *vs.* Slope	1.4468	0.03

In bold the main differences identified for the zooplankton community from Rio Grande do Norte in the Tropical Western Atlantic. Perm = PERMANOVA.

temperature was the macrozooplankton biomass. Coastal and temperature vectors explained together 33% of the variability.

A cluster analysis of the samples based on Copepoda presented four groups (Cophenetic $r = 0.89$), which corresponded to the four campaigns (**Figure 8**). In the groups corresponding to Campaigns 1 and 2, two subgroups were formed and consisted of Coastal and Inner Shelf samples at one subgroup, and Shelf Break and Slope samples at the other. In Campaigns 3 and 4, the Coastal stations were separated from the subgroups formed by Inner Shelf, Shelf Break, and Slope.

Functional Traits

The major functional traits dividing the Copepoda community was the reproductive and trophic attributes, which formed three main groups: herbivorous and broadcaster (Group 1), omnivorous-detritivorous, omnivorous-herbivorous, carnivorous and sac-spawner (Group 2), and carnivorous-omnivorous and sac-spawner (Group 3) (**Figure 9**). These groups each included different lengths, costal distances and vertical migration.

Group 1 comprised mostly species with broadcaster reproduction, with epipelagic offshore distribution, herbivorous and filter feeding, non-migrant behavior and smaller sizes varying from 500 to 1500 μm. This group contained mainly calanoids of the genera *Acartia*, *Calocalanus*, *Temora, Paracalanus*, *Calanopia, Undinula* and *Centropages*. Group 2 consisted mostly of sac-spawner species, neritic or neritic-oceanic, epi-meso-bathipelagic and presented three sub-groups, sub-group 1: carnivorous, sub-group 2: omnivorous-herbivorous and sub-group 3: omnivorous-detritivorous. All *Oithona* spp., which exhibit active ambush behavior belonged to sub-group 2. Group 3 also consisted of sac-spawners and included the large (2,500–6,500 μm) oceanic calanoids *Euchaeta*, *Candacia, Labidocera* and *Haloptilus*, and cyclopoids *Saphirina* and *Copilia* which exhibit omnivorous or carnivorous feeding habits, cruising or active ambush behavior types, and vertical diel migration that varies from weak to strong.

DISCUSSION

The study of the zooplankton community structure and function between coastal and oceanic regions from Rio Grande do Norte in the Tropical Western Atlantic showed the great spatial diversity, seasonal variations and the productive potential, chiefly of the coastal region (<10 m depth), possibly caused by continental influence. The coastal zone is extremely complex and is affected by a variety of oceanographic processes (Walsh, 1976; Sousa et al., 2016) that are influenced by diverse anthropic impacts related to continental sources (Mee, 2012). In general, the seasonal distribution presented higher densities for the communities in the rainy season, when fertilization and discharge of nutrients from the continent are more intense.

Our study revealed a high number of taxa occurring in the mesozooplankton community and a greater numerical importance of the microzooplankton community. These results show that net mesh selectivity is an important factor to be considered in studies of the zooplankton community structure. The mesh size effect has already been investigated on the copepod assemblage in the South China Sea (Tseng et al., 2011) and on planktonic cnidarians from neritic and oceanic habitats in the equatorial Atlantic Ocean (Tosetto et al., 2019). The results of the mentioned studies demonstrate that the mesh size directly affects important descriptors (abundance and diversity) which

TABLE 5 | Results of SIMPER analysis for micro-, meso- and macrozooplankton and the zooplankton taxa that contributed to the composition and their values in %, off Rio Grande do Norte, Southwestern Atlantic.

	Coastal	Slope	
Taxa	**Average abundance**	**Average abundance**	**Cumulative contribution (%)**
(A) Coastal *vs.* Slope (Average dissimilarity = 46.01) – Microzooplankton			
Oithona hebes	**10.07**	**5.04**	**9.82**
Euterpina acutifrons	**7.35**	**1.72**	**18.91**
Parvocalanus crassirostris	**8.51**	**4.4**	**27.86**
Oikopleura dioica	**6.83**	**3.52**	**36.03**
Oithona (Copepodito)	**6.24**	**2.29**	**43.97**
Oithona sp.	**7.07**	**3.43**	**51.86**
Foraminifera	6.11	2.16	59.54
Gastropoda (veliger)	8.48	6.05	66.4
Oikopleura sp.	4.83	2.23	73.14
Oithona nana	5.85	6.31	79.45
Bivalvia (veliger)	8.75	6.58	85.58
Tintinnopsis sp.	3.51	1.5	90.64
(B) Coastal *vs.* Slope (Average dissimilarity = 64.49) – Mesozooplankton			
Oithona nana	**6.06**	**1.49**	**10.91**
Nannocalanus minor	**6.11**	**2.08**	**20.55**
Temora turbinate	**4.44**	**0.11**	**30.05**
Oithona hebes	**3.85**	**0.74**	**37.97**
Parvocalanus crassirostris	**3.45**	**0.4**	**45.3**
Clausocalanus furcatus	**3.26**	**3.14**	**52.26**
Undinula vulgaris	2.56	4.09	59.18
Bivalvia (veliger)	5.72	3.29	65.64
Euterpina acutifrons	3.19	1.38	71.99
Gastropoda (others)	2.8	1.66	77.78
Oikopleura sp.	2.98	1.46	83.4
Oithona plumifera	0.7	2.32	89.01
Oithona oswaldocruzi	1.72	1.46	94.09
(C) Coastal *vs.* Shelf Break (Average dissimilarity = 75) – Macrozooplankton/Dry			
Temora turbinata	**2.74**	**0.29**	**11.68**
Undinula vulgaris	**0.48**	**2.6**	**22.12**
Luciferidae (mysis)	**1.78**	**0.08**	**29.48**
Luciferidae (protozoea)	**1.42**	**0.21**	**35.23**
Centropages furcatus	**1.23**	**0.23**	**40.59**
Oikopleura longicauda	**1.18**	**0.77**	**45.81**
Flaccisagitta enflata	**0.23**	**1.15**	**50.94**
Brachyura (zoeae)	1.01	0.66	55.81
Parasagitta tenuis	1.26	0.55	60.68
Brachyura (zoeae)	0.79	0.81	65.33
Teleostei (egg)	0.7	1.06	69.89
Calanopia americana	0.96	0.42	74.41
Onychocorycaeus giesbrechti	0.75	1	78.35
Gastropoda (veliger)	0.73	0.51	81.92
Temora stylifera	0.27	0.78	85.41
Oikopleura sp.	0.46	0.46	88.56
Subeucalanus pileatus	0.28	0.69	91.61
(D) Coastal *vs.* Shelf Break (Average dissimilarity = 79.66) – Macrozooplankton/Rainy			
Undinula vulgaris	**0.48**	**3.1**	**12.61**
Temora turbinata	**2.74**	**0.01**	**25.11**
Luciferidae (mysis)	**1.78**	**0.01**	**32.71**
Sagitta enflata	**0.23**	**1.53**	**39.47**
Luciferidae (protozoea)	**1.42**	**0.07**	**45.33**
Centropages furcatus	**1.23**	**0.02**	**50.85**
Oikopleura longicauda	1.18	0.57	55.83
Parasagitta tenuis	1.26	0.54	60.37
Brachyura (zoeae)	1.01	0.26	64.68
Calanopia americana	0.96	0.35	68.75
Brachyura (zoeae)	0.79	0.34	72.76
Temora stylifera	0.27	0.85	76.72
Onychocorycaeus giesbrechti	0.75	0.8	80.15
Membranipora sp.	0.58	0.38	83.5
Subeucalanus pileatus	0.28	0.64	86.83
Gastropoda (veliger)	0.73	0.36	90.13

In bold the main taxa, whose cumulative contribution corresponds to ≥50%.

are particularly useful for the management of marine resources, mostly of the marine regions studied (Coastal, Inner Shelf, Shelf Break and Slope).

Spatial differences were observed for the zooplanktonic communities among the marine regions investigated with a Coastal and Inner Shelf group (related to higher chlorophyll-*a*, shallow area and higher meroplanktonic forms) and Shelf Break and Slope group (linked to lower chlorophyll-*a*, deeper areas and higher percentage of holoplanktonics). However, greater dissimilarity was registered between the Coastal and the Slope areas (e.g., microzooplankton extremely high density was associated with the shallower coastal area). This Coastal region is enriched by rivers discharges from the continent (including outflow from the intensive shrimp culture ponds), delivering nutrients to the marine system. These nutrients stimulate the phytoplankton growth, favoring most zooplankton species, which are characteristically herbivores or omnivores (Johnson and Allen, 2005). This pattern is commonly found in Continental shelves (Neumann-Leitão et al., 1999, 2008; Dias et al., 2015; Bueno et al., 2017) and oceanic islands (Campelo et al., 2018; Santana et al., 2018) in Brazil and reflect the typical coast-ocean gradient.

An increase in macrozooplankton density was observed near the Shelf Break, caused by local topographic upwellings (Stramma et al., 1990). However, the condition of each location may strongly affect the distribution of the zooplankton, such as reefs currents, canyons, ravines, eddies and vortices (Regner, 1985), and alter the general pattern of the studied area. For instance, the Rio Grande do Norte coast has a narrow continental shelf; therefore, the zooplankton community has a high degree of

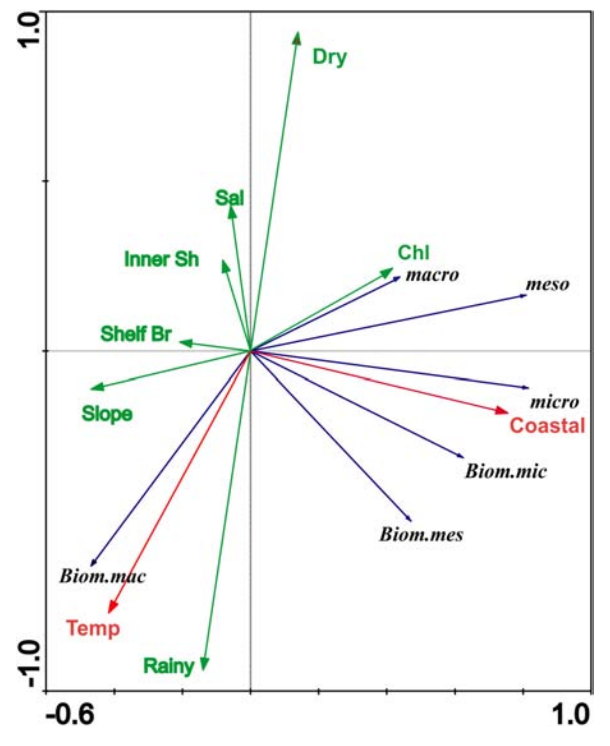

FIGURE 7 | Ordination diagram of the Redundancy Analysis (RDA). Significant vectors of spatial-temporal are in red, non-significant vectors in green, and taxon classification in blue for Zooplankton at the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic. Areas: Coastal, Inner Shelf, Shelf Break, and Slope; Rainy: Rainy season; Dry: Dry season: Sal: Salinity; Chl: Chlorophyll *a*; macro: macrozooplankton; meso: mesozooplankton; micro: microzooplankton; Bio_macro: biomass macrozooplankton; Bio_meso: Biomass mesozooplankton, and Bio_micro: biomass microzooplankton.

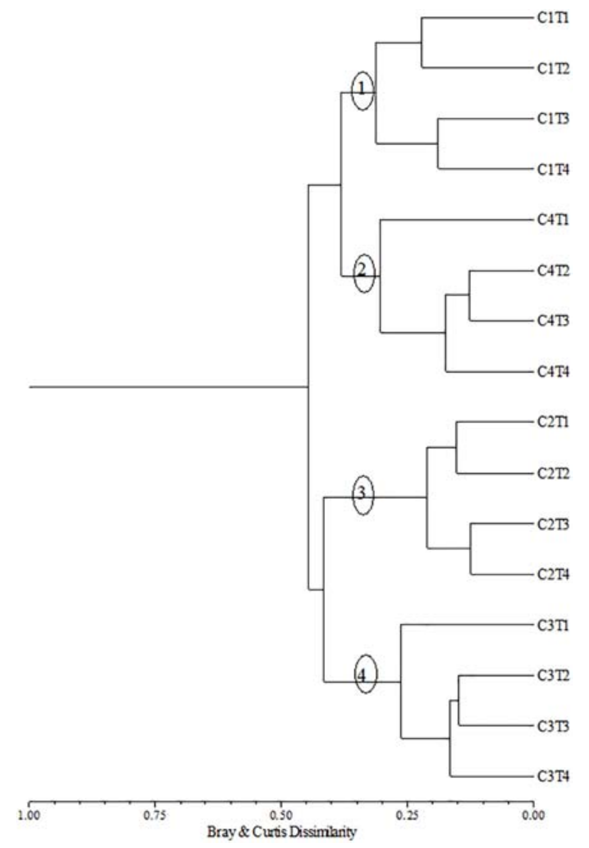

FIGURE 8 | Dendrogram of samples based on Copepoda density from the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic. Bray–Curtis index and Ward linkage clustering. C = Campaign (C1 = July 21–30, 2002, C2: May 12–30, 2003, C3: November 14–23, 2003, C4: May 17–31, 2004). T = Transect (T1: <10 m, T2: 10–20 m, T3: 20–50 m, and T4: >50 m).

influence from oceanic intrusions. Thus, a mixture of oceanic and neritic micro-, meso-, and macrozooplankton was observed, which resulted in difficulties separating the communities. As expected, diversity increased from inshore to offshore. This pattern is usual for SWA (Boltovskoy, 1981; Neumann-Leitão et al., 1999, 2008; Dias and Bonecker, 2009; Dias et al., 2015); however, due to the reproductive requirements, some species prefer shallow waters.

The high biomass of micro- and mesozooplankton was mainly recorded in the Coastal area in both studied seasonal periods, being able to consider that these fractions of the community are key elements in the planktonic food chain of this region. In addition, it is important to consider the large amount of particulate matter from the estuaries and bays (Lopes, 2007). These particulates matter (plankton, marine snows and detritus) are important components of the pelagic system because they are a food source for the zooplankton, being sampled more efficiently by smaller mesh sizes (Silva et al., 2019). In general, the lowest values of biomass observed for the macrozooplankton community occurred in the coastal area and the largest on the slope. This is a result of a coast-ocean size gradient (Marcolin et al., 2013), implying a change in the taxonomic composition of the organisms, with a greater contribution of siphonophores and fish larvae in the slope, considered organisms of larger body size, better sampled with the a net of 300 µm mesh size. A maximum of zooplankton biomass occurs in neritic waters of SWA (Boltovskoy, 1981; Dias et al., 2015), with 100 mg·m^{-3} in the top layer (200 m).

Copepoda were the most diverse group in all fractions, accounting for 93 species. This result is expected for the SWA tropical waters (Boltovskoy, 1981, 1999; Neumann-Leitão et al., 1999, 2008; Lopes et al., 1999; Bueno et al., 2017). Highest Copepoda diversity were registered in the mesozooplankton fraction during this study and most of them were of small size. In oligotrophic areas, species occur with smaller sizes and in developmental stages that are important in planktonic communities and these areas are dominated by microbial components (Calbet et al., 2001; Turner, 2004; Calbet, 2008). Small-sized copepods are a pivotal link between the classical and microbial food webs (Nakamura and Turner, 1997; Melo et al., 2014); they present a much higher growth rate (Peterson et al., 1991; Hopcroft et al., 1998) and influence the effectiveness of the trophic connection between primary

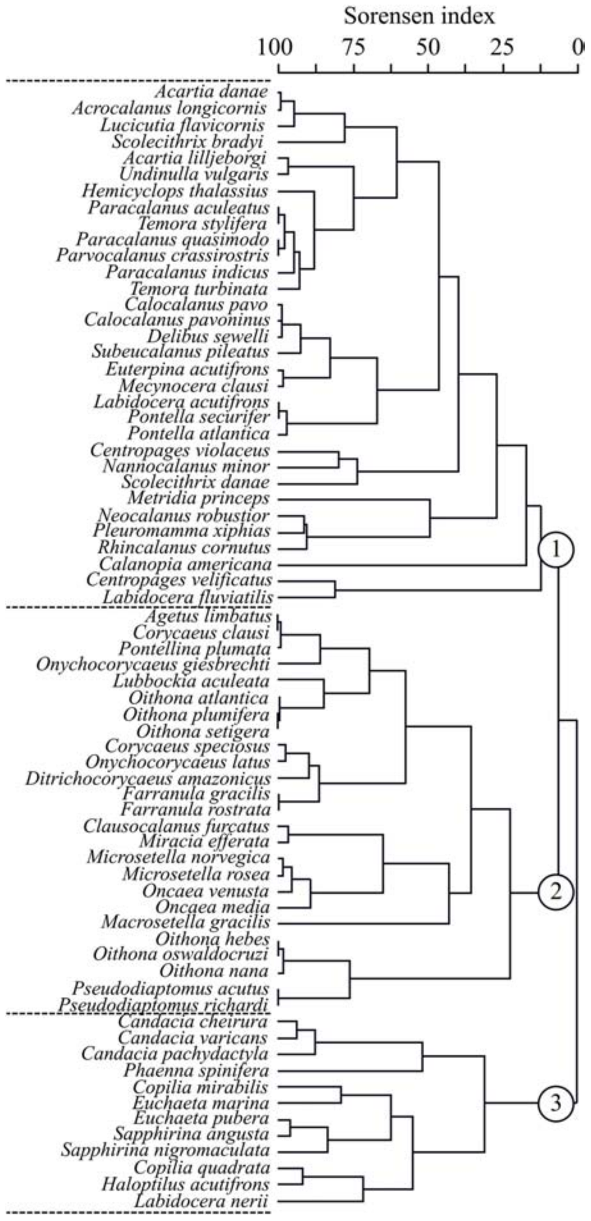

FIGURE 9 | Dendrogram of the Copepoda species that have been clustered by functional traits identified from July 2002 to May 2004 in coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic. The numbers 1, 2 and 3 represent the main groups. Sorensen index and average linkage clustering.

producers/protozooplankton and larger species (Zervoudaki et al., 2007). One of the most oligotrophic oceans in the world is the Southwest Atlantic Ocean (Andrade et al., 2007); and, Dias et al. (2015) mention that oligotrophic areas present higher production than formerly supposed and have an extraordinary amount of biotic complexity, encompassing nearly 75% of marine surfaces.

Young forms (copepodites) of *N. minor, Temora stylifera, C. furcatus, Centropages velificatus*, and *O. giesbrechti* and adults of *Microsetella norvegica* and *Macrosetella gracilis* predominated the microzooplankton fraction. The species *M. norvegica* and *M. gracilis* were generally associated with the cyanobacterium *Trichodesmium eritheum*. Pelagic harpacticoids can also be found in close association with floating substrates, such as *Trichodesmium* (Calef and Grice, 1966; O'Neil and Roman, 1994; O'Neil, 1998; Uye et al., 2002). These blue-green colonies offer both a firm substratum and food for the accompanying plankton in tropical and subtropical oligotrophic oceans, thus supporting multifaceted microenvironments (Sheridan et al., 2002; Bergman et al., 2013).

The copepod *P. crassirostris* is very important to the microzooplankton community of the Coastal stations; *P. crassirostris* commonly occurs in nearly all Brazilian estuaries and the estuarine plume (Björnberg, 1981; Eskinazi-Sant'Anna and Björnberg, 2006), including those that are severely anthropically impacted (Schwamborn et al., 2004; Silva et al., 2004). This species forages mainly on pico- and nanoplankton fractions, behaving as an *r*-strategist (opportunistic) particle feeder and revealing high ingestion rates of the most profuse cells (2–5 μm nanoplankton) (Calbet et al., 2000). *P. crassirostris* is dominant in eutrophic systems, evidencing the estuarine effect in the coastal studied area. In the offshore direction, a characteristic zooplanktonic community is commonly found in reef areas. The high abundance of the Oithonidae and Paracalanidae families is typical of the coastal waters of Brazil (Björnberg, 1981; Dias and Bonecker, 2009).

Epipelagic, oceanic, and widespread species were the dominant groups in this region, and they occur in tropical and subtropical oceans (Atlantic, Pacific, and Indian), except for *U. vulgaris* and *O. nana*, which demonstrate neritic occurrence (Björnberg, 1981; Bradford-Grieve et al., 1999). There is a reported relation between *U. vulgaris* and coastal areas due to its occurrence in neritic environs; *U. vulgaris* exhibits a high abundance in many inshore plankton hauls in the surface layer (Razouls et al., 2005). However, *U. vulgaris* dominated among copepods in samples from oceanic provinces in the economic exclusive zone (EEZ) of Northeastern Brazil (Cavalcanti and Larrazábal, 2004; Melo et al., 2014; Campelo et al., 2018). In our study, *U. vulgaris* was also abundant at young stages under oceanic influence, which suggested that it also inhabits oceanic regions with an epi-mesopelagic distribution.

The wide distribution of numerous Copepoda species in our study is due their passive transportation by currents (*Calocalanus pavo, U. vulgaris*, *Oithona plumifera, Oncaea venusta*, *M. gracilis, Microsetella rosea*, and *Corycaeus speciosus*), Chaetognatha (*F. enflata* and *Serratosagitta serratodentata*), and Appendicularia (*Oikopleura* spp.) results in circumglobal distribution patterns. This occurs much more commonly than endemism for pelagial plankton (Boltovskoy et al., 2002; Pierrot-Bults and Angel, 2012). Species with high proportions of neritic organisms and benthopelagic forms are excluded from this pattern (Angel, 1993).

Chaetognatha predominated in the macrozooplankton fraction and comprised species from coastal and oceanic provinces; oceanic origin was predominantly represented. *F. enflata*, *S. serratodentata, Flaccisagitta hexaptera,* *Sagitta bipunctata*, and *Krohnitta subtilis* are indicators of the Tropical Water, and *Parasagitta tenuis* a coastal-water indicator. *Pterosagitta draco* have a wide distribution recorded in both oceanic and costal water masses (Boltovskoy, 1981). High densities of *F. enflata* are common to this area (Boltovskoy, 1981, 1999; Gusmão, 1986; Neumann-Leitão et al., 1999, 2008).

The zooplankton species indicator classified by Björnberg (1963, 1981) and Bradford-Grieve et al. (1999) showed that the most relevant Copepoda group in our analysis included a mixture of neritic and oceanic species from the North Brazil Current, which is under the Shelf Break influence that presents the general scenario of a huge reef system. Campos et al. (2017) found a similar result to a coastal area north of the present studied area. Also, holoplanktonic organisms, mainly the oceanic Copepoda, predominated the entire studied region, including the inshore area. This pattern is a consequence of the weak continental freshwater runoff over the shelf due to arid climate and geomorphology. Thus, freshwater flux fertilizes the very coastal area under 10 m depth. Other authors for Northeastern Brazil (e.g., Gusmão et al., 1998; Neumann-Leitão et al., 1999, 2008; Campos et al., 2017) registered this same pattern. The constant northeast tradewinds and arid climate in this area permits for the establishment of widespread beaches and dunes, which are in continuous movement due to the absence of anchoring vegetation (Mabesoone and Coutinho, 1970). These dunes prevent the free flux of rivers to the sea during dry season, and many freshwater lakes form behind the dunes. The changes recorded along the shelf seem to be chiefly driven by the rain and periodic blooms of benthic invertebrate larvae.

The role of zooplankton through functional groups involves information that precisely capture their complex dynamics (Everett et al., 2017). The zooplankton are represented by many functional groups, that oscillate in size from small (>0.002 μm) to large (>5000 μm) organisms. Zooplankton also presents vast trophic malleability that can modify considerably along a time interval as the community structure changes. Many external factors (e.g., nutrients, temperature, phytoplankton, competition, predation) regulate the growth of an organism and/or of a population, that by its turn is strongly connected to life cycles, such as reproduction with generations fluctuating (from days to years) (Williams and Conway, 1982). Zooplankton species modify its diet preferences throughout different periods or life stages, or substitute a food item behavior (Stibor et al., 2004; Sommer and Sommer, 2006). To complicate the dynamics of the zooplankton community, several species of microzooplankton are mixotrophic (Caron, 2016), the phytoplankton succession is seasonal (Pingree et al., 1976; O'Boyle and Silke, 2010) and many meroplanktonic species emerge in the shelf (Williams and Collins, 1986). Thus, zooplankton within a specified size class (e.g., microzooplankton, mesozooplankton, macrozooplankton) are thus unlikely to behave reliably over a spatial-temporal scale.

The main traits separating the Copepoda groups were the reproductive and trophic strategies, and a very similar outcome was found by Campos et al. (2017) to a shelf area located North of the present studied area; and, by Neumann-Leitão et al. (2018) for the reef system in the Amazonas coastal area. Trophic stratagems and reproduction are normally controlled by female weight, ecosystem temperature, and diet (Blaxter et al., 1998; Bunker and Hirst, 2004; Brun et al., 2017). In terms of feeding, Kiørboe and Sabatini (1995) presented three strategies in copepods: filtering, active ambushing and cruising; and, Kiørboe (2011) presented the following not necessarily exclusive feeding strategies: Passive (Ambush feeding, particle feeding) Active (Feeding currents, cruise feeding) Mixed (Combination of active and passive modes) and Other (Parasitic).

In conclusion, the study area presents spatial heterogeneity, with low diversity limited to Coastal stations; high diversity and low abundance occur along the Inner Shelf, Shelf Break, and Slope. This is a pelagic oligotrophic habitat located off the coast of tropical Brazil over a diverse, high biomass benthic habitat, which is mostly covered by calcareous algae functioning on the shelf as a large reef system. The narrow and shallow shelf is responsible for the strong connectivity between nearshore enriched coastal water and the oceanic oligotrophic Tropical Water mass, which results in a complex mixed system that is critical to the food web structure and forms a peculiar pattern of zooplankton diversity and distribution.

AUTHOR CONTRIBUTIONS

SNL and RS coordinated the project. SNL, RS, AS, PM, and VP designed and coordinated the fieldwork. SNL, FPN, MMJ, RS, AS, and LF wrote and reviewed the manuscript. SNL, RS, MMJ, FPN, TS, DNV, PM, XD, AS, VP, LF, AC, RC, JS, and SL contributed with data and data analyses.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00287/full#supplementary-material

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