



Genetic connectivity of black drum (*Pogonias courbina*) stocks in the southwestern Atlantic Ocean

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Received: 9 October 2019 / Accepted: 14 June 2020 / Published online: 27 June 2020
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Abstract The delimitation of fishery stocks is an important aspect for the development and implementation of fishery stock management and sustainable use programs. Genetic analyses can provide useful information for the definition of population units, migration rates and changes in effective population sizes over long time frames. The black drum *Pogonias courbina* (Lacepede, 1803) is a marine fish that inhabits estuaries, bays and coastal waters of both hemispheres of the Western Atlantic, including Brazil, Uruguay and Northern Argentina. Intensely exploited at the Lagoa dos Patos Estuary in South Brazil, it is considered locally collapsed and since 2014 it is included in the National List of Endangered Fauna. Here we studied the population genetics of *Pogonias courbina* from South Brazil and the Argentinean and Uruguayan margins of the Río de la Plata Estuary, using the mitochondrial DNA control region. We showed that along the study area *Pogonias courbina* groups present high genetic diversity, no genetic structure, and are undergoing slight expansion. These characteristics favor resilience of the population, decreasing the extinction risk of local stocks. However, the slow recovery after the black drum fisheries collapse at Lagoa

dos Patos indicates that the recolonization process is slow; this is corroborated by migration estimates, in which we observe a low number of migrants between Argentina/Uruguay and South Brazil. Therefore, we suggest that the South Brazil reproductive stock, impacted by regional fisheries, can be considered a unique stock in terms of management, independent of Uruguayan and Argentinean management strategies. However, an integrated management plan should ideally be considered for these groups, since impacts and conservation efforts are likely shared between areas.

Keywords Fisheries management · Genetic diversity · mtDNA D-loop · Population structure · South Atlantic

Introduction

Marine sciaenid fishes inhabit mainly unconsolidated substrates in estuarine and coastal areas and are valuable fishery resources (Nelson et al. 2016). Two of the largest species of the Sciaenidae family are the black drum *Pogonias cromis* and its recently redescribed congeneric species *Pogonias courbina* (Lacepede, 1803) (Azpelicueta et al. 2019). This demersal species has its first maturation with approximately 3–4 years, lives up to 55 years, can reach over 60 kg and 1400 mm total length (Murphy and Taylor 1989; Haimovici 1997; Azpelicueta et al. 2019) and are estuarine-dependent, tolerating a wide range of salinities and temperatures and inhabiting coastal marine areas such as bays and estuaries of the Western Atlantic Ocean. These species

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10641-020-00993-6>) contains supplementary material, which is available to authorized users.

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present a large tropical distribution gap of ~8000 km, with *P. cromis* occurring from the state of Massachusetts (U.S.A.) to the Gulf of Mexico and *Pogonias courbina* from Rio de Janeiro (Brazil) to the San Matías Gulf (Argentina) (Azpelicueta et al. 2019). In the South-west Atlantic, *Pogonias courbina* supports commercial fisheries in Argentina, Uruguay and, until the early 1980s, in Brazil (IBAMA/CEPERG 2011; CTMFM 2019; MAGyP 2019).

Adult *Pogonias courbina* form large aggregations during reproductive and spawning seasons, and females present high fertility rates spawning multiple times over several months, with a larval phase of about 4 months (Peters and McMichael 1990; Macchi et al. 2002). At the Río de La Plata Estuary along northern Argentina and Uruguay, spawning occurs between October and January (Urteaga and Perrotta 2001) at the estuary's inner portion, where the saline front presents largest horizontal salinity gradients (Militelli et al. 2013). At the Lagoa dos Patos Estuary and adjacent coastal waters in South Brazil, female black drum occur in advanced stages of maturation mainly from October to November, but can also be observed in low frequencies until March (Haimovici and Cardoso 2017).

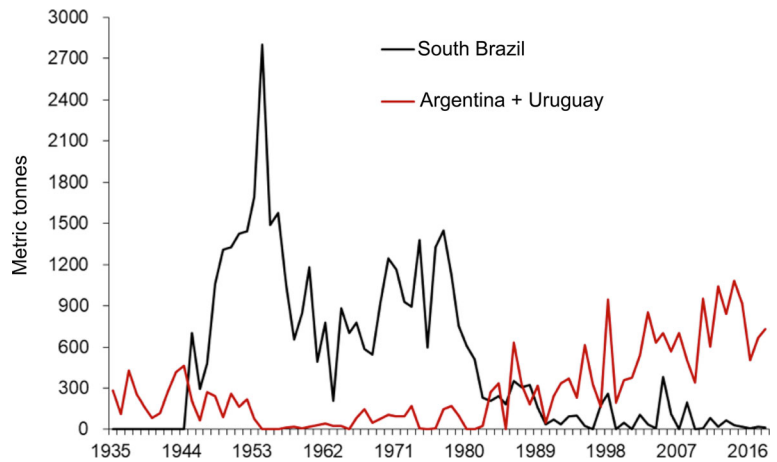
At the Río de la Plata Estuary and adjacent marine coastal waters fishing occurs mainly between February and November, with highest efforts from June to August. Annual landings at the region were of several hundred tones between 1935 and the 1950s, followed by several decades of almost no commercial fishing, and increasing again in the 1980s; between 500 and 1000 t were fished annually over the last two decades (Sanchez et al. 2012; MAGyP 2019; CTMFM 2019) (Fig. 1). At the Lagoa dos Patos Estuary, black drum has been exploited since the mid-nineteenth century (Odebrecht 2003), being caught mainly in the spring season with gill and beach nets, and occasionally throughout the year with bottom trawlers. From 1945 to 1981 annual landings usually surpassed 1000 t per year, but decreased sharply to a few tons over the last decades (IBAMA/CEPRG 2011) (Fig. 1). The Brazilian black drum stock is considered collapsed, and recovery is occurring at a very slow rate (Chao et al. 2015; Haimovici and Cardoso 2017). This species was included in the National List of Endangered Species of the Environmental Ministry as 'Endangered' (MMA 2014), with its fishery being prohibited. The slow of recovery of the *Pogonias courbina* stock in South Brazil after 30 years of its collapse has been attributed to its high

vulnerability to fishing during its seasonal reproductive migration into the Lagoa dos Patos Estuary (Haimovici and Cardoso 2017), and could indicate little or no exchange of migrants with the Río de la Plata group, which is still being exploited in high numbers.

The populational relationships between fishery stocks is commonly evaluated through genetic markers, which can help understand the degree of connectivity between them and evaluate how fishing pressures or stock recovery at one region can affect the abundance at another. Genetic markers are especially useful for understanding connectivity of organisms that present continuous distributions and high potential for gene flow, as is the case of several species of the Sciaenidae family (Cadrin et al. 2014). Mitochondrial DNA (mtDNA) markers are widely utilized due to the large number of copies per cell (i.e. easy isolation), high mutation rates, generally maternal inheritance, and almost inexistent recombination (Freeland 2011). Although nuclear markers should ideally be used along with mtDNA in order to understand additional factors such as male-mediated gene flow and migrations (Prugnolle and Meeus 2002), mtDNA is still predominantly studied, and the genetic population structure of several coastal sciaenid fish in the southwestern Atlantic (SWA) has been described using mtDNA markers. For instance, distinct genetic populational units of the royal weakfish *Macrodon atricauda* (Rodrigues et al. 2014) and the kingcroaker *Menticirrhus americanus* (Freitas et al. 2017; Márquez et al. 2017) were found to occur at the Río de la Plata front and South Brazil. On the other hand, the weakfish *Cynoscion guatucupa* presents a single genetic populational unit including groups from Argentina to South Brazil. Despite the commercial importance of *P. courbina*, there are no studies on the population structure over its entire distribution range.

Population connectivity in marine fish populations can be influenced by several factors, including life history traits such as duration of larval phases and migratory behavior, and environmental factors such as temperature, nutrients, fronts and ocean current patterns (Cowen et al. 2007). At an evolutionary scale, the characteristics of marine and estuarine species/populations were largely affected by Pleistocene glaciations at tropical and temperate regions (Santos et al. 2006; González-Wevar et al. 2015). During glaciation cycles, fluctuations in temperature and sea levels, as well as changes in ocean current patterns and loss of coastal habitats, resulted in physical or oceanographic barriers

Fig. 1 Annual *Pogonias courbina* landings by fishing fleets of Argentina, Uruguay and South Brazil between 1935 and 2016



that influenced connectivity between populations and possibly led to bottleneck events with reduction of abundance and genetic diversity (Durand et al. 2005). Pleistocene climatic fluctuations along the SWA may also have been responsible for the origin of some coastal estuarine fish species (e.g., Beheregaray et al. 2002). Several studies on marine fish along the SWA show population expansions with star-like phylogeographic patterns, likely a result of such fluctuations (e.g., Beheregaray et al. 2002; Santos et al. 2006; Pereira et al. 2009).

Understanding the genetic characteristics of exploited marine fish populations is crucial for adequate management and recovery of stocks. In this manner, to provide baseline genetic information on black drum groups in the Southwestern Atlantic and test the hypothesis of genetic isolation between the Río de la Plata and Lagoa dos Patos estuaries, in this work we evaluated the genetic diversity, demography and structure of *Pogonias courbina* groups sampled along its southernmost distribution range (between South Brazil and Argentina), based on the mitochondrial DNA control region.

Material and methods

We sampled 91 *Pogonias courbina* individuals. Thirty were imported *in natura* from Uruguay, most likely fished along the Uruguayan portion of the Río de la Plata estuary as informed by the local fishers upon sampling. Thirty-one individuals were sampled in 2016 at Samborombón Bay, located in the Argentinean portion of the Río de la Plata, and thirty in 2013 at the

Lagoa dos Patos Estuary, South Brazil, from small-scale gillnet fisheries (Fig. 2). A small portion (~2 g) of muscle from each individual was removed and stored in absolute ethanol at -20 °C for further genetic analyses.

DNA extraction and mtDNA amplification

Genomic DNA was extracted using a saline purification protocol, as described in Aljanabi and Martinez (1997). DNA integrity was evaluated visually through electrophoresis in 1% agarose gels, and quantified through spectroscopy using a BioDrop®. Amplification of 950 bp of the mitochondrial DNA control region (D-loop) was achieved using specific primers designed in this study for the target species. Primers Pogo 100 (5'-CCCACCACTAACTCCCAAAGCTAGTA-3') and Pogo 1100 (5'-CGGAGCTTTCTAGGGCTCATCTTAAC-3') were developed based on mtDNA D-loop sequence alignments of the following species: *Argyrosomus amoyensis*, *Chrysochir aureus*, *Collichthy sniveatus*, *Larimichthys crocea* and *Protonibea diacanthus*. These sequences were edited using BioEdit 7.2.5. (Hall 1999) and aligned with CLUSTAL W (Thompson et al. 1994), and primers were manually selected and had their properties checked with the OligoEvaluator™ tool (<http://www.oligoevaluator.com/>). Each 25 µl PCR reaction contained 1X buffer solution (10 mM TrisHCl pH 8.5 and 50 mM KCl), 2.5 mM MgCl₂, 0.4 mM dNTP, 0.2 pmol of each primer, 2.5 U Taq DNA polymerase and 40 ng of DNA. Thermal cycles consisted of: an initial denaturation of 2 min at 94 °C; 5 cycles of 1 min at 95 °C, 1 min at 60 °C and 1.5 min at 72 °C; 30 cycles of 1 min at 93 °C, 1 min

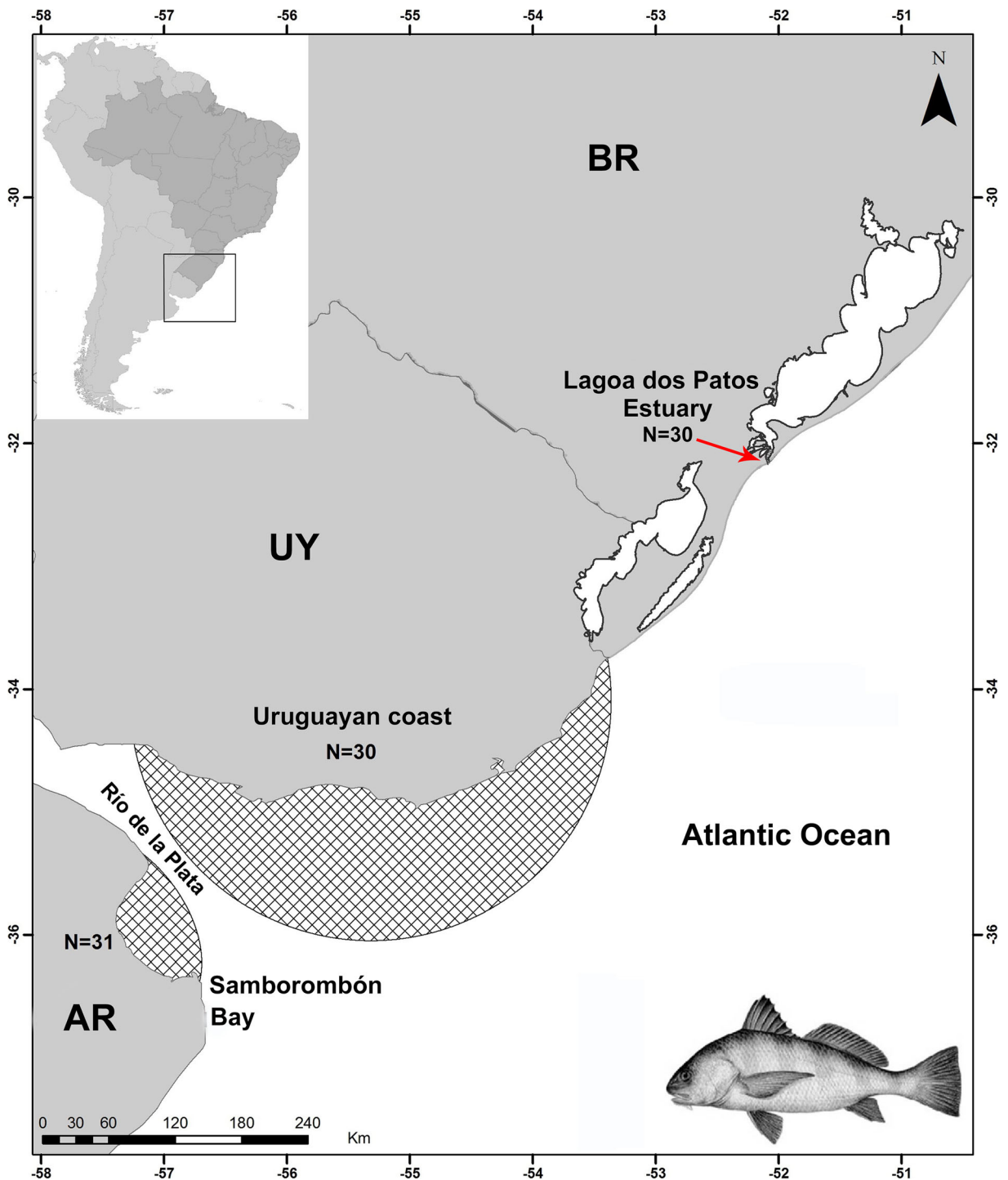


Fig. 2 *Pogonias courbina* sampling locations and sample sizes at Samborombón Bay, Argentina, and the Uruguayan coast (hashed areas); and Lagoa dos Patos Estuary, South Brazil (red arrow)

at 59 °C, 1.5 min at 72 °C; and a final extension of 5 min at 72 °C. To assure lack of contamination, negative controls were used in all reactions. Amplification

products were submitted to electrophoresis in 1% agarose gels in order to evaluate amplification efficiency. A molecular weight marker (100 bp or

1 kb, KASVI) was used to determine size of amplified fragments. The amplified material was purified by precipitation with 15% Polyethylene Glycol (PEG) 8000 (Hartley and Bowen 1996), and resuspended in pH 7 TE buffer. Purified products were sequenced in both directions by the chain termination method in capillary sequencers at Macrogen (<http://dna.macrogen.com/eng/>).

Data analysis

Forward and reverse sequences were visually checked and edited in BioEdit 7.2.5 (Hall 1999) and aligned with CLUSTAL W (Thompson et al. 1994). To evaluate the genetic diversity of populations, the number of D-loop polymorphic sites, haplotypes (H), haplotype diversity (h) and nucleotide diversity (π) were determined in Arlequin 3.5 (Excoffier and Lischer 2010). Genetic structure between black drum groups sampled at the three localities was estimated through Phi ST (Φ_{ST}), using the Tamura-Nei model of nucleotide substitution (Tamura and Nei 1993); this model was determined as most suitable for our data using jModel test 2.1.10 (Darriba et al. 2012). A haplotype network was built using PopART software using the Median Joining method (Bandelt et al. 1999). Migration rates were estimated between populations using the maximum likelihood approach, based on the coalescence method, in MIGRATE 4.4.3 (Beerli and Felsenstein 1999). The mean values of θ and M were used to calculate $\gamma_{ab} = \theta_b M_{ab}$, where γ is the number of effective migrants, θ is the population size, and $M = m/\mu$ (where m is the immigration rate and μ is the mutation rate) (Beerli and Felsenstein 1999; Beerli 2006). The migration rates are presented as the effective number of migrants per generation.

The demographic history of *Pogonias courbina* was inferred through a mismatch distribution analysis, which evaluates the distribution of the number of nucleotide differences between sequences, using Arlequin 3.5 (Rogers and Harpending 1992). Tajima's D (Tajima 1989) and Fu's FS (Fu 1997) neutrality tests were also performed with this software to detect possible population expansions or reductions. Raggedness indexes (Harpending 1994) and the Sum of Squared Deviations (SSD) between the observed and simulated mismatch distributions were used to validate the expansion models (Schneider and Excoffier 1999). SSD significance was evaluated through parametric initialization. This test

was also used to estimate the mutation parameters before ($\theta_0 = 2N_0u$) and after ($\theta_1 = 2N_1u$) expansion – where N_0 is the effective size of the initial population, N_1 new population size and u the mutation rate of the sequence – and the mismatch distribution mode (τ). Time since population expansion (t) was calculated using the equation $\tau = 2ut$ (Rogers and Harpending 1992), where u is the mutation rate of the sequence, calculated as $u = 2\mu k$, where μ is the mutation rate per nucleotide and k is the number of nucleotides. For this analysis, the mutation rate of 3.6% per million years was used, as proposed by Donaldson and Wilson (1999) for the control region of fish.

Results

A total of 841 bp were sequenced for all samples, 825 of the D-loop region and 16 of the initial phenylalanine tRNA. *Pogonias courbina* presented a high number of D-loop haplotypes, with a total of 57 haplotypes defined by 48 parsimony-informative sites (43 transitions, three transversions and two indels). The obtained sequences were deposited in FigShare (available at <https://doi.org/10.6084/m9.figshare.12574013.v1>). The haplotypic diversities of the three regions were high, with the highest observed at Samborombón Bay, Argentina ($h = 0.995 \pm 0.009$), and the Uruguayan coast ($h = 0.993 \pm 0.010$), and being slightly smaller at the Lagoa dos Patos Estuary, Brazil ($h = 0.889 \pm 0.042$). Nucleotide diversities were also similar at the three sites, with Lagoa dos Patos presenting $\pi = 0.014$ and Samborombón Bay/Uruguayan coast presenting $\pi = 0.013$ (Table 1).

As can be observed in the haplotype network (Fig. 3), only two haplotypes (17 and 24) were shared between the three groups. Haplotypes 2, 5, 9, 12, 21 and 22 were shared between Samborombón Bay and the Uruguayan coast. The Lagoa dos Patos Estuary and the Uruguayan coast shared haplotype 35. The other haplotypes were exclusive to each region. No regional separation of haplotype distribution among the three *Pogonias courbina* groups can be observed in the haplotype network, which presented an overall panmictic shape with small distances between haplotypes of all regions. Φ_{ST} results confirmed this, showing a very low, non-significant differentiation between groups (Table 2). The migration rates from Lagoa dos Patos Estuary to

Table 1 Mitochondrial DNA control region diversity for *Pogonias courbina* from Samborombón Bay (Argentina), Uruguayan coast, and Lagoa dos Patos Estuary (South Brazil)

Locations	N	H	<i>h</i>	π
Samborombón Bay	31	28	0.995 ± 0.009	0.013 ± 0.006
Uruguayan coast	30	26	0.993 ± 0.010	0.013 ± 0.007
Lagoa dos Patos	30	14	0.889 ± 0.042	0.014 ± 0.007
Total	91	57	Mean = 0.959	Mean = 0.013

N = number of individuals, *H* = number of haplotypes, *h* = haplotype diversity and π = nucleotide diversity

Samborombón Bay and the Uruguayan coast were respectively $\gamma = 53.78$ and $\gamma = 48.24$. Meanwhile, Lagoa dos Patos received $\gamma = 2.44$ and $\gamma = 1.89$ migrants from Samborombón Bay and the Uruguayan coast; these last two areas exchanged $\gamma = 30.30$ (Samborombón to Uruguay) and $\gamma = 36.85$ (opposite migration) migrants (Fig. 4).

The mismatch distributions were multimodal for the three black drum groups, indicating demographic equilibrium (Fig. 5). However, only the Brazilian group presented a truly multimodal distribution, with the groups from Uruguay and Argentina presenting bimodal distributions. Tajimas's *D* and Fu's *F_s* confirm that *Pogonias courbina* from the Lagoa dos Patos Estuary are in equilibrium (*D* = 0.76 and *F_s* = 1.23). However, for groups sampled from the Uruguayan coast and Samborombón Bay, these indexes contradicted mismatch results and indicated demographic expansion (*D* = -0.24 and *F_s* = -13.38, *D* = -0.62 and *F_s* = -17.64) (Fig. 5). SSD values and the Raggedness index (Table 3) differ from the distribution models described in Fig. 5. The Raggedness index and the low SSD values indicate that the three analyzed groups are in demographic expansion. For Samborombón Bay, Uruguayan coast and Lagoa dos Patos the Raggedness index was respectively 0.006, 0.010 and 0.056, while SSD was 0.091, 0.024 and 0.025 (Table 3). The estimated time since demographic expansion indicates that the group from the Lagoa dos Patos Estuary suffered expansion around 163 thousand years ago, followed by the Uruguayan coast and Samborombón Bay, respectively 27 and 36 thousand years ago. In this way, the Brazilian group is more likely to be truly in equilibrium, while the groups in Uruguay and Argentina are possibly undergoing slight expansion.

Discussion

Genetic diversity

In this study, we analyzed for the first time the genetic diversity, population structure and demographic history of *Pogonias courbina* in the Southwestern Atlantic, evaluating regional groups from Lagoa dos Patos in the extreme South of Brazil, the Uruguayan coast and Samborombón Bay in Argentina. Evaluation of the mtDNA control region revealed high intra-population genetic diversity but no inter-population differentiation, indicating that the analysed black drum groups share a similar gene pool due to gene flow between areas. This is corroborated by migration estimates, which show a relatively high number of migrants from South Brazil to Uruguay/Argentina.

The highest genetic diversities were observed in black drum groups from Samborombón Bay and the Uruguayan coast (*h* = 0.99), and were slightly lower in those from the Lagoa dos Patos estuary (*h* = 0.90). Regarding the congeneric *Pogonias cromis* along the Gulf of Mexico and Atlantic coast of the United States, moderate genetic diversity (*h* ranging from 0.47 to 0.89) and high gene flow among groups was found (Grant and Bowen 1998; Leidig et al. 2015). The nucleotide diversity of *Pogonias courbina* from our study areas was low (mean π = 0.013), but slightly higher when compared to other marine and estuarine fishes studied in the Southwestern Atlantic: *Atherinella brasiliensis* (Cortinhas et al. 2016), *Micropogonias furnieri* (Pereira et al. 2009), *Cynoscion guatucupa* (Iriarte et al. 2011) and *Macrodon atricauda* (Rodrigues et al. 2014) (Table 4). This low nucleotide diversity (π), when considered with the high haplotype diversity (*h*), indicates that the population could have undergone a population reduction (e.g., through a bottleneck event) followed by growth, leading to an accumulation of mutations of few bases between haplotypes (Grant and Bowen 1998; Iriarte et al. 2011).

Two haplotypes were shared between the three regions, six between only Samborombón and Uruguay, and one only between Uruguay and Lagoa dos Patos Estuary; none was shared exclusively between Samborombón and Lagoa dos Patos, the two most distant areas. Most haplotypes were unique to each locality, but showed few differences between them. This can be observed in the haplotype network (Fig. 2), which exhibits an unstructured pattern with few shared

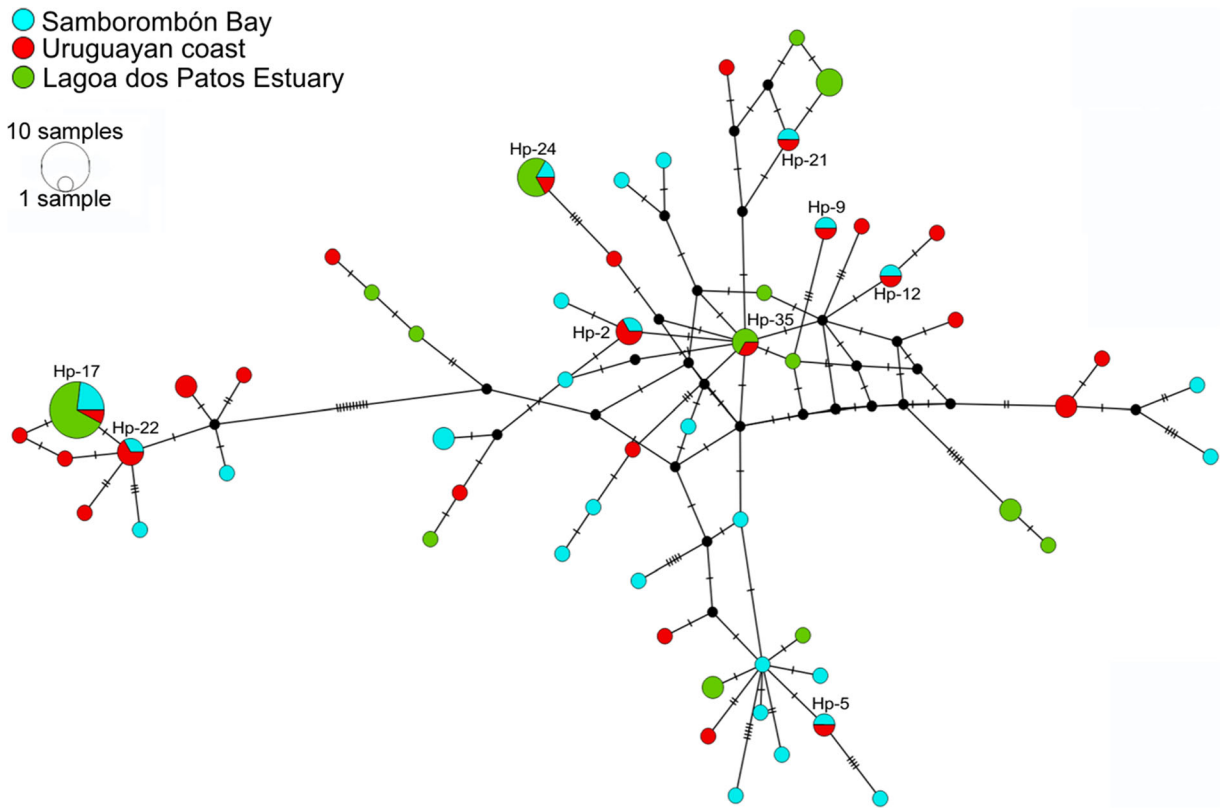


Fig. 3 *Pogonias courbina* haplotype network for the studied regions (Argentina, Uruguay and South Brazil). Each circle represents a distinct haplotype, with size being proportional to

frequency. Colors represent sampling locations and dashes indicate the number of mutations between haplotypes

haplotypes and a predominance of scattered, unique haplotypes separated by a small number of mutations. Similar mitochondrial DNA haplotype networks have been observed for other species at the region: *Macrodon atricauda*, with an extensive mixture between fish from Argentina and South Brazil (Rodrigues et al. 2014); and *Cynoscion guatucupa*, which did not display distinction

between groups from Argentina and the coast of São Paulo (Southeast Brazil) (Iriarte et al. 2011).

Population structure and connectivity

No genetic isolation was observed among the *Pogonias courbina* groups sampled from northern Argentina to southern Brazil, with very low Φ_{ST} rates suggesting genetic homogeneity. Migration rates also indicate high connectivity between areas, although the South Brazil group receives few (1.89 to 2.44) and exports many (48.24 to 53.78) individuals. In pelagic spawning fish, genetic flow between neighboring regions without physical barriers can be maintained by the mobility of adults from different regions during reproduction, as well as through the dispersal of eggs and larvae that recruit to areas far from the spawning site. For example, in *Gadus macrocephalus* groups in the northeastern Pacific Ocean, gene flow was maintained by a small number of migrants ranging from one to ten individuals per generation (Cunningham et al. 2009). Gene flow

Table 2 Phi ST (Φ_{ST}) values between *Pogonias courbina* sampled at Samborombón Bay (Argentina), Uruguay and Lagos dos Patos (South Brazil)

	Samborombón Bay	Uruguayan coast	Lagoa dos Patos
Samborombón Bay	–	0.551	0.192
Uruguayan coast	–0.008	–	0.627
Lagoa dos Patos	0.013	–0.011	–

Φ_{ST} is given below the diagonal, respective *p* values above diagonal

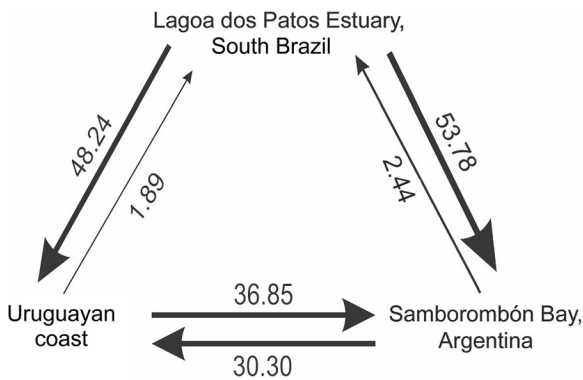


Fig. 4 Migration rates (number of migrants per generation) among *Pogonias courbina* groups from Argentina, Uruguay and South Brazil

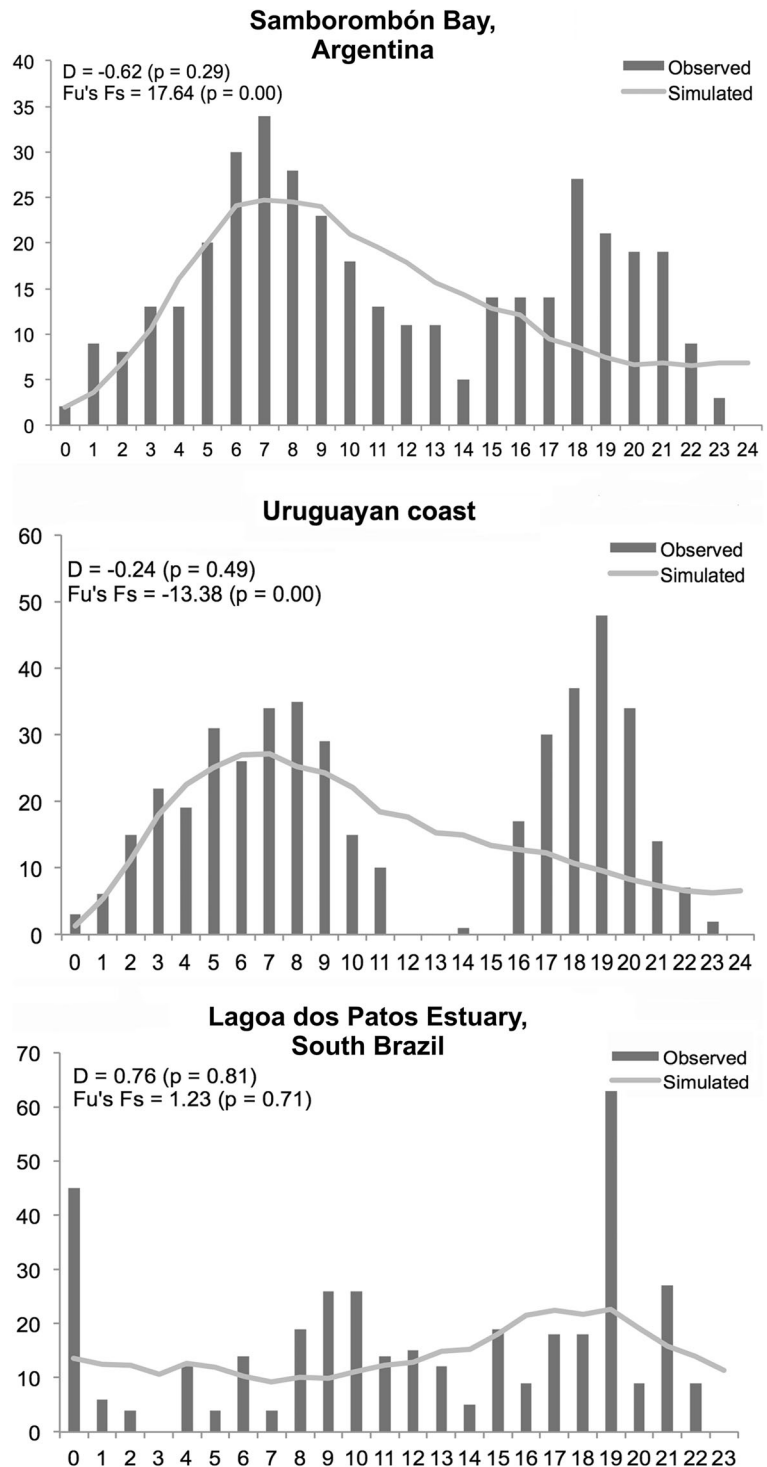
may occur between distant populations in species with continuous distribution, but reproduction is generally more frequent between geographically close individuals (Cunningham et al. 2009). However, despite having observed a larger number of haplotypes shared between groups of more proximal areas when compared to those of more distant ones, the migration rates we found did not show a clear pattern in terms of geographical distance. Mark/recapture studies at the eastern coast of the United States have shown that juvenile and adult (total length of 150 to 414 mm) *P. cromis* can occasionally perform long displacements, but shorter movements are predominant (Murphy et al. 1998; Leidig et al. 2015). The proximity between habitats (e.g., estuaries and bays) suitable for *P. cromis* could explain why most tagged individuals moved over short distances (Music and Pafford 1984; Murphy et al. 1998), and since *P. courbina* uses the same habitats, this could also explain our observations.

Factors such as coastal geomorphology, temperature, food availability and ocean currents can influence the migrations of marine animals (Beheregaray et al. 2002; Lima et al. 2016). Coastal circulation between northern Argentina and southern Brazil is dominated by the cool, north-flowing western branch of the Malvinas/Falkland current, which mixes with the Río de la Plata plume in the cold season, and the warmer and more saline south-flowing coastal waters of the Brazil current in the warm season; these currents meet at the Brazil-Malvinas Confluence Zone (Stramma and England 1999). Along the continental shelf of the region, two water masses predominate: Subantarctic Shelf Water (cold, low salinity) and Subtropical Shelf Water (warm, high salinity). Shelf circulation consists of the northern flow of

Subantarctic waters and the southern flow of Subtropical waters, which meet at the Subtropical Shelf Front that is also influenced by the Río de la Plata plume (Piola et al. 2000; Möller et al. 2008). These oceanographic features do not seem to represent a barrier for the displacement of marine fish at the region, since many species of teleosts and elasmobranchs carry out seasonal migrations across these confluence/frontal zones (Haimovici 1997; Vooren 1997). In fact, the genetic homogeneity observed between groups from northern Argentina and southern Brazil in our work has also been reported for other species of fish and crustaceans, such as *Macrodon atricauda* (Rodrigues et al. 2014), *Mugil liza* (Mai et al. 2014) and *Atherinella brasiliensis* (Cortinhas et al. 2016). In contrast, a recent study analyzing mtDNA D-loop sequences of *Menticirhus americanus* suggest a separation between the populations of Río de la Plata and southern Brazil (Márquez et al. 2017); however, this study evaluated a low number of individuals from the Brazilian group, which may have influenced results.

Although there are no apparent restrictions to gene flow between the studied black drum groups, the slow recovery of the southern Brazil stock after more than 30 years of its collapse indicates that displacement of individuals from Río de la Plata to the Lagoa dos Patos Estuary is likely small. Indeed, the migration rates showed a low number of migrants from Uruguay and Argentina to South Brazil, and a high number of migrants in the opposite direction. However, even the lowest number of migrants (1.89, from South Brazil to Uruguay) may be sufficient to indicate genetic connectivity between regions: if one to ten individuals per generation migrate between sites and reproduce, structure may no longer be detected (Slatkin 1987; Palumbi 2003). Apart from low number of migrants, seasonal migratory movements and the reproductive strategy of the species could explain the slow recovery of the Brazilian stock. In Argentina, *Pogonias courbina* is commercially fished Río de la Plata Estuary mostly throughout the reproductive season until November (Urteaga and Perrotta 2001). After reproduction, black drums move southwards along the coast where is targeted mainly by local recreational fisheries (Sentí la Pesca 2016) and reach south of the Buenos Aires province around February (Sentí la Pesca 2018). In southern Brazil, fishers report reproductive migrations of *Pogonias courbina* towards the estuarine region of the Lagoa dos Patos in the spring and there are no reports of

Fig. 5 Mismatch distribution, simulated expansion models and Tajimas's D and Fu's Fs values with associated probabilities for the sampled *Pogonias courbina* groups from Argentina, Uruguay and South Brazil, based on the mitochondrial DNA D-loop region



a directional migration when it returns to the ocean, as occurs in Argentina. In fact, black drum landings from industrial trawl fisheries in southern Brazil occurred throughout the year (IBAMA/CEPRG 2011), which

could be an indication of more limited movements when compared to stocks in Río de la Plata. A possible explanation for such limited movements could be the changes in mouth width and water mass circulation at the Lagoa

Table 3 Demographic parameters of the studied *Pogonias courbina* groups from Samborombón Bay (Argentina), the Uruguayan coast and Lagoa dos Patos estuary (South Brazil)

	Samborombón Bay	Uruguayan coast	Lagoa dos Patos
S	29	27	14
θ_0	0.000	11,781	0.000
θ_1	99,999	99,999	25,410
τ	4.381	3.270	19.811
t (years)	36,175	27,002	163,586
SSD	0.091	0.024	0.025
p (SSD)	0.000	0.154	0.099
Raggedness	0.006	0.010	0.056
p (Raggedness)	1.000	0.470	0.034

number of polymorphic sites (S); population size before expansion (θ_0); population size after expansion (θ_1); expansion parameter (τ); time since possible population expansions (t) (years); Sum of Squared Deviations (SSD) and p value; Raggedness index and p value

dos Patos Estuary due to the construction of two jetties (3.1 and 4.2 km in length) from 1911 to 1915 to provide access to the estuary's canal. From 2001 to 2011 the jetties were extended to 3.8 and 4.6 km, further altering circulation and likely leading to additional difficulty for marine organisms such as zooplankton, mollusks, crustaceans and fish to access the estuary (Odebrecht et al. 2010). The reduction in recruitment of fish larvae and juveniles directly affects adult stocks, and consequently reduces the abundance of fishery resources at the estuary (Fernandes et al. 2005).

Table 4 Haplotype (h) and nucleotide (π) diversities of marine and estuarine fish species from different areas of the Southwestern Atlantic

Species	Location	h	π
<i>Atherinella brasiliensis</i>	Lagoa dos Patos ^a	0.75	0.001
<i>Cynoscion guatucupa</i>	Río de la Plata ^b	1.000	0.019
<i>Macrodon atricauda</i>	Río de la Plata ^c	0.576	0.001
	Lagoa dos Patos ^c	0.591	0.0008
<i>Menticirrhus americanus</i>	Río de la Plata ^d	0.901	0.003
<i>Micropogonias furnieri</i>	Uruguayan coast ^e	0.455	0.003
<i>Pogonias courbina</i>	Samborombón ^f	0.995	0.014
	Uruguayan coast ^f	0.993	0.013
	Lagoa dos Patos ^f	0.889	0.013

^a Cortinhas et al. 2016; ^b Iriarte et al. 2011; ^c Rodrigues et al. 2014; ^d Freitas et al. 2017; ^e Pereira et al. 2009; ^f this work

At the Río de la Plata Estuary, *Pogonias courbina* spawns in low-salinity estuarine waters (Macchi et al. 2002), which limits the possibility of eggs developing and hatching at other distant estuaries, especially one with altered access such as Lagoa do Patos. This supports the hypothesis of limited gene flow between Río de la Plata and Lagoa dos Patos, since eggs and larvae transport between estuaries is likely low. As breeding areas are also estuarine, there may also be relative isolation of young fish between regions. The collapse of the black drum fishery in the Lagoa dos Patos Estuary lasted three decades, and only in 2010 the recruitment of *Pogonias courbina* juveniles began to be once again reported by artisanal fishers in Lagoa dos Patos (Santos et al. 2016). This interval corresponds to around 7–10 generations, but there is still no large-scale spawning as occurred in the decades prior to the fishery's collapse (Haimovici and Cardoso 2017). Since *Pogonias courbina* is a large species with prolonged spawning and high individual fecundity, the recolonization process could begin with the successful recruitment of the spawn of few specimens from neighboring regions; however, the slow of recovery of the stock indicates that these displacements are not frequent.

Historical demography

The studied black drum groups presented multimodal mismatch distributions, indicating demographic equilibrium. Neutrality indexes also indicated demographic equilibrium in the group from Lagoa dos Patos (positive Tajima's D and Fu's Fs); *P. courbina* landings in South Brazil decreased after 1981 (Fig. 1) due to overfishing, and the population that could have been expanding likely began a period of demographic equilibrium. Since the early 2010s the species seems to be undergoing a slow recovery process in Lagoa dos Patos Estuary, evidenced by a small number of captures at the region; however, this recovery is still likely undetectable in mtDNA. For the groups from Samborombón Bay and the Uruguayan coast, neutrality indexes indicated a recent subtle expansion (negative Tajima's D and Fu's Fs). This has also been observed for the Atlantic bonito (*Sarda sarda*) in the Mediterranean, which presented bimodal mismatch distribution and negative neutrality indexes suggesting population expansion (Viñas et al. 2004).

Regarding the estimated times since population expansion, *Pogonias courbina* from Samborombón Bay

and the Uruguayan coast presented shorter times since expansion (respectively 36,175 and 27,002 years) in relation to the Lagoa dos Patos Estuary (163,586 years). This period (Pleistocene) was characterized by several sea level transgressions and regressions, causing species expansions and retractions around the world and directly affecting their distribution and demography (Hewitt 1996). At Lagoa dos Patos several cycles of sea level transgressions/regressions occurred after the quaternary glaciations 230,000 years ago, strongly influencing the continental shelf and shaping the current Patos – Mirim estuarine system (Villwock 1984; Norris and Hull 2012). These cycles likely affected the movement of *Pogonias courbina* between regions, with groups from Lagoa dos Patos Estuary undergoing demographic expansions and possibly connecting with those from Río de la Plata during periods of high sea levels; this could explain the genetic similarity observed in the studied *Pogonias courbina* groups.

Implications for management and conservation

Pogonias courbina is currently classified as endangered in Brazil (MMA 2014) due to the drastic reduction of its abundance in the 1980's. Although it is currently beginning to recover, the black drum group from Lagoa dos Patos still has low abundance due to the slow recovery rates, especially in terms of large adults. Meanwhile, black drum stocks from Uruguay and Argentina did not suffer such reduction despite intense exploitation. Our mtDNA control region analyses indicated no structure between the *P. courbina* stocks from the three sampled areas in South Brazil, Uruguay and Argentina. However, considering that fleets operating at the regions are from different national jurisdictions, with different fishing gears, bycatch rates, conservation strategies and abundances, we suggest that the stocks be considered separate units that, at the moment, should be managed separately. More specifically, considering that the reproductive stock at Lagoa dos Patos is still technically collapsed, with annual catches well under 10% of the historical maximums, it is a management priority to recover the size and age structure that guarantees stock maintenance at the Lagoa dos Patos Estuary. Current measures ban targeted fishing but do not contemplate reductions in bycatch. On the other hand, the rare remaining large adults are vulnerable to the intense gillnet and trawl fishing that

occurs at the region (Santos et al. 2016). Theoretically, the black drum's high fecundity could allow that only a small number of breeders help recover recruit production at Lagoa dos Patos, as apparently began occurring from 2010. Nevertheless, the lack of adult black drum in landings at the area could be a result of untargeted bycatch that affects stock recovery and limits the practical effects of bans (Pauly 2009).

Conclusions

This work successfully described the population genetics of *Pogonias courbina* at the southern end of its distribution range, defining the sampled groups as a slightly expanding, connected population with high genetic diversity. These characteristics favor the resilience of populations, reducing the risk of extinction of local stocks. However, the low recovery after the collapse of the fishery at Lagoa dos Patos Estuary shows that the recolonization process is slow, possibly due to a low number of migrants arriving from Río de la Plata, and will require a longer timeframe. Despite the lack of genetic structure between regions, due to the reasons described above, we believe that the Brazilian reproductive stock should be considered unique and a priority in terms of management strategies. Management of the *Pogonias courbina* stock in the common fishery zone of Uruguay and Argentina could benefit from taking into account the slow recovery observed in South Brazil, in order to avoid further depletion of the adult fraction of their stocks. Finally, we suggest analysis of additional molecular markers and individuals from other sampling areas, as well as a better characterization of black drum movements and adult rearing sites (e.g., through tagging and stable isotope analysis), be conducted in order to aid management plans for this species in the Southwestern Atlantic.

Acknowledgements We thank Coordination for the Improvement of Higher Education Personnel (*Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* - CAPES), which provided access to the *Portal de Periódicos* and financial support through *Programa de Excelência Acadêmica* – PROEX. The National Council for Research and Development (*Conselho Nacional de Desenvolvimento Científico e Tecnológico* - CNPq) provided a research fellowship to M.H. (303561/2015-7) and M.C.P. (312470/2018-5).

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