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Resilience despite overfishing? Microsatellites reveal high genetic diversity and connectivity for *Umbrina canosai* (Acanthuriformes: Sciaenidae) in the Southwestern Atlantic

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Marine connectivity and demographic changes are important factors in the conservation and management of commercially exploited marine fishes. This study used seven microsatellite markers to evaluate the connectivity and potential loss of genetic diversity for the Argentine croaker (*Umbrina canosai*), a coastal sciaenid fish endemic to the Warm Temperate Southwestern Atlantic Province. Sampling was conducted across almost the entire species distribution: Southeastern Brazil, Southern Brazil, and Argentine-Uruguayan Common Fishing Zone. Despite historical overfishing, the analyses revealed high genetic diversity and connectivity, with no evidence of a genetic bottleneck. Previous studies based on phenotypical and ecological markers have proposed two distinct stocks for *U. canosai*. We hypothesized that a bidirectional gene flow between these stocks is promoted by the dispersal of planktonic eggs and larvae via marine currents in the Southwestern Atlantic, as well as by adult migrants. These conclusions support the species resilience and its IUCN classification as "Least Concern". Nevertheless, transboundary management measures by Brazil, Uruguay, and Argentina are necessary to prevent the economic collapse of *U. canosai* stocks.

Keywords: Conservation genetics, Fish migration, Fishery resources, Gene flow, Population genetics.

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Conectividade marinha e mudanças demográficas são fatores importantes para a conservação e manejo de peixes marinhos comercialmente explorados. Este estudo utilizou sete marcadores microssatélites para avaliar a conectividade e a potencial perda de diversidade genética da "castanha" ou "pargo blanco" (*Umbrina canosai*), um peixe cienídeo costeiro endêmico da Província do Atlântico Sudoeste Temperado Quente. A amostragem foi realizada em quase toda a distribuição da espécie: Sudeste do Brasil, Sul do Brasil e Zona Comum de Pesca Argentino-Uruguaia. Apesar da sobrepesca histórica, as análises revelaram altas diversidade genética e conectividade, sem evidências de gargalo genético. Estudos anteriores baseados em marcadores fenotípicos e ecológicos propuseram dois estoques distintos para *U. canosai*. Nós apresentamos a hipótese de que há um fluxo gênico bidirecional entre esses estoques, promovido pela dispersão de ovos e larvas planctônicas ao longo das correntes marinhas no Atlântico Sudoeste, bem como por migrantes adultos. Essas conclusões corroboram a resiliência da espécie e sua classificação pela IUCN como "Menos Preocupante". Contudo, medidas de manejo transfronteiriço por parte do Brasil, Uruguai e Argentina são necessárias para evitar o colapso econômico dos estoques de *U. canosai*.

Palavras-chave: Fluxo gênico, Genética populacional, Genética da conservação, Migração de peixes, Recursos pesqueiros.

INTRODUCTION

Understanding marine connectivity and demographic changes is important for the conservation and management of marine species, especially for marine fishes with commercial interest (Lowe, Allendorf, 2010; Cadrin *et al*., 2014). Genetic markers offer important information about ecological questions and are well-established techniques in fisheries science (Mariani, Bekkevold, 2014). Microsatellites are repetitive, noncoding regions of the DNA with high mutation rates, and have become popular tools for investigating genetic diversity, population structure, gene flow and demographic changes, as they can reflect the recent past of organisms (10–100 generations ago) (Selkoe, Toonen, 2006; Mariani, Bekkevold, 2014). Microsatellites have been applied to investigate the population genetics of important fisheries resources, including fishes of the family Sciaenidae, which are exploited worldwide (Vasconcellos *et al*., 2015; Almeida *et al*., 2022; Franco *et al*., 2023; Yu *et al*., 2024). Studies using these markers have indicated that fishing pressure can reduce the genetic diversity of marine fishes due to depleted population sizes, genetic drift and selection (Hauser *et al*., 2002; Pinsky, Palumbi, 2014).

The Warm Temperate Southwestern Atlantic Province (22°–41°S) includes three important marine ecoregions: Southeastern Brazil, Rio Grande and Uruguay-Buenos Aires Shelf (Spalding *et al*., 2007), which are limited by marine fronts (Acha *et al*., 2004). This Province supports highly productive fisheries in its ecoregions: Southeastern Brazil, Southern Brazil, and the Argentine-Uruguayan Common Fishing Zone (Defeo *et al*., 2025). Sciaenid fishes represent a significant portion of the captures in this Province

(Haimovici, Cardoso, 2017; Defeo *et al*., 2025), among which is the Argentine croaker, *Umbrina canosai* Berg, 1895. The Argentine croaker is a demersal fish endemic to the Warm Temperate Southwestern Atlantic Province, with a continuous distribution between São Tomé Cape in Brazil (22°S) and the Gulf of São Matias in Argentina (41°30'S) (Cousseau, Perrota, 2013). *Umbrina canosai* is a relatively small fish that reaches over 400 mm in total length, may live up to over 25 years, and has a relatively slow growth (Haimovici, Reis, 1984). The species produces high number of pelagic eggs (Haimovici, Cousin, 1989) and feeds on benthic organisms, mainly crustaceans and polychaetes (Haimovici *et al*., 1989). As a typical sciaenid, *U. canosai* produces species-specific croaking sounds in agonistic and reproductive situations (Tellechea *et al*., 2017).

During the austral summer, *U. canosai* is abundant in Northern Argentina, which is used as feeding ground. In the autumn, large numbers of breeders migrate towards Southern Brazil (28°40' to 33°50'S) to reproduce during winter and spring (Gonzalez Alberdi, Nani, 1967; Haimovici, Cousin, 1989), and the juveniles use this region as a nursery ground (Haimovici *et al*., 1996). Spawning females are also observed off the coast of Uruguay and Argentina in late spring (Militelli *et al*., 2013) and some adults remain along Southern Brazil in the summer, suggesting that there are possibly other shorter migratory patterns (Kikuchi *et al*., 2021). Additionally, the presence of both juveniles and adults in Southeastern Brazil (Zaneti-Prado, 1979; Haimovici *et al*., 2007, 2008, 2017), including individuals with mature gonads (DMV, 2019, pers. obs.), indicates that the species also reproduces along this region.

The occurrence of two *U. canosai* stocks was proposed by Zaneti-Prado, Vazzoler (1976) based on first maturity size: a north stock in Southeastern Brazil and a south stock from Southern Brazil to Northern Argentina. The two-stocks hypothesis was maintained in subsequent works (Haimovici, Cousin, 1989; Haimovici *et al*., 2006, 2008). Posteriorly, ecological and phenotypic approaches supported it: Canel *et al.* (2019) identified distinct parasitic assemblies, while Kikuchi *et al.* (2021) found different growth rates and sagittal otoliths shapes from these two regions.

Fisheries exploit the Argentine croaker throughout its entire distribution: Southeastern Brazil (FIPERJ, 2016; Instituto de Pesca/SP, 2026, www.propesq.pesca.sp.gov.br), South Brazil (FURG/SEMA/MPA, 2026), Uruguay (Uruguay/DINARA, 2019) and Northern Argentina (Navarro *et al*., 2022). The recorded catches peaked twice over time: more than 25,000 tons in the 1970's and more than 15,000 tons in the 2000's, both followed by a drastic decrease in catches (Haimovici *et al*., 2006, 2022). The industrial fleets include bottom trawls, gillnets and, since the 2000's, midwater trawls equipped with sonars, which target spawning adults on the external shelf of Southern Brazil (Haimovici, Cardoso, 2016). Consequently, this fishery is considered to be at risk of commercial collapse (Haimovici *et al*., 2006, 2022).

The mitochondrial genome of *U. canosai* was recently sequenced, along with several other bony fishes from the South Atlantic Ocean (Alvarenga *et al*., 2024); however, to the best of our knowledge, there are no studies focusing on its population genetics. Considering the importance of understanding genetic factors for fisheries management, in this work we used microsatellite markers to investigate 1) genetic diversity, 2) potential genetic bottleneck events, and 3) genetic connectivity for *U. canosai* throughout most of its distribution area in the Southwest Atlantic. We also evaluated the gonadal maturity stage of some individuals from Brazil in order to infer spawning seasonality and to associate it with larval dispersion.

MATERIAL AND METHODS

Study area. The Warm Temperate Southwestern Atlantic Province (22°–41°S) is dominated by the warm and saline Brazil Current flowing southwards, and the cold and less saline Malvinas Current flowing northwards, with both meeting at the Brazil-Malvinas Confluence at around 38°S; this latitude can vary according to the season (Fig. 1; map built in QGIS 3.34.11, QGIS Development Team, 2024) (Matano *et al*., 2010). On the continental shelf, these oceanic currents are diluted by fluvial drainage systems, and the Brazil Current originates the Subtropical Shelf Water, while the Malvinas Current originates Subantarctic Shelf Water (Piola *et al*., 2000). These shelf waters meet at the Subtropical Shelf Front at around 33°S, as an extension of the Brazil-Malvinas Confluence (Fig. 1) (Piola *et al*., 2000; Acha *et al*., 2004).

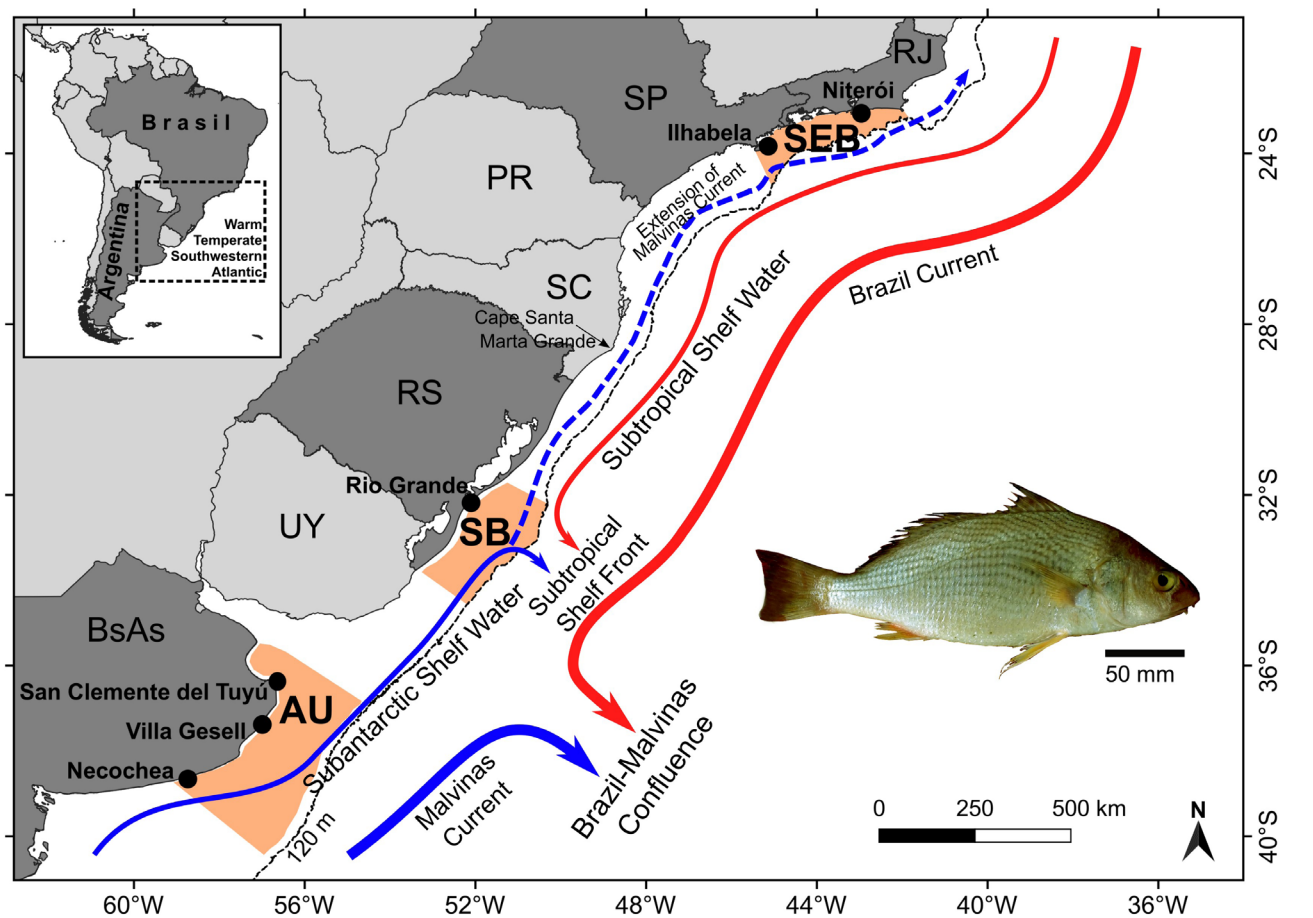

FIGURE 1 | Study area and sample design of Argentine croaker *Umbrina canosai* along its distribution range in the Warm Temperate Southwestern Atlantic Province. Genetic analyses considered the three regions in orange: 1) Southeastern Brazil (SEB), 2) Southern Brazil, and 3) Argentine-Uruguayan Common Fishing Zone (AU). Sampling locations are represented by black dots in the dark grey areas. In Brazil, samples were collected in Niterói, Rio de Janeiro State (RJ); Ilhabela, São Paulo State (SP); and Rio Grande, Rio Grande do Sul State (RS). In Argentina, samples were collected in San Clemente del Tuyú, Villa Gesell and Necochea in the Buenos Aires Province (BsAs). Adjacent areas in light gray: Uruguay (UY) and Brazilian States of Paraná (PR) and Santa Catarina (SC). Curved arrows indicate the warm (red) and cold (blue) marine currents of the Southwestern Atlantic.

Sampling. Adult specimens of *U. canosai* were collected along approximately 2,400 km of coastline in the Warm Temperate Southwestern Atlantic Province. Samples were obtained from commercial trawl and gillnet fisheries between 2015 and 2019, supported by partner institutions (Tab. 1). Three sampling regions were defined according to the marine ecoregions (Spalding *et al*., 2007), the main fishing areas of the species (Kikuchi *et al*., 2021; Defeo *et al*., 2025) and the previous studies evaluating their stocks (Canel *et al*., 2019; Kikuchi *et al*., 2021). The sampling regions are: 1) Southeastern Brazil (SEB), comprising samples from Niterói (Rio de Janeiro State) and Ilhabela (São Paulo State); 2) Southern Brazil (SB), comprising samples from Rio Grande (Rio Grande do Sul State); and 3) Argentine-Uruguayan Common Fishing Zone (AU), comprising samples from San Clemente del Tuyú, Villa Gesell and Necochea (Buenos Aires Province) (Fig. 1).

All fish have the sex, total length (TL, mm) and total weight (WT, 1 g precision) recorded. The gonads collected from each specimen from Brazil were weighed (WG, 0.01 g precision) and the maturity stage was recorded following the scale proposed by Haimovici, Cousin (1989), as was the gonadosomatic index: GSI = 100 x (WG/WT). The maturity stage and spawning seasonality were related to larval dispersion.

Voucher specimens. Muscle and DNA samples of *Umbrina canosai* (UC) were numbered from UCRS001 to UCSP251 and deposited in the Laboratório de Ecologia Molecular Marinha (LEMM) from Instituto de Oceanografia (IO), Universidade Federal do Rio Grande (FURG), Rio Grande, Brazil. The Tab. **S1** lists the voucher specimens analyzed in this study, according to Tab. 1.

DNA extraction, amplification and genotyping. For each region, over 30 individuals were selected for molecular analysis, with a similar number of females and males to avoid putative sex biases (Tab. 1). Approximately 2 g of muscle was collected from each individual and stored in absolute ethanol at -20 °C for further analyses. Genomic DNA was extracted with the saline method (Aljanabi, Martinez, 1997), and its concentration and purity were quantified with a BioDrop™ spectrophotometer (Biochrom™). DNA concentrations were standardized to 35-65 ng/µL (~50 ng/µL) by diluting in ultrapure water prior to amplifications.

Microsatellite loci were amplified via Polymerase Chain Reaction (PCR). Since no microsatellite primers specific for *Umbrina canosai* have been reported, we used cross-species transferability of markers (Barbará *et al*., 2007). Twelve primers from other species of sciaenids were tested: 1) primers for eight loci developed for *Micropogonias furnieri* and polymorphic for *U. canosai*: Mfur02, Mfur03, Mfur06, Mfur13, Mfur14, Mfur19, Mfur25 and Mfur26 (Vasconcellos, 2012; Molecular Ecology Resources Primer Development Consortium *et al*., 2012); and 2) primers for four loci developed for *Sciaenops ocellatus* (Turner *et al*., 1998; Saillant *et al*., 2004) and polymorphic for *M. furnieri* (D'Anatro *et al*., 2011): Soc049, Soc050, Soc085 and Soc204.

PCRs were performed with M13 tails with fluorescences 6-FAM, HEX, and NED (Tab. 2), in order to identify different loci during genotyping (Schuelke, 2000; Blacket *et al*., 2012). The reactions were carried out in a final volume of 20 µL each, containing: 1 x buffer (Buffer), 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.13 µM of the M13 tailed forward primer, 0.5 µM of the reverse primer, 0.25 µM of M13 tailed fluorescences, 1 U Platinum Taq DNA Polymerase (Invitrogen) and ~50 ng/µL of genomic DNA template,

TABLE 1 | Origin and characterization of *Umbrina canosai* specimens from the Southwestern Atlantic used for molecular analyses, with the region, location, partner institution that provided the specimens, fishing gear and type, sampling period, depth (m), number of individuals (n), sex, total length (mm) and total weight (g) of individuals. Und. = undefined.

Region	Location	Sampling institution	Fishing gear and type	Period	Depth	n	Sex	Total length	Total weight
Southeastern Brazil (SEB)	Niterói (RJ)	Fundação Instituto de Pesca do Estado do Rio de Janeiro (FIPERJ)	Bottom trawl (industrial)	Feb/2019	80–120	31	15 ♀ 16 ♂	282–361	250–542
	Ilhabela (SP)	Instituto de Pesca do Estado de São Paulo (IP/SP)	Gillnets (artisanal)	Sep/2019	16–25	33	15 ♀ 18 ♂	250–303	227–387
Southern Brazil (SB)	Rio Grande (RS)	Universidade Federal do Rio Grande (FURG)	Bottom and midwater trawls and gillnets (industrial)	Aug and Sep/2018	18–105	34	18 ♀ 16 ♂	225–411	144–982
Argentine-Uruguayan Common Fishing Zone (AU)	San Clemente del Tuyú (BsAs)	Universidad Nacional de Mar del Plata (UNMdP)	Bottom trawl (industrial)	Jan/2019	-	15	-	310–405	388–824
	Villa Gesell (BsAs)			Dec/2015	-	4	3 ♀ 1 ♂	340–375	498–640
	Necochea (BsAs)			Apr/2017	-	16	10 ♀ 5 ♂ 1 und.	250–355	238–528

and completed with ultrapure water (Schuelke, 2000; Vasconcellos *et al*., 2015). Most microsatellite markers were amplified separately (singleplex), and Mfur19 and Mfur25 were amplified simultaneously (multiplex) (Guichoux *et al*., 2011). Multiplex PCRs were performed with almost the same concentrations, but with 2 x buffer (Markoulatos *et al*., 2002), primer pairs of both markers, and twice the concentration of fluorescence. For each PCR reaction, a negative control (sample without DNA template) was included, in order to detect possible contamination.

PCRs were performed in a Veriti™ 96-Well thermocycler (Applied Biosystems). Thermocycling conditions for the *M. furnieri* microsatellites were: initial denaturation at 94°C for 5 min; 30 cycles of denaturation at 94°C for 45 s, primer annealing at 62 °C for 45 s, extension at 72°C for 45 s; followed by eight cycles of denaturation at 94 °C for 45 s, M13 tail annealing at 53°C for 45 s, extension at 72°C for 45 s; and a final extension at 72°C for 30 min (Schuelke, 2000; Vasconcellos *et al*., 2015). Thermocycling conditions for the *S. ocellatus* microsatellites were: initial denaturation at 94°C for 3 min; 35 cycles of denaturation at 94°C for 30 s, primer annealing at 60–62°C for 30 s, extension at 72°C for 30 s; followed by eight cycles of denaturation at 94°C for 45 s, M13 tail annealing at 53°C for 45 s, extension at 72°C for 45 s; and a final extension at 72°C for 30 min (Schuelke, 2000; D'Anatro *et al*., 2011).

To verify amplifications success, PCR products were subjected to electrophoresis with 1.8–2.0% agarose gel stained with GelRed (0.001%), along with a molecular-weight size marker, and visualized with a U.V. transilluminator. The concentrations of PCR products were estimated based on the molecular-weight size marker. Among the tested primers, Mfur13 and Soc049 were eliminated, as they did not amplify the *U. canosai* samples analyzed in this study. To maximize the number of loci per genotyping reaction, we combined the PCR products marked with different fluorescences in the same reaction (poolplex, Tab. 2) (Guichoux *et al*., 2011), and genotyping was done in an automated sequencer at Macrogen (South Korea, dna.macrogen.com).

TABLE 2 | Sequences, repetition motifs, annealing temperature, allele size and total number of alleles of the microsatellite primers used for *Umbrina canosai*, with the M13 tail underlined in the 5' region of each forward primer. To optimize genotyping, loci were combined in poolplex reactions according to the associated fluorescences. Mfur19 and Mfur25 were amplified in multiplex reactions. Soc050, Soc085 and Soc204 were amplified in the original species without the M13 tail; therefore, original allele sizes are smaller than those in this study.

Poolplex group	Locus	Primer sequences (5'- 3')	Repetitions	Fluorescence	Annealing temperature		Allele size (basepairs)		Total alleles in *U. canosai*	Original species
					Original	This study	Original species	*U. canosai*		
1	Mfur02	F: TGTAAAACGACGGCCTTT-GAGTTGGATGGATGAGC	$(CA)_{21}$	HEX	50 °C	62 °C	194–296	218–284	30	*Micropogonias furnieri* (Vasconcellos, 2012; Molecular Ecology Resources Primer Development Consortium *et al.*, 2012)
		R: AGTGAGTTTAGAGGGTCTGC								
	Mfur03	F: TGTAAAACGACGGCCATG-GAGCGATTAGGATGTGAAT	$(CA)_{19}$	FAM	50 °C	62 °C	240–336	226–286	26	
		R: CTGAAATGACTGAATGA-GGCTG								
	Mfur06	F: TGTAAAACGACGGCCTTCA-CGTCTGTAGCTGTGTGTG	$(TG)_{14}$	NED	50 °C	62 °C	245–267	255–323	30	
		R: GGAGACATCTGCCTGTT-GAAG								
2	Mfur14	F: TGTAAAACGACGGCCTCGT-GATGTAGGGTGAAATCAG	$(CA)_{22}$	FAM	50 °C	62 °C	244–284	238–280	20	
		R: TGTGCGAGTGTGAGTTTGCT								
	Mfu-r19a	F: TGTAAAACGACGGCCATT-CAGGTTTTGAGTACCG	$(TG)_{20}$	HEX	50 °C	62 °C	302–332b	278–354	28	
		R: TTGAACGACATGGTGCTAGG								
	Mfu-r25a	F: TGTAAAACGACGGCCCATG-GCTGTCAAAGAAAAGGA	$(TG)_{22}$	HEX	50 °C	62 °C	150–220	146–228	34	
		R: TGCCTGTAAGCATCAGCAAC								
	Mfur26	F: TGTAAAACGACGGCCGAG-GATTTTATTGGCTCGCA	$(GT)_{24}$	NED	60 °C	62 °C	264–326	264–280	8	
		R: GCCTGAGACGTGTTGACTGA								
3	Soc050	F: TGTAAAACGACGGCCCCCG-TGATTTTAGGCTCAGATA	$(GT)_{7}$	HEX	58 °C	62 °C	183c	195–279	31	*Sciaenops ocellatus* (Turner *et al.*, 1998; Saillant *et al.*, 2004)
		R: CCTTTAGAGTGCAGTAAG-TGATTT								
	Soc085	F: TGTAAAACGACGGCCTTTT-GGACCTACACTAGAGTAGC	$(AC)_{17}$	FAM	58 °C	62 °C	80–122c	114–186	35	
		R: CGTGGGAGACTAGCGAT-GTAGAT								
	Soc204	F: TGTAAAACGACGGCCACAG-CAGTACCTGCCCAAAACTG	$(CTG)_{12}$	NED	58 °C	60 °C	193c	205–235	11	
		R: TCCCCTTCGTCTTCTTC-CACTTC								

Data analysis. Genotype profiles were read on Peak Scanner™ 1.0 (Applied Biosystems). The true peaks (alleles) were visually differentiated from the stutter peaks and other types of artifacts, following the patterns described in literature (Selkoe, Toonen, 2006, appendix S2; Arif *et al.*, 2010; Guichoux *et al.*, 2011; Flores-Rentería, Krohn, 2013). Based on the peak readings, the distribution of raw genotype size was analyzed in the MsatAllele 1.05 package (Alberto, 2009) in R studio 4.0.2 (R Development Core Team, 2024), where each read mode was established as an allele class (bins). We verified if the allele classes followed the repetition motifs of each microsatellite (di- or trinucleotide), and we manually corrected them according to the read modes when necessary (DeWoody *et al.*, 2006).

Since the microsatellite markers used in this study were transferred from other sciaenid genera, limitations to amplify some loci were expected (Barbará *et al.*, 2007). Thus, Micro-Checker v. 2.2.3 (Van Oosterhout *et al.*, 2004) was used to inspect the

genotypes and estimate the frequencies of null alleles. Loci with high frequencies of null alleles (> 0.10) were excluded from analysis, while loci with moderate frequencies of null alleles (≤ 0.10) had the genotypes adjusted by the Oosterhout method. The input files for each analysis were formatted using Convert v. 1.31 (Glaubitz, 2004) and PGDSpider v. 2.1.1.5 (Lischer, Excoffier, 2012).

The genetic diversity was analyzed in different softwares: allele frequencies, number of alleles (N_A), allelic richness (A_R) and inbreeding coefficient (F_{IS}) were calculated in FSTAT v. 2.9.4 (Goudet, 2001); observed heterozygosity (H_O) and expected heterozygosity (H_E) were calculated in Arlequin v. 3.5.2.2 (Excoffier, Lischer, 2010). Hardy-Weinberg Equilibrium (HWE) and linkage disequilibrium were tested in GenePop v. 4.7.5 (Raymond, Rousset, 1995) using Markov Chains with 10,000 dememorization steps, 1,000 batches and 10,000 iterations per batch. The False Discovery Rate (FDR) procedure was used to correct the level of significance (α) in multiple tests (Benjamini, Hochberg, 1995; Waples, 2015).

To verify if *U. canosai* suffered loss of genetic diversity due to recent population decline, three bottleneck methods were applied to each region separately, as well as to the pooled sampling areas. The first method was the Wilcoxon test for heterozygosity excess, performed with 1,000 iterations in Bottleneck v. 1.2.02 (Piry *et al*., 1999). This test compares the expected heterozygosity under the Hardy-Weinberg Equilibrium (H_E) with the expected heterozygosity under the mutation-drift equilibrium (H_{EQ}), and a genetic bottleneck is inferred when there is a significant heterozygosity excess, *i.e*., $H_E > H_{EQ}$ (Luikart, Cornuet, 1998). H_{EQ} was calculated under the infinite alleles model, stepwise mutation model, and two-phase model. The two-phase model parameters were chosen following Peery *et al.* (2012): variance of mutations with more than one repetition $\sigma_g^2 = 12$ (corresponding to mean $\delta_g = 3.1$) and 78% of mutations with one repetition (22% with more than one repetition). The second method was the graphical test of rare allele deficit, also calculated in the Bottleneck software, under the previously described conditions. For stable populations, the allele frequencies present a L-shaped distribution; when there is a bottleneck, rare alleles are lost and the distribution changes its mode (Luikart *et al*., 1998). The third bottleneck method was the M ratio (Garza, Williamson, 2001), calculated in Arlequin, which is the ratio between the number of alleles (N_A) and the microsatellite size range (r) in terms of number of repetitions. A genetic bottleneck is assumed for populations with $M < 0.68$ (Garza, Williamson, 2001).

The genetic structure was investigated between pairwise localities by the exact G test of population differentiation in GenePop (with the same Markov Chain parameters described above), and by F_{ST} indices estimated in Arlequin. Two independent Molecular Analysis of Variance (AMOVA) were also conducted in Arlequin, each with 10,000 permutations, in order to compare: 1) the north stock (SEB) *vs*. south stock (SB + AU); and 2) among the three regions (SEB, SB, AU). Additionally, Structure v. 2.3.4 (Pritchard *et al*., 2000) was used to assign individuals with similar genotypes to the most likely population. For this, 1 to 3 populations (K) were simulated, with 20 replicates each, using a Markov Chain with 100,000 burn-in steps, followed by 200,000 simulation steps. The most likely number of K populations was chosen by the probability of individuals belonging to each K population and the largest L(K). The ΔK Evanno method (Evanno *et al*., 2005) could not be used because only three K populations were simulated.

The statistical power to identify a possible genetic differentiation was assessed by Chi-square and Fisher's exact tests in Powsim v. 4.1 (Ryman, Palm, 2006), which simulates the Wright-Fisher model for genetic drift. For this, we simulated a genetic differentiation of F_{ST} = 0.05 (combination of generation time of drift t = 200 with effective population size N_e = 2,000) and F_{ST} = 0.01 (t = 40; N_e = 2,000) for our sampling design and our allele frequencies. The type I error (α) was also assessed with the same scenario, simulating the base population before drift (t = 0). The Markov Chain parameters used for Powsim were the same for GenePop, running 1,000 replicates.

Migrations among the three regions were estimated in Migrate v. 5.0.4, a software based on the coalescence theory and Bayesian approach (Beerli, 2006). For this, the mean number of migrants per generation (γ) between regions was calculated as $\gamma_{ab} = \Theta_b.M_{ab}$, where Θ represents the mutation-scaled population size and M represents the mutation-scaled migration rate, from region *a* to *b*. Migrate combines the genetic data with an arbitrary prior distribution to the parameters Θ and M and generate a posterior distribution (Beerli, 2006; Beerli *et al*., 2019). The Brownian motion was employed, which is more suitable to microsatellite data. Different runs were performed, considering the default priors of the software, as well as arbitrary priors to Θ and M, using uniform or exponential distributions, with a range 0–20 to simulate a smaller population and a range 0–200 to simulate a larger population (Peter Beerli, 2025, pers. comm.). Better models were choose using the following diagnostics: higher marginal likelihood, calculated by the Bezier-approximated Thermodynamic integration (BTI); and Effective MCMC Sample Size (ESS) >1000 to each posterior parameter (Beerli *et al*., 2019).

RESULTS

Biological characterization. The genotyped fishes presented total lengths ranging from 225 to 411 mm and total weights ranging from 144 to 982 g (Tab. 1). The age classes varied from 1 to 12 years, representing an age-mixed sample (Kikuchi *et al*., 2021). Higher gonadosomatic index (GSI) means and the prevalence of mature females were observed in Rio Grande (SB) during August and September, and in Ilhabela during September (SEB), while lower GSI means and the prevalence of spawned females were observed in Niterói (SEB) during February. The GSI pattern observed in this study is in accordance with the reproductive seasonality for the species in Southern Brazil, as previously described by Haimovici, Cousin (1989) (Fig. 2). Therefore, we concluded that *U. canosai* spawns from late winter to spring in both Southeastern and Southern Brazil.

Molecular marker validation. The ten genotyped loci were polymorphic, totalizing 253 alleles identified (Tab. 2). The highest estimated frequencies of null alleles were found for Mfur26 (mean 0.338), Mfur19 (mean 0.205) and Mfur03 (mean 0.136); therefore, these three loci were excluded from all analyses. The loci Mfur02, Mfur06, Mfur14 and Soc204 presented null alleles for some regions in moderate estimated frequencies (mean ≤ 0.10) and were adjusted in Micro-Checker. The null alleles probably were the cause of two deviations from HWE for Mfur06 in SEB, and for Mfur14 in AU (Tab. 3), as well as of linkage disequilibrium in SEB for the loci pairs Mfur02-Soc204, Mfur14-

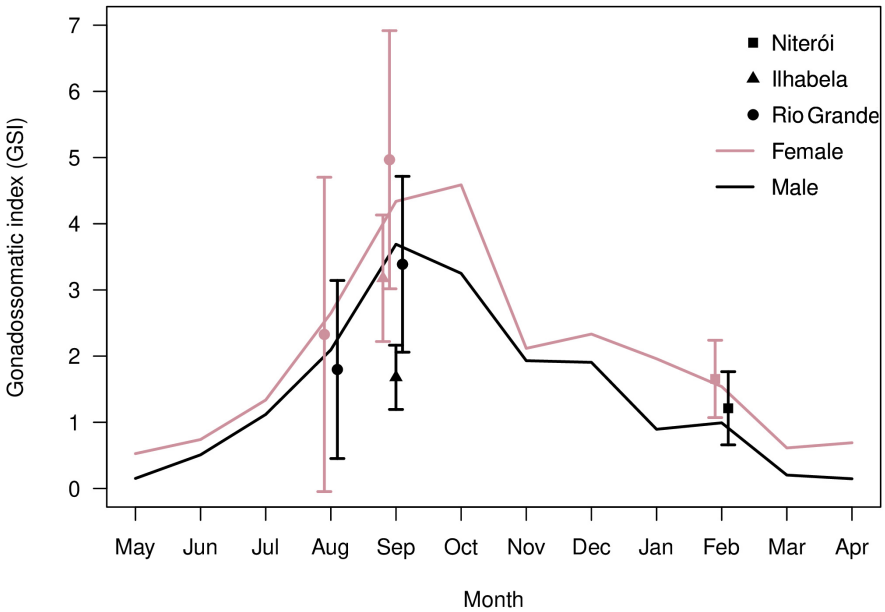

FIGURE 2 | Mean gonadosomatic indices (GSI) throughout the months of the year for both sexes of *Umbrina canosai* (pink for females, black for males). Lines represent previous data from Southern Brazil (Haimovici, Cousin, 1989). Shapes and standard deviation bars represent the data from this study. Squares: Niterói (February: 27 females, 70 males); Triangles: Ilhabela (September: 43 females, 79 males); Circles: Rio Grande (August: 26 females, 20 males; September: 25 females, 14 males).

TABLE 3 | Genetic diversity of *Umbrina canosai* from the Southwestern Atlantic, evaluated by seven microsatellite loci in three regions: Southeastern Brazil (SEB), Southern Brazil (SB) and Argentine-Uruguayan Common Fishing Zone (AU). For each locus and region, number of genotypes used (N), number of alleles (N_A), allelic richness (A_R), observed heterozygosity (H_O), expected heterozygosity (H_E), probability of conformity to Hardy-Weinberg Equilibrium (HWE) and inbreeding coefficient (F_{IS}) are shown. Asterisks indicate significant deviations from HWE after the False Discovery Rate procedure. Mfur = *Micropogonias furnieri*, Soc = *Sciaenops ocellatus*.

Locus	Index	SEB	SB	AU	All sampling area
Mfur02	N	51	33	34	118
	N_A	19	25	25	31
	A_R	16.132	22.152	22.378	19.642
	H_O	0.8039	0.8788	0.8235	0.8305
	H_E	0.9286	0.9552	0.9587	0.9437
	HWE	0.0645	0.4576	0.0248	
	F_{IS}	0.135	0.081	0.143	
Mfur06	N	34	28	29	91
	N_A	23	22	22	30
	A_R	21.11	21.198	20.732	22.247
	H_O	0.6471	0.9286	0.7931	0.7802
	H_E	0.9596	0.9565	0.9552	0.9588
	HWE	*<0.0001	0.4833	0.0117	
	F_{IS}	0.329	0.03	0.172	
Mfur14	N	47	30	26	103

TABLE 3 | (Continued)

Locus	Index	SEB	SB	AU	All sampling area
	N_A	17	16	17	20
	A_R	14.694	15.386	16.804	15.61
	H_O	0.8298	0.7667	0.6923	0.7767
	H_E	0.9153	0.9096	0.9163	0.9128
	HWE	0.0081	0.0949	*0.0004	
	F_{IS}	0.094	0.159	0.248	
Mfur25	N	58	29	26	113
	N_A	31	22	19	34
	A_R	22.157	20.791	18.728	20.919
	H_O	0.9138	0.9655	1.0000	0.9469
	H_E	0.9483	0.9480	0.9419	0.9448
	HWE	0.1139	0.4541	0.9138	
	F_{IS}	0.037	-0.019	-0.063	
Soc050	N	58	27	28	113
	N_A	27	21	20	32
	A_R	20.56	20.234	18.977	19.898
	H_O	0.8448	0.8889	0.8571	0.8584
	H_E	0.9267	0.9252	0.8974	0.9181
	HWE	0.0781	0.5793	0.6079	
	F_{IS}	0.089	0.04	0.046	
Soc085	N	54	25	28	107
	N_A	29	22	20	36
	A_R	20.154	22	18.782	19.799
	H_O	0.8148	0.8800	0.8214	0.8317
	H_E	0.9079	0.9200	0.9091	0.9100
	HWE	0.5674	0.5092	0.2398	
	F_{IS}	0.103	0.044	0.098	
Soc204	N	38	29	28	95
	N_A	8	10	6	11
	A_R	7.264	9.307	5.679	7.668
	H_O	0.6842	0.6207	0.6429	0.6526
	H_E	0.7368	0.6461	0.5753	0.6659
	HWE	0.0168	0.1954	0.7719	
	F_{IS}	0.072	0.04	-0.12	
All loci	N mean	48.6	28.7	28.4	105.7
	N_A mean	22.0	19.7	18.4	27.7
	A_R mean	17.4387	18.7240	17.4400	17.8676
	H_O mean	0.79120	0.84702	0.80434	0.8110
	H_E mean	0.90332	0.89438	0.87914	0.8934
	F_{IS} all loci	0.125	0.054	0.086	0.0883

Soc204, Mfur06-Mfur14 and Mfur02-Mfur14. Finally, Mfur25, Soc050 and Soc085 did not present null alleles, HWE deviations or linkage disequilibrium. Data analysis was performed only with the loci Mfur02, Mfur06, Mfur14, Mfur25, Soc050, Soc085 and Soc204.

Genetic diversity. The genetic diversity indices for the seven analyzed loci, with 217 alleles in total, are presented in Tab. 3. The indices ranges were: allele number (N_A) from 6 to 31; allelic richness (A_R) from 5.68 to 22.38; observed heterozygosity (H_O) from

0.62 to 1; expected heterozygosity (H_E) from 0.57 to 0.96; and inbreeding coefficient (F_{IS}) from -0.12 to 0.33. Soc204 was the unique trinucleotide locus analyzed, which showed lower diversity indices in comparison to the dinucleotide loci. Total means for diversity indices were: N_A = 27.7; A_R = 17.867; H_O = 0.811; H_E = 0.893; and F_{IS} = 0.088.

Genetic bottleneck. The data showed insufficient evidences of genetic bottleneck for *U. canosai* (Tab. 4). Under the infinite allele mutation model, which is more likely to indicate heterozygosity excess, the Wilcoxon tests were significant when considering only SEB and all sampling areas together (p-values < 0.05). Under the stepwise mutation and two-phase models, which are considered more suitable for microsatellites, all Wilcoxon tests were non-significant. After FDR procedure, all Wilcoxon tests were also non-significant. The allele frequency in the three regions, as well as when considering all sampling areas together, presented a L-shaped distribution, which indicates population stability. All mean M ratios were higher than the critical value M_C = 0.68, indicating absence of bottleneck effects.

Genetic connectivity. Our analyses indicated absence of genetic population structure and high connectivity of *U. canosai* among the three studied regions. None of the exact G tests between pairs of localities were significant (χ^2 from 10.96 to 21.67; df = 14; p-values > 0.08), and all F_{ST} indices were negative and non-significant (Tab. **S2**). The AMOVAs also showed negative fixation indices (F_{CT}, F_{SC}, F_{ST}) and all variations were attributed to within the regions (SEB, SB, AU), with no variation among regions or among the two stocks (north versus south) (Tab. **S3**). Since fixation indices are a measure between 0 and 1 (Wright, 1978), negative values were considered as near zero in pairwise tests and AMOVAs.

The Structure software also indicated lack of genetic population structure, with all individuals being equally likely to belong to any simulated population (Fig. 3). The highest L(K) values (mean = -4216.15) were found for K = 1 population. The genetic drift simulated by Powsim considered the allele frequencies, seven loci, three regions and the mean sample size in each region: 48 individuals in SEB, 28 in SB and 28 in AU (Tab. 3). Powsim showed a probability of 100% to detect genetic differentiations in these conditions, indicating a satisfactory statistical power for our analyses. The estimated type I error (α) was 0.042 for Chi-square test and 0.053 for Fisher's test, which approximate the conventional 0.05 limit for significance testing.

TABLE 4 | Genetic bottleneck methods for *Umbrina canosai* in the Southwestern Atlantic: Wilcoxon test of heterozygosity excess (p-values), under three mutational models; Garza-Williamson M ratio. Analyses were done separately for each region, and for all sampling area integrated.

Region	Wilcoxon test of heterozygosity excess			M ratio	
	Infinite alleles	Two-phase	Stepwise	Mean	Standard deviation
Southeastern Brazil (SEB)	0.0273	0.6562	0.9609	0.7646	0.0757
Southern Brazil (SB)	0.4062	0.8125	0.9609	0.7524	0.1584
Argentine-Uruguayan Common Fishing Zone (AU)	0.1484	0.8125	0.9609	0.7083	0.1378
All sampling area integrated	0.0391	0.9609	0.9805	0.8864	0.0899

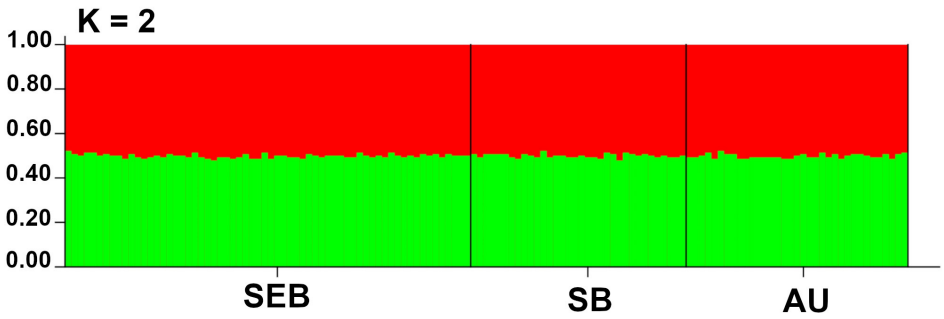

FIGURE 3 | Structure assignment probabilities for *Umbrina canosai* in the Southwestern Atlantic, simulating two populations (K = 2). Each vertical bar represents one individual, and vertical black lines separate the three regions analyzed: 1) Southeastern Brazil (SEB), 2) Southern Brazil, and 3) Argentine-Uruguayan Common Fishing Zone (AU).

A bidirectional gene flow among regions was estimated by Migrate, and the migration magnitude varied according to the arbitrary priors (Tab. **S4**). Model 0 was not considered, since the default priors of the software are not customized to microsatellite data (Peter Beerli, 2025, pers. comm.). In Models 1 and 2 (smaller population), the mean numbers of migrants per generation (γ) ranged, respectively, from 86.7 to 149.2 (general mean 107.16) and from 153.9 to 207.2 (general mean 179.93). In Model 3 (larger population), γ ranged from 498.1 to 3286.8 (general mean 1630.35). This last model achieved better diagnostics: higher log-marginal-likelihood (Bezier-approximated: -21559.57), and all parameters estimated showed Effective MCMC Sample Size (ESS) > 1000. Likely due to the highly variable dataset, the models did not agree on which region showed the largest migration (Tab. **S4**).

DISCUSSION

Genetic diversity and bottleneck. All sampled regions showed relatively high genetic diversity for *U. canosai*, with no evidences of a bottleneck event. The mean heterozygosities for this species were among the highest, considering exploited crustaceans and coastal bony fishes in the study area (Tab. 5). Decades of intensive fishing of the Argentine croaker led to the loss of larger, older female fishes, decrease of spawning potential and changes in populational parameters, such as sex rate, individual growth, and length and age of first maturity (Haimovici *et al*., 2022). Given this alarming scenery, why is there no evidence of a genetic bottleneck for *U. canosai*? Two aspects can be discussed: 1) the life history of *U. canosai*, and 2) the information provided by microsatellites.

Genetic diversity of marine fishes is usually positively correlated with population size (McCusker, Bentzen, 2010), and our data indicated that *U. canosai* still has a genetically stable population. Therefore, the demographic decline of *U. canosai* was not severe enough to implicate a genetic bottleneck (Chapman *et al*., 2011; Pujolar *et al*., 2011). As thousands of tons of individuals are still landed each year (Haimovici, Cardoso, 2016; Haimovici *et al*., 2022), the population size is likely still in the order of millions. Moreover, the high genetic connectivity observed in *U. canosai* could be counteracting genetic bottlenecks, since recovery of genetic diversity after a bottleneck event is faster if migrations occur between areas (Luikart, Cornuet, 1998; Chapman *et al*., 2011).

TABLE 5 | Coastal crustaceans and fishes evaluated by microsatellites in the Warm Temperate Southwestern Atlantic Province. Spawning and nursery environments by Castro *et al.* (2002), Capparelli *et al.* (2012), Haimovici, Cardoso, 2017. Microsatellite studies: area evaluated, number of loci, mean observed heterozygosity (H_O), mean expected heterozygosity (H_E), F_{ST} range, references. N = north; SE = southeast; S = south.

Group	Species	Spawning environment	Nursery environment	Area evaluated	Microsatellite loci evaluated	Mean H_O	Mean H_E	F_{ST} range	References
Decapoda, Penaeidae	White shrimp *Penaeus schmitti*	Shelf	Estuary	SE Brazil (24°S) to S Brazil (27°S)	6	0.8502	0.8633	-0.001 to 0.036	Maggioni *et al.* (2003)
Decapoda, Portunidae	Blue crab *Callinectes sapidus*	Shelf and estuary	Estuary	S Brazil (27–33°S)	9	0.5025	0.5466	-0.001 to 0.023	Lacerda *et al.* (2016)
Teleostei, Mugilidae	Mullet *Mugil liza*	Shelf	Shelf and estuary	SE Brazil (23°S) to N Argentina (36°S)	9	0.6774	0.6952	0 to 0.018	Mai *et al.* (2014)
Teleostei, Paralichthyidae	Mud flounder *Paralichthys orbignyanus*	Shelf	Shelf and estuary	S Brazil (32°S) to N Argentina (41°S)	7	0.866	0.848	0.003 to 0.023	Fainburg *et al.* (2023)
Teleostei, Sciaenidae	Striped weakfish *Cynoscion guatucupa*	Shelf	Shelf	N Argentina (36–40°S)	2	0.3990	0.8330	0.007	Sabadin *et al.* (2010)
	Jamaica weakfish *Cynoscion jamaicensis*	Shelf	Shelf	SE Brazil (23°S) to S Brazil (33°S)	6	0.3780	0.3908	-0.011 to 0.028	Silva (2015)
	Whitemount croaker *Micropogonias furnieri*	Shelf	Shelf and estuary	Uruguay and Rio de la Plata (34–35°S)	7 (including 2 non-neutral loci, D'Anatro 2017)	0.6656	0.7464	0.036 to 0.274	D'Anatro *et al.* (2011)
				SE Brazil (23°S) to Uruguay (34°S)	13	0.7187	0.7671	-0.027 to 0.013	Vasconcellos (2012)
				SE Brazil (23°S) to S Brazil (33°S)	4 (plus 4 introns)	-	-	0 to 0.096	Vasconcellos *et al.* (2015)
				SE Brazil (22–23°S)	12	0.6805	0.7503	0.012 to 0.101	Franco *et al.* (2023)
	Argentine croaker *Umbrina canosai*	Shelf	Shelf	SE Brazil (23°S) to N Argentina (38°30'S)	7	0.8110	0.8934	-0.072 to -0.001 (near zero)	This study

Microsatellites are neutral genetic markers, *i.e.* they do not directly influence phenotype and fitness (Kirk, Freeland, 2011; Mariani, Bekkevold, 2014). The selective harvesting that reduces larger and more fertile fishes (Haimovici, Cardoso, 2016; Haimovici *et al.*, 2022) can remove important alleles of genes influencing body size, reproduction traits, and adaptation to environmental conditions (Pinsky, Palumbi, 2014). This loss could be reflected by adaptive genetic markers, but not by using neutral microsatellites (Kirk, Freeland, 2011). Similarly, microsatellites did not detect genetic bottleneck in other overexploited bony fishes and elasmobranchs: *Micropogonias furnieri* and *Mugil liza* in the Southwestern Atlantic (D'Anatro *et al.*, 2011; Mai *et al.*, 2014), as well as *Pristis pectinata* and *Anguilla anguilla* in the North Atlantic (Chapman *et al.*, 2011; Pujolar *et al.*, 2011).

Genetic connectivity. Microsatellite analysis revealed "drift connectivity" for *U. canosai*, in which the gene flow is enough to maintain similar allele frequences in different regions (Lowe, Allendorf, 2010). This homogeneity may occur because throughout the Warm Temperate Southwestern Atlantic Province there are no obvious geographical barriers with the potential to stop gene flow (Acha *et al*., 2004; Spalding *et al*., 2007). Therefore, *U. canosai* eggs and larvae can be carried both northwards and southwards by marine currents before their larval settlement. Surface drifters have shown that an extension of the Malvinas Current can carry Subantarctic Shelf Water from 33°S in Southern Brazil up to 22°S in the Southeastern region during autumn and winter, mainly due to the action of cold fronts (Fig. 1) (Campos *et al*., 1996). This current can present linear displacements of 300 to 500 km per month, which corresponds to approximately 10 to 17 km per day, and is capable of carrying planktonic fauna from temperate to tropical zones (Campos *et al*., 1996; Stevenson *et al*., 1998). Conversely, the Brazil Current could carry eggs and larvae southwards.

The planktonic larval duration of *U. canosai* is not reported in literature, but can be inferred from related species. Sciaenid eggs take one day on average to hatch, as is the case of *Pogonias cromis* (Joseph *et al*., 1964) and *Micropogonias furnieri* (Albuquerque *et al*., 2009). Wild larvae of *Micropogonias undulatus* take approximately 40–50 days to attain 10 mm of standard length (Cowan, 1988; Nixon, Jones, 1997), which is the approximate settlement size for sciaenids and other coastal bony fishes, when larvae are capable of actively swimming to the bottom (reviewed by Clark *et al*., 2005; Leis *et al*., 2006). At 10 mm of total length, *U. canosai* larvae still have a frontal oblique mouth, and at 22 mm the mouth moves slightly to the inferior position, indicating the transition between the plankton phase and the settlement (Weiss, 1981). Therefore, *U. canosai* larvae likely remain in the plankton for at least 40 days, assuming that planktonic larval duration is similar in benthic feeding sciaenids from warm temperate waters. Forty days is probably sufficient for some larvae spawned in the southern range of the species to reach and recruit in its northern range or vice-versa. *U. canosai* spawns during from late winter to spring in Southern Brazil (Haimovici, Cousin, 1989), and the gonadal data observed in this study suggests that the spawning in Southeastern Brazil occurs during the same period (Fig. 2). This overlap can favor the mixture of larvae, contributing to the lack of genetic differentiation between regions.

In terms of migrations, large schools of breeders are known to migrate hundreds to a thousand kilometers between Northern Argentina and South Brazil during the reproductive season, reaching up to the Cape Santa Marta Grande (28°40'S) (Haimovici, Cousin, 1989). It is possible that some move further north to spawn, aided by the extension of the Malvinas Current in winter and early spring (Campos *et al*., 1996). Individuals can also migrate in the opposite direction in late spring, favored by the Brazil Current. The genetic mixture of *U. canosai* could be occurring in a "stepping stone" manner, with individuals in Southern Brazil as a midpoint for gradual migrations over generations between Southeastern Brazil and Northern Argentina. Different tagging experiments have shown that coastal bony fishes travel on average tens of kilometers in periods from ~200 days to more than one year. On the other hand, some individuals can move over larger distances, with records of more than a thousand kilometers traveled (Iversen, Tabb, 1962; Murphy *et al*., 1998; Dunlop *et al*., 2013).

Genetic patterns in the Warm Temperate Southwestern Atlantic. Populations of crustaceans and coastal bony fishes have been investigated by microsatellites in the Warm Temperate Southwestern Atlantic Province (Tab. 5). Their life cycles include spawning and nursery on the continental shelf (*Callinectes sapidus*, *Cynoscion guatucupa*, *Cynoscion jamaicensis*, *U. canosai*), use of estuaries as nurseries (*C. sapidus*, *Penaeus schmitti*, *Micropogonias furnieri*, *Mugil liza*, *Paralichthys orbignyanus*) or even spawning in estuaries (*C. sapidus*) (Castro *et al*., 2002; Capparelli *et al*., 2012; Haimovici, Cardoso, 2017). Most of them exhibited low genetic structure across the Province (F_{ST} < 0.05; Tab. 5) and corroborate the general pattern of connectivity for marine fishes with planktonic larvae, which can be dispersed via ocean currents (Cooke *et al*., 2016).

Nonetheless, some studies reported moderate to high genetic structure to *M. furnieri* along the Province (F_{ST} > 0.05; Tab. 5). Three aspects can explain this genetic contrast between *M. furnieri* (structured) and *U. canosai* (high connectivity). First, *U. canosai* was evaluated here only by neutral microsatellites, while some studies evaluated *M. furnieri* using microsatellites jointly to intron length polymorphisms (Vasconcellos *et al*., 2015) or linked to non-neutral regions (D'Anatro *et al*., 2011; D'Anatro, 2017), which probably influenced F_{ST} values. Second, a study sampled *M. furnieri* along the Rio de Janeiro coast and included an area north of Cape Frio (23°S), considering individuals outside of the Warm Temperate Southwestern Atlantic Province (Franco *et al*., 2023). Third, both sciaenid species have distinct life cycles, and this likely drives their population genetics. *M. furnieri* uses estuaries and lagoons as nursery ground; this strategy, associated with semi-closed environments, can favor a partial genetic isolation, as observed along the Uruguay coast (D'Anatro *et al*., 2011). On the other hand, *U. canosai* completes the entire life cycle in the continental shelf. In the ocean, F_{ST} values accumulate slowly along vast distances. At least 5,000 km would be necessary for a fish of median size to achieve high genetic structures between populations (F_{ST} > 0.15) (Cooke *et al*., 2016). Since the Warm Temperate Southwestern Atlantic Province has approximately 2,500 km in a straight line, this is not likely to occur.

Implications for conservation and management. The conservation status of *U. canosai* was categorized in 2019 as "Least Concern" by the International Union for Conservation of Nature (IUCN), since the global declines were not considered to result in the endangerment of the species (Haimovici *et al*., 2021). Despite its overfishing, *U. canosai* could be resilient due to its biological characteristics: relatively small-body, high fecundity, long spawning season, flexible and early age maturity, and flexible and fast individual growth (Haimovici, Cousin, 1989; Haimovici *et al*., 2022). These characteristics contrast to those of more vulnerable marine fishes, which are usually large-bodied and have late age at maturity (Reynolds *et al*., 2005; Olden *et al*., 2007). Genetic data can provide information on the risks of local and global extinctions (Collen *et al*., 2016) and the microsatellite data corroborated the low risk of extinction reported by IUCN (Haimovici *et al*., 2021), as well as the resilience capacity observed for the species (Haimovici *et al*., 2022).

In fisheries management, a holistic approach to fish stock identification is desirable (Begg, Waldman, 1999; Cadrin *et al*., 2014). For *U. canosai*, previous studies on the parasitic assembly, growth and otolith shape identified two demographically distinct stocks: one in Southeastern Brazil, and another from Southern Brazil to Northern

Argentina (Canel *et al*., 2019; Kikuchi *et al*., 2021). These environment-based techniques can be complemented by the inheritance-based microsatellites, which showed high connectivity between stocks. In this scenario, the removal of individuals from a stock can be recovered by immigrants from the neighboring stock, a phenomenon known as "rescue effect" (Benestan, 2019). Conversely, overexploitation can cause the gradual depletion of both stocks. Therefore, a collaborative management by Brazil, Uruguay, and Argentina is necessary for the *U. canosai* conservation, given that it is a migratory, transboundary and genetically connected marine fish (Defeo *et al*., 2025).

Caution is needed considering the limitations of a standard panel of microsatellites (Mariani, Bekkevold, 2014; Benestan, 2019). Measures should be considered to prevent the risk of economic collapse for Argentine croaker, *i.e.* when stocks decline and no longer contribute to the fisheries production (Haimovici, Cardoso, 2016; Haimovici *et al*., 2022). Moreover, the Southwestern Atlantic is considered an ocean-warming hotspot. In this sense, climatic changes can drive new impacts on *U. canosai* not considered in this study, such as the reduction of larval connectivity caused by tropicalization and alterations in current routes (Defeo *et al*., 2025).

Finally, additional studies with non-neutral/adaptive genetic markers and genomic methods, such as single nucleotide polymorphisms (SNPs) (Benestan, 2019), should be conducted to further enlighten the resilience and population genetics of *U. canosai*, and increase the resolution for stock delimitations.

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AUTHORS' CONTRIBUTION

Davi M. Vasconcellos: Data curation, Formal analysis, Investigation, Methodology, Software, Writing-original draft, Writing-review and editing.

Ana Luzia Lacerda: Formal analysis, Software, Validation, Writing-review and editing.

Maíra Carneiro Proietti: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing-review and editing.

Manuel Haimovici: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing-review and editing.

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ETHICAL STATEMENT

All animals used in this study were obtained by commercial fishery; therefore, no ethics approval was needed.

DATA AVAILABILITY STATEMENT

The microsatellite data are available in the Figshare repository at https://doi.org/10.6084/m9.figshare.30615713. The DMV's M.Sc. dissertation (Portuguese and English) is available at https://argo.furg.br/?BDTD12916 and includes a guide in Portuguese to interpret genotype profiles.

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Neotropical Ichthyology

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