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Close genetic similarity among populations of the white croaker (*Micropogonias furnieri*) in the south and south-eastern Brazilian coast. I. Allozyme studies

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Abstract

Micropogonias furnieri (*white croaker*) is a demersal sciaenid species highly exploited along the south-eastern coast of South America. Off the Brazilian Coast some morphological and population dynamic characters suggested the presence of two partially isolated populations between 23°S and 33°S latitude. To study the white croaker population structure in this area, 17 enzyme and one protein-encoding loci were examined by starch and polyacrylamide gel electrophoresis in seven sampling sites for a total of 638 individuals.

The allozyme results showed a high degree of genetic homogeneity in allele frequencies (F_{st}=0.005) and also high levels of gene flow were found among the sampled populations. Therefore, the results do not support the hypothesis of the presence of two partially isolated populations of the white croaker in the studied area. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: White croaker; *Micropogonias furnieri*; Population genetics; Isozymes; South Brazil

1. Introduction

The white croaker *Micropogonias furnieri* Desmarest (Sciaenidae) is a bottom dwelling marine species, long lived and with high adaptive capability to the variable conditions of its habitat. The family Sciaenidae contains more than 245 species, and 57 are described for the western Atlantic Ocean (Chao, 1978). The species that belong to this family are mainly marine, usually inhabit coastal areas, and reproduction may take place close to bay entrances, estuaries or open sea where eggs are dispersed by currents. The white croaker is distributed from the Yucatan Peninsula (Gulf of Mexico, 20°N) to the Gulf of San Matias (Argentina, 41°S) (Chao, 1978; Isaac, 1988). The species shows a high preference for estuarine areas, using them as nursery grounds, but this behaviour appears not to be strict (Castello, 1986). Despite its wide distribution it is commercially fished only from Cabo Frio (Brazil, 23°S) to the south (Vazzoler, 1991), where because of its abundance, it is heavily exploited. (Haimovici et al., 1989).

Studies in the Brazilian coast show different abundance patterns for the white croaker (for review see Vazzoler, 1991). Along the south-eastern coast (23°S–29°S) the abundance is low and homogeneous, while in the south (29°S–33°S) it is about eight times greater, and there is schooling with seasonal displacement

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according to the oceanographic conditions. The analysis of some life-history parameters show differences, for example, in time and area of spawning, and size and age of sexual maturation. Therefore, the presence of two fishery stocks is suggested described as population I (23°S–29°S) and population II (29°S–33°S); these populations would be isolated to some degree by a convergence system, the Subtropical Convergence (Vazzoler, 1971). Nevertheless, the genetic differentiation between these populations, although suggested, remains to be studied.

A thorough understanding of white croaker population structure is necessary for the effective management of this economically important marine resource for Brazil, Uruguay and Argentina. In marine environments the geographical structure of populations may be influenced by local environmental requirements and the species life-history, so, the potential for dispersal of a species does not always predict the amount of gene flow among geographical populations (Burton, 1983; Palumbi, 1995). Several geographical and ecological factors have been considered to constrain the dispersal capability of marine species (Palumbi, 1995), for example, spawning home behaviour, sharp temperature or hyaline gradients, and larval retention mechanisms (Sinclair, 1988). The geographical structure of a species is due not only to the actual gene flow but more important, to historical gene flow between geographical populations (Slatkin, 1993).

Recently, many studies have been carried out to assess levels of genetic differentiation and gene flow within several economically important marine fish species (e.g. Ramsey and Wakeman, 1987; Bowen and Avise, 1990; Elliott et al., 1994; Gold et al., 1994; Grewe et al., 1994; Ward et al., 1994a). These studies are relevant not only to evolutionary biology but also to the management of these stocks, providing information to adjust regulations according to the stock structure.

The aims of this study are to characterise the genetic structure of *M. furnieri* in the Brazilian Coast, and to estimate the levels of gene flow between the populations through allozyme electrophoresis.

2. Materials and methods

Samples were taken by trawling with a bottom gear between 13 and 65 m depth from seven locations (Fig. 1). Six hundred and thirty eight individuals were sampled for liver and skeletal muscle, and 389 for blood. The blood samples were taken by cardiac puncture and centrifuged at $3000\times g$ for 5 min to separate the plasma. All samples were stored at -20°C for no longer than a month.

Muscle and liver samples were macerated on Tris–Hcl 0.05 M pH 7.5 buffer and homogenates were centrifuged at $3000\times g$ for 5 min. Preliminary screening of 21 enzyme systems for liver and muscle resolved 12 enzymes which showed enough activity and good resolution to be genetically interpreted. Moreover, transferrin was also assayed and resolved (Table 1). Vertical 10% polyacrylamide-gel electrophoresis was used for esterase and transferrin, whereas for the remaining enzymes systems horizontal 14% starch-gel electrophoresis was carried out. Polyacrylamide gels were prepared with Tris–citrate–borate–lithium hydroxide pH 8.15 buffer (Shaklee and Keenan, 1986), and starch gels were prepared with Tris–citrate pH 8.0 buffer (Siciliano and Shaw, 1976). Staining solutions followed those proposed by Harris and Hopkinson (1978) and Levy (1995). Transferrin electrophoresis was done by defrosting plasma samples and treating them with rivanol 0.4%. The mixture was then incubated for 1 h at 5°C and centrifuged at $3000\times g$ for 10 min. The gels were stained with Coomassie Blue 0.1% and the position of transferrin bands was confirmed through staining with R nitrous salt (Mueller et al., 1962).

Alleles were designated by letters and the loci by numbers, both in order of decreasing mobility. The nomenclature used for designating loci was the one described by (Shaklee et al., 1990). Intrapopulation genetic variation was assessed by using the following measures: mean proportion of polymorphic loci (P) (frequency of the most common allele not greater than 0.95 and 0.99), mean observed heterozygosity per locus (Ho), and the unbiased estimate of mean expected heterozygosity per locus under random mating (He) (Nei, 1978). Departures of genotype frequencies from those expected under Hardy–Weinberg equilibrium were tested either using chi-square goodness-of-fit analysis or using an exact test. If more than two alleles were present at a locus, rare alleles were pooled for the analysis (Sokal and Hohlf, 1995). Deviations from random-mating expectations within populations were estimated for all loci using F_{is}

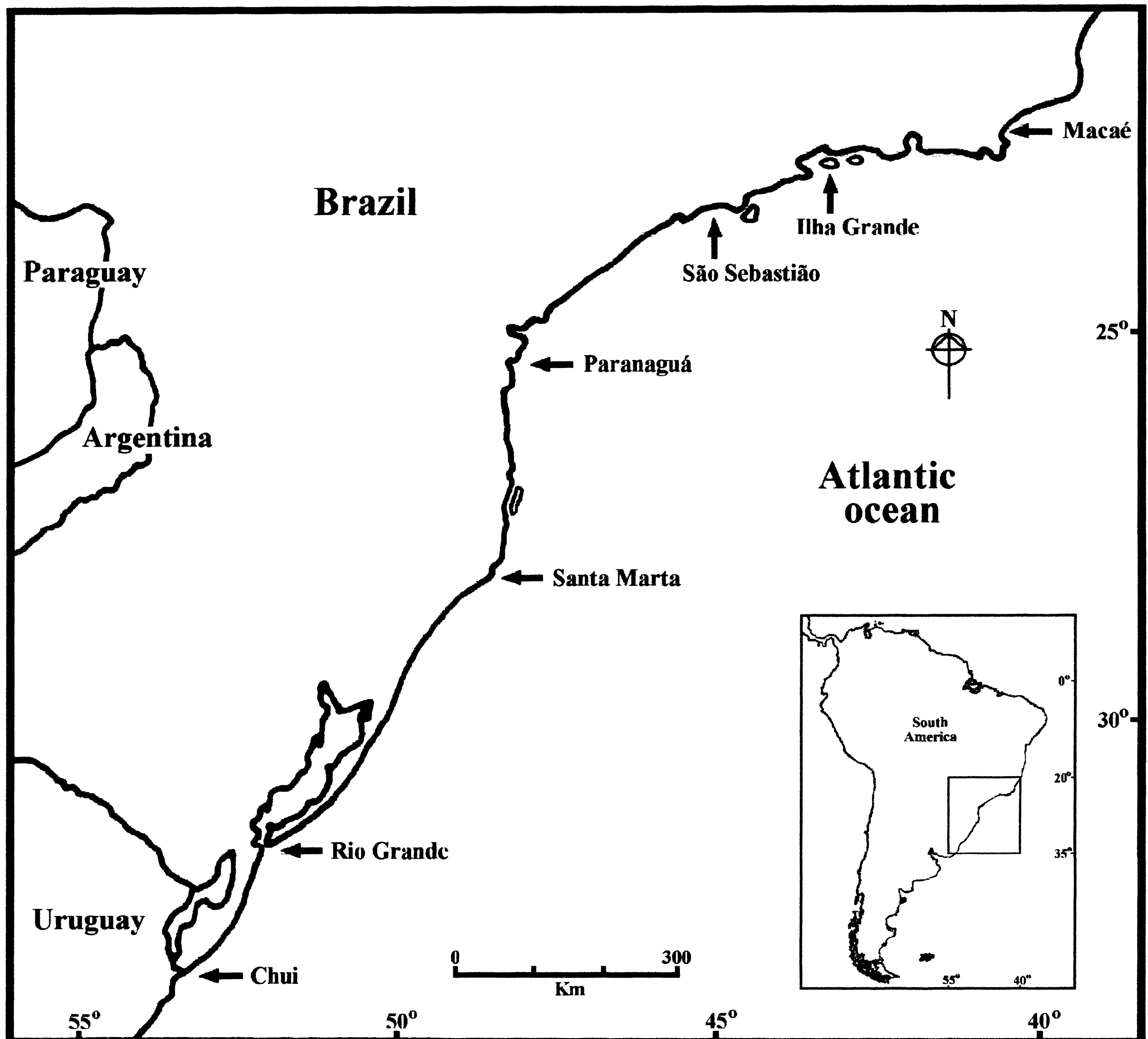

Fig. 1. Sampling sites of *Micropogonias furnieri* in the south and southern coast of Brazil.

(Wright, 1978), and the statistical significance of each F_{is} was tested using the relationship $\chi^2 = F_{is}^2 N(k-1)$, d.f. $= k(k-1)/2$, where N is the sample size for the populations, and k is the number of alleles at the locus (Li and Horvitz, 1953).

Inter-population comparisons of allele frequencies were made using contingency chi-square analysis. Genetic differentiation among populations was estimated as Wright's standardised variance in allele frequencies (F_{st}). F_{st} for each locus between samples was calculated using the formulations of Wright (1978), and the significance of F_{st} estimates was tested using the relationship with $\chi^2{=}2NF_{st}(k{-}1)$ with $(k{-}1)(s{-}1)$ degrees of freedom, where N is the total number of individuals sampled across s populations, and k is as defined above (Workman and Niswander, 1970). The Biosys-1 programme (Swofford and Selander, 1981) was used to analyse the genotypic data. The average number of migrants per generation (N_m) was estimated using the equation for an Island Model,

Table 1
Enzyme systems assayed, enzyme abbreviations (Abbrev.), EC numbers; tissue and number of loci obtained for those systems that were successfully scored

Enzyme system	Abbreviation	EC number	Number of loci	Tissue
Aspartate aminotransferase	AAT	2.6.1.1	1	Liver
Acid phoshpatase	ACP	3.1.3.1	1	Liver
Alcohol dehydrogenase	ADH	1.1.1.1	–	–
Aldehyde oxidase	AO	1.2.3.1	–	–
Alkaline phosphatase	ALP	3.1.3.1	1	Liver
Esterase	EST	3.1.1.-	3	Muscle
Glucose dehydrogenase	GDH	1.1.1.47	–	–
Glucose-6-phosphate isomerase	GPI	5.3.1.9	2	Muscle
Glutamate dehydrogenase	GLUDH	1.4.1.2	–	–
Glycerol-3-phosphate dehydrogenase	G3PDH	1.1.1.8	1	Muscle
Glucose-6-phosphate dehydrogenase	G6PDH	1.1.1.49	–	–
3-Hydroxybutyrate dehydrogenase	HBDH	1.1.1.30	–	–
Hexokinase	HK	2.7.1.1	–	–
L-Iditol dehydrogenase	sIDDH	1.1.1.14	–	–
Isocitrate dehydrogenase ($NADP^+$)	IDHP	1.1.1.42	1	Liver
L-Lactate dehydrogenase	LDH	1.1.1.27	2	Liver
Malate dehydrogenase	sMDH	1.1.1.37	2	Muscle
Malic enzyme ($NADP^+$)	sMEP	1.1.1.40	1	Muscle
Phosphoglucomutase	PGM	5.4.2.2	1	Muscle
Superoxide dismutase	sSOD	1.15.1.1	1	Liver
Xanthine dehydrogenase	XDH	1.1.1.204	–	–
Transferrin	TF	–	1	Blood

(–) Not enough activity and resolution to be scored.

$N_m=(1/F_{st}-1)/4$, at equilibrium (Slatkin, 1993). Estimated levels of gene flow are averages over a large number of generations. All chi-square tests were appropriately corrected for multiple tests with the sequential Bonferroni procedure (Rice, 1989).

3. Results

All individuals were successfully analysed for 12 enzyme systems and for transferrin, coded by a total of 18 putative loci. The loci *AAT**, *G3PDH**, *LDH-1**, *sMDH-1**, *sMDH-2**, *MEP**, *ACP**, and *ALP** were monomorphic. The allele frequencies for the polymorphic loci are shown in Table 2.

No significant deviations from Hardy–Weinberg expectations were observed for the polymorphic loci analysed after the correction for multiple simultaneous tests using the sequential Bonferroni procedure (cf. Rice, 1989). The locus *EST-3** showed the highest F_{is} value, however, this value was not significantly different from zero after the correction for multiple tests (data not shown). Since no overall trend in heterozygote deficiency or excess was found for any locus, the basic genetic model of inheritance for the enzyme systems analysed cannot be rejected. Summary statistics on genetic variability are provided in Table 3. The mean observed heterozygosity ranged from 0.044 for Chuí population (CH) to 0.063 for Paranaguá population (PR).

Results for the chi-square contingency analysis indicated that there were no significant differences in allele frequencies among the sampled populations (Table 4). The analysis of the genetic structure of the studied populations by means of *F*-statistics and the estimates of gene flow among the populations are shown in Table 5. Low estimates of F_{st} (mean F_{st}=0.005) suggested a high level of homogeneity between the populations and the lack of a genetic structure. Estimates of gene flow among populations also demonstrated high levels of gene flow. The mean estimated effective number of migrants (N_m) among the populations was 49 migrants per generation.

Table 2
Allele frequencies in the seven sampling sites for the 10 variable loci

Locus	Allele	Sampling sites						
		CH	RG	SM	PR	SS	IG	MC
*EST-1**	A	0.020	0.012	0.020	0.000	0.005	0.036	0.025
	B	0.000	0.018	0.007	0.019	0.010	0.005	0.000
	C	0.775	0.741	0.743	0.791	0.785	0.745	0.809
	D	0.205	0.229	0.230	0.190	0.195	0.214	0.167
	E	0.000	0.000	0.000	0.000	0.005	0.000	0.000
*EST-2**	A	0.000	0.000	0.000	0.000	0.015	0.010	0.000
	B	1.000	1.000	1.000	1.000	0.985	0.990	1.000
*EST-3**	A	0.010	0.066	0.059	0.057	0.060	0.036	0.069
	B	0.990	0.934	0.941	0.943	0.940	0.964	0.931
*GPI-1**	A	0.000	0.006	0.000	0.006	0.005	0.010	0.010
	B	0.960	0.940	0.954	0.937	0.935	0.944	0.946
	C	0.040	0.054	0.046	0.057	0.060	0.041	0.044
	D	0.000	0.000	0.000	0.000	0.000	0.005	0.000
*GPI-2**	A	0.000	0.006	0.000	0.006	0.000	0.000	0.005
	B	1.000	0.994	1.000	0.994	1.000	1.000	0.995
*sIDHP**	A	0.000	0.000	0.000	0.000	0.000	0.010	0.015
	B	0.995	0.982	0.987	0.987	0.990	0.969	0.971
	C	0.000	0.012	0.013	0.013	0.005	0.015	0.005
	D	0.000	0.006	0.000	0.000	0.005	0.005	0.005
	E	0.005	0.000	0.000	0.000	0.000	0.000	0.005
*LDH-2**	A	0.925	0.958	0.928	0.918	0.915	0.959	0.975
	B	0.075	0.042	0.072	0.082	0.085	0.041	0.025
*PGM**	A	0.000	0.000	0.000	0.006	0.000	0.005	0.000
	B	0.955	0.958	0.928	0.975	0.985	0.974	0.961
	C	0.045	0.042	0.072	0.019	0.015	0.020	0.039
*sSOD**	A	0.040	0.066	0.059	0.076	0.060	0.082	0.064
	B	0.960	0.934	0.941	0.924	0.940	0.918	0.936
	(*N*)	100	83	76	79	100	98	102
*TF**	A	0.010	0.006	0.007	0.000	0.000	0.025	0.009
	B	0.010	0.032	0.027	0.063	0.049	0.038	0.027
	C	0.980	0.956	0.966	0.938	0.951	0.938	0.964
	D	0.000	0.006	0.000	0.000	0.000	0.000	0.000
	(*N*)	50	79	74	40	51	40	55

CH, Chuí; RG, Rio Grande; SM, Santa Marta; PR, Paranaguá; SS, São Sebastião; IG, Ilha Grande; MC, Macaé; (*N*) sample size.

4. Discussion

The estimated values of genetic variation for *M. furnieri* (Table 3) are close to the mean heterozygosities proposed by Nevo et al. (1984); Ward et al. (1992) (H=0.051, ±0.003) for 183 and 195 fish species, respectively, and to the estimates proposed by Smith and Fujio (1982) (H=0.055, ±0.036) for 106 marine teleost species. However, the mean H found for *M. furnieri* in the present study is relatively high when compared to other sciaenids species: *Genyonemus lineatus* (H=0.030) and *Seriphus politus* (H=0.043) (Beckwitt, 1983); *Nibea albiflora* (H=0.043) and *Pennahia argentata* (H=0.046) (Menezes et al., 1990); *Cynoscion nebulosos* (H=0.009) and *Sciaenops ocellatus* (H=0.029) (Ramsey and Wakeman,

Table 3
Summary statistics on genetic variability for *M. furnieri* populations

Population	Ho	He	P (0.95)	P (0.99)
Chuí	0.044	0.045	0.111	0.389
Rio Grande	0.052	0.059	0.222	0.444
Santa Marta	0.058	0.060	0.278	0.444
Paranaguá	0.063	0.059	0.333	0.444
São Sebastião	0.055	0.057	0.278	0.500
Ilha Grande	0.062	0.059	0.222	0.500
Macaé	0.054	0.052	0.222	0.444
Mean	0.055	0.056	0.238	0.452

Table 4
Results for the contingency chi-square analysis of allele frequencies at polymorphic loci in *M. furnieri*

Locus	No. of alleles	Chi-square	DF	Probability
*EST-1**	5	26.769	24	0.3153
*EST-2**	2	11.738	6	0.0681
*EST-3**	2	10.431	6	0.1076
*GPI-1**	4	10.590	18	0.9109
*GPI-2**	2	4.349	6	0.6295
*sIDHP**	5	22.866	24	0.5277
*LDH-2**	2	11.663	6	0.0699
*PGM**	3	17.187	12	0.1427
*sSOD**	2	3.464	6	0.7488
*TF**	4	13.489	18	0.7617
Total		132.546	126	0.3273

Table 5
F-statistics and gene flow estimates for the polymorphic loci among *M. furnieri* populations

Locus	F_{is}	F_{it}	F_{st}	N_m
*EST-1**	−0.036	−0.032	0.003	83.08
*EST-2**	0.013	−0.004	0.009	27.53
*EST-3**	0.108	0.115	0.008	31.00
*GPI-1**	0.051	0.053	0.001	249.75
*GPI-2**	0.006	−0.002	0.003	83.08
*sIDHP**	0.027	0.032	0.004	62.25
*LDH-2**	0.050	0.058	0.009	27.53
*PGM**	−0.008	0.001	0.009	27.53
*sSOD**	−0.042	−0.039	0.003	83.08
*TF**	−0.044	−0.038	0.006	41.42
Mean	0.000	0.005	0.005	49.75

1987); and *Sciaenops ocellatus* (H=0.047) (Bohlmeyer et al., 1991). These differences may be due to the relatively small number of loci (18 loci) assayed in this study. Ward et al. (1994b) showed that subpopulation heterozygosity was significantly less in freshwater than in marine fish, however the average degree of genetic subpopulation differentiation was significantly greater for freshwater species, suggesting that marine fish subpopulations have higher gene flow than freshwater subpopulations. The differences in subpopulation heterozygosities showed are probably due to reduced subpopulation sizes of freshwater relative to marine species.

The high homogeneity in allele frequencies detected by the contingency chi-square analysis (Table 4) and the small values for F_{st} denote the lack of genetic structuring between *M. furnieri* populations in the sampled area. Therefore, the hypothesis of a single panmitic population could not be rejected by our data.

Several other studies have demonstrated an absence or a very reduced level of population structuring in sciaenids and other teleost species (e.g. Beckwitt, 1983; Grant, 1985, 1986; Ramsey and Wakeman, 1987; Ward et al., 1994b). Usually, the absence of population genetic structuring is associated with environmental conditions and organism life-history parameters. For example, species with high egg or larval dispersal and with mobile adults, tend to display lower values of F_{st} (Waples, 1987; but see Palumbi, 1995). *M. furnieri* is a pelagic spawner and with adults capable of large movements along its wide and continuous distributional area in the Brazilian coast. Therefore, the results are consistent with its life-history attributes, despite some morphological differences observed by Vazzoler (1991). This may also be due to the fact that small amounts of gene flow are enough to homogenise even a demographically fragmented species (Slatkin, 1987).

The levels of gene flow estimated for *M. furnieri* populations (Table 5) suggested that the number of migrants per generation among populations is high enough to maintain the homogeneity in allele frequencies, and therefore, avoid differentiation by genetic drift. The absence of patterns of isolation by distance also corroborate the high levels of gene flow estimated for the species.

The view that species dispersal capability results from the interaction between physical environmental

conditions and species ecological requirements, is supported by our data and by many other studies (e.g. Winans, 1980; Beckwitt, 1983; Grant, 1986; Rosenblatt and Waples, 1986; Waples, 1987; Bohlmeyer et al., 1991; Gold et al., 1994). Lima et al., 1996 showed that the general form of the circulation in the southern Brazilian shelf can be characterised by a combination of different processes that can restrict the possibilities of population subdivision and present high levels of gene flow in this area. Studies showing high genetic homogeneity for this area have been reported in other species of molluscs and crustaceans (Silva, 1991; Weber et al., 1993; Levy, 1997).

For natural populations under exploitation, an incorrect interpretation of the genetic structure can lead to overexploitation and to erosion of genetic resources via depletion of some or all of the population' spawning components. This problem is particularly relevant to marine fish, like the white croaker, which for political or administrative convenience are often managed under assumptions of single, homogeneous and large breeding populations. If indeed there are separate breeding components parameters such as population growth rate and fishing mortality should be estimated separately for each component (Ruzzante et al., 1996). Population structure is typically manifested as the spatial or temporal partitioning of genetic variation. Other approaches are necessary to uncover more genetic variation like the use of other molecular markers such as mitochondrial and nuclear markers.

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