MORPHOMETRIC AND MITOCHONDRIAL DNA ANALYSES OF THE CARIBBEAN RED SNAPPER, *Lutjanus purpureus* (TELEOSTEI, LUTJANIDAE), IN WESTERN ATLANTIC OFF NORTHERN BRAZIL

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ABSTRACT

The present work aims at evaluating the hypothesis that the population of Caribbean red snapper, *Lutjanus purpureus* Poey, 1867, is segregated into two stock units in northern Brazil, corresponding to eastern and western sub-areas on either side of the Amazon Environmental Barrier located around 47º W. Evidence has been gathered from space-related modifications in body proportions and genetic variation on sequences of the mitochondrial cytochrome b gene among individuals. Discriminant analysis showed that 67% of the individuals were identified as belonging to one of the stocks while 33% may be allocated to either of them. Specimens from the eastern sub-area have head, eye diameter and pectoral fin of a larger size than specimens from the western sub-area, the reverse being true of body depth, features somehow related to the activities of capture and/or processing of prey. Four different haplotypes were identified, two (A and B) associated to the western sub-area, and the other two (C and D) to the eastern sub-area. It is suggested that fishery management should be conducted considering the existence of two conservation units, within which data should be collected and analyzed separately so as to enable administrators to take the appropriate regulatory measures.

Key words: *Lutjanus purpureus*; morphometry; mitochondrial DNA; stock discrimination; conservation units; northern Brazil

ANÁLISES MORFOMÉTRICA E DO DNA MITOCONDRIAL DO PARGO, *Lutjanus purpureus* (TELEOSTEI, LUTJANIDAE), NO ATLÂNTICO OCIDENTAL, EM FRENTE À REGIÃO NORTE DO BRASIL

RESUMO

Este trabalho tem por objetivo avaliar a hipótese de que a população do pargo, *Lutjanus purpureus* Poey, 1867, está fragmentada em duas unidades de estoque no norte do Brasil, correspondentes às subáreas leste e oeste em cada lado da Barreira Ambiental do Amazonas, localizada em torno de 47º W. A base de dados foi obtida através de modificações espaciais relacionadas com as proporções corporais e variações genéticas nas seqüências do gene do citocromo-b mitocondrial, entre indivíduos. A função discriminante mostrou que 67% dos indivíduos foram identificados como pertencentes a um dos estoques, enquanto 33% podiam ser alocados a um ou outro estoque. Os

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espécimes do estoque da subárea leste têm cabeça, diâmetro do olho e nadadeira peitoral maiores do que os do estoque da subárea oeste, ocorrendo o contrário com relação à altura do corpo, características das quais depende, provavelmente, o sucesso das atividades de captura e/ou processamento das presas. Quatro diferentes haplótipos foram determinados, dois dos quais (A e B) associados com a subárea oeste, e os outros dois (B e C), com a subárea leste. Sugere-se que a administração pesqueira seja conduzida considerando a existência de duas áreas de gerenciamento, para cada uma das quais os dados devem ser coletados e analisados separadamente, de modo a permitir a adoção das medidas regulatórias pertinentes a cada estoque.

Palavras-chave: pargo; *Lutjanus purpureus*; morfometria; DNA mitocondrial; identificação de estoques; norte do Brasil

INTRODUCTION

The genus *Lutjanus* (family Lutjanidae) has a worldwide distribution with many species making up important fishery resources. One of those species, the Caribbean red snapper, *Lutjanus purpureus* Poey, 1867, is distributed along the tropical western Atlantic Ocean (CARPENTER and NELSON, 1971; ALLEN, 1985). In Brazil, being a commercially important species, it has been extensively studied in several aspects of its morphometry, fisheries biology, fishing technology and population dynamics (FONTELES-FILHO, 1972; GESTEIRA *et al.*, 1972; IVO, 1976; IVO and HANSON, 1982; IVO and SOUSA, 1988; XIMENES and FONTELES-FILHO, 1988; SALLES, 1997; HOLANDA, 2001).

The red snapper population has been fished over an area as large as 32,625 sq. mi that includes both oceanic banks and the continental shelf (Figure 1). The analysis of a time series that spans the period 1962-1992 shows that fish production underwent the phases of growth, stabilization and depletion during the fishery on the oceanic banks from 1962 to 1974, the same process being repeated as the fleet was deployed over to the continental shelf fishing grounds off northern Brazil, at first on middle distance waters (1966-1982) and, later, on far distance waters (1974-1992) from Fortaleza home-port (Figure 2).

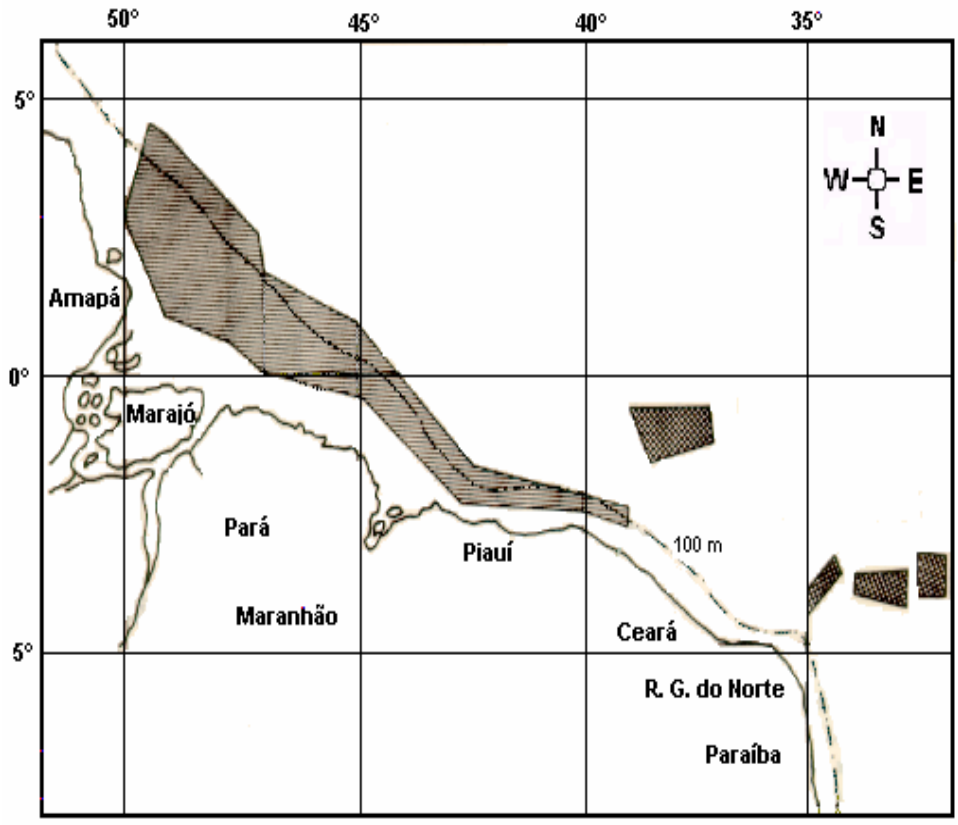

Figure 1. Distribution area of Caribbean red snapper, *Lutjanus purpureus,* on the oceanic banks and continental shelf of northern Brazil

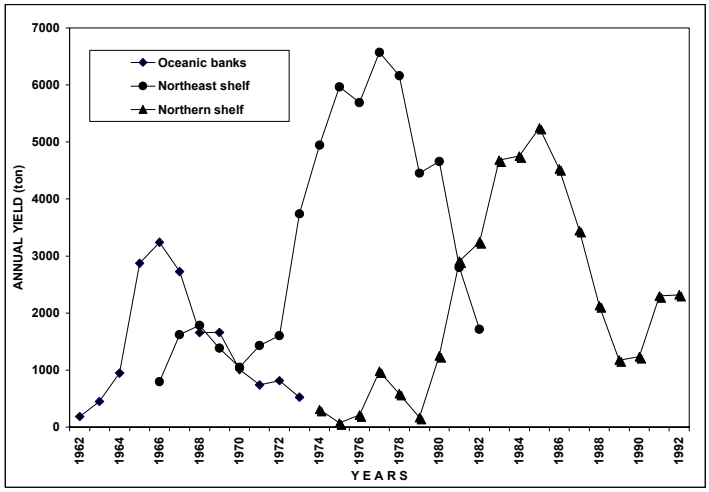

Figure 2. Variation of the annual yield of Caribbean red snapper, *Lutjanus purpureus*, off northern Brazil (SALLES, 1997)

Most species are considered as belonging to a single-stock population, and Caribbean red snapper is not an exception, despite the evidence provided by early papers (FONTELES-FILHO, 1972; COELHO, 1974) so as the differences in length composition in different parts of the distribution area. As a result, fish inhabiting the oceanic banks were shown to be much bigger than those of the continental shelf. In the recent past, a new taxon might be under way as shown by the occurrence of individuals anatomically similar to both Caribbean red snapper and mutton snapper, *Lutjanus analis*, but whose number of scales in the lateral line refers to neither of them.

In this study, **stock** has been considered as a statistical population that inhabits a geographically defined region which generates the biomass that supports the fishery and wherein changes in abundance and behavior throughout life history take place (GAULDIE, 1991). According to MARR (1957), the environment plays a substantial role in defining characteristics of individuals belonging to such units, that should not necessarily be genetically transmitted to their offspring.

The comprehensive analysis of biological aspects carried out by IVO (1979) reveals that, to some extent, feeding habits, growth and reproduction features vary in accordance with the area from which fish are sampled. The spatial variability found on some environmental factors, mainly temperature and salinity, over the distribution area leads to the hypothesis of there being more than one stock of Caribbean red snapper along northern Brazil. Earlier on, an analysis of morphometric and meristic characters has been presented by GESTEIRA *et al*. (1972), but the absence of information on their spatial variation made it impossible to use the results for stock unit identification.

Thus, the inconclusiveness of such studies made it clear that a more extensive investigation of the population was called for, such as that performed by FURTADO-NETO (1998) on Brazilian marine vertebrates. Restriction endonuclease analysis of mitochondrial cytochrome-b and 12S ribosomal RNA gene fragments has already been used as a method for stock identification of thirteen snapper species (CHOW *et al*., 1993), and phylogenetic relationships of ten species of genus *Lutjanus* were also studied by SARVER *et al*. (1996), in the western Atlantic Ocean. GOLD *et al.* (1997), using variation in mitochondrial DNA, arrived at the hypothesis of there being a single breeding population of *L. campechanus* in northern Gulf of Mexico.

Genetic studies have lately shown that wide-ranging populations are likely to be fragmented (HARTL and CLARK, 1997) and the only previous attempt at investigating the hypothesis of population fragmentation in Caribbean red snapper has been made on the basis of reproduction data, under the assumption that spawning takes place on different oceanic banks off northeast Brazil by individuals of either of two stocks, in March-April and October (IVO and HANSON, 1982). Further, the fact that the Amazon River freshwater drainage is supposed to reach out as far as 50 km from the coastline, makes it an environmental barrier which is bound to divide the influence area into a eastern sub-area having higher temperature (28 °C) and salinity (36‰) and a western sub-area having lower temperature (27 °C)

and salinity (20‰), according to RYTHER *et al*. (1967), and roughly corresponding to Ceará/Piauí/Maranhão States and Pará/Amapá States, respectively.

With the ever-increasing expansion of the fishing area westwards up to the boundary with French Guiana (Figure 1), the hypothesis of the existence of different stocks called for new evidence to support it. The usefulness of morphometric characteristics depends on the application of multivariate statistical techniques since none of the individual variables is likely to promote a good separation of individual stocks from a fish population.

The objectives of the present study are to assess and describe geographic variation in morphological and genetic characters of *L. purpureus* from different sites along northern Brazil, using the best set of morphometric characters for group separation by means of the discriminant function, and the DNA sequence variation of the mitochondrial cytochrome **b** gene. The outcome of this research work is expected to support the hypothesis of the population being segregated into stock units whose individuals would be so influenced by the Amazon Environmental Barrier (AEB) as to acquire morphometric and genetic specific features. In this connection, the counterintuitive notion of two stock units and one breeding population requires the necessary explanation.

MATERIAL AND METHODS

Laboratory work

Between January and April 1996, a total of 494 red snappers were sampled between latitudes 01º54' S and 03º45' N and longitudes 42º53' W and 49º14' W, at depths from 45 to 140 meters. The data were obtained through one research cruise on board fishing vessels. Square sampling was adopted in order to minimize variation arising from different numbers of observations over the size range and the 42 – 49º W longitude range, broken down by 1 degree strata.

For the morphometric analysis, the following body measures were taken in centimeter, chosen as the most representative according to GESTEIRA *et al*. (1972): total length (TL), fork length (FL), head length (HL), lower jaw length (LJL), eye diameter (ED), body depth (BD), width of dorsal fin's base (DFB), width of anal fin's base (AFB), and pectoral fin length (PFL).

For the genetic analysis, samples of heart tissue were obtained from twelve fish. DNA was isolated from frozen or DMSO-preserved specimens by an acid guanidium thiosulfate-phenol-chloroform extraction procedure modified from CHOMCZYNSKI and SACCHI (1987). DNA was extracted with chloroform-isoamyl alcohol, precipitated with isopropanol, washed with 75% ethanol, and resuspended in 50 µL distilled water.

The polymerase chain reaction (PCR) was used to amplify 307-base pair sequences of the mitochondrial DNA cytochrome b gene from each collected individual. The primers used were:

L14724(5-CGAAGCTTGATATGAAAAACCATCGTTG-3') and

H15149(5'-GCCCCTCAGAATGATATTTGTCCTCA-3'), according to FURTADO-NETO (1998). DNA was quantified with a DNA Fluorometer model TKO 100 and measurements of its concentratiom (ng/µL) were obtained using fluorochrome bis-benzimide-zole, which binds to DNA and allows rapid quantification.

Sequencing reactions were carried out in 25 cycles, on the following step-cycle profile: 98 °C for 1 sec, 50 °C for 15 sec, and 60 °C for 4 min, using the same primers. The eluted DNA was then dried under reduced pressure and resuspended in 5 µL of 5:1 mixture of deionized formamide and 50 mM Na_2EDTA. Sequencing of both strands of the 401 base pair region was done on an ABI 373A Automated DNA Sequencer. Alignment of sequences in a publishable format was obtained from the Eyeball Sequence Editor (ESEE) (CABOT and BECKENBACH, 1989).

Data analysis

The variation that may have occurred in the morphometric and genetic characters according to a longitudinal gradient was dealt with grouping the data into two broad strata, named Sub-area I (43º-46º W) and Sub-area II (47º - 49º W). They have been separated by the Amazon Environmental Barrier (AEB) set up at 47° W (Figure 1), according to reasoning put forward by IVO and HANSON (1982).

The discriminant analysis generates a rule of elements classification into different groups, for which data were collected on nine variables and classified *a priori* as belonging to either sub-area by the discriminant Fisher's linear function represented by a multivariate regression equation.

The Wilks' l was used to test equality among groups in order to classify the morphometric ratios that should make up the discriminant function, by choosing the best ones out of the seven whose statistical significance was determined by means of Snedecor's F statistic. Genetic heterogeneity among samples was tested with the Monte Carlo c^2 test (ROFF and BENTZEN, 1989) from REAP (Restriction Enzyme Analysis Package). Phylogenetic analyses were performed with the PAUP 3.0 program of SWOFFORD (1993). Maximum parsimony trees were identified with the heuristic search algorithm (tree-bisection-and-reconnection) with random addition and delayed-character-transformation optimization.

RESULTS

Morphometric analysis

Although linearity and normality are usually more closely approximated by logarithms, the original variables made up the basic material due to the high correlation observed among characters. However, because of the variation in size of fish from different sampled strata, morphometric data were made amenable to analysis as ratios between the independent variable (fork length) and all other dependent variables. This procedure allowed size-independent comparisons given the isometric relationship between body linear measurements, the variables being statistically cross correlated at 1% significance level (Table 1).

It can be seen there to be little scatter in the size of the various morphometric characters as shown by the regularity of the variation coefficient, around 20% except for eye diameter with a variation of 10.43% of the standard deviation about the mean, what attests to the homogeneity of the basic data (Table 2).

Among the analyzed variables, the following were found to present the most significant results and so being amenable to take part in the discriminant function: TL/FL, HL/FL, ED/FL, BD/FL and PFL/FL (Table 2). The canonic discriminant function, considering the variables classified according to the Wilks' λ test (Table 3), was jointly represented by the following multivariate regression equation:

$$Y = 7.7 + 14.5\,(TL/FL) - 75.4\,(HL/FL) + 150.5\,(ED/FL) + 15.2\,(BD/FL) - 54.4\,(PFL/FL)$$

Classification into each of the sub-areas was performed by means of the following multivariate regression equations:

Eastern sub-area

$$Y = -455.1 + 312.1\,(TL/FL) + 1437.2\,(HL/FL) - 1170.8\,(ED/FL) + 178.6\,(BD/FL) + 623.6\,(PFL/FL)$$

Western sub-area

$$Y = -461.9 + 299.2\,(TL/FL) + 1504.3\,(HL/FL) - 1305.0\,(ED/FL) + 165.1\,(BD/FL) + 672.0\,(PFL/FL)$$

The results of correct classification show mean proportions of 71.1% and 68.9% in the eastern and western sub-areas, respectively, while the proportions of misplaced classification were 28.9% of fish as belonging to the eastern sub-area when they should be taken as coming from the western sub-area, and 31.1% of fish in the western sub-area when they should be taken as coming from the eastern sub-area (Table 4). In general, taking the whole 494-individual sample, the correct classification percentage was 70%, revealing that 30% of the fish were incorrectly classified.

Genetic analysis

Within the 307-bp amplified segment, five variable sites were identified among the twelve individual snappers. All substitutions occurred in the third codon position and would not result in an amino acid substitution. These variable sites define four haplotypes that differ by one to three nucleotide substitutions. A maximum parsimony network identified two different monophyletic groups: one including haplotypes A and B, and the other including genotypes C and D with bootstrap value of 100%. Genotype A was found in five individuals collected in the northwest of the Amazon River mouth (LP01-LP05) and in one individual collected in front of the river mouth (sample LP07). Genotype B was detected in two samples collected just in front of the river mouth (LP06 and LP08). Genotype C was from three samples collected in the southeast of the Amazon River mouth (LP09-LP11), and genotype D was represented by a single individual (LP12) from a southeastern location off Maranhão State (Figure 3).

The Monte Carlo χ^2 test indicates significant differences of haplotype distributions between the samples from the eastern and western sub-areas ($\chi^2 = 12.03$; df = 3; $P < 0.05$).

Table 1. Correlation coefficients between morphometric ratios of Caribbean red snapper, *Lutjanus purpureus*, off northern Brazil

	LT/FL	HL/FL	JL/FL	ED/FL	BD/FL	DFB/FL	AFW/FL	PFL/FL
LT/FL	1.000							
HL/FL	0.394	1.000						
LJL/FL	0.234	0.720	1.000					
ED/FL	0.116	0.593	0.565	1.000				
BD/FL	0.247	0.450	0.382	0.198	1.000			
DFB/FL	0.292	0.265	0.177	0.096	0.216	1.000		
AFB/FL	0.276	0.483	0.388	0.282	0.314	0.335	1.000	
PFL/FL	0.345	0.616	0.496	0.449	0.349	0.269	0.353	1.000

Table 2. Descriptive measures of morphometric variables of Caribbean red snapper, *Lutjanus purpureus*, over the range 42° W - 49° W, off northern Brazil (N=494 individuals) (See text for acronyms.)

Variable	***Length measure (cm)***			***SD (cm)***	***CV (%)***
	min.	max.	mean		
TL	24.0	72.2	42.9	8.94	20.84
FL	22.1	65.4	39.5	8.02	20.30
HL	6.5	19.2	11.7	2.16	18.51
LJL	2.4	7.1	4.3	0.77	17.91
ED	1.3	3.1	2.3	0.24	10.43
BD	6.3	19.8	11.4	2.28	20.01
DFB	9.5	28.0	17.0	3.57	21.00
AFB	2.8	7.6	4.7	0.92	19.57
PFL	5.7	15.7	10.3	1.95	18.93

Table 3. Results of the entry classification of morphometric ratios of Caribbean red snapper, *Lutjanus purpureus,* into the discriminant function

Variable	***Wilks' λ test***				***Snedecor-F test***			
	estimate	df_1	df_2	df_3	estimate	df_1	df_2	*P*
TL/FL	0.885	3	1	492	21.167	3	490	< 0.001
HD/FL	0.845	4	1	492	22.434	4	489	< 0.001
BD/FL	0.837	5	1	492	19.046	5	488	< 0.001
ED/FL	0.914	2	1	492	23.013	2	491	< 0.001
PFL/FL	0.975	1	1	492	12.846	1	492	< 0.001

Table 4. Results of the data classification into eastern and western stocks of the Caribbean red snapper, *Lutjanus purpureus,* population, according to the discriminant function

Frequency	*Localization*	*Predicted stock*		*Total*
		eastern	western	
Absolute	eastern	150	61	211
	western	88	195	283
Relative (%)	eastern	71.1	28.9	100.0
	western	31.1	68.9	100.0

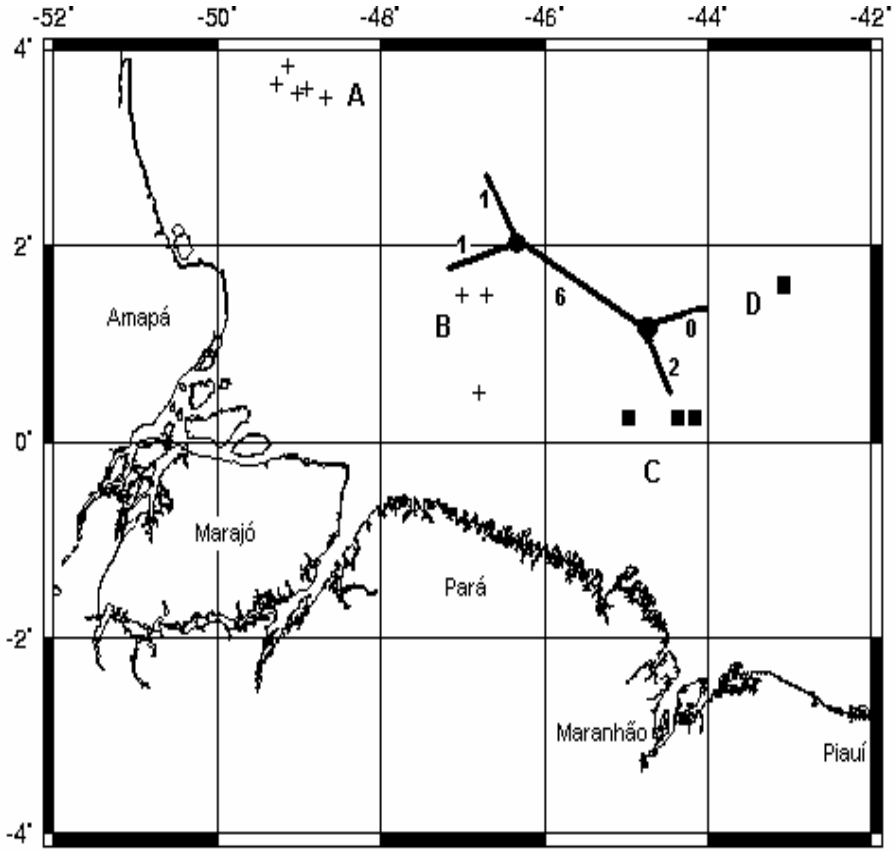

Figure 3. Map of northern Brazil showing twelve locations where samples of Caribbean red snapper, *Lutjanus purpureus* Poey were collected. Maximum parsimony network based on 307-bp sequences of cytochrome b mitochondrial DNA gene of four different haplotypes A (+), B (+), C (■) and D (■) . Numbers show nucleotide differences between branches. Bootstrap value 100%

DISCUSSION

The hypothesis addressed previously in the literature, e.g. IVO and HANSON (1982), about the fragmentation of Caribbean red snapper population along northern Brazil, was not fully confirmed in the present paper. This situation seems to result from the vastness of the analyzed area and the lack of environmental factor powerful enough to determine an overwhelming isolation of the individuals over a longitudinal gradient. Nevertheless, morphometric and genetic analyses revealed a good deal discrimination between *L. purpureus* stocks from the eastern and western sub-areas of northern Brazil. Thus, the so-called Amazon Environmental Barrier, supposed to function through a subsaline wedge, which would likely impair the free movement of individuals along the same salinity-gradient, apparently was able to isolate a reasonable proportion of the total population as indicated by a mean 70% of correct classification through the discriminant

analysis. The remaining 30% which could not be explained by the discriminant function may be ascribed to differences in sample size along the distribution area, which would likely cause different size ranges to be dealt with in the morphometric analysis.

In the eastern sub-area most of the river drainage lies between 44°00′ W and 45°30′ W, whereas in the western sub-area the much greater nutrient-richer river drainage comes from the Amazon system to the west of 47°00′ W (BOISVERT, 1967; RYTHER *et al*., 1967). The impact of the difference in discharge intensity is mainly brought to bear upon the salinity so much so that its mean values are 36‰ and 20‰ in the eastern and western sub-areas respectively, while the temperature is roughly the same in both of them, namely 28 °C and 27 °C (RYTHER *et al*., 1967). Granting that there is a reproduction-related fragmentation in the Caribbean red snapper population (IVO, 1973 and 1975**),** most spawning grounds would be located on the eastern sub-area and most feeding grounds, on the western sub-area (IVO, 1979).

Non specific longitude-related differences in morphometry were expected to occur, so that the basic hypothesis of negligible within-sub-area variation and significant between-sub-area variation was confirmed to a reasonable extent. Yet it is worth pointing out that a more detailed analysis by longitude stratum might have thrown some further light on the causing factors of the arrived at results. Nevertheless, the fact that the outer continental shelf and the continental upper slope, which make up the main habitat for Caribbean red snapper, are located further off the coast in the western sub-area than in the eastern one (Figure 1), could account for differences in quantity and quality of the food supply to such an extent as to make the "eastern" stock more dependent upon the coastal zone than the "western" one.

Specimens from the eastern sub-area have head, eye diameter and pectoral fin of a larger size than specimens from the western sub-area, the reverse being true of body depth (SALLES, 1997). The western sub-area, being a richer environment because of the huge outflow from the Amazon River should be more suitable as feeding ground, while the eastern sub-area would more likely be reproductive ground. Thus, a large share of the population would inhabit the eastern sub-area and part of it would migrate westwards to feed, and most of the population in the western sub-area would be there to feed, with a smaller proportion eventually migrating eastwards to reproduce.

Morphometric discrimination between the two stocks is probably a result of the feeding/reproductive strategies adopted in each of their respective sub-areas. In fact, the diet of *L. purpureus* may include a large fraction of bottom-dwelling prey associated with rocky substrates, such as spiny lobsters of genus *Panulirus*, a variety of crabs, pteropod mollusks, tunicate cordates, and demersal fishes (FURTADO-OGAWA and MENEZES, 1972). Populations (stocks) were found to differentiate from each other mostly regarding head length, body depth, eye diameter and pectoral fin, which seem to be somehow related to the capture and/or processing of prey. A large head apparently favors the ingestion of hard and massive prey such as lobsters, crabs, mollusks (squids) and some fish species. Variation in eye diameter may reflect a clear advantage for detection of prey associated with the water column, like mysids, shrimp and some fish. Pectoral fins are supposed to be important for a very rapid projection of individuals in the water column when they are moving about aimlessly near the bottom. Thus, a high development of the pectoral fin seems to be a very helpful physical aid for the detection and capture of fast prey associated with the water column, like squid and fish.

The presence of different stocks or populations in a determined area is generally associated with a reasonable amount of genetic variation (SCOLES and GRAVES, 1993; AVISE, 1994). The number of nucleotide substitutions among haplotypes recorded in the present study is higher than that verified by CRUTCHER and CARR (1996) among codfish from North Atlantic, considered by these authors as different populations. Therefore, the results obtained by the genetic analyses identified four different haplotypes of *L. purpureus* sampled off northern Brazil suggesting that this species has high genetic diversity in the studied area.

The present phylogenetic analysis also suggests that haplotypes C and D, which occupy waters with average temperature of 28 °C and high salinity of 36‰, are probably derived from the basal haplotypes A and B, which occupy waters with average temperature of 27 °C and low salinity of 20‰ (IVO and HANSON, 1982). Temperature and salinity variation could be responsible for isolation of marine

fish populations according to PEPIN and CARR (1993). Recent studies of Caribbean spiny lobster, *Panulirus argus* (CARREIRO, 2001), and yellowfin tuna, *Thunnus albacares* (VIEIRA *et al*., 2000) point out to the existence of different stocks over a distribution area about the same as the one inhabited by Caribbean red snapper.

Spatial and temporal patterns of mtDNA haplotype variation among Caribbean red snapper in northern Brazil are consistent with the hypothesis of there being two stock units, but probably comprised into a single breeding population. However, genetic homogeneity and absence of spatial patterns in allele distributions in marine fishes typically have been interpreted to indicate existence of a single breeding population or gene pool, and since Caribbean red snapper has sedentary or demersal adult phases, hydrodynamic transport of pelagic eggs and larvae (LEIS, 1987) may be inferred as the mechanism promoting gene flow (JOHNSON *et al*., 1993).

The two methodologies used in this work demonstrate that in the studied area at least two populations of *L. purpureus* inhabit the continental platform. Both morphometric and genetic results agree with an early study based on reproduction, growth and feeding habits of this species in northern Brazil (IVO and HANSON, 1982).

The results obtained in the present study, that are important for the complete characterization of the populations of the Caribbean red snapper, have shown that two basic premises were not still verified: a) the study of the reproductive and migratory behavior of each population along the time; b) area of distribution of each population. However, the evidence of population fragmentation, albeit incomplete, turns possible in a certain logical way to treat each population as a potential and administratively independent stock, but additional confirmation needs to be investigated by a more extensive survey. These suggestions are compatible with WARD (2000), who recently reviewed the application of genetics in fisheries management.

Conservation units can be thought of as of evolutionary or management significance, as put forward by MORITZ (1994), in the sense that they represent population groups which are treated as demographically independent while containing a changing degree of genetic variability of the species. Therefore, under the assumption that individuals inhabiting either the eastern or the western sub-area have their own life history, the ideal situation should be for them to be classified by assignment to a specific stock and have their relative contribution in a mixed-stock estimated sample. However, given the difficulties of attaining this goal, the practical outcome of this finding is that hereafter the Caribbean red snapper fishery administration ought to be conducted considering the existence of management units within which all data obtained on life history, fishing effort distribution, abundance and population dynamics should be collected and analyzed separately under the assumption that their individuals react differently to fishing pressure, so as to enable administrators to take the appropriate conservation measures.

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