

Spatial distribution of fish species in a tropical estuarine lagoon: a geostatistical appraisal

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ABSTRACT: The density and spatial distribution of 3 commercial fish species and coincident abiotic factors were analyzed seasonally in the Ciénaga Grande de Santa Marta between 1993 and 1994. Geostatistical techniques were used to model and estimate spatial structure (variographic analysis) and to predict local fish density and salinity (ordinary kriging). Salinity showed a persistent spatial and temporal gradient determined by climatic seasons. *Eugerres plumieri*, *Cathorops spixii* and *Mugil incilis* showed different spatial correlations that determined different patch distribution patterns among seasons. The highest densities of *E. plumieri* and *M. incilis* and a secondary peak of *C. spixii* occurred during the rainy season, near the lagoon-sea connection. Statistically significant multiple regression models could account for 13, 2 and 30% of the variance of *E. plumieri*, *C. spixii* and *M. incilis* densities respectively, using a combination of salinity, depth and substrate type; temperature was consistently rejected as predictor. *E. plumieri*, *C. spixii* and *M. incilis* preferred fine sands, shells, and mud respectively, and euryhaline behavior was observed for all species.

KEY WORDS: Fish density · Spatial distribution · Geostatistics · Abiotic factors · Tropical estuarine lagoon · Colombia

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INTRODUCTION

The ecological and socio-economic importance of estuaries has been well documented in temperate and tropical environments (Yañez-Arancibia et al. 1985, Day et al. 1989, Kjerfve 1994, Blaber 1997). Amongst the numerous subjects for ecological research, knowledge about spatial distribution patterns of estuarine fish and abiotic influencing factors has been identified as being central to the implementation of fishery management strategies (Blaber 1997). Studies carried out mainly in temperate estuaries have identified patterns of spatial and temporal variation in composition, abundance and distribution of fishes related to gradients in rainfall, salinity, temperature, depth, light, turbidity, substrate type and tides (Kinne 1971, Day et al. 1989, Pollard 1994, Armstrong 1997, Brown 2000). Although the few studies in tropical estuaries have shown that

fish communities are determined by the interplay of interrelated abiotic factors such as tides, turbidity, salinity and habitat structure (Cyrus & Blaber 1992, Yañez-Arancibia et al. 1993, Sánchez-Velasco et al. 1996, Guillard 1998), detailed spatial analyses are still scarce (Blaber 1997). In this respect, geostatistical techniques constitute powerful tools for estimating the spatial distribution of marine populations (Freire et al. 1992, Simard et al. 1992, Petitgas 1993, Pelletier & Parma 1994, Fletcher & Sumner 1999). They are more suitable for mapping purposes than conventional statistical methods because they explicitly consider spatial correlation between observations (Warren 1998). Geostatistical techniques may become important for stock assessment and fishery management, because certain biological categories, such as spawning females or juveniles, may be protected by seasonal closures of fishing areas.

Eugerres plumieri, *Cathorops spixii* and *Mugil incilis* are the most important commercial fish species in the

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Cienaga Grande de Santa Marta (CGSM), Colombia, accounting for 81% of the annual catch during 1993 to 1994 (Santos-Martínez & Vilorio 1998). These species belong to characteristic families (Gerreidae, Ariidae and Mugilidae respectively) in tropical and subtropical estuaries (Blaber 1997, Whitfield 1999), and in CGSM are categorized as marine migrants (*M. incilis*) or estuarine residents (*E. plumieri* and *C. spixii*). In addition, in the fisheries of CGSM, other species are also caught in any given area, due to the underlying species assemblages that reflect ecological communities dominated by clupeoids, scianids, carangids, centropomids and elopids. The fisheries of this estuarine lagoon are of considerable socio-economic importance, and studies of the spatial distribution patterns of the species are essential for stock assessment and management purposes. The objective of this study is to determine seasonal fluctuations in the spatial distribution of the 3 main commercial species in the CGSM through geostatistical techniques using data from surveys conducted on a fixed grid of stations. The potential effects of salinity, temperature, depth and substratum type on spatial variations in fish density are also evaluated by multiple regression analysis.

MATERIALS AND METHODS

Study area and fishing surveys. CGSM is the largest (450 km²) estuarine lagoon in Colombia, located on the Caribbean coast (10° 43'–11° 00' N, 74° 16'–74° 35' W; Fig. 1). The lagoon has an annual mean depth of 1.5 m and a mean temperature of 30°C, while salinity varies from 2 to 36 according to 4 seasons: (1) 'major dry' from December to April; (2) 'minor rainy' from May to June; (3) 'minor dry' from July to August; and (4) 'major rainy' from September to November (Botero & Salzwedel 1999). The fishery is artisanal and multispecific, including fish, mollusks and crustaceans (Santos-Martínez & Acero 1991, Mancera & Mendo 1996, Sánchez & Rueda 1999).

Fishery-independent surveys were conducted for each season at the CGSM: (1) November 1993 (major rainy); (2) March 1994 (major dry); (3) June 1994 (minor rainy); and (4) August 1994 (minor dry). Systematic sampling, consisting of 115 stations spaced 2 km apart and located using a GPS NAV 5000D, covered the whole surveyed area (Fig. 1). At each station, a haul was carried out using a 'boliche' or encircling gillnet of 5 cm mesh size, which enclosed an average circular area of 0.005 km² (Rueda et al. 1997, Rueda & Santos-Martínez 1999). Eight boliches, transported in canoes with outboard motors, were used simultaneously to cover all stations; each survey took approximately 8 h to complete. Each fish collected at each station was identified to species level. In addition, temperature, salinity, and depth were recorded at each station. Additional substrate information was obtained from a sedimentology survey carried out in 1994 (Bernal & Betancur 1996).

Environmental data analysis. Differences in temperature, depth and salinity among seasons were tested using 1-way ANOVA, using previous confirmation of normality and homoscedasticity assumptions for the first 2 environmental variables, and using a Kruskal-Wallis test by ranges for salinity because the normality assumption was not fulfilled. When significant differences were found, Tukey's pairwise (parametric) and Mann-Whitney *U* (non-parametric) comparisons were performed.

Spatial analysis. The spatial structure of salinity and fish density was analysed by the use of semivari-

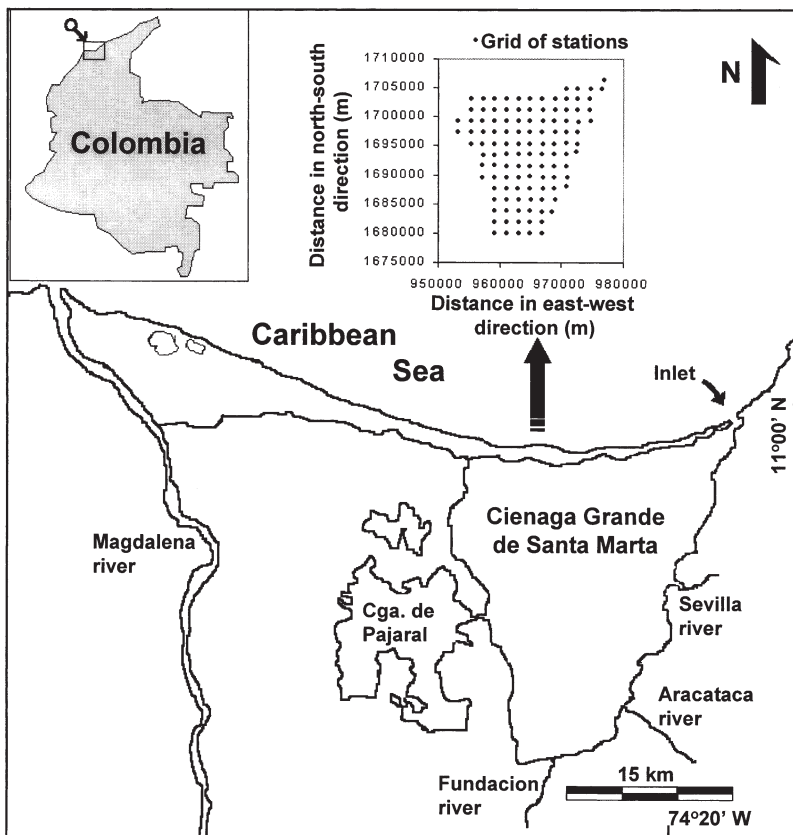


Fig. 1. Cienaga Grande de Santa Marta (CGSM), Colombia, showing fixed grid of 115 stations sampled during each season

ograms. Each spatial process consisted of 115 observations measured at a location x , where x is defined by latitude and longitude in a 2-dimensional space for each season. It was assumed that: (1) the spatial distribution of each process was stable throughout the survey and (2) the observations and spatial processes differ only through white-noise measurement error (Pelletier & Parma 1994). The assumption that the observations were second-order stationary (sensu Cressie 1991) was tested by analysis of covariance (ANCOVA), with the direction (south-north and east-west) as the independent variable, salinity and density as dependent variables and distance as the covariate. In all cases, normality, homoscedasticity and parallelism assumptions of ANCOVA were fulfilled. Five stations located in the northeast of CGSM were excluded from the salinity ANCOVA, because they showed extreme values that indicated trends in the data. Observations were normalized [salinity and density, $\log(x+1)$], and then a nondirectional experimental semivariogram $\gamma(h)$ was estimated by pooling pairs of observations in all directions, using Matheron's (1965) estimator:

$$\gamma(h) = \frac{\sum_{i=1}^{N_h} \{Z(x_i + h) - Z(x_i)\}^2}{2N(h)} \quad (1)$$

where $Z(x_i)$ is the value of the variable at Stn x_i , $Z(x_i + h)$ is another value separated from x_i by a discrete distance h (measured in meters) and $N(h)$ is the number of pairs of observations separated by h . Spherical and exponential theoretical models (Cressie 1991) were fitted to the experimental semivariograms to estimate the semivariogram values for each distance within the range of observations. The following parameters were estimated: (1) the nugget effect (C_0), that reflects variation at distances less than the sample spacing in the data set; (2) the sill ($C_0 + C$), which defines the asymptotic value of semivariance; and (3) the range (A_0), defined as the maximum distance at which spatial effect or covariance is detected. The number of pairs of observations from which each semivariogram estimate was computed, the proportion of sample variance accounted for by spatially structured variance [$C/(C_0 + C)$], the coefficient of determination (r^2) and the reduced sum of squares (RSS) were used as goodness of fit criteria.

The expected values of salinity and fish density $\hat{Z}(X_0)$ were estimated for each season by kriging, using data stations $Z(X_i)$ in the surrounding neighborhood (Matheron 1965):

$$\hat{Z}(X_0) = \sum_i^n \lambda_i Z(X_i) \quad (2)$$

where λ_i is the vector of observations that minimizes prediction error (Cressie 1991). Kriging results were

evaluated using 'jackknife' cross-validation. To this end, the observed (O) and estimated (E) values were plotted and fitted to a linear regression of the form $O = \alpha + \beta E$. If predictions are identical to actual observations, then the points form a 45° line through the origin. Departures from the line indicate model inadequacy, and thus the significance of α and β was tested under the null hypotheses that $\alpha = 0$ and $\beta = 1$ with standard t -tests (Power 1993). Model adequacy was also evaluated by means of kriging standard deviations. The salinity and fish density predicted by kriging were displayed in 2-dimensional maps. In cases where spatial covariance was not detected, quartile maps were displayed to identify any spatial order in the data.

Relationships between environmental data and fish density. Multiple regression analysis was used to relate fish density for each species (dependent variable) to salinity, temperature, habitat structure (i.e. substrate type) and depth (independent variables), with data pooled from all seasons. Fish density data were log-transformed to remove differences due to scaling and deviations from normality, whereas the Durbin-Watson test showed no correlation between residuals and data. Categorical substrate type variables (S_1, S_2, S_3) were used to classify fine sands ($S_1 = 0, S_2 = 0, S_3 = 0$), shells ($S_1 = 0, S_2 = 0, S_3 = 1$), mixed 'mud-shells' ($S_1 = 0, S_2 = 1, S_3 = 0$), and mud ($S_1 = 1, S_2 = 0, S_3 = 0$). Multiple regressions were generated by a forward stepwise selection technique with F values of 1 and 0 chosen *a priori* for variable entry and removal respectively, until the best regression model was obtained. The contribution of each independent variable to the prediction of fish density was examined by partial correlation. The redundancy of independent variables was evaluated by model tolerance, defined for the respective variable as $(1 - R^2)$, with all other variables currently included in the model.

Fish densities recorded in each season were grouped in salinity ranges and used to explain the distribution patterns observed. Two-way ANOVA with unequal replication (Zar 1996) was performed on fish densities, using seasons and substratum type as main effects. Assumptions of normality and homoscedasticity were tested and data were log-transformed when necessary. When significant differences were found, Tukey's pairwise comparisons were performed.

RESULTS

Environmental data

Temperature differed significantly among seasons (ANOVA $F_{3,451} = 11.48$; $p < 0.01$), while depth did not ($F_{3,451} = 2.51$; $p = 0.058$). The lower temperature was

during the major rainy season (Tukey test: $p < 0.01$). Salinity was significantly different among seasons (Kruskal-Wallis test $H_{3,455} = 292.4$; $p < 0.01$), being lower during the major rainy season (U -test: $p < 0.01$) and higher in major and minor dry seasons (U -test: $p < 0.01$ in both cases). Variations of salinity indicated the presence of 4 seasons in the CGSM defined by rainfall regime (Table 1).

Spatial analysis

ANCOVA tests performed with the distance as covariate, and the direction (south-north and east-west) as the main factor, did not reveal significant differences in salinity and fish density ($p > 0.05$). Hence, no geographical trend was observed in the dependent variables. This indicated that the covariance of salinity and fish density between 2 stations only depended on the distance and that the expected values at any station were constant.

All points of the semivariograms for salinity and fish density included more than 200 pairs, conferring power for parameter estimation. The spatial correlation of salinity fit an exponential model in the major rainy season, while in the remaining seasons the experimental semivariograms best fit a spherical model (Table 2). In all cases the ranges indicated a spatial dependence >26 km and the small-scale spatial variation was very low ($C_0 < 0.01$). The highest semivariance occurred in the major rainy season ($C_0 + C = 0.209$), while in the remaining seasons the values ranged from 0.004 to 0.063. Different degrees of exponential spatial correlation were fitted to *Eugerres plumieri*, *Cathorops spixii* and *Mugil incilis* according to the seasons (Table 2), with a spatially structured density component [$C/(C_0 + C) = 57$ to 84%] that indicated instability in the fish distribution. *E. plumieri* density was lowest in the minor rainy season (2.1 ind. 0.005 km^{-2}), where spatial correlation was not detected. In the remaining seasons, with highest mean densities (3.0 to 6.2 ind. 0.005 km^{-2}),

Table 1. Seasonal mean (\pm SD) values of abiotic factors in the CGSM. Mean monthly precipitation (Pr) was registered at an airport nearby from 1952 to 1994

Season	Salinity			Pr (mm)	Temperature ($^{\circ}\text{C}$)			Depth (m)		
	\bar{X}	SD	n		\bar{X}	SD	n	\bar{X}	SD	n
Major rainy	15.6	5.4	113	65.0	31.5	1.4	113	1.6	0.4	113
Major dry	30.9	1.7	115	5.4	32.0	1.8	115	1.5	0.3	115
Minor rainy	26.1	2.4	115	46.0	32.3	1.4	115	1.6	0.4	115
Minor dry	30.1	3.4	112	44.0	31.3	1.3	112	1.7	0.4	112

Table 2. Statistics, model parameters and goodness of fit criteria of exponential (Exp) and spherical (Sph) models, fitted to salinity and fish density (ind. 0.005 km^{-2}) experimental semivariograms during the 4 seasons. C_0 : nugget effect; $C_0 + C$: sill; A_0 (in m): range; $C/(C_0 + C)$: spatially structured component; r^2 : coefficient of determination; RSS: reduced sum of squares

Spatial process	Season	\bar{X}	SD	Model	Parameters			Goodness of fit			
					C_0	$C_0 + C$	A_0	$C/(C_0 + C)$	r^2	RSS	
Salinity	Major rainy	15.6	5.4	Exp	0.011	0.209	67320	0.94	0.96	3×10^{-4}	
	Major dry	30.9	1.7	Sph	3×10^{-5}	0.004	26600	0.99	0.99	2×10^{-8}	
	Minor rainy	26.1	2.4	Sph	0.002	0.016	34450	0.83	0.97	2×10^{-6}	
	Minor dry	30.1	3.4	Sph	1×10^{-3}	0.063	61100	0.99	0.81	4×10^{-4}	
Density	<i>Eugerres plumieri</i>	Major rainy	6.2	11.1	Exp	0.570	2.05	34320	0.72	0.90	0.115
		Major dry	3.3	4.0	Exp	0.160	0.75	6840	0.80	0.75	0.041
		Minor rainy	2.1	3.4	None	0.513					
		Minor dry	3.0	3.9	Exp	0.570	1.35	85800	0.57	0.82	0.042
<i>Cathorops spixii</i>	Major rainy	2.0	4.3	None	0.704						
	Major dry	2.3	3.5	Exp	0.193	0.83	9480	0.76	0.51	0.080	
	Minor rainy	2.7	6.9	Exp	0.200	0.90	6390	0.78	0.45	0.096	
	Minor dry	2.5	3.6	Exp	0.114	0.68	8010	0.83	0.66	0.047	
<i>Mugil incilis</i>	Major rainy	4.6	14.2	Sph	0.360	1.24	12190	0.70	0.86	0.078	
	Major dry	0.14	0.48	None	0.065						
	Minor rainy	0.21	0.74	None	0.161						
	Minor dry	0.39	1.17	Exp	0.500	3.27	45310	0.84	0.81	0.470	

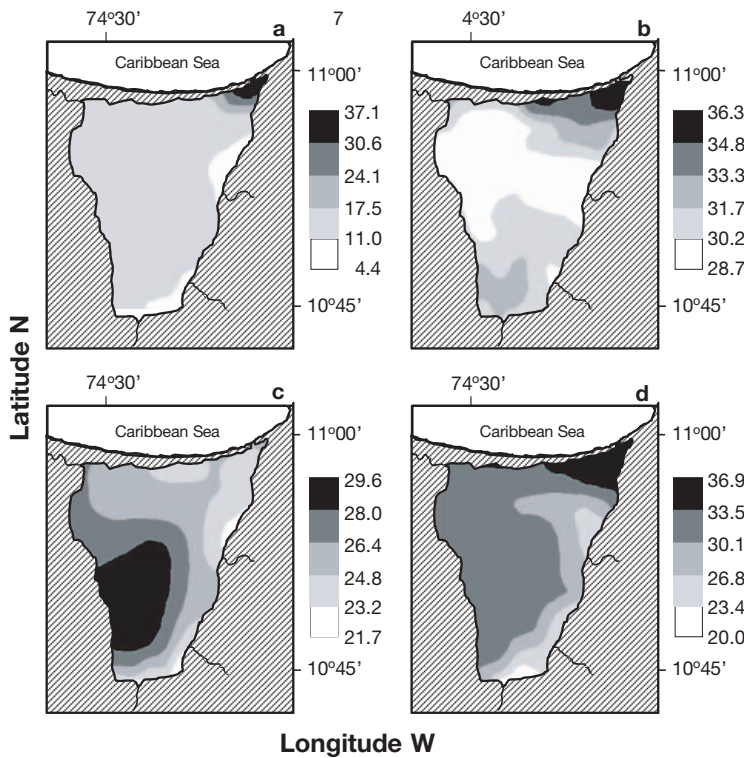


Fig. 2. Kriging maps of salinity for: (a) major rainy, (b) major dry, (c) minor rainy and (d) minor dry seasons

the range of spatial influence oscillated between 6.8 and 85 km, with C_0 between 0.16 and 0.57. *C. spixii* presented the lowest mean density (2.0 ind. 0.005 km⁻²) and absence of spatial correlation in the major rainy season, while in the remaining seasons, with densities around 2.5 ind. 0.005 km⁻², the spatial dependence oscillated between 6.4 and 9.5 km, with $C_0 \leq 0.20$. *M. incilis* had highest mean density in the major rainy season (4.6 ind. 0.005 km⁻²), with a well-defined spatial structure of 12 km and with $C_0 = 0.36$. Its mean density decreased in the remaining seasons (<0.39 ind. 0.005 km⁻²), and only in the minor dry season was spatial correlation in a range of 45 km, with $C_0 = 0.50$.

Salinity increased along a gradient from the southeast border of the lagoon to the inlet, and at areas close to the Caribbean Sea, except during the minor rainy season (Fig. 2). This range varied from 4.4 to 37.1 in major rainy season, describing a spatial process that alternated oligohaline, mesohaline and polyhaline conditions. In all seasons the observed and estimated salinity values were fitted to a 45° line through the origin

($-0.6 \leq \alpha \leq 1.7$; $0.96 \leq \beta \leq 1.10$; $p > 0.05$ in both cases) and the kriging standard deviations ranges on sampling area were low (0.3 to 3.0), indicating good salinity predictions by kriging.

Eugerres plumieri, *Cathorops spixii* and *Mugil incilis* were distributed in irregular patches within and among seasons (Figs 3–5). *E. plumieri* density was highest in the major rainy season (global kriging mean and SD of 3.8 and 22.3 ind./0.005 km² respectively) with a patch in the northeast of CGSM (Fig. 3a). Densities decreased from major to minor dry seasons (kriging \bar{X} and SD 2.9 to 5.8 and 1.9 to 1.4 ind. 0.005 km⁻² respectively), with patches in the north and southwest respectively (Fig. 3b–d). Kriging predictions for *E. plumieri* density were good (given that $0.6 \leq \alpha \leq 1.7$, $0.94 \leq \beta \leq 1.20$, $p > 0.05$ in both cases) and kriging SD ranges on sampling area were low (1.0 to 2.4 ind. 0.005 km⁻²). The spatial ordination of densities in the minor rainy season showed that 75% of data were ≤ 3 ind. 0.005 km⁻², while 100% of data were ≤ 25 ind. 0.005 km⁻² (Fig. 3c).

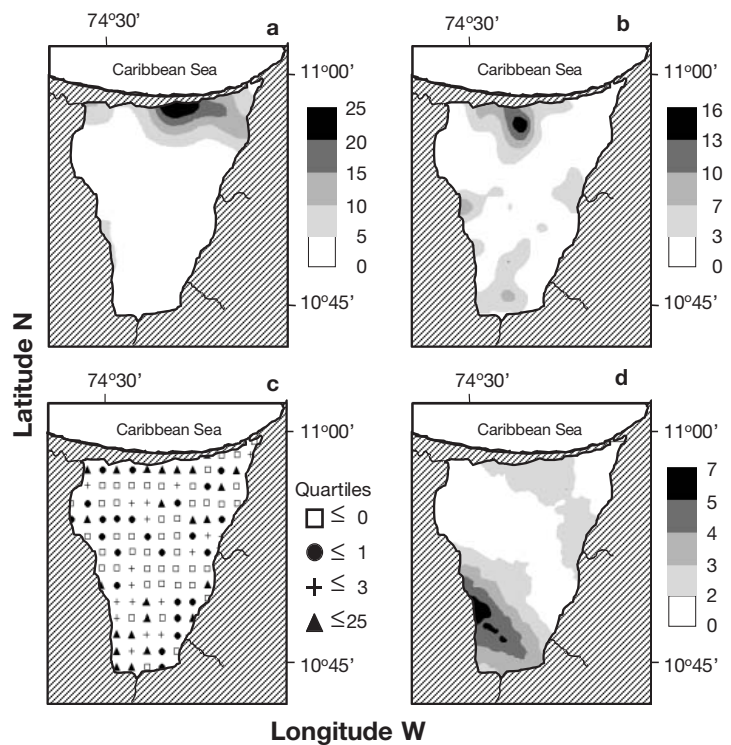


Fig. 3. Kriging maps of *Eugerres plumieri* density (ind. 0.005 km⁻²) for: (a) major rainy, (b) major dry, (c) minor rainy and (d) minor dry seasons

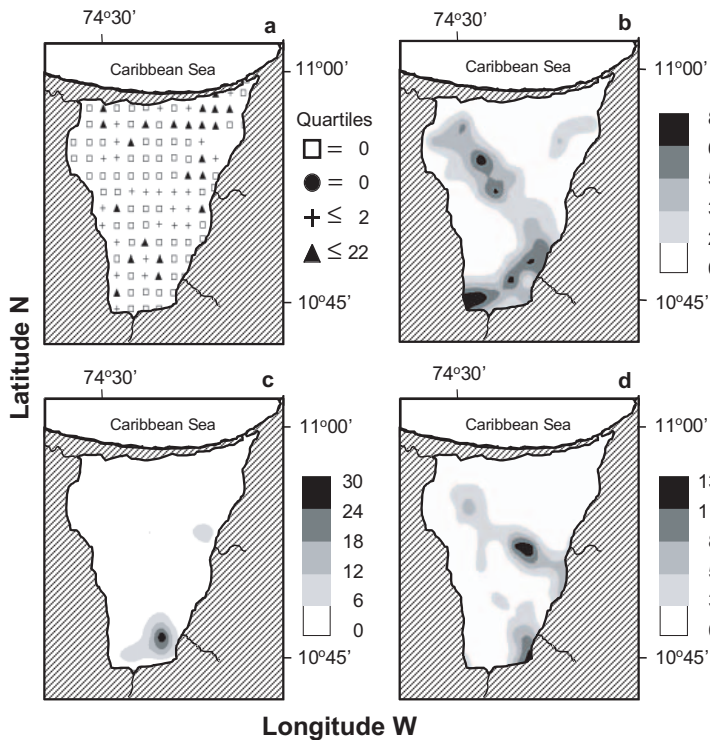


Fig. 4. Kriging maps of *Cathorops spixii* density (ind. 0.005 km^{-2}) for: (a) major rainy, (b) major dry, (c) minor rainy and (d) minor dry seasons

Cathorops spixii showed a higher number of patches than other species, which also varied within and among seasons (Fig. 4). In the major rainy season, 75% of densities were ≤ 2 ind. 0.005 km^{-2} , while 100% of densities were ≤ 22 ind. 0.005 km^{-2} (Fig. 4a). In the remaining seasons, kriging \bar{X} were near 2 ind. 0.005 km^{-2} , with SD between 3.2 and 9.5 ind. 0.005 km^{-2} in the major dry and minor rainy respectively (Fig. 4b,c,d). α and β values were not significant ($-0.8 \leq \alpha \leq 0.6$, $0.90 \leq \beta \leq 1.50$, $p > 0.05$ in both cases) and kriging SD between 1 and 1.7 ind. 0.005 km^{-2} denoted good model predictions.

Mugil incilis presented highest densities in the major rainy season (kriging \bar{X} and SD of 2.4 and 19.2 ind. 0.005 km^{-2} respectively), with a main patch located in the east (Fig. 5a). Density decreased markedly in the minor dry season (kriging \bar{X} and SD of 0.32 and 0.43 ind. 0.005 km^{-2} respectively), while during the remaining seasons, 75% of densities were zero (Fig. 5b–d). α and β values were not significant in major rainy and minor dry seasons ($\alpha = 0.0$ to 1.4, $\beta = 0.86$ to 1.30, $p > 0.05$ in both cases) and SD were between 0.4 and 0.5 ind. 0.005 km^{-2} , indicating good model predictions.

Relationship between environmental data and fish density

Statistically significant multiple regression models were able to account for 13, 2 and 30% of the variance of *Eugerres plumieri*, *Cathorops spixii* and *Mugil incilis* densities, consistently rejecting temperature as a predictor and including only those variables that were not statistically redundant (tolerance > 0.5 ; Table 3). Substrate type accounted for 55% of the variance in *E. plumieri* density, while salinity and depth accounted for the remaining variance. Densities were inversely related to salinity, depth, shell, mixed and mud substrates (see partial correlations in Table 3). All independent variables were rejected as predictors of *C. spixii* density, except shell substrate (partial correlation = 0.14). The density of *M. incilis* was inversely correlated with salinity and depth, and positively with the presence of mud (Table 3). Salinity ranges within which the mean *E. plumieri*, *C. spixii* and *M. incilis* densities were recorded in each season showed wide tolerances (Fig. 6). Each range corresponded to the maximum feasible partitioning of salinity values observed that included fish density data. During the rainy season, *E. plumieri* and *C. spixii* had highest density at salinities > 30 , which

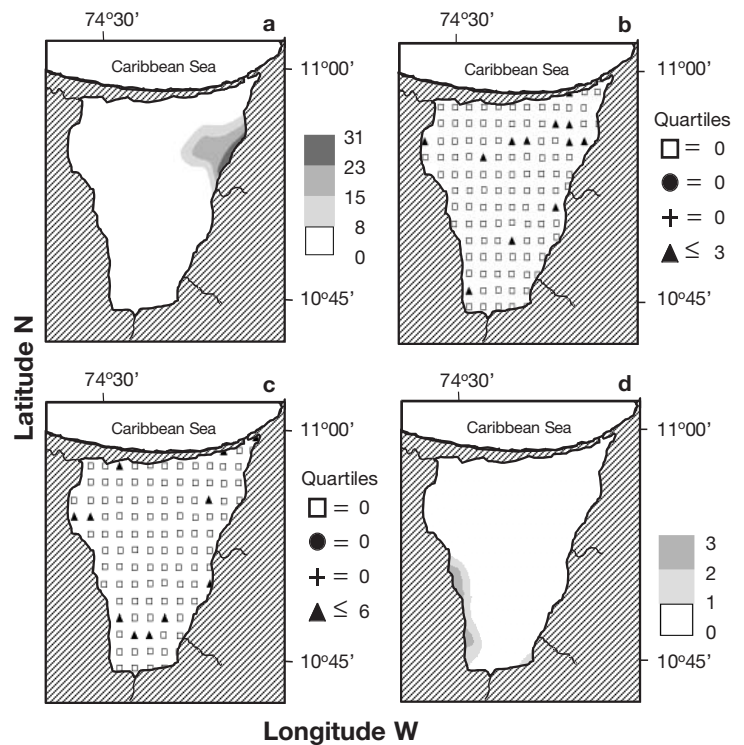


Fig. 5. Kriging maps of *Mugil incilis* density (ind. 0.005 km^{-2}) for: (a) major rainy, (b) major dry, (c) minor rainy and (d) minor dry seasons

Table 3. Best multiple regression models for predicting fish density [$\ln(\text{ind. } 0.005 \text{ km}^{-2})$]. Mean (\pm SE) of intercept and regression coefficients for each predictor variable. PC: partial correlation; T: tolerance; ns: variable removed (not significant). * $p < 0.05$; ** $p < 0.01$

	<i>Eugerres plumieri</i>	<i>Cathorops spixii</i>	<i>Mugil incilis</i>
Intercept	3.23 (0.36)**	2.12 (0.24)**	3.19 (0.51)**
Salinity	-0.02 (0.01)**	ns	-0.05 (0.01)**
PC	-0.17		-0.43
T	0.97		0.96
Temperature (°C)	ns	ns	ns
PC			
T			
Depth (m)	-0.54 (0.16)**	ns	-1.11 (0.27)**
PC	-0.19		-0.38
T	0.94		0.94
Mud (S1)	-0.56 (0.18)**	ns	0.44 (0.23)*
PC	-0.18		0.19
T	0.51		0.60
Muds-shells (S2)	-0.63 (0.18)**	ns	ns
PC	-0.20		
T	0.51		
Shells (S3)	-0.85 (0.20)**	1.75 (0.58)**	ns
PC	-0.24	0.14	
T	0.57	1.0	
R ² adj	0.126	0.019	0.300
p	<0.01	0.002	<0.01
SE of estimate	0.930	4.758	0.916
N	298	455	105

were not very frequent. In the remaining seasons, densities tended to be clustered from mean to upper salinity ranges. *M. incilis* presented highest densities at low salinities during the major rainy season, while in the remaining seasons the lowest densities were recorded in mean to upper salinity ranges.

Eugerres plumieri density (Fig. 7) differed significantly among seasons ($F_{3,439} = 4.94$; $p = 0.0022$) and substrate type ($F_{3,439} = 5.92$; $p = 0.0006$), preferring fine sands (Tukey test: $p < 0.05$) and having highest densities in the major rainy season (Tukey test: $p < 0.01$). *Cathorops spixii* density did not show significant differences among seasons ($F_{3,439} = 1.35$; $p = 0.2576$), but differed among substratum type ($F_{3,439} = 7.44$; $p = 0.0001$), preferring shells substratum (Tukey test: $p < 0.01$). It was not feasible to carry out the 2-way ANOVA for *Mugil incilis* due to the non-parametric nature of the data; however, the preference for mud during the major rainy season was clear (Fig. 7).

DISCUSSION

Salinity varied markedly according to seasonal changes in precipitation (Table 1) and freshwater dis-

charges (Kaufmann & Hervert 1973), and showed a clear spatial gradient and strong seasonal patterns typical of estuarine ecosystems (Day et al. 1989, Cyrus & Blaber 1992, Sánchez-Velasco et al. 1996). The analysis of salinity using semivariograms determined spatial dependence along the CGSM and little unobserved micro-scale variability, indicating that the observation scale was suitable for modelling spatial structure correctly (Table 2).

The study presented here constitutes one of the first examples in which geostatistical techniques have been used to model the spatial structure of fish populations in tropical estuaries based on intensive and systematic sampling. The spatial distribution pattern of main commercial species of the CGSM showed unstable patches between seasons. Different degrees of spatial correlation described ranges of dependence from 6 km up to and greater than 25 km, which provides an idea of patch size. This is inferred from the fact that stationarity conditions were satisfied and the exponential model gave the best

fit, describing a continuous decay of spatial correlation with distance. The cases where spatial correlation was not detected were due to the high number of zero densities; quartile maps then gave a discrete picture of the spatial distribution pattern (Figs 3c, 4a & 5b,c). The presence of anisotropy was explored by assessing the autocorrelation function in different geographic directions—directional variograms did not differ significantly from isotropic variograms. Therefore, isotropic variograms for salinity and fish density showed a better fit, with low nugget components [$C_0/(C_0 + C)$, Legendre & Legendre 1998] of <25% in 9 of the cases, and between 30 and 43% for 3 remaining cases. This is widespread in fisheries data (Freire et al. 1992, Simard et al. 1992, Petitgas 1993, Pelletier & Parma 1994).

Zonation schemes exhibited by each species accounted for the characterization of seasonal changes of fish density subject to exploitation in the CGSM. The highest densities of *Eugerres plumieri*, *Mugil incilis* and *Cathorops spixii* during the major rainy season coincided with commercial catches (Santos-Martínez & Vilorio 1998) and fish community structure analysis (Santos-Martínez 1989, Sánchez 1997), which reflects the high fishery production of this season. Fish density decreased in the remaining seasons and patch location

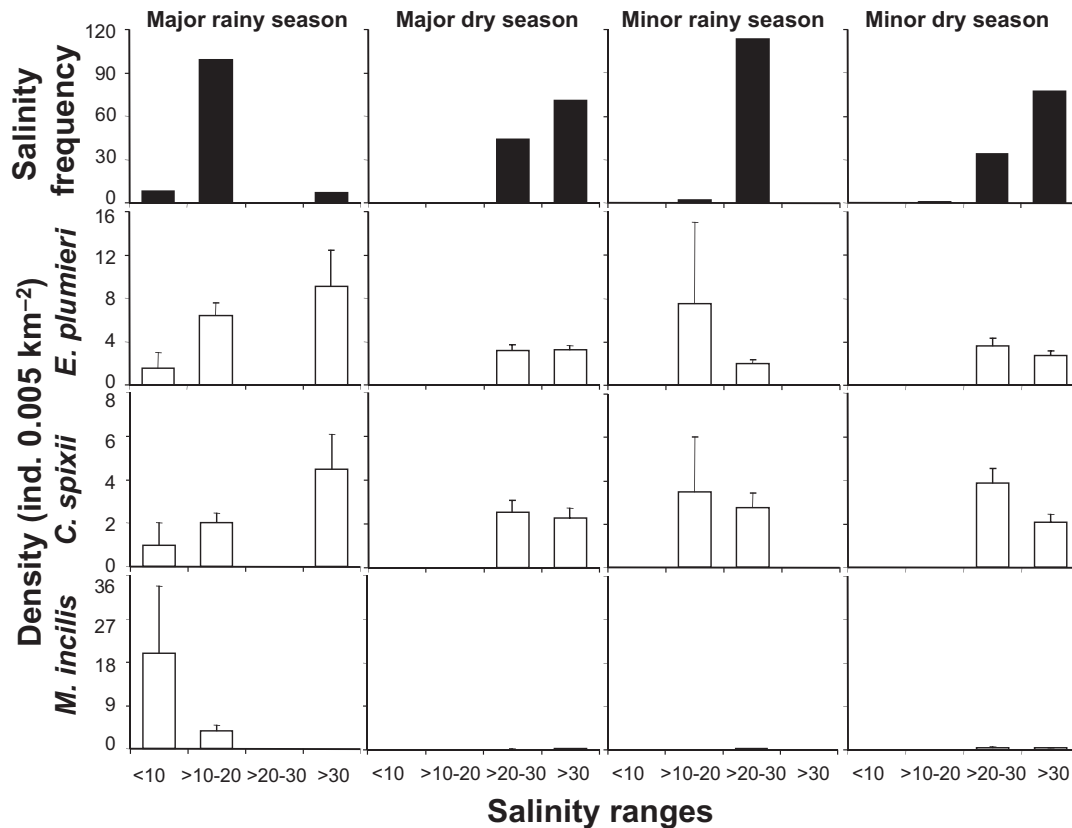


Fig. 6. Salinity frequency distributions and fish density (mean \pm SD) by salinity range for each season

was heterogeneous. Kriging predictions were good, with significant cross-validation and smaller kriging SD values near sampling stations. The global kriging \bar{X} fish densities were lower than the arithmetic mean; however the same trend was not consistent among standard deviations. This is due, first of all, to the existence of a relative high proportion of zero densities and, secondly, to the positive skew exerted by extreme values. This implies that for estimating total abundance a careful choice between kriging and simple arithmetic mean should be made (Warren 1998).

The negative effect of salinity on *Eugerres plumieri* and *Mugil incilis* density (Table 3) and observed seasonal spatial distribution patterns (Figs 3 & 5) probably reflect the seasonality in primary productivity (highest in rainy season) and flushing of organic matter in the CGSM (Hernández & Gocke 1990, Mancera 1991). This picture is characteristic of estuarine tropical systems (Flores-Verdugo et al. 1990, Whitfield 1993, Sánchez-Velasco et al. 1996, Blaber 1997). *E. plumieri*, *Cathorops spixii* and *M. incilis* showed high densities in particular salinity ranges between seasons, possibly due to their individual reproductive behavior (Arango & Rodas 1978, Blanco 1983, Sánchez et al. 1998). Moreover, the analysis revealed the euryhaline characteristics of

these marine-estuarine species (Santos-Martínez & Acero 1991). Since these species are euryhaline, multiple regression models (Table 3) and 2-way ANOVA results (Fig. 7) suggested that substratum type linked to food availability might play an important role in fish distribution. A negative effect of shell, mixed and mud substrata on *E. plumieri* was equivalent to an additive positive effect of fine sands, where the species finds benthic invertebrates that constitute the main dietary component (Arenas & Acero 1992). Shell substrate was the single significant predictor of *C. spixii* density; this could be attributed to high abundance of macro-invertebrates and fish larvae, which constitute the basic food source of this generalist predator (Galvis 1983). *M. incilis* had the highest density on mud, which provides the detritus that constitutes the main food source (Osorio 1988). The negative effect of depth on *E. plumieri* and *M. incilis* (Table 3) suggests the preference of these species for shallow waters. The lack of effect of temperature on species abundance could be attributed to the lower variability ($<4^{\circ}\text{C}$) described for the CGSM (Botero & Salzwedel 1999).

The above discussion shows the disparate influences of abiotic factors on seasonal and spatial distribution of *Eugerres plumieri*, *Cathorops spixii* and *Mugil incilis* in

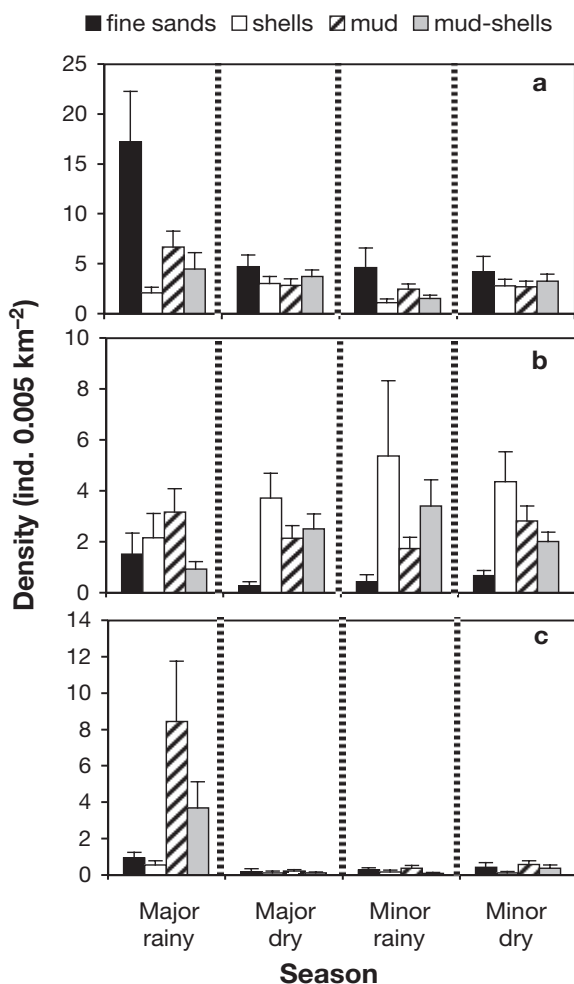


Fig. 7. Mean (\pm SD) fish density by substratum type for each season in the CGSM. (a) *Eugerres plumieri*, (b) *Cathorops spixii*, and (c) *Mugil incilis*

the CGSM. Multiple regression models were highly significant but accounted for a relatively low percentage of variance. The remaining variance could be explained by other variables (see Blaber 1997). However, turbidity could not be significant in this system, because the suspended load, an important part of any turbidity measurement, did not differ among different places in the lagoon ($F_{5,18} = 2.09$; $p = 0.112$) or between seasons ($F_{3,20} = 3.03$; $p = 0.052$) during the same analysis period (INVEMAR unpubl. data). Additional biotic factors influencing fish distribution in tropical and subtropical estuaries such as reproductive condition, competition and predation (Blaber 1997, Whitfield 1999) were not considered in this study and could reduce precision in the regression models. However, the results of these analyses, corroborated by the 2-way ANOVA, are relevant given the complex matrix of interacting factors influencing fish distribution in tropical estuaries (Blaber 1997).

The estimates provided here of spatial and temporal variability in abundance of the most important species of the CGSM could be beneficial for the purpose of stock assessment and fishery management, in order to assess the harvestable biomass and to protect certain biological categories. For example, regulation of fishing effort during the major rainy season would protect the high-biomass patches of *Eugerres plumieri* (immature individuals, Rueda & Santos-Martínez 1999) and *Mugil incilis* (spawning biomass, Sánchez et al. 1998) that are present and vulnerable. Moreover, an additional use could be as baseline information to evaluate the recent impact of dredging canals in the system (Botero & Salzwedel 1999). It would be interesting to implement seasonal surveys and the geostatistical methodology laid out here in order to generate fishery indicators that provide adequate signs of fishery status.

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