

A bioeconomic multispecies analysis of an estuarine small-scale fishery: spatial structure of biovalue

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We estimated the spatial population structure by size and the economical potential (biovalue) of a multispecies fish resource in an estuarine lagoon in Colombia, based on fishery-dependent (catch and effort) and independent (seasonal fishing surveys) data. Model-based (geostatistics, kriging) estimations of such performance variables were used to quantify the uncertainty in abundance, individual price by size and variable costs per haul. Monte Carlo analysis was used to assess the status of the fishery. The spatial dimension of risk analysis was explored by indicator kriging, whereas effects of biovalue on the spatial allocation of fishing effort were evaluated using contingency tables. Fish abundance, individual sizes and biovalue were spatially structured, but the spatial patterns varied between seasons and species. Analysis of biovalue showed a moderate risk that fishers had economic losses derived from the fishing activity. Spatial risk analysis showed that no more than 30% of the total area from the lagoon registered profitable levels of fish abundance, which affected the spatial allocation of fishing effort. Management implications supported by our study suggest seasonal and spatial fishing closures to protect juveniles and spawning stock of fish species.

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Introduction

The spatial structure of the environment and of the biological communities is not only one of the most important determinants of ecosystem functioning (Legendre, 1993), but it also defines the spatial allocation of fishing effort which affects fishery management (Castilla and Defeo, 2001). Indeed, spatially explicit analyses of exploited fish populations have demonstrated a strong spatial structure in abundance and in the fishing process (Pelletier and Parma, 1994; Orensanz and Jamieson, 1998; Caddy and Carocci, 1999; Rueda, 2001). However, the integrated analysis of the spatial dynamics of the composition by size and population abundance, jointly with concurrent spatio-temporal changes in the economic benefit, has been rarely documented (Anderson, 1989; Caddy, 1999; Pauly et al., 2001). This is relevant in small-scale fisheries located on tropical estuaries, where the unselective harvest of a multispecies stock of short-lived species (Blaber, 1997) together with economic

pressures, cause fishers to allocate fishing effort in areas closer to port (Defeo and Castilla, 1998; Cabrera and Defeo, 2001).

The application of spatial models, both analytical (Hilborn and Walters, 1987; Caddy and Seijo, 1998) and empirical (Caddy and Carocci, 1999; Taconet and Bensch, 2000) arise as a powerful tool for stock assessment and fishery management. In this setting, geostatistics has obtained increasing acceptance to address the spatial structure of variables observed across geographical space. Such applications in marine science have been mainly used to describe spatial patterns of benthic and pelagic species (Maravelias et al., 1996; Rueda, 2001; Defeo and Rueda, 2002) and to interpolate abundance at unsampled locations (Petitgas, 1993; Maynou et al., 1998; Rueda and Defeo, 2001). In this study we integrate biological and economic information for modeling and interpolate the spatial structure of fish abundance, individual size and the economic potential of the abundance (biovalue) in the Ciénaga Grande de Santa Marta (CGSM). This is a multispecies (Rueda and Urban, 1998; Sánchez and Rueda, 1999) and multifleet fishery (Rueda and Defeo, in press) based on the exploitation of the fishes *Eugerres plumieri*, *Mulgil incilis* and *Cathorops spixii*, whose harvestable biomass is mainly formed by juveniles (Rueda and Defeo, 2001). In addition, the effect of the abundance of different population components on the biovalue was assessed to quantify the uncertainty in fishery performance variables and to estimate the probability of exceeding limit reference points (LRPs) defined in terms of critical threshold values of biovalue. Potential consequences of biovalue spatial dimension on the spatial allocation of fishing effort are also explored.

Methods

Study area and sampling

The CGSM is the most important estuarine lagoon of Colombia (Figure 1), because its fishery constitutes the main source of both food and income for ca. 20000 persons

(3500 fishers: Botero and Salzwedel, 1999). Four alternating seasons affect the life history traits of the fish fauna in the CGSM (Rueda and Santos-Martínez, 1999; Sánchez and Rueda, 1999); however, for the purpose of this study, we only considered data gathered in the contrasting rainy and dry seasons. One fishing survey was conducted in November 1993 (rainy season) and another in March 1994 (dry season), based on a systematic design of 115 stations spaced 2000 m apart and located using a GPS, covering the whole CGSM (Figure 1). At each station, a haul was carried out using a "boliche" or encircling gillnet, which enclosed an average circular area of 5000 m². Eight "boliches" were used simultaneously to conduct each survey, which took approximately 8 h to be completed (see Rueda, 2001; Rueda and Defeo, 2001 for details). Individuals of E. plumieri, M. incilis and C. spixii collected per station were counted and measured for total length to the nearest 0.5 cm. Information on fishing effort of the "boliche" and bioeconomic variables was obtained from a fishery monitoring program conducted between 1993 and 1994 (Santos-Martínez and Viloria, 1998). Effort data (number of trips

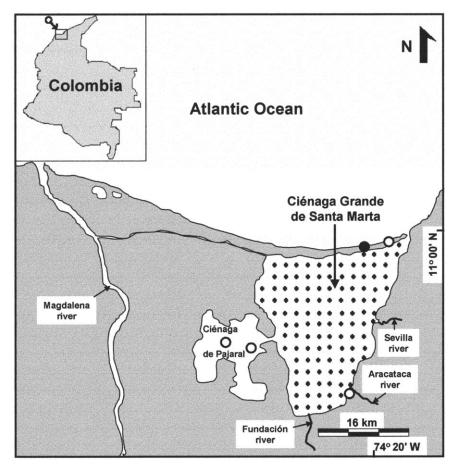


Figure 1. CGSM—Colombia, showing the fixed grid of 115 stations (+) sampled during rainy (1993) and dry (1994) seasons. (O) Denotes fishing ports, highlighting the port of Tasajera (\bullet).

day⁻¹) and location of fishing grounds were recorded during November 1993 and March 1994 using random sampling of commercial catches. Bioeconomic variables gathered per month focused on individual price by size (measurement of length–frequency samples and collection of size-at-price data). Variable costs of the "boliche" (VC; gas, gear repair, food and beverages) were obtained from logbooks and interviews with the fishers from the main port on the north of the CGSM (Tasajera, see Figure 1), where 80% of the "boliche" activity was carried out. Additional information on national minimum salary for 1993 and 1994 was gathered from Colombian government statistics (Banco de la República, 2002).

Differences in fish abundance between seasons for each species were tested by the Kruskal–Wallis test by ranges, because the normality assumption was not fulfilled. Concerning the population structure by size, length–frequency distributions of *E. plumieri*, *M. incilis* and *C. spixii* were subjected to Kolmogorov–Smirnov (K–S) goodness of fit to test for differences between seasons. The length–price (L–P) relationship was modeled by the power function of the form $P = aL^b$, where a and b are parameters, and were employed to calculate the price for each average size estimated per sampling station. An analysis of covariance (ANCOVA) was employed to compare the L–P relationship fitted for each species between seasons, using length as the covariate.

Assessing spatial structure of fish abundance, size and biovalue

Variographic analysis (Matheron, 1971) was used to characterize the spatial structure of fish abundance, size and biovalue. Each variable was considered as a spatial process observed in each season by means of 115 observations measured at a location x, defined by latitude and longitude in a two-dimensional space. Seasonal experimental semivariograms were estimated. Confirmation of a second-order stationarity assumption and assessing the possibility of isotropic and anisotropic processes were conducted by computing semivariogram surfaces (Isaaks and Srivastava, 1989). Structure functions for fish abundance, size and biovalue were estimated fixing the active lag distance to 20400 m (65% of the maximum lag). This was done after looking for the large number of pairs available to estimate semivariograms which avoids the situation where they decompose at large lag intervals close to the maximum lag interval (Robertson, 2000). Calculated mean individual size per station was used to estimate experimental semivariograms of fish size, whereas the spatial autocorrelation of biovalue took into account species-specific information on individual price by size. The seasonal biovalue (BV_{iikl}) for each species was calculated as $BV_{ijkl} = (NP)_{ijkl}$, where N and P are the fish abundance and price, respectively, of the species i by size j at station k in season l. In all cases, theoretical models were fitted to the experimental semivariograms to relate the observed structure to hypothesized generating processes (Isaaks and Srivastava, 1989). The model that best explained the spatial structure was selected according to the coefficient of determination (r^2) and the residual sum of squares. Semivariogram models provided the following parameter estimates: (1) the nugget effect (C₀), which reflects microscale variation; (2) the sill (C₀ + C), which defines the asymptotic plateau in the semi-variance; and (3) the range (A₀), defined as the distance at which the variables ceases to be autocorrelated (Isaaks and Srivastava, 1989). An analysis of the residual sum of squares (ARSS; Chen *et al.*, 1992) was performed to compare the semivariograms for fish abundance, size and biovalue fitted for each season.

Spatial prediction of fish abundance, size and biovalue

Maps of fish abundance, size and biovalue per species and seasons were obtained by block kriging (Matheron, 1971). Kriging predictions were evaluated using jackknife crossvalidation, fitting observed (O) and estimated (E) values to a linear regression of the form $O = \alpha + \beta E$ and testing the significance of α and β (t-test) under the null hypotheses $\alpha = 0$ and $\beta = 1$ (Power, 1993). Maps were performed over a regular interpolating grid of $424 \times 414 \text{ m}^2$ (internodal distances) covering the whole area of the CGSM (450 km^2) , whereas the neighborhood comprises at least the 16 nearest neighbors. Global biovalue and the standard deviation per species and seasons were computed as a linear combination of block estimates, with each estimate receiving a weight proportional to the sampled area (Journel and Huijbregts, 1978). Global estimates were corrected by the vulnerability of each species to the sampling gear experimentally estimated as 0.5, 0.43 and 0.4 for E. plumieri, M. incilis and C. spixii, respectively (Rueda and Defeo, 2001).

Risk analysis and indicator probabilistic kriging

We estimated multispecies biovalue (BV) by summing up the global biovalues obtained for each species, given by multiplying the mean fish abundance of block kriging analyses by its mean unit price per size. Thus, estimates of BV, VC and minimum threshold profit (Z) in each season were used to quantify the risk of falling below undesirable biovalue thresholds per haul. As a typical trip of the "boliche" involves around 20 hauls day⁻¹ allocated to any site in the lagoon from any port (Rueda, 1995), VC corresponded to one global seasonal estimate weighed to a single haul. Z was fixed at 1.6 times the daily national minimum salary for 1993 (rainy season) and 1994 (dry season), representing revenue levels that fulfill daily economic expectations of fishers (Santos-Martínez and Viloria, 1998). This risk analysis was done with LRPs defined by two thresholds (1) prob(BV \leq VC) and (2) prob(BV \leq Z), representing two scenarios of fishery status. Scenario (1)

could be considered as risk-prone, on the basis that BV <VC implies economic losses or zero quasi rent, whereas scenario (2) is a risk-averse desirable profit margin. Monte Carlo analysis was used to explicitly account for the uncertainty associated with fish abundance, unit price per species and the variable costs per haul in order to quantify the BV risk of falling below the LRPs mentioned above. These variables were randomly generated by Monte Carlo resampling with lognormal (N and P; Chi-square test: p > 0.05 in all cases) probability density functions, which allowed us to estimate the mean and standard deviation parameters needed for the simulation process. The VC was fitted to a uniform distribution, assuming that all values between the minimum and maximum, both fixed, occur with equal likelihood (Werckman et al., 2000). Two Monte Carlo runs of 1000 simulation trials were conducted for each year to obtain the probability distributions of BV by which the LRPs were assessed.

To provide adequate signs of fishery status, the spatial dimension of the LRPs (Seijo and Caddy, 2000) were determined by indicator kriging (Burrough and McDonnell, 1998), by which we estimated the probability that the BV exceeds desirable thresholds [prob(BV > VC) and prob (BV > Z)] over the study area in each season. For this purpose, original BV data were transformed from a continuous to a binary scale to apply ordinary indicator kriging (Goovaerts, 1997) as follows:

$$i(X_i; Z_k) = \begin{cases} 0 & \text{if } BV(X_i) \le Z_k \\ 1 & \text{if } BV(X_i) > Z_k \end{cases}$$
(1)

where X_i is the BV datum location and Z_k are the k thresholds (VC and Z). Indicator kriging is a non-linear form of ordinary kriging, where semivariograms are computed for the binary data in the usual way, and ordinary kriging proceeds with the transformed data (Burrough and McDonnell, 1998). The resulting maps displayed continuous data in the range 0–1, indicating the probability that BV has exceeded desirable thresholds.

Effects of biovalue on temporal and spatial allocation of fishing effort

Seasonal variations in fishing effort (daily number of fishing trips) were tested using a standard t-test. We do not have effort allocation data with the same spatial resolution as fishing surveys. To circumvent this, potential effects of the spatial structure of BV on spatial allocation of fishing effort were explored by dividing the CGSM area into three discrete sub-areas (fishing zones). These zones were defined according to the number of fishing trips per season allocated on each one, which significantly differed from a hypothesized 1:1:1 ratio for the rainy (χ^2 test = 159.34; p \ll 0.01) and the dry (χ^2 test = 381.96; p \ll 0.01) seasons. The distribution of the occurrence of the binary scale of BV (1 if BV > VC, and 0 otherwise) in each fishing zone

was analyzed for each season by computing a 2×2 contingency table to test the null hypothesis that fishing effort between fishing zones is independent of the prob(BV > VC).

Results

Fish abundance and population structure by size

Abundance of *E. plumieri* and *C. spixii* did not differ between seasons (Kruskal–Wallis test $H_{1,228} = 0.29$ and $H_{1,228} = 0.31$; p > 0.05, respectively). However, fish abundance in the rainy season showed higher variability (Table 1). Although *M. incilis* presented higher abundance in the rainy season, seasonal comparison was not tested due to high number of hauls with zero catch in the dry season. The population structure by size of *E. plumieri* and *C. spixii* did not differ between seasons (K–S test: p > 0.05), while *M. incilis* presented significantly lower mean lengths in the dry season (22.5 ± 3.1 cm) with respect to the rainy season (26.3 ± 2.6 cm) (K–S test: p < 0.05, Table 1).

Structural analysis and spatial prediction

In four of the six cases analyzed, the spherical model described the spatial structure of *E. plumieri*, *M. incilis* and *C. spixii* abundance, which was unstable between seasons, as highlighted by significant differences in semivariograms (ARSS analyses: F-test >100; $p \ll 0.01$) and the different values of variance explained by the spatial models $[C/(C_0 + C)]$ (Table 2). The semivariance for each species was higher in the rainy season than in the dry season. This trend was also found for the range parameter A₀, which describes the distance at which the variables ceases to be autocorrelated, indicating larger areas of spatial dependence in the rainy season. Consistent with this spatial heterogeneity, kriging maps of fish abundance showed a patchy structure, although *M. incilis* did not present

Table 1. Seasonal mean (\pm s.d.) values of fish abundance and individual fish length in the CGSM. Different sample sizes (n) are due to a breakdown of the "boliche" (abundance data for rainy season) or stations with zero individuals (length data).

Species		Abundanc nd 5000 m	Total length (cm)			
	Ā	s.d.	n	Ā	s.d.	n
1993/Rainy						
E. plumieri	6.2	11.1	113	17.6	3.1	70
M. incilis	4.6	14.7	113	26.3	2.6	59
C. spixii	2.0	4.4	113	22.3	2.6	48
1994/Dry						
E. plumieri	3.3	4.0	115	17.5	2.3	85
M. incilis	0.1	0.5	115	22.5	3.1	12
C. spixii	2.3	3.5	115	23.3	2.0	62

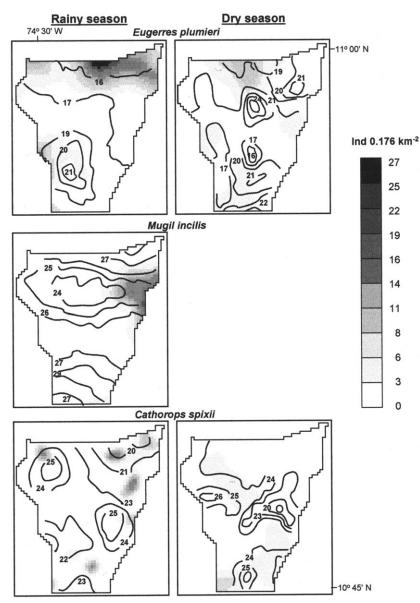
Table 2. Parameters, goodness of fit criteria and cross-validation of the exponential (Exp), spherical (Sph) and Gaussian (Gau) models, fitted to fish abundance, size, biovalue and indicator experimental semivariograms during rainy and dry seasons in the CGSM. (Co) nugget effect, (C_0+C) sill, $(A_0, in m)$ range, (%) spatially structured component, (r^2) coefficient of determination, (RSS) reduced sum of squares, (α) intercept, (β) slope, (r) coefficient of correlation. For all surveys, α and β were not significantly different from 0 and 1, respectively, and r was significant (p < 0.05), both for the geostatistical models fitted and the jackknife cross-validation. (BV) multispecies biovalue, (VC) variable costs of the "boliche" and (Z) minimum threshold profit.

Species	Model	Parameters			Goodness of fit		Cross-validation			
		C ₀	$C_0 + C$	A ₀	%	r ²	RSS	α	β	r
Abundance										
1993/Rainy										
E. plumieri	Sph	0.490	1.580	12 530	70	0.96	5×10^{-2}	1.90	1.03	0.47
M. incilis	Sph	0.432	1.295	13 750	66	0.91	6×10^{-2}	0.91	1.60	0.40
C. spixii	Gau ^a	0.001	1.106	4587	99	0.44	5.1	1.9	0.40	0.20
1994/Dry							2			
E. plumieri	Sph	0.371	0.743	7180	50	0.81	1×10^{-2}	0.58	1.03	0.43
M. incilis	None	-	-	-	65	-	5×10^{-2}	-	-	
C. spixii	Sph	0.270	0.766	6370	65	0.62	5×10	0.77	1.65	0.42
Fish length										
1993/Rainy		0.014	0.056	51 100	- 4	0.00	2 10-4		0.75	0.00
E. plumieri	Exp	0.014	0.056	51 100 51 100	74 79	0.82 0.88	3×10^{-4} 8×10^{-7}	4.54 5.71	0.75	0.32
M. incilis C. spixii	Exp Exp ^b	0.002 3.250	0.007 6.980	3610	78 53	0.88	8×10^{-2} 8×10^{-2}	5.71 8.60	0.80 0.65	0.39 0.26
1	Ехр	3.230	0.980	3010	55	0.37	8×10	8.00	0.05	0.20
1994/Dry	a 1	0 000 -		2250	0.4	o 1 -	0 10-5		0.44	
E. plumieri M. incilis	Sph None	0.0005	0.014	3370	96	0.47	9×10^{-5}	5.72	0.66	0.28
M. incliis C. spixii	Exp ^b	0.4000	3.990			0.10	2.4	11.30	0.52	0.20
-	слр	0.4000	3.990	040	90	0.10	2.4	11.50	0.52	0.20
Biovalue										
1993/Rainy E. plumieri	Sph	0.083	0.173	21 780	51	0.89	8×10^{-3}	0.04	1.10	0.35
L. plumleri M. incilis	Sph	0.085	0.173	15 660	72	0.89	2×10^{-3}	0.04	1.10	0.33
C. spixii	Sph	0.0001	0.166	3830	99	0.56	2.4	0.35	0.26	0.40
1994/Dry	opn	010001	0.100	2020		0100	2	0100	0.20	0.10
E. plumieri	Sph	0.003	0.099	4090	96	0.56	4×10^{-4}	0.14	0.62	0.40
M. incilis	None	0.005	0.099	4090	-	0.50	4×10	-	0.02	0.40
C. spixii	Sph	0.053	0.249	4940	79	0.51	7×10^{-3}	0.29	0.60	0.34
Risk	~									
1993/Rainy										
prob(BV > VC)	Sph	0.134	0.270	11 590	50	0.94	7×10^{-4}	0.05	0.90	0.47
prob(BV > Z)	Sph	0.110	0.221	15 240	50	0.92	8×10^{-4}	0.05	0.87	0.41
1994/Dry	I									
prob(BV > VC)	Exp	0.019	0.146	1320	87	0.24	2×10^{-3}	0.05	0.83	0.42
prob(BV > VC) prob(BV > Z)	Exp	0.019	0.140	680	90	0.24	1×10^{-4}	0.05	0.83	0.42
F100(D (> D)	LAP	0.017	0.170	000	20	0.22	1/10	0.00	0.07	0.55

^aAnisotropic model in northeast direction (64°). Only the value of A_0 for the major axis is reported. ^bData non-transformed.

spatial dependence in the dry season (Figure 2). C. spixii showed different distribution patterns between seasons, whereas E. plumieri consistently presented high-abundance patches in the north of CGSM. Mean sizes for each species tended to show patchy distribution with smooth autocorrelation between stations, as indicated by the best fit of exponential models in most cases (Table 2). Semivariograms for E. plumieri and C. spixii differed between seasons (ARSS analysis: F test >80; p < 0.01). This was consistent with the variability in the spatially structured component of sizes, which ranged from 53 to 96%. Kriging maps of individual size evidenced the spatial segregation of different population components in each species, which varied seasonally (Figure 2). A simple visual inspection of abundance and size maps showed that high-abundance patches and larger sizes did not overlap in space (Figure 2), mainly in the rainy season. Negative correlations between mean size and abundance for *E. plumieri* (r = -0.40; p = 0.009) and C. spixii (r = -0.26; p = 0.047) corroborate our observations.

The relationship between price and size was statistically significant for each species, accounting in all cases for ca. 50% of the total variance; moreover, parameters a and b were highly significant in all cases (p < 0.001; Figure 3).



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Figure 2. Ordinary kriging maps overlaying fish abundance $(Ind 0.176 \text{ km}^{-2})$ and individual mean size (cm) for rainy (1993) and dry (1994) seasons in the CGSM. Darker surfaces correspond to fish abundance, whereas the numbers labeling isolines indicate mean length estimates for each species. For *M. incilis*, maps of fish abundance and sizes were not performed in the dry season, due to the lack of spatial autocorrelation.

For a same size, the price of *E. plumieri* was higher in the dry season (ANCOVA $F_{1,147} = 6.32$; p = 0.012), whereas the price of *M. incilis* was higher in the rainy season (ANCOVA $F_{1,51} = 4.71$; p = 0.034). Alternatively, the L– P relationship for *C. spixii* did not differ between seasons (ANCOVA $F_{1,162} = 0.009$; p = 0.924).

The spatial structure of BV for *E. plumieri* and *C. spixii* differed between seasons (ARSS analysis: F test >112; p < 0.01), with areas of spatial dependence well defined by spherical models (Table 2). The spatially structured component of BV ranged between 51 and 99%, confirming

different spatial features in the economic potential denoted by kriging maps (Figure 4). The distribution patterns of BV were very similar to those shown for abundance data (Figures 2 and 4). *E. plumieri* presented high-BV patches mainly in the north of CGSM in both seasons, with some important clusters in the dry season located toward southern, eastern and western ends of the lagoon. Consistently, *C. spixii* showed an aggregated distribution in each season, whereas the BV of *M. incilis* was clustered on the eastern coast during the rainy season. In all cases, cross-validation analysis showed that kriging predictions for fish abundance,

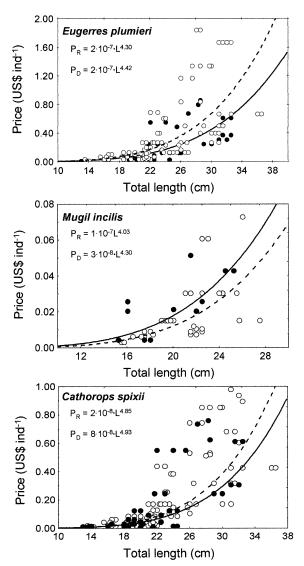


Figure 3. L–P relationship fitted for fish species in rainy $(R, - \bullet)$ and dry $(D, - \circ)$ seasons in the CGSM. Fitted models are also shown. P, price; L, total length. Note the different scale in the X-axis for *M. incilis*.

size and biovalue were suitable, because the null hypotheses $\alpha = 0$ and $\beta = 1$ were never rejected (p > 0.05; Table 2). Global estimates of biovalue were higher in the dry season than in the rainy season, both for *E. plumieri* (13%) and *C. spixii* (37%) (Table 3). These estimates evidenced the combined effect of abundance by size and individual size price variations for each species on the economic potential of fish abundance.

Risk analysis and indicator kriging

Both LRPs [prob(BV \leq VC) and prob(BV \leq Z)] varied between seasons (Figure 5). For the first scenario, the

probability that the BVs were equal or less than the variable costs (US\$0.68 haul⁻¹ in the rainy season and US\$0.81 haul⁻¹ in the dry season) was 0.47 and 0.58, respectively, suggesting a moderate risk that fishers obtain zero quasi rent or economic losses. The second scenario showed a high risk (0.79 and 0.92 for rainy and dry seasons, respectively) that fishers obtain a minimum profit threshold equal or less than that expected (Z = US1.48 haul⁻¹ in the rainy season and US\$1.6 haul⁻¹ in the dry season). Consequently, the probability of obtaining some fishing profit ranged between 0.53 in the rainy and 0.42 in the dry seasons. Such probabilities were substantially reduced under the second scenario (0.21 in the rainy and 0.08 in the dry season).

Spatial risk analysis showed that probabilities of exceeding desirables thresholds of biovalue had spatial structure, which differed between seasons consistently with changes in the spatial variance explained by spherical (50%, rainy season) and exponential models (87-90%, dry season) (Table 2). Cross-validation analysis corroborated the appropriateness of the semivariogram models (0.33 < r < 0.47; p < 0.05). Risk maps (Figure 6) showed that patches with probability of getting some profit [prob(BV > VC)] varied in location and size, being the smaller patches when the probability of achieving the expected rent by fishers was considered [(prob(BV > Z)]]. Taking into account an arbitrary value of probability higher than 0.7, the potential areas for getting profits did not exceed 30% of the CGSM total area.

Effects of biovalue on temporal and spatial allocation of fishing effort

The number of fishing trips day⁻¹ was significantly higher in the dry season than in the rainy season (t - test =-6.84; p $\ll 0.01$) (Figure 7b). Moreover, the number of trips was significantly higher on fishing zone A, both in the rainy (55% of 571 trips) and dry (48% of 1882 trips) seasons. The lowest number of trips was allocated on zone B (12 and 13% of the total trips in rainy and dry seasons, respectively), whereas zone C had intermediate values (33 and 39% of the total trips in rainy and dry seasons, respectively) (Figure 7a, c, d). Consistent with this spatiotemporal pattern, the number of fishing trips between zones was dependent on the probability of obtaining some profit prob(BV > VC) in the rainy ($\chi^2 = 10.07; \ p \ll 0.01)$ and in the dry (χ^2 test = 6.06; p < 0.05) seasons. In this sense, zones A (in the rainy season) and C (in the dry season) were the most successful, considering that the higher frequency of indicators revealed the probability of finding fish abundance at profitable levels (Figure 7c, d).

Discussion

The spatial dimension has played an important role in building paradigms in ecological research, and currently

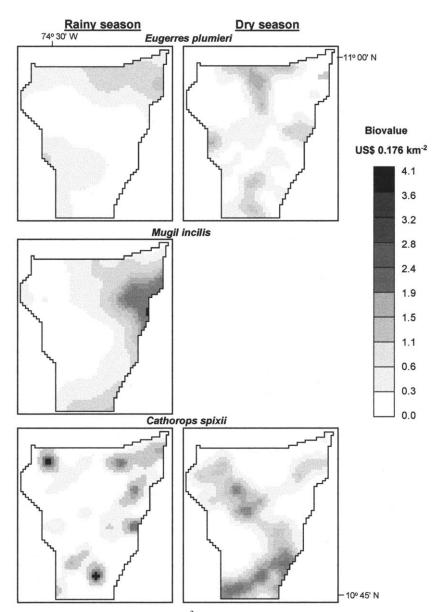


Figure 4. Ordinary kriging maps of biovalue (US 0.176 km^{-2}) for each species in rainy (1993) and dry (1994) seasons in the CGSM. The kriged map was not performed for *M. incilis* in the dry season, due to the lack of spatial autocorrelation.

constitutes one of the challenges to overcome in fisheries science for the present century (Caddy, 1999). In this study, model-based (e.g. geostatistics) approaches allowed us to describe successfully the spatial structure of fish abundance, individual size and biovalue in a tropical estuarine small-scale fishery. Such an approach was also useful to test hypotheses related to the spatial dynamics of those performance variables and to assess the status of fishery using bioeconomic reference points.

Abundance of *E. plumieri*, *M. incilis* and *C. spixii* showed a strong spatial structure in the CGSM, and this was

consistent with spatial variations in the population composition by size and the BV (Table 2). Fish distribution of these species has been related to gradients in salinity and to habitat features like substrate type (Rueda, 2001). The reproductive migration of *M. incilis* toward adjacent marine waters (Sánchez *et al.*, 1998) precluded the determination of spatial structure for the abundance, size and biovalue in the dry season. Size distribution maps showed different spatial structures of population components (e.g. juveniles, spawning stock) within and between seasons, as a result of the co-occurrence of multiple annual cohorts (Sánchez

Table 3. Block kriging estimates of fish biovalue during rainy and dry seasons in the CGSM. $\bar{B}\bar{V}$ (US\$0.176 km⁻²) is the mean biovalue and s.d._{BV} is its standard deviation; BV_t and s.d._{BVt} are the mean total biovalue for the whole area (US\$) and its standard deviation, respectively.

	Biovalue						
Species	$\bar{B}\bar{V}$	s.d. _{BV}	BV_t	s.d. _{BVt}			
1993/Rainy							
E. plumieri	0.37	0.08	28712	6208			
M. incilis	0.37	0.09	28786	7002			
C. spixii	0.48	0.11	31 680	7260			
1994/Dry							
E. plumieri	0.42	0.08	32 424	6176			
M. incilis	_	_	_	_			
C. spixii	0.66	0.21	43 560	13 860			

et al., 1998; Tíjaro *et al.*, 1998; Rueda and Santos-Martínez, 1999). High-abundance patches corresponded to juveniles, mostly for *E. plumieri* (L < 17 cm) and *C. spixii* (L < 23 cm) in the rainy season, whereas most aggregations of adults were present in the dry season (Figure 2). This picture was consistent with recruitment and sexual maturity peaks

reported for these species during the rainy and dry seasons, respectively, in the CGSM (Tíjaro *et al.*, 1998; Rueda and Santos-Martínez, 1999). Negative correlations between mean size and abundance for *E. plumieri* and *C. spixii* suggest spatial density dependence in the rainy season, thus giving strong support to our findings. Alternatively, *M. incilis* showed adult individuals (L > 24 cm) in the rainy season, mainly clustered in the eastern part of the CGSM before migrating to the sea to spawn.

The L–P relationship fitted for each species was very useful to estimate spatial and temporal variations in the biovalue. In spite of this, abundance and structure by size did not differ between seasons for *E. plumieri* and *C. spixii*, and BV of these species was consistently higher in the dry season as a response to seasonal price-at-size variations. This demonstrates one of the main characteristics of artisanal fisheries, where market forces regulating prices affect the potential value of the catch (Defeo and Castilla, 1998; Castilla and Defeo, 2001). Higher BV values (Figure 4) coincided with scarce high-abundance patches for the three species (Figure 2). Such spatio-temporal heterogeneity of the economical potential determined that fishers had moderate probabilities of realizing economic losses from their fishing activity; whereas the risk of falling below an

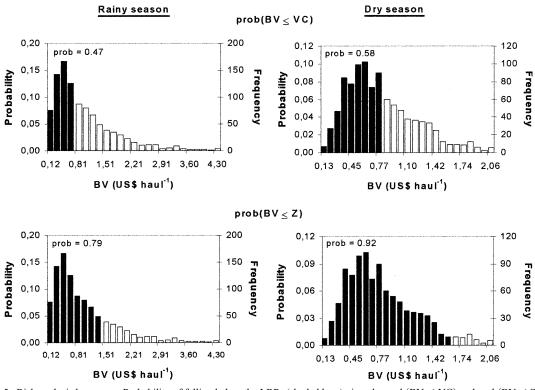
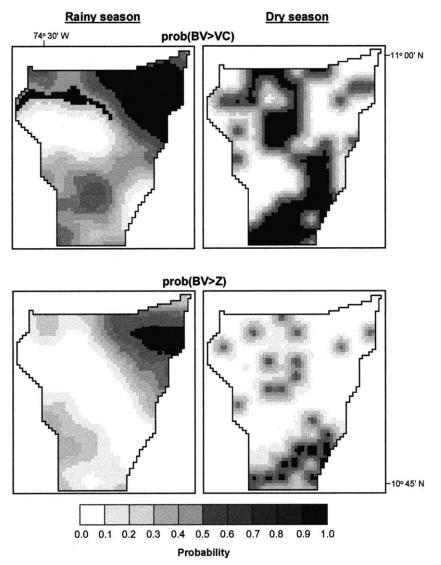


Figure 5. Risk analysis by season. Probability of falling below the LRPs (shaded bars) given by $prob(BV \le VC)$ and $prob(BV \le Z)$. The corresponding probability values are also shown. BV is the multispecies biovalue by haul. VC denotes variable costs by haul of the "boliche", and Z is a minimum threshold profit (see text for details). Probabilities of falling below these undesirable thresholds are based on 1000 Monte Carlo simulation trials for rainy and dry seasons.



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Figure 6. Probability maps of exceeding desirable thresholds given by prob(BV > VC) and prob(BV > Z) for rainy and dry seasons in the CGSM. Maps were produced by ordinary indicator kriging. BV, VC and Z are as defined in Figure 5.

undesirable threshold of rent expected was always high. In agreement with this scenario, maps of risk emphasized that only a small portion of the stock could be harvested with high probabilities of obtaining profits and that, in general, when fish abundance was low variable costs were higher than the biovalue. The above situation determines high concentrations of fishers over the most productive grounds, generating crowding externalities (Seijo *et al.*, 1998). Conflicts between fishers of different ports employing several gears support this assertion due to overlapping of fishing grounds (Santos-Martínez and Viloria, 1998). These findings were confirmed by the analysis of commercial fishing data, which showed: (1) higher amounts of fishing effort in the dry season in accordance with higher BV levels and (2) dependence between fishing effort allocated among zones and the probability of finding profitable levels of abundance [prob(BV > VC)].

In conclusion, the analysis of spatial structure of fishery performance variables allowed us to map variations in abundance of different population components and in the economical potential of targeted species. These modelbased estimates were useful to quantify spatially explicit probabilities of exceeding bioeconomic LRPs, which may be used to explain potential changes in the spatial and temporal allocation of fishing effort. In this context, a precautionary approach could include the reduction of fishing effort in areas and seasons with high concentration of juveniles (e.g. *E. plumieri* on the north of the lagoon during the rainy season), even though high abundance could generate high economic revenues. Moreover, effort

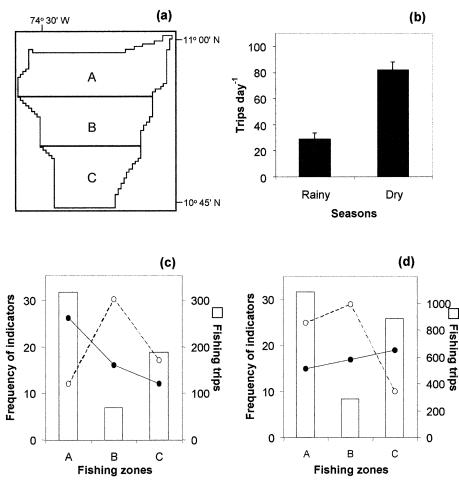


Figure 7. Linkage between biovalue and spatial allocation of fishing effort in the CGSM. (a) Fishing zones (A, B and C). (b) Seasonal variations in fishing effort (fishing trips day⁻¹: mean \pm SE). Frequency of indicators (— \oplus —, BV > VC; —O—, BV \leq VC) and total fishing effort (fishing trips) discriminated by fishing zones for rainy (c) and dry (d) seasons.

on *M. incilis* should be restricted at the northeast of the lagoon during the rainy season, in order to protect the spawning stock. Such strategies might be combined with selectivity controls of the "boliche" (Rueda and Defeo, in press) and an appropriate institutional framework directed to strengthen the actually poor implementation and enforcement of management measures in this artisanal fishery.

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