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Seasonal patterns of three fish species in a Caribbean coastal gill-net fishery: Biologically induced or climate-related aggregations?

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ABSTRACT

Although both seasonal patterns and short-term variation in CPUE are known to occur in most fisheries, particularly small-scale coastal fisheries, the analysis of their underlying factors have received little attention to date. When these factors become part of the local fishermen's ecological knowledge, the resulting peak abundances are often intensively fished, as a result of their predictability, both in space and time. This study, conducted in the Caribbean Sea of north-eastern Colombia, tests hypotheses derived from local fishermen of seasonal patterns of the demersal species *Lutjanus analis* and the two pelagic species *Caranx crysos* and *Scomberomorus cavalla*, and of the possible wind- or swell-driven aggregations of *L. analis*. ARIMA modelling and Fourier analysis were used to identify seasonal patterns from time series of monthly mean catch per unit effort. Available biological information and, concerning *L. analis*, also data on wind speed and significant wave height anomalies were used to analyse the intra-annual patterns. Evidence of biologically induced seasonal migrations was found for the two pelagic species. Concerning *L. analis*, in the windy season the timing of these aggregations and therefore peak CPUE values appear correlated with the wind forcing occurring a few days before, but in the last months of the wet season these peak abundances seem to be mainly related to pre-spawning migrations and spawning aggregations. Thus, we state that both kinds of events should be taken into account for the implementation of precautionary measures aimed to reduce the vulnerability to overfishing of these aggregations.

1. Introduction

Knowledge of temporal fluctuations in the availability of fisheries resources and their underlying migration or aggregation behaviour are critical for effective management and sustainable exploitation (Lucas and Batley, 1996; Healy, 2000; Borges et al., 2003), because a great proportion of the stocks become extremely vulnerable to heavy exploitation during such periods (Munro et al., 1973; Domeier and Colin, 1997; Burton et al., 2005; Matos-Caraballo et al., 2006), particularly when this behaviour is related to seasonal variations in the abundance (Lucas and Batley, 1996). Considerable evidence has been provided on seasonal fish migrations and aggregations linked to growth, survival and reproduction in various regions (e.g., Jennings et al., 2001; Borges et al., 2003; Suárez-Sánchez et al., 2004; Graham et al., 2008). Most documented of these seasonal variations are attributed to fish spawning aggregations (FSA) (e.g., Munro et al., 1973; Domeier and Colin, 1997; Claro and Lindeman, 2003; Matos-Caraballo et al., 2006). A common recommendation of these studies is the advice of applying management strategies for preserving spawning stock biomass.

However, many studies have called "spawning aggregations" any gathering of fish, although in strict terms such gatherings may not necessarily be the vehicle for spawning (Domeier and Colin, 1997). Moreover, several studies have also highlighted climate-related effects on the migratory behaviour (Healy, 2000; Páramo et al., 2003; Lloret et al., 2004) or the temporal dynamics (Borges et al., 2003; Hänninen et al., 2003; Bondi and Overland, 2005) of fisheries resources (Robins, 1957; Pati, 1982; Longhurst and Pauly, 1987), including offshore oceanographic events that affect onshore fishery dynamics. In the specific case of the north-eastern

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Colombian Caribbean Sea (NCCS), temporal patterns concomitant with environmentally or biologically forced processes, as well as trends in fishing production indices, have so far received little research attention, despite the extreme vulnerability of such aggregations to heavy exploitation. In this region there are few continuous, methodical, multi-year, and regular-interval records of landings or CPUE, an important requirement for detecting seasonality and trends in fisheries resources (Wolfe et al., 1987). One of the few exceptions is the series of artisanal fishery statistics for the NCCS, recorded directly at the landing sites and systematized using a fishery statistical system known as "PICEP", a database funded by several government fishery agencies and research institutions (Manjarrés, 2004). Nevertheless, studies focusing on the effect of storms or swells on tropical fish resources are scarce in the Caribbean, particularly those studying daily-scale effects.

Three commercially important fish species frequently found in the NCCS catches are the demersal species mutton snapper *Lutjanus analis* (Cuvier, 1828), and the pelagic species blue runner *Caranx crysos* (Mitchill, 1815) and king mackerel *Scomberomorus cavalla* (Cuvier, 1829). Mutton snapper, the second most important lutjanid in the artisanal fisheries of the NCCS, are found in a variety of habitats, from shallow seagrass beds and patch reefs to deep barrier reefs (Domeier and Colin, 1997). For the NCCS, Manjarrés-Martínez et al. (2004) reported a gill-net mean catch size of 35.5 cm TL and a maximum of 60 cm TL. Peak abundances due to large transient FSA have been reported for mutton snapper, a species normally solitary (Domeier and Colin, 1997; Burton et al., 2005; Graham et al., 2008). The blue runner is a fast-growing, coastal species, with a mean catch size of 36.5 cm TL and a maximum of 62 cm TL (Barros, 1996), occurring in loose shoals in the neritic region (Longhurst and Pauly, 1987). The king mackerel is a shoaling fish, the largest species of its genus, with a maximum recorded catch size of 84 cm TL (Perrota, 2003). A traditional, year-round fishery that exploits these resources in the NCCS is that constituted by artisanal boats using mainly synthetic monofilament gill nets, commonly deployed as stationary bottom sets. These gears usually are 160 meshes deep (8.9–11.4 cm stretch-measure mesh) and are used in sheltered inlets, where a large proportion of the entire water column can be fished. Historical recorded data (Manjarrés, 2004) indicate that at least 131 taxa are caught by this fishery. Mutton snapper, blue runner, and king mackerel accounted for about 41%, 10% and 6% of the sampled fishery catch, respectively, and were mutually exclusive in 75.5% of the total gill-net hauls, while co-occurrences of two of these species were recorded in 21.3% of hauls. The three species were recorded together in the rest of the hauls (3.2%).

According to the local ecological knowledge (LEK) of the NCCS artisanal fishermen, the three species studied have seasonal patterns. Local fishermen relate the seasonal pattern of mutton snapper to a natural event occurring generally twice a year, known as the "bajanza" ("runs" hereafter). LEK claims that these events lasts for about 2 to 4 days and are characterized by an increased abundance of large specimens of mutton snapper and other commercial species in the coastal zone, sometimes a few days after strong swells events. Thus, the first objective of this study is to identify intra-annual patterns in mutton snapper, blue runner and king mackerel, and in particular to verify the seasonal behaviour attributed to these resources in LEK, through time series and Fourier analyses. A second objective is to determine the extent to which these patterns are related to available biological or climate data, and, in the specific case of mutton snapper, to analyse the LEK-based hypothesis of a significant role of the "runs" in the seasonal availability of this resource, sometimes related to swell events.

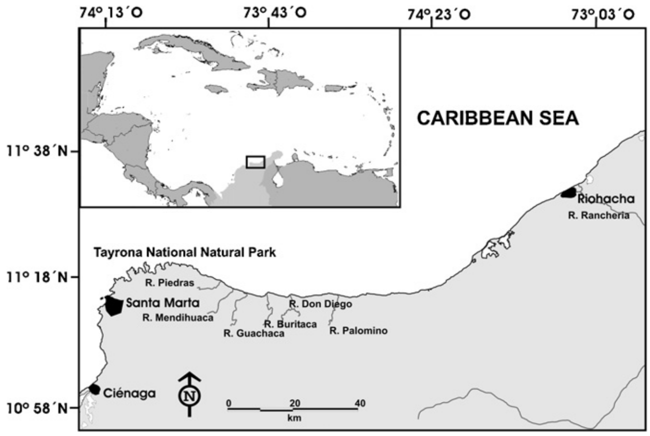

Fig. 1. Study area: north-eastern Colombian Caribbean Sea. A black square encompasses the specific area where landings were recorded.

2. Material and methods

Data on monthly gill net catch and effort for mutton snapper, blue runner, and king mackerel taken in the NCCS (Fig. 1), from May 1993 to December 1998, were obtained from the PICEP database and used for generating the time series used for ARIMA modelling (Fig. 2). We use kg/100 m net-day as a CPUE index for this fishery (Chu-fa et al., 1996; Zuur and Pierce, 2004), because net sizes differ basically in their lengths, and fishing times tend to be similar. In fact, the gill net fleet operates on a nightly trip basis, deploying the gear at dusk and retrieving it at dawn. Although some differences occur in mesh sizes, the probable effect of this factor is assumed to be compensated, since the spatial distribution of sampling effort was similar throughout the time series. Furthermore, gill net sets with several mesh sizes are common. Catches of these species are never discarded and are only exceptionally gut-

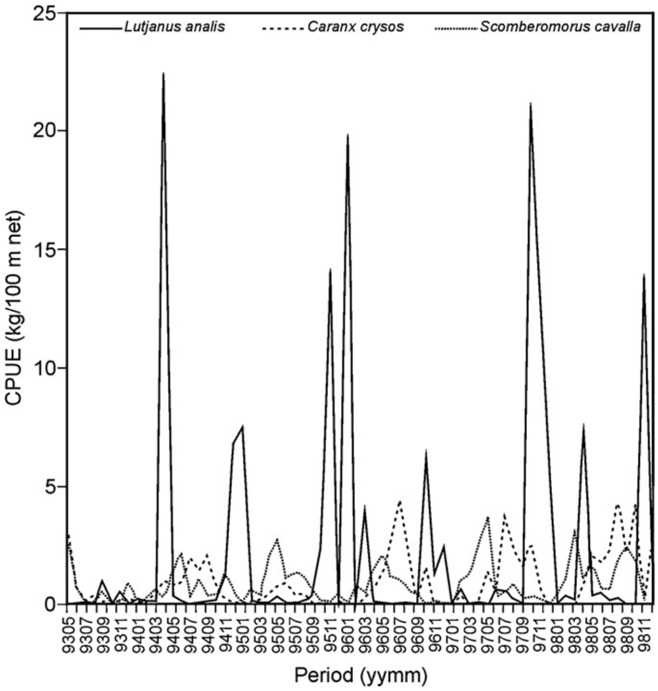

Fig. 2. Time series of monthly mean gill net catch per unit effort (CPUE) of mutton snapper *L. analis*, blue runner *Caranx crysos* and king mackerel *Scomberomorus cavalla* from the north-eastern Colombian Caribbean Sea, for the period May 1993 to December 1998.

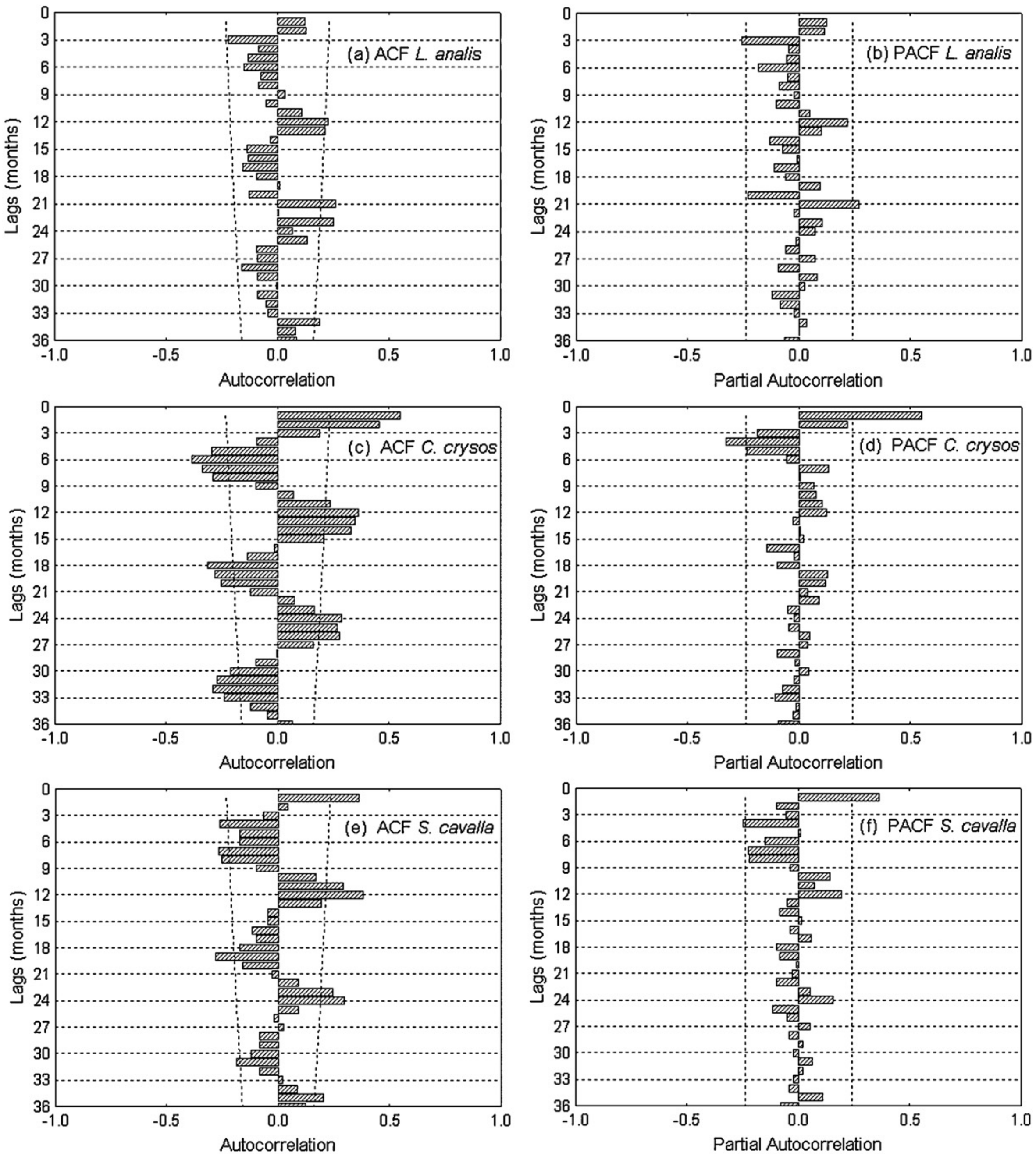

Fig. 3. ACF and ACFP autocorrelograms of the log-transformed CPUE series for mutton snapper (*Lutjanus analis*) and blue runner *Caranx crysos*, and of the CPUE series for king mackerel *Scomberomorus cavalla*.

ted before landing, so differences between landings and captures may be deemed negligible (González Herraiz et al., 2009), therefore the term CPUE has been used instead of LPUE (landings per unit effort).

Among the various methods used to describe temporal fishery dynamics, ARIMA modelling has proven to be an important tool for revealing hidden trends and seasonal patterns in time series with high inter-annual variability, such as artisanal landings and catch per unit effort (CPUE) series (e.g., Farley and Murphy, 1997; Stergiou et al., 1997; Park, 1998; Lloret et al., 2000; Becerra-Muñoz et al., 2003; Koutroumanidis et al., 2006; Czerwinski et al., 2007, González Herraiz et al., 2009). ARIMA models were basically intended to identify and compare seasonal signals and trends in the three time series. Although a longer time series would be recommendable to generate forecasts with reasonable accuracy, the forecasting power of the ARIMA models generated for each species was only measured for model selection purposes. We used the multiplicative seasonal model, which has the general form of an ARIMA (p,d,q)(P,D,Q)s, in which p is the order of the regular (non-seasonal) autoregressive term (AR), q is the order of the regular moving average term (MA), and d is the order of the regular differentiation, while the respective upper-case letters correspond to the seasonal part.

As for the homogeneity of variances (homoscedasticity), Bartlett's and Levene's tests indicated that only the original CPUE time series for king mackerel showed homoscedasticity ($P > 0.05$). Thus, for mutton snapper and blue runner variances, stationarity was obtained by taking the natural-log of the time series (Box − Cox $\lambda = 0$). The appropriate degree of regular (Δd) and/or seasonal (ΔD) differentiation was established through the autocorrelograms. Neither the autocorrelation (ACF) nor the partial autocorrelation function (PACF) suggested the presence of a regular trend in any of the three series. Each time series showed significant correlation at lags 12 and 24, indicating the presence of seasonal non-stationarity, hence the first seasonal difference was applied (Chu-fa et al., 1996; Stergiou et al., 1997; Brockwell and Davis, 2002).

ACF and PACF analyses were conducted on the stationary time series to establish the orders of the AR (p) and MA (q) polynomials of the transformed and/or differentiated time series (Chu-fa et al., 1996). The need to adjust seasonal ARIMA models was also evaluated using periodograms (Chu-fa et al., 1996; Brockwell and Davis, 2002). An exceptional peak in the frequency λ in the periodogram indicates a relatively large contribution to the variance from frequencies near λ, whose period T—i.e., the reciprocal of the frequency—is then brought into line with the seasonality of the series (Brockwell and Davis, 2002).

Models were constructed using the STATISTICA® v. 7.0 and ITSM 2000® v. 7.1 softwares (Brockwell and Davis, 2002). The latter permits the analysis of short-term time series (from 60 data points onwards). Alternative models were evaluated by comparing the following indicators: (1) bias-corrected Akaike's information criterion (AICc), which quantifies model parsimony; (2) various diagnostic checks performed to test the assumption of uncorrelated random residuals with a zero mean and constant variance; and (3) six accuracy measures to evaluate the forecasting power of the models (Stergiou et al., 1997; Czerwinski et al., 2007), resulting from comparing the 12 real CPUE data for the year 2000 (in 1999 no fishery statistics were recorded in the area) with the last 12 CPUE data of the 24 forecasted by the ITSM software from the models. The assumptions of independent and identically distributed (iid) residuals were verified using a number of diagnostic tests: Ljung–Box Portmanteau, McLeod–Li Portmanteau, Turning point, Difference-sign, and Rank. The hypothesis of normality of residuals was checked through the Jarque–Bera's Test (Brockwell and Davis, 2002). Neither this hypothesis nor the IID residual one were rejected for any of the 4 models selected for each species at the parameter estimation phase. An α of 0.05 was used in all statistical tests.

The forecasting accuracy was assessed on several statistical measures: root of the mean square error (RMSE), mean absolute error (MAE), percent standard error of prediction (%SEP), coefficient of efficiency (E_2) (Nash and Sutcliffe, 1970; Kitanidis and Bras, 1980; Czerwinski et al., 2007), average relative variance (ARV) (Griñó, 1992), and persistence index (PI)(Kitanidis and Bras, 1980; Czerwinski et al., 2007). E_2 represents the proportion of the variation of the observed data explained by the model. A value of zero for E_2 indicates that the observed average CPUE is as good a predictor as the model, while negative values indicate that the observed average is a better predictor than the model (Legates and McCabe, 1999; Czerwinski et al., 2007). A PI value of 1 implies a perfect fit between predicted and observed values, whereas a value of zero indicates that a "naïve" model, whose prediction is always equal to the previous observation, is a better model. A negative PI value denotes a performance worse than that of the naïve model (Anctil and Rat, 2005; Czerwinski et al., 2007). A benchmark of the worst permissible value was calculated for each measure of accuracy. This benchmark is proven by a naïve model, known as naïve Forecast 1 (NF1), whose forecast for each period is the same as that of the preceding period. If the forecasting model cannot do better than the NF1, then it is rejected (McLaughlin, 1983; Czerwinski et al., 2007).

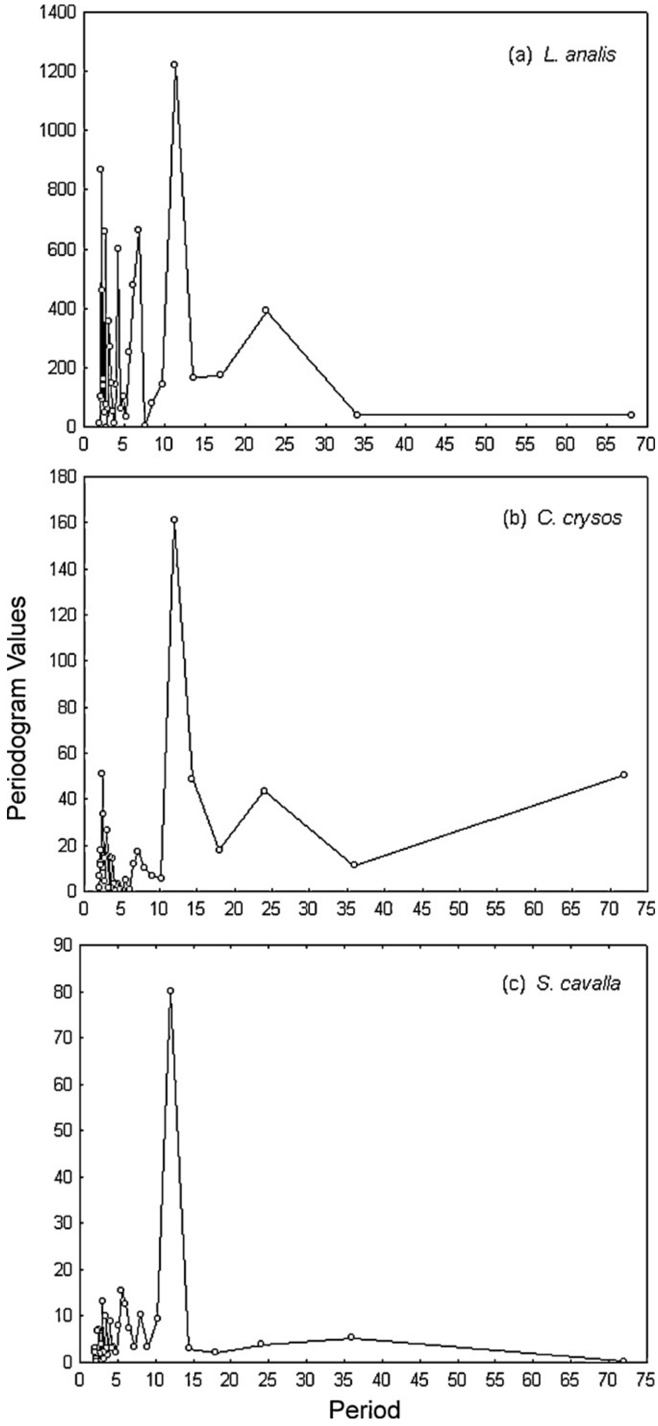

Fig. 4. Periodogram values plotted against the respective periods, from the Fourier (spectral) analysis applied to the mean-corrected and detrended time series for (a) mutton snapper *Lutjanus analis*, (b) blue runner *Caranx crysos*, and (c) king mackerel *Scomberomorus cavalla*.

We used the module TRAMO SEATS of the TSW software (http://www.bde.es/webbde/es/secciones/servicio/software/econom.html) that carries out an iterative procedure developed by Gómez and Maravall (1994) as a kind of intervention analysis, to estimate the magnitude, timing and type of outliers in the time series. The effect of level shifts and temporal outliers was practically negligible; therefore only additive outliers (AOs), which affect the time series at one period (Zaharim et al., 2009), were considered. While the seasonal patterns were contrasted with the available biological information on a monthly basis, the analysis had to be shifted from a monthly to a daily resolution for studying the LEK claim of a short-term lag (of days) cause-effect relationship between strong swells and major peaks in mutton snapper catches. Box-plots were used to display the chronological distribution of individual CPUE data (kg/100 m net-day) within the AO

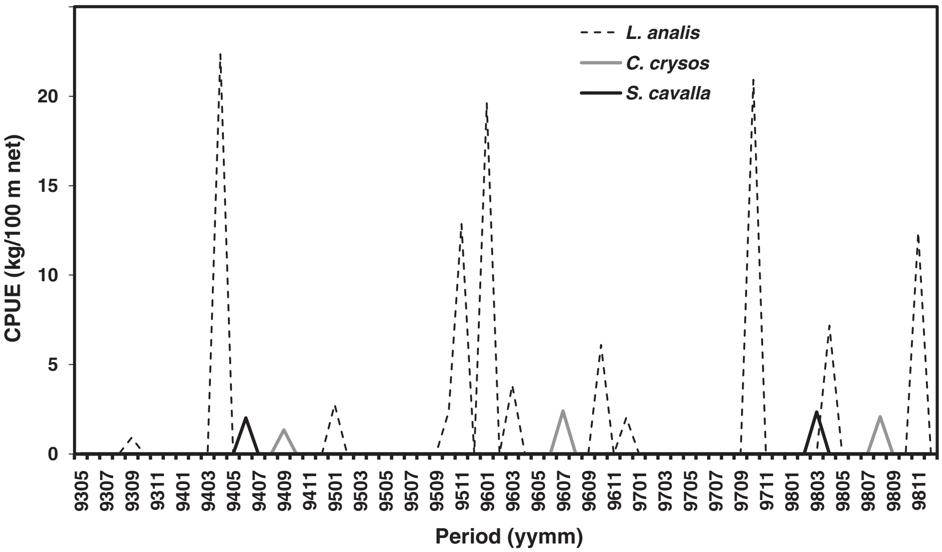

Fig. 5. Additive outliers in the time series of monthly mean gill-net catch per unit effort (CPUE) of the three species studied.

months, and next the relationship of wind speed (WS) and significant wave height (SWH) with CPUE of mutton snapper was analyzed within some AO months, in three ways: (i) by contrasting graphically daily mean CPUE of mutton snapper and buoy recorded data of SWH and WS (transformed to anomalies) for three periods where both fisheries and buoy data were available; (ii) by calculating correlation coefficients for all possible paired data (73) for lags of 0–5 days between the daily mean CPUE anomaly of mutton snapper and the daily mean anomalies in WS and SWH; and (iii) by contrasting graphically daily mean CPUE of mutton snapper and onshore WS data, as reported by the coastal meteorological station 1506501 (Simón Bolívar Airport) of the IDEAM (Colombian Hydrology, Meteorology and Environmental Research Institute), located approximately 30 km southweast from the main artisanal landing sites of the study area. Buoy data were collected from historical hourly observations provided by the National Oceanographic Data Center (NODC) for the buoy 41018 (15°00′00″ N, 075°00′00″ W), only available for some months of the 1994–1996 period (http://www.nodc.noaa.gov/BUOY/41018.html).

3. Results

None of the species showed a unidirectional trend (Figs. 2 and 3). Considering the mutton snapper time series, highest values tend to occur more frequently from November to January, which seemed to indicate a seasonal pattern. November is frequently a peak month. Some years also showed peaks in March or April. For the blue runner, the time series showed higher CPUE values between April and October, with recurrent peaks in April–May and September–October, suggesting a seasonal bimodality in the series. For the king mackerel time series, peaks were remarkably persistent in the month of May, followed by some minor peaks in June, October and November (Fig. 2).

All the ACF autocorrelograms for the stationary series showed significant positive correlations at lag 12, which indicated 12-month cycles for all species, but the seasonal signal was less evident for mutton snapper. Turning now to the PACF autocorrelograms, seasonal behaviours were again apparent although correlations at lag 12 did not reach statistical significance (Fig. 3). The periodogram plots (Fig. 4) showed that maximum values correspond to a 12-month period for the three species. Furthermore, seasonal parameters were found significant in all the different models preselected from the parameter estimation process (Table 1). For mutton snapper the minimum AICc value corresponded to the MS-3 model; for blue runner, the minimum value was that of the BR-2 model; and for king mackerel it was clear that the KM-2 and KM-3 models minimized this criterion (Table 1). Very deficient fit statistics were obtained for all the mutton snapper models, largely because

Table 1

Estimated parameters (standard error in parentheses) for the tested autoregressive integrated moving average (ARIMA) models, and their respective subtracted mean and bias-corrected Akaike's information criterion (AICc).

Species	Model code	ARIMA model	Estimated parameters		Subtracted mean	AICc
			Regular part	Seasonal part		
Mutton snapper (*L. analis*)	MS-1	$(0,0,0)(1,1,0)_{12}$	–	$\phi_{12} = -0.3547$ (0.15)	0.0159	171.2
	MS-2	$(0,0,3)(0,1,1)_{12}\ \theta_{1-2=0}$	$\theta_3 = -0.3469$ (0.16)	$\theta_{12} = -0.7726$ (0.30)	0.0159	161.4
	MS-3	$(0,0,3)(1,1,0)_{12}\ \theta_{1=0}$	$\theta_2 = 0.2641$ (0.12) $\theta_3 = -0.5783$ (0.16)	$\phi_{12} = -0.4083$ (0.14)	0.0159	160.9
	MS-4	$(2,0,0)(1,1,0)_{12}\ \phi_{1=0}$	$\phi_2 = 0.2419$ (0.12)	$\phi_{12} = -0.3133$ (0.14)	0.0159	169.7
Blue runner (*C. crysos*)	BR-1	$(0,0,0)(0,1,1)_{12}$	–	$\theta_{12} = -0.6756$ (0.30)	0.1287	81.7
	BR-2	$(1,0,0)(0,1,1)_{12}$	$\phi_1 = 0.3973$ (0.15)	$\theta_{12} = -0.4448$ (0.21)	0.1287	77.9
	BR-3	$(0,0,1)(1,1,0)_{12}$	$\theta_1 = 0.3606$ (0.13)	$\phi_{12} = 0.3303$ (0.15)	0.1287	80.6
	BR-4	$(0,0,0)(1,1,0)_{12}$	–	$\phi_{12} = -0.4141$ (0.13)	0.1287	84.5
King mackerel (*S. cavalla*)	KM-1	$(0,0,0)(1,1,0)_{12}$	–	$\phi_{12} = -0.5357$ (0.13)	0.2143	151.0
	KM-2	$(0,0,4)(1,1,0)_{12}\ \theta_{1\text{-}3=0}$	$\theta_4 = -0.4733$ (0.14)	$\phi_{12} = -0.5565$ (0.13)	0.2143	145.7
	KM-3	$(8,0,0)(1,1,0)_{12}\ \phi_{1\text{-}3=0,5\text{-}7=0}$	$\phi_4 = -0.3327$ (0.11) $\phi_8 = -0.2480$ (0.12)	$\phi_{12} = -0.6138$ (0.12)	0.2143	146.6
	KM-4	$(4,0,0)(1,1,0)_{12}\ \phi_{1\text{-}3=0}$	$\phi_4 = -0.2327$ (0.10)	$\phi_{12} = -0.5360$ (0.12)	0.2143	148.5

Table 2

Forecasting accuracy statistics of the models with significant parameters, independent and identically distributed (iid) residuals and positive forecasted CPUE values. Accuracy statistics for the benchmark are also included. RMSE, root of the mean square error; MAE, mean absolute error; %SEP, percent standard error of prediction; ARV, average relative variance; E_2, coefficient of efficiency; PI, persistence index.

Species	Model code	Accuracy statistics					
		RMSE	MAE	%SEP	ARV	E_2	PI
Mutton snapper (*L. analis*)	MS-1	4.257	1.906	482.231	6.736	−5.736	−3.870
	MS-2	2.884	1.429	326.734	3.092	−2.092	−1.196
	MS-3	4.266	1.958	483.344	6.767	−5.767	−3.841
	MS-4	4.256	1.919	482.130	6.733	−5.733	−3.868
	Benchmark	2.015	1.131	228.229	1.383	−0.383	0.000
Blue runner (*C. crysos*)	BR-1	1.264	0.993	76.130	0.976	0.024	0.142
	BR-2	1.419	1.006	75.795	1.230	−0.230	−0.067
	BR-3	1.649	1.086	79.799	1.661	−0.661	−0.452
	BR-4	1.619	1.063	80.670	1.601	−0.601	−0.425
	Benchmark	1.414	1.045	74.622	1.120	−0.120	0.000
King mackerel (*S. cavalla*)	KM-1	0.581	0.718	37.132	1.002	−0.002	0.043
	KM-2	0.619	0.739	42.644	1.137	−0.137	−0.015
	KM-3	0.548	0.672	35.311	0.889	0.111	0.101
	KM-4	0.558	0.701	35.759	0.923	0.077	0.097
	Benchmark	0.590	0.684	46.056	0.946	0.054	0.000

the effects on the error statistics of the one-lag difference between forecasted and observed maximum peaks are quite large. In fact, while the main forecasted seasonal CPUE peak corresponded to November, the highest observed peak occurred in December 2000. Only models BR-1, KM-3 and KM-4 presented better forecasting accuracy statistics values than their corresponding benchmarks (Table 2).

The outlier analysis produced 11 AOs for the mutton snapper time series, which are almost 4 times as many positive AOs as for blue runner and 5 times as many as for king mackerel (Fig. 5). Almost half the AOs for mutton snapper meant relatively major shifts in CPUE, in comparison with those for blue runner and king mackerel. Also, AOs occurred for all years of the mutton snapper time series and just corresponded to months when atypical CPUE data were recorded on 2 or 3 successive days (Fig. 6). The analysis of trends in both CPUE and the environmental variables WS and SWH (Fig. 7) shows that a sharp peak in daily mean CPUE (an anomaly of 474%) occurred on 950105 (date format: yymmdd), after a 4-day period of positive anomalies in both WS (>9.11 m s^{-1}) and SWH (>2.10 m) (Fig. 7a). A negative trend in CPUE was observed when negative anomalies occurred in both WS (<7.33 m s^{-1}: moderate breeze on the Beaufort Scale) and SWH (<1.65 m) (Fig. 7b). Another peak in catches (about +150%) occurred for three days (951103–951105), following a 4-day period of positive anomalies in both WS (>8.84 m s^{-1}) and SWH (>2.15 m) (Fig. 7c). From the 73 WS-CPUE and SWH-CPUE data that could be paired, the stronger relationships between CPUE and both environmental vari-

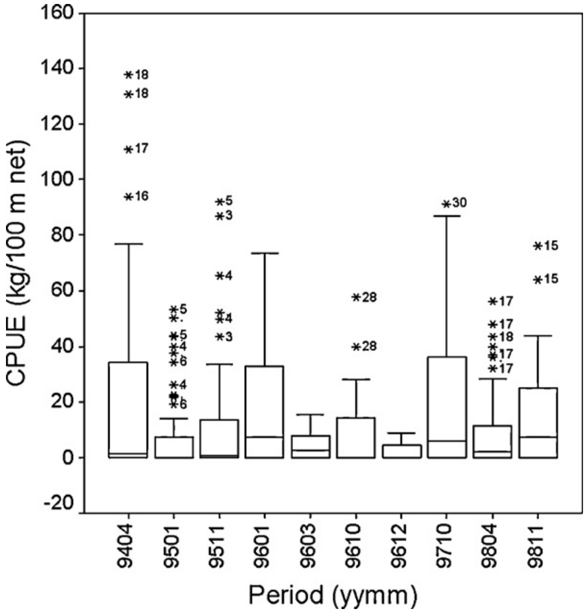

Fig. 6. Intra-monthly variability of mutton snapper (*L. analis*) CPUE data in the months classified as additive outliers. Each box contains the central 50% of the data (interquartile range IQR). The line across the box indicates the median and the plus sign indicates the location of the mean. CPUE data beyond 1.5 IQR are considered as outliers and represented as asterisks labelled with the corresponding sampling day.

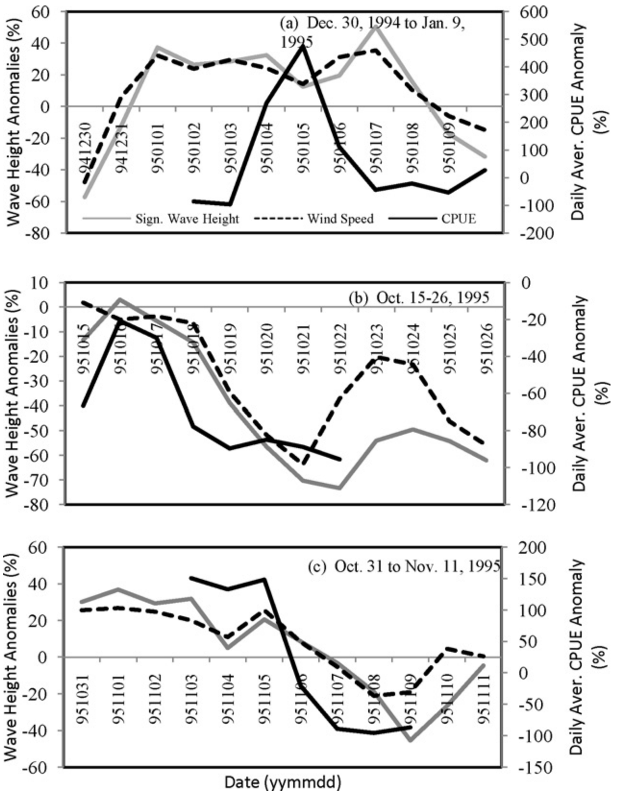

Fig. 7. Daily variations in mean CPUE of mutton snapper *L. analis*, wave height and wind speed in the north-eastern Colombian Caribbean Sea, for three periods where both fisheries and oceanographic data were available, expressed as percentage deviations from the overall mean. Wind Speed and Significant Wave Height data came from National Oceanographic Data Center (NODC) databases (buoy 41018).

Table 3
Correlation coefficients (r) for lags of 1–5 days between daily mean CPUE anomalies of mutton snapper *L. analis* and daily mean wave height and wind speed anomalies in the north-eastern Colombian Caribbean Sea. Historical wave height and wind speed data for some months of the 1994–1996 period were available for buoy 41018 from National Oceanographic Data Center (NODC). $n = 73$ in all cases.

Environmental anomaly	Lag (days)					
	0	1	2	3	4	5
Signif. wave height (SWH)	0.25*	0.24*	0.25*	0.30**	0.24*	0.06^{NS}
Wind speed (WS)	0.27*	0.30**	0.32**	0.33**	0.30**	0.14^{NS}

NS, non-significant.
* $P < 0.05$.
** $P < 0.01$.

ables were those at lag 3 days. An upward trend in r-values was observed from lag 0 to lag 3, especially for the correlation between WS and CPUE anomalies, which was higher than the SWH-CPUE correlation for all lags (Table 3).

The analysis of trends in both daily CPUE of mutton snapper and onshore WS (Fig. 8) confirm the higher frequency of the relationship between these two variables at lag 3 days. Furthermore, it makes clear that in fact positive CPUE anomalies recorded on months of

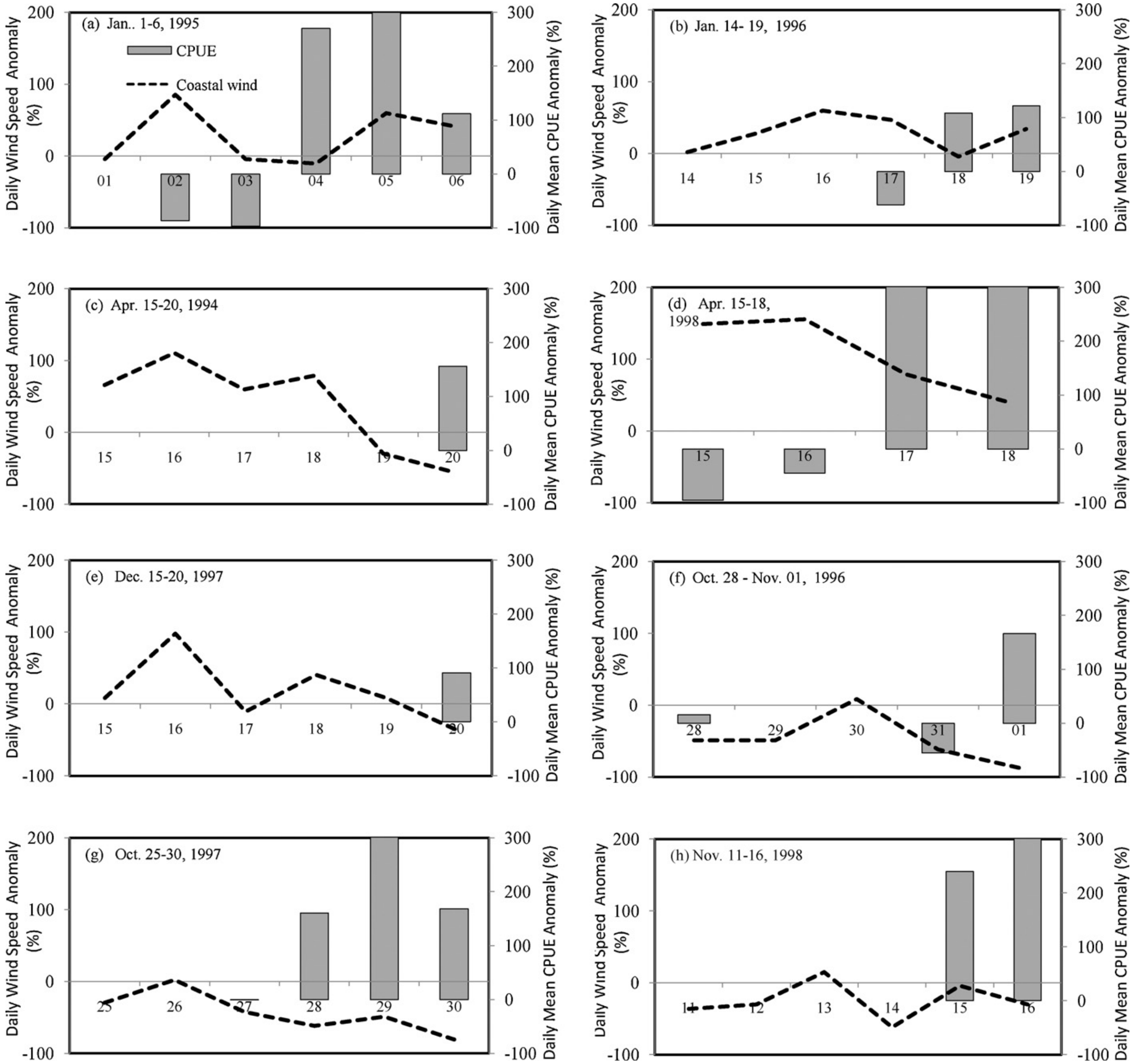

Fig. 8. Daily anomalies in mean CPUE of mutton snapper *L. analis* and onshore wind speed, for eight periods where both kinds of data were available. Wind Speed data came from the meteorological station 1506501 (Simón Bolívar Airport) of the IDEAM (Colombian Hydrology, Meteorology and Environmental Research Institute).

the windy season (December–April) followed positive anomalies in onshore WS, with lags of 2–4 days (Fig. 8a–e). In contrast, negative or no anomalies in onshore WS were observed 1–4 days before the positive CPUE anomalies occurred on October (Fig. 8f–g) and November (Fig. 8h).

4. Discussion

The time series analysis showed the seasonal behaviour attributed to blue runner, king mackerel and mutton snapper in LEK. A seasonal model (BR-1) with a MA of order 1 and a mixed model (KM-3) with a AR of order 1 in the seasonal component and ARs of order 4 and 8 in the regular component were found to be appropriate for modelling the monthly CPUE time series of blue runner and king mackerel, respectively. The AR in lag t−12 for king mackerel indicates density-dependent effects and strong seasonal cycles (Stergiou et al., 1997; Becerra-Muñoz et al., 2003). In contrast, seasonal MA for blue runner indicates a linear relationship between the seasonally differenced rates of change and the prior error term, i.e., there is a density-independent effect, which has been attributed to changes in the particular conditions of each annual class (Becerra-Muñoz et al., 2003) or to variations in catches and fishery activity (González and Lorenzo, 1995). The absence of any pattern in the regular component of the best ARIMA model for blue runner indicates that this species follows a pulsing variability pattern from one month to the next, in a framework of low-frequency cyclic change showed by the seasonal component. This feature causes the king mackerel model selected to be notably different from the blue runner model, whose AR in the regular component suggests that this series does incorporate serial correlation, i.e., persistence shorter than seasonal (Zwieter et al., 2002). On the other hand, the very few AOs in these time series suggest the multiplicative effect of good survival at several different life history stages (Farley and Murphy, 1997).

Reproductive behaviour seems to explain the seasonal pattern of blue runner. Observed data showed that lower CPUE values tended to be concentrated at the beginning and end of each year, while higher values occurred in April–May and September–October. Information from LEK indicates that a migration of mature, fat individuals from north-eastern areas occurs in April–May (Manjarrés et al., 2007). Furthermore, reproductive peaks were found from June to August in the area (Reyes, unpublished data), while Munro et al. (1973) found that the spawning season of some species of Caranx off Jamaica might be from February to June. The nucleus of the seasonal upwelling is located to the north-east of the study area. This upwelling occurs during the dry season (December–April) in the NCCS, resulting from the parallel-to-coast action of the trade winds when the Inter Tropical Convergence Zone (ITCZ) moves to the south (Andrade-Amaya, 2000; García et al., 2007). This event modulates the spatial distribution of the small pelagic species in the NCCS (Páramo et al., 2003) and the survival of species throughout their life stages (Borges et al., 2003; Hänninen et al., 2003; Suárez-Sánchez et al., 2004). Thus, during April and May, the zone covered by the coastal gill-net fishery seems to be part of the spawning migration route of the blue runner, towards the south-west, from growth zones, in the context of a reproductive strategy aimed at maximizing the survival of the offspring.

According to LEK (Manjarrés et al., 2007), a migration of immature, medium-sized individuals of blue runner in the opposite direction to the spawning migration accounts for the increased abundance in September–October. Both environmental and biological factors suggest a feeding-modulated migration event in this period, preceding the period of maximum phytoplankton production by some two months. LEK refers to an increased abundance of juveniles of sardine-like species (e.g., *Odontesthes* spp., *Sardinella* sp.) in the coastal zone from October to January (Manjarrés et al., 2007). Abundance of these preys is favoured by run-off from the main rivers discharging in or near the area (Magdalena and Piedras); this run-off reaches its maximum mean levels in October and November, as a result of maximum rainfall from September to November (IDEAM, unpublished data). Blue runner feed on zooplankton and fishes (Gómez et al., 2004). Thus, peaks of September–November match up with improved catchability due to increased fish density during feeding migration. On the other hand, the period of minimum CPUE values of blue runner (from January to March) clearly matched up with the smaller catch sizes in that zone (Manjarrés et al., 2007). Therefore, this last period could be one of recruitment, although with low monthly CPUE levels, perhaps due to the selectivity of most of the gill nets used in the area.

As with the second migration of blue runner, access to food resources could also partially influence the seasonal pattern of king mackerel, whose maximum CPUE values tend to occur primarily in March–May, and secondarily in June, October and November. The migratory king mackerel feed on nekton, mainly adults of small pelagic species (engraulids and clupeids) and medium pelagic fish to a lesser extent (Collette and Nauen, 1983). Several sources (e.g., Manjarrés et al., 1993; Gómez et al., 2004) agree that there is great availability of adult Atlantic thread herring (*Opisthonema oglinum*), the most abundant small pelagic species in the NCCS, during May and June, followed by a second peak in October–November. Additionally, local fishermen speak of an increased abundance of adults of *O. oglinum* in the coastal zone during the calm, rainy season (from May to November), a period called the “bonanza” by the fishermen (Manjarrés et al., 1993, 2007). They also argue that this abundance is related to the arrival of schools of large pelagic species (i.e., king mackerel, albacore and tunas) throughout the first months of the “bonanza”. On the other hand, spawning of this species takes place over the middle and outer continental shelf (Collette and Nauen, 1983), offshore from the artisanal gill-netters grounds. Thus, this suggests that we are facing a case of schooling and food-induced migration of a large pelagic species.

Concerning the mutton snapper, its fluctuating seasonal behaviour is attributed to the high inter-annual variability in the timing of the “runs” and the occurrence of two such events in most years: one in the calm, wet season and other in the dry, windy season. This variability is shown by the relatively high frequency of AOs throughout the time series. It is known that unexpected environmental changes can hinder predictability of the marine ecosystem (Becerra-Muñoz et al., 2003; Bondi and Overland, 2005). In fact, Graham et al. (2008) also found a great variability in the periodicity of the mutton snapper fishery in Belize. Therefore this indicates that at least one of the two yearly shoreward migrations of mutton snapper may be triggered by episodic weather events.

Available biological data support the occurrence of mutton snapper pre-spawning migrations and therefore FSA events in October and November, months belonging to the calm, wet season. An annual fishery biological sampling of mutton snapper landed in the same area from June 1995 to May 1996 (Data from Arévalo-Garzón, unpublished thesis, University Jorge Tadeo Lozano, Faculty of Marine Biology) showed that peaks in mature individuals occurred just in these two months, whereas post-spawned individuals peaked in December. Domeier and Colin (1997) define a FSA as a group of conspecific fish gathered for the purposes of spawning, with any increase in density of spawning fish greater than 3-fold, much like occurs in these “runs”. Considering that these FSA only persist for a period of days, do not occur year around and seem to exhibit high site-fidelity, we think that this corroborate the description of a “Transient Spawning Aggregation” claimed by Domeier and Colin (1997) for this species.

Spatio-temporal distribution of the FSA events in the NCCS seems to have relevant features. Carter and Perrine (1994) stated that spawning in snapper populations may be timed to coincide with pulses in production cycles and associated plankton densities. The timing of spawning of mutton snapper with respect to the timing of availability of sufficient concentrations of larval food particles—which in the present case occur from December to April, during the seasonal wind-driven upwelling—seems to meet up with the "match-mismatch" hypothesis (Cushing, 1990). On the other hand, reef FSA generally occur on the outer reef edge, on seaward extensions or promontories, near the shelf-edge break, on the reef slope or near drop-offs (Claro and Lindeman, 2003; Burton et al., 2005). Besides being a reef area, the continental shelf of the area is very narrow or absent, since the high tropical coastal mountainous system, the Sierra Nevada de Santa Marta, plunges abruptly into the sea in that zone (Díaz et al., 2000).

The same FSA-related argument does not apply for the "runs" that, in some years, occurred in the dry, windy season, when the relationship with anomalous climate events does seem to occur, as claimed by LEK. The annual sampling of mutton snapper (Data from Arévalo-Garzón, unpublished thesis) gives no indication that windy season peaks are in any way related to FSA, since most individuals were immature and with abundant fat over the digestive tube. Recruitment is not thought either to be the factor that triggers the "bajanza", since small individuals are scarce during this event. As indicated by the local fishermen for some "runs" and revealed by our analyses, the timing of this events in the windy season is related to sea movements, with sharp CPUE increases taking place two or three days after high WS or SWH. Our results show that, whether or not the WS was high enough to generate heavy swell events in the coastal zone, persistent offshore WS above 33 km h^{-1} or SWH above 2.10 m were enough to yield a migratory response by the mutton snapper—among other species—toward the coastal zone two or three days later than the beginning of the environmental anomaly. This agrees with the statements of the local fishermen that the "runs" do not necessarily occur after swell events. It is not clear the mechanism underlying the "runs" of mutton snapper in the windy season. A hypothesis could be that such events may be attributed to the shoreward migration of fish avoiding the disturbances caused by wind stress forcing in the open sea (Pati, 1982), moving from offshore banks or demersal shoals in the middle and outer continental shelf or from shallower grounds, to the sheltered bays and inlets where artisanal fishing activity takes place, chiefly in windy seasons, like the effect on gillnetting reported by Pati (1982) for the Bay of Bengal.

In the entire time series of mutton snapper, "runs" were recorded in November 1995, 1997 and 1998, for which monthly CPUE values become AOs. Positive anomalies both in WS and WSH were recorded a few days before the 1995 "runs", so this would seem indicate an climate-induced "runs", instead of the FSA-related "runs" that we have attributed to the peak abundances occurring in the October–November period. Nevertheless, we think that this apparent contradiction is due to an episodic event. In fact, a historical database of hurricanes in the Atlantic (http://weather.unisys.com/hurricane/atlantic/1990.data) gives an account of the occurrence of the hurricane "Tanya" in the north-eastern sector of the Caribbean Basin, from October 27 to November 3 1995, whereas the corresponding "run" occurred on November 3–5 (Fig. 7c). Depressions, storms or hurricanes were not recorded in the Caribbean Basin within the windy seasons of the time series.

In conclusion, whereas evidence of biologically induced seasonal peak abundances was found for the two pelagic species, with remarkable differences between them both in periodicity and underlying mechanism, the seasonality of mutton snapper appear related both to FSA in the last months of the wet season and to weather stress forcing in the windy season. Hence, it can be stated that both kind of events are of great importance in predicting peak abundances of mutton snapper and understanding the temporal pattern of this species. Considering that depletion or elimination of FSA is one of the most damaging of globally documented population-level impacts (e.g., Claro and Lindeman, 2003; Matos-Caraballo et al., 2006; Graham et al., 2008), a precautionary approach to FSA management must be adopted. Although full protection from fishing would be desirable to improve population persistence (Graham et al., 2008), we think that a more realistic and achievable target would be to regulate the use of set nets across the spawning migrations routes in order to reduce the vulnerability to overfishing of the pre-spawning fishes migrating to the outer spawning site, a measure that has been implemented in Cuba for mutton snapper (Claro and Lindeman, 2003). Moreover, the management scheme should also include handlines as they can also exert strong pressure on fish stocks when aggregating to spawn (Graham et al., 2008). For these management goals, strong LEK of the fishermen of the area should be taken advantage of, linking them actively to the regulation design. On the other hand, the need for a long-term monitoring of fishery biological variables in the NCCS is emphasized, to make possible two main goals: (i) the application of transfer function models that could help, for instance, to better elucidate the mechanisms and processes involved in the relation between "run" of mutton snapper in the NCCS and both physical forcing and spawning; and (ii) the assessment of long-term biologically meaningful changes in CPUE, mean size and age at first maturity, as result of increasing effort on reproductive populations of these resources.

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