

Relationship of precipitation, freshwater input, and sea level height with the abundance of the white shrimp (*Litopenaeus occidentalis*; Street, 1871) off Buenaventura, eastern tropical Pacific

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Abstract

Penaeid shrimp fisheries are an important source of income for the fishing communities that live in estuarine zones around the world. Off Buenaventura, the habitat of the western white shrimp (*Litopenaeus occidentalis*) is subject to high precipitation associated with the intertropical convergence zone, contributions from numerous short rivers descending from the Andes Mountains, and seasonal alternations in Trade Winds directions responsible for the upwelling in the Panama Bight. This work analyzes the relationship of precipitation, the San Juan River runoff, and sea level height with *Litopenaeus occidentalis* abundance in fishing areas between 1968 and 1989. The results indicate that precipitation is significantly correlated ($p < 0.01$) with the catch per unit effort on a monthly scale with a lag of approximately 1 calendar year but the inclusion of the data in a transfer function model does not improve considerably the forecasting power of a simpler autoregressive moving average model of the catch per unit effort. On an annual scale, the catch per unit effort for white shrimp depends significantly [$r^2 = 0.36$, p (corrected for autocorrelation) $\ll 0.01$] on the precipitation that fell the previous December, whereas the residuals of this regression are significantly associated with variations of mean sea level between January and March (the upwelling season in the Panama Bight) of the current year at Buenaventura ($r^2 = 0.61$, p (corrected for autocorrelation) $\ll 0.01$). The inclusion of these two variables in a multiple linear regression model accounted for a substantial proportion of the total annual variance of the mean CPUE ($r^2 = 0.54$), suggesting that freshwater contributions (lower salinities) and offshore transport during the main settlement period of postlarvae in the estuaries play a significant role in determining the strength of the cohorts recruited in the fishing areas. The industrial fishing yield decreased sharply after the 1982–1983 El Niño event. However, a high percentage of this change can be explained not by invoking El Niño effects but by a decreasing tendency of precipitation and offshore advection of early life stages between December and March, which took place on a multi-annual scale since the mid 1980s

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1. Introduction

The western white shrimp (*Litopenaeus occidentalis*), a penaeid decapod, has been commercially exploited in the Colombian Pacific (Fig. 1) since 1957 when the first trawling ships were introduced (Palacio, J. fide Forsbergh, 1969; Mora, 1988; Pineda et al., 1992), constituting one of the area's

most important fishery resources (Mora, 1988; INPA, 1999; MinAgricultura, 2005). However, landing time series exhibited a decreasing trend that became more pronounced since the mid-1980s, coinciding with a substantial increase of artisanal landings (e.g. Mora, 1988). In the Colombian Pacific, the artisanal fishery is carried out by small boats equipped with 6–7 cm mesh gill nets mainly operating in shallow waters close to the nurseries. It is likely that the decrease in industrial yields is associated, at least in part, with competition between industrial and artisanal fisheries (e.g. Pineda et al., 1992) as verified elsewhere (e.g. Gracia and Vázquez-Bader, 1998 in the Gulf of Mexico; Gracia and Le Reste, 1986 for some African penaeid

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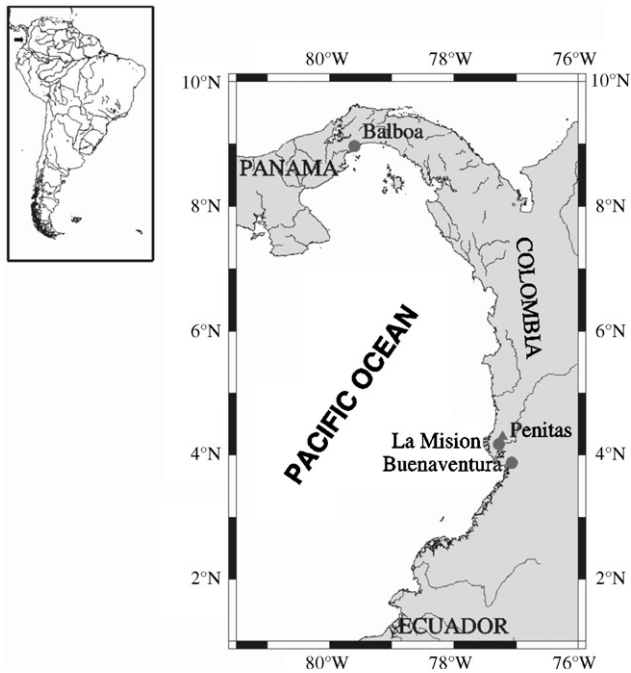


Fig. 1. The Colombian Pacific and the Panama Bight (stations used for precipitation and runoff analysis are represented by circles and a triangle, respectively).

shrimp fisheries). Nevertheless, the trawling fleet was indeed operating off the Colombian Pacific well before the onset of artisanal fisheries in the early 1980s (Mora, 1988). From 1957 onwards, the industrial fleet grew rapidly and by 1960 a mean of 54 vessels extracted a maximum yield of 1017 tons (Palacio, J. fide Forsbergh, 1969; Mora, 1988). Such a record was close to the maximum sustainable yield of ~ 900 tons year⁻¹ corresponding to an optimal effort of 56 ships estimated by Mora (1988). On the other hand, due to the use of non-standardized effort units, an attempt was made to reconstruct the fishery statistics between 1972 and 1984 (Pineda et al., 1992). From the figures presented by these authors, we estimate that between 1957 and 1980 the catch per unit effort (CPUE) from the industrial fishery was decreasing at a mean rate of ~ -0.045 kg-headless vessel⁻¹ h⁻¹ year⁻¹ whereas, between 1980 and 1988, this rate doubled to ~ -0.09 kg-headless vessel⁻¹ h⁻¹ year⁻¹ (Pineda et al., 1992). In addition, during the first quarter of 1983, shrimp catches were anomalously low; some speculated that this was due to the strong 1982–1983 El Niño. However, the yields returned to their “normal” behavior in 1984 (Pineda et al., 1992). It is interesting to note that, despite the different methods used for computing the CPUE, Pineda et al. (1992) arrived at a maximum sustainable yield of ~ 800 tons with 95 standard 300 HP vessels, which is similar to the value estimated by Mora (1988).

Along with fishing-related factors, changes in the *Litopenaeus occidentalis* abundance are likely to have been modulated by environmental variability. In general, penaeid shrimp have short life cycles (~ 1 – 2 years), rapid growth, and high rates of natural mortality associated with the early stages (e.g. Garcia and Le Reste, 1986; Hendrickx, 1995).

Some studies have shown that penaeid recruitment and population dynamics are strongly influenced by a wide range of physical mechanisms that affect the migration of planktonic stages (larvae and postlarvae) from spawning grounds in the open ocean to coastal nursery areas (Garcia and Le Reste, 1986; Rothlisberg et al., 1995; Criales et al., 2006). Survival during the first stages of development is highly associated with abiotic variables such as salinity (e.g. Pérez-Farfante, 1969, for *Litopenaeus setiferus* in Texas, USA; Haas et al., 2001 for *Farfantepenaeus aztecus* in Louisiana, Gulf of Mexico, USA; Ramírez-Rodríguez et al., 2003 for recruitment of *Farfantepenaeus duorarum* in the Campeche Sound, southern Gulf of Mexico). In addition, sea surface temperature may regulate both juvenile shrimp growth (e.g. Pérez-Farfante, 1969 for *Litopenaeus setiferus* in Texas; O’Brien, 1994 for *Penaeus sculentus* in Queensland, Australia; Haas et al., 2001 for all stages except postlarvae of *Farfantepenaeus aztecus* off Louisiana, northern Gulf of Mexico) and adult shrimp yields (e.g. *Litopenaeus occidentalis* off Ecuador during El Niño: Klima, 1989; *Litopenaeus vannamei* off northern Peru, during years with and without El Niño: Mendo and Tam, 1993). Another important abiotic variable for determining penaeid shrimp abundance is freshwater input. Rainfall was negatively correlated with *Litopenaeus setiferus* juvenile abundance in the Terminos Lagoon, southwest Gulf of Mexico (Gracia, 1989) whereas a parabolic relationship was found between rainfall and the CPUE of *Fenneropenaeus merguensis* in Papua, New Guinea (Evans et al., 1997). Runoff was positively associated with catches of *Metapenaeus macleayi* and *Fenneropenaeus merguensis* in southeast Queensland, Australia (Loneragan and Bunn, 1999) whereas Diop et al. (2007) found a negative association between the abundance of juvenile *Litopenaeus setiferus* and both river discharge and cumulative wetland loss in Louisiana. The extent of suitable nursery habitats such as mangroves has also been considered crucial for determining penaeid shrimp abundance (a negative effect associated with mangrove loss), for instance for *Fenneropenaeus merguensis* in northern Australia (Vance et al., 1990) and Malaysia (Loneragan et al., 2005) and for nine penaeid species off the Philippines (Primavera, 1998). In addition, recruitment success has been associated with physical transport mechanisms such as tides (e.g. Criales et al., 2005 for *Farfantepenaeus duorarum* in Florida Bay, USA), meander rings (e.g. Criales and Lee, 1995; Criales et al., 2003 also for *Farfantepenaeus duorarum* off Florida), and the direction of subtidal currents for entering the nurseries (e.g. for *Litopenaeus setiferus* postlarvae in Georgia, USA; Wenner et al., 2005).

In the Panama Bight, an association between *Litopenaeus occidentalis* yields and upwelling has been suggested (e.g. Forsbergh, 1969). Such a relationship is inferred from significant lagged (3 months) correlations between catches in the coastal area of Panama and sea level height, temperature, and precipitation (e.g. D’Croz et al., 1979). In fact, mean monthly catches of white shrimp in the Colombian fishery between 1958 and 1966 were also negatively correlated with the mean monthly sea level at Buenaventura between 1951 and 1965 with a lag of 4–6 months (Forsbergh, 1969). Such a relationship was interpreted to be a response of white shrimp populations to upwelling under

the assumptions of an omnivorous diet and the sea level as a proxy for upwelling (Forsbergh, 1969).

In the Colombian Pacific, white shrimp fishing grounds are located on the continental shelf between 1°38'N and 7°08'N (Fig. 1), at depths between 5 and 50 m, depending on the thermocline depth (Herazo, 1981). Temperature profiles made with data collected during the early 1970s revealed that the thermocline depth varies considerably along the year (Squires et al., 1971; FAO, 1973; Herazo, 1981). In October, the thermocline is ~10 m thick and is located between 45 and 50 m whereas, in February, it is ~20 m deep and is more diffuse (Squires et al., 1971; Herazo, 1981). On average, the width of the continental shelf in the Colombian Pacific is 23 km and its maximum extension is found off Buenaventura. Because sea temperature over the shelf is usually between 27 and 29 °C, it has been hypothesized that penaeid shrimps off Buenaventura are more dispersed than in other locations along the coast, and consequently, they are less vulnerable to the industrial fleet near the shore (Herazo, 1981).

1.1. Climatology and oceanography in the study area

The climate of the Colombian Pacific is highly influenced by the migrations of the intertropical convergence zone (ITCZ) that generate high precipitation as of the second trimester of the year (Forsbergh, 1969; Tchantsev and Cabrera, 1998; Poveda et al., 2001). In turn, the displacements of the ITCZ are associated with changes in the direction of the trade winds from the southeast that direct the surface currents towards the coast between November and May (Philander, 1990; Andrade, 1992; Tchantsev and Cabrera, 1998). The atmospheric circulation pattern in the oceanic area favors the divergence of water offshore at the beginning of the year, increasing productivity due to upwelling in the Panama Gulf (Forsbergh, 1969). The information on primary productivity in the area is scarce but, in March 1997, in the oceanic zone, the greatest concentrations of chlorophyll (>20 mg m⁻³) were located to the east of the basin, coinciding with the intensification of the Panama wind stream from the north-northwest (Rodríguez and Stuardo, 2002).

The Colombian Pacific basin covers a total of 76,365 km² between 0°36'N–7°45'N and 75°51'W–79°02'W (Fig. 1), including the western branch of the Andes Mountains. The main river in this basin is the San Juan River, which has the greatest discharge of water and sediments on the western coast of South America (Restrepo and Kjerfve, 2000). The San Juan basin receives an average of 7277 mm annual precipitation, with 78% in May–November and 22% in December–April. The greatest precipitation is captured in the apex of the delta near the mouth of the river that drains into the Pacific Ocean (Restrepo and Kjerfve, 2000). On an interannual scale, low-frequency, large-scale phenomena of the ocean–atmosphere system are closely linked to the region's hydroclimatology, including periodic occurrences of the extreme stages of the El Niño Southern Oscillation (ENSO) cycle (Poveda and Mesa, 1997; Restrepo and Kjerfve, 2000; Waylen and Poveda, 2002).

1.2. Distribution and life cycle of the white shrimp

Litopenaeus occidentalis is distributed between the Gulf of Tehuantepec (Mexico) and the Lobos de Tierra Islands (Peru) (Wicksten and Hendrickx, 2003). This is an important species for fisheries in Nicaragua, Costa Rica, Panama, and Colombia (Hendrickx, 1995). In Ecuador, due to the growth of the farming industry since 1976, statistics of both marine penaeid shrimp fisheries and aquaculture are mixed because they are “based on export records which do not distinguish farm and sea production” (Klima, 1989 and references within). However, it is evident that catches of the white shrimp (also the dominant penaeid species in Ecuador) between 1958 and 1964 were similar to the CPUEs off Colombia and Panama, with an annual mean of ~70–90 kg day⁻¹ (e.g. Forsbergh, 1969; Klima, 1989).

In the Colombian Pacific the white shrimp fishery is based on *Litopenaeus occidentalis*, which shares the bottom habitat with other two shrimp species (*Litopenaeus stylirostris* and *Xiphopenaeus rivetti*) and is caught near the coastline at depths not usually exceeding 20 m and at maximum depths of 80 m (e.g. Forsbergh, 1969; Squires et al., 1971; Herazo, 1981). This species spawns in the Gulf of Nicoya (Costa Rica) throughout the year (Alfaro et al., 1993) with two main spawning pulses: one in August–October and the other in April–June (Tabash and Palacios, 1996) or June–August (Palacios and Vargas, 2000). The postlarvae are found in the nursery areas between November and February (Kitani, 1997). In Panama, the largest shrimp (i.e. spawning females) caught in the industrial fishing areas were obtained in September–November, whereas the main peak in spawning occurs toward the end of the year or at the beginning of the following year. Therefore, maximum juvenile densities in the Panama coast estuaries are observed in the first semester (principally March–May); as the growing season progresses (April–July), these individuals emigrate toward the adult areas (D'Croze et al., 1979). As observed off the Panama coast, in the Colombian Pacific, the life cycle of the white shrimp is developed in approximately 1 calendar year. Between October and December, high percentages of gravid females are observed in the fishing areas near Buenaventura (Ramírez, 1994), whereas the settlement of postlarvae takes place between December and February (Pineda, 1992). Finally, the juvenile shrimp enter the fishing areas in pulses, with the main pulse in January–May and the secondary one in July–November (Herazo, 1981).

Herein, we researched the influence of precipitation in the Buenaventura area (eastern tropical Pacific), the San Juan River runoff and sea level height on the abundance of *Litopenaeus occidentalis* in fishing areas. This work is based on the formulation of *a priori* hypotheses of the environment–recruitment relationship (Tyler, 1992) generated with the information available on the white shrimp's biology and habitat, thereby avoiding spurious correlations. Any causal association between these environmental variables and shrimp abundance should be associated with the entry of the shrimp into the fishing areas with a delay of about 1 year. Due to the strong influence of the ENSO cycles on the study area, the results are put into context with respect to the occurrence of El Niño events.

2. Materials and methods

2.1. Sources of information

The first statistics of the white shrimp fishery in Buenaventura were collected by the Ministry of Agriculture of Colombia, between 1958 and 1966, and were used in a comprehensive analysis of the fisheries and oceanography of the Panama Bight (Forsbergh, 1969). This database was summarized on an annual basis including information such as total shrimp landings (headless weight) and fishing effort measured in days (Forsbergh, 1969, his Table 31). The task of collecting fisheries statistics was continued by the Instituto Nacional de los Recursos Naturales (INDERENA) between 1968 and 1989 and, with the data accumulated until 1986, the maximum sustainable yield of the industrial fishery was estimated by Mora (1988). The INDERENA methodology for data collection consisted of reviewing landing certificates directly in the fishing companies (Mora, 1988). Those certificates contained information such as the landing date, vessel name, and corresponding weight of shrimp landed (Pineda et al., 1992). In contrast with fishing effort measurements made by the Ministry of Agriculture, the INDERENA reported fishing effort as the number of vessels active and the corresponding number of trips with fishing per month. Although published statistics of the fishery before 1990 were accumulated by year, the original INDERENA database was collected with a resolution of 1 month. This information was stored in electronic worksheet files (LOTUS® and QPRO®) and was available from Argiro Ramírez, Instituto Colombiano de Desarrollo Rural (INCODER). By the early 1990s, the Colombian Government introduced a new fishing law that transferred fisheries administration, enforcement, and research responsibilities to the new Instituto Nacional de Pesca y Acuicultura (INPA). This agency redirected efforts to develop alternative new fisheries and limited white shrimp data collection to landing statistics to be published in statistical bulletins (INPA, 1991–1999); however, some personnel continued registering fishing effort. Currently, fishing effort statistics for the fishery are incomplete for the period after 1992 (between 1989 and 1992 the INPA continued recording fishing effort statistics using the same methodology as the INDERENA), and they are not used herein.

In this work we use the time series of total monthly landings (headless weight in tons) and the number of fishing trips (Buenaventura port industrial fleet) between January 1968 and September 1989 (i.e. the INDERENA database) and calculate the CPUE by dividing the total landing by the number of fishing trips carried out by the trawling fleet. On the other hand, river runoff ($\text{m}^3 \text{s}^{-1}$) and precipitation (mm) time series were purchased from the Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM), and sea level heights at Balboa (Panamá) and Buenaventura (both in mm) were available on the Internet (University of Hawaii Sea Level Center, <http://ilikai.soest.hawaii.edu>). In addition, El Niño events are classified according to the multivariate El Niño index (MEI) from Wolter (NOAA, <http://www.cdc.noaa.gov/people/klaus.wolter/MEI>), the Standardized Southern Oscillation Index (Climate Prediction Center,

<http://www.cpc.ncep.noaa.gov/data/indices/soi>), and the sea surface temperature anomaly in the Niño 3–4 region (IRI/LDEO Climate Data Library, <http://ingrid.ldeo.columbia.edu/SOURCES/Indices/.nino/.EXTENDED/.NINO34>).

2.2. Time series analysis

2.2.1. Monthly scale

More than 250 monthly observations were available, making possible the use of autoregressive integrated moving average models (ARIMA, Box and Jenkins, 1976). The sum of the precipitation at two meteorological stations (i.e. La Misión, near the mouth of the San Juan, and Colpuertos, in Buenaventura, Fig. 1) was used as a representative variable for precipitation in the fishing areas. Missing data from these time series were estimated by means of linear regression between these two stations ($r=0.71$, $p \ll 0.01$), following a similar strategy to that used for estimating sea level height at Buenaventura from the data recorded at Balboa ($r=0.89$, $p \ll 0.01$). Freshwater input from the San Juan River was taken from Peñitas station at the most northern mouth of the delta (Fig. 1). In the case of landing and fishing effort time series, although we had data available until 1992, for the ARIMA model, we decided to use only the data up to 1989, 1 year before this agency was replaced by the INPA.

As part of the analysis, time series were differentiated with 1- and 12-month periods to achieve stationarity (Box and Jenkins, 1976; Makridakis et al., 1983; Vandaele, 1983), whereas the natural logarithmic transformation was necessary to stabilize the variance of the CPUE. The ARIMA models estimated for the independent variables (i.e. river runoff, precipitation, sea level) were used to remove the autocorrelation of the CPUE as part of the estimation of the crosscorrelation functions. If significant crosscorrelations were found, we proceeded to estimate transfer functions (TFs) models including both the environmental variable and the autoregressive structure of the CPUE. The standard stages of identification, estimation, and prediction were followed in the analysis (e.g. Box and Jenkins, 1976; Makridakis et al., 1983; Fogarty, 1989; Rothschild et al., 1996; Lloret et al., 2004). Time series modeling was accomplished with the program SAS Version 9 (The SAS Institute Inc., 2002).

2.2.2. Interannual scale

On this scale, the CPUE observations were averaged for 12-month intervals and correlated with annual series of the environmental variables for specific months corresponding to the main recruitment pulse in the nursery area (i.e. river runoff or precipitation considering only data from all the months of December, January, etc.). Since the sea level between January and March is considered to be a proxy for upwelling in the Panama Bight (e.g. Forsbergh, 1969), we averaged the sea level height at Buenaventura for the first trimester to investigate the effects of upwelling on the interannual shrimp abundance. Due to the short extension of the time series, instead of the ARIMA models (Box and Jenkins, 1976), simple linear regression models were used and the effective number of independent observations for judging the significance of the correlation coef-

ficient was calculated with the Pyper and Peterman formula (1998):

$$\frac{1}{n^*} = \frac{1}{n} + \frac{2}{n} \sum_{i=1}^{n/5} r_{XX}(i) r_{YY}(i) \quad (1)$$

where n is the number of data in the time series, n^* the number of independent observations, and $r_{XX}(i)$ and $r_{YY}(i)$ are the autocorrelation coefficients for the lag (i) in the time series X and Y . The autocorrelation coefficient was calculated as below (Emery and Thompson, 2001):

$$r_k = \frac{\sum_{t=1}^{n-k} (X_t - \bar{X})(X_{t+k} - \bar{X})}{\sum_{t=1}^n (X_t - \bar{X})^2} \quad (2)$$

where X_t is a current observation of the series at time t , X_{t+k} an observation of the same series, but in a later period $t+k$, and \bar{X} is the series average. The p values corrected for autocorrelation with the Pyper and Peterman (1998) method are represented by p_{corr} . Additionally, residual diagnostic tests were conducted to verify the adequacy of the linear regression models. Furthermore, these residuals were checked for correlation with the other environmental or fishing predictors looking for an eventual improvement of the percent of total variance of the CPUE explained by a multiple linear regression model (e.g. Kutner et al., 2004).

3. Results

3.1. Monthly scale

3.1.1. Landings and fishing effort

Landings of the industrial fleet in Buenaventura between 1968 and 1985 fluctuated around $\sim 70 \pm 24$ tons month⁻¹ and showed a rather slow decreasing trend superimposed over high frequency oscillations (Fig. 2A). Artisanal landings began growing in 1984 and attained several consecutive records each year throughout the 1990s (B). In fact, the artisanal fishery accounted for $\sim >70\%$ of total monthly white shrimp landings between 1996 and 1999 (C).

With respect to fishing effort, both the number of active vessels and the number of trips with fishing showed similar trends (Fig. 2D and E). Our record shows that fishing effort grew during the late 1960s, attaining a maximum of 170 ± 18 trips month⁻¹ (101 ± 9 vessels month⁻¹) in 1972. These figures remained high during most of the 1970s with >120 trips month⁻¹ (>80 vessels month⁻¹). After 1978, however, the trawling fleet activity experienced a substantial decline so that, by 1982, the fishing effort was as low as 86 ± 21 trips month⁻¹ (56 ± 12 vessels month⁻¹) (Fig. 2D and E). During the rest of the 1980s and the early 1990s, the number of active vessels and fishing trips recovered to $\sim 66 \pm 20$ vessels and $\sim 100 \pm 36$ trips, respectively (Fig. 2D and E). It is worth mentioning that landing and fishing effort time series had several extreme values (i.e. values $<3\sigma$ the mean

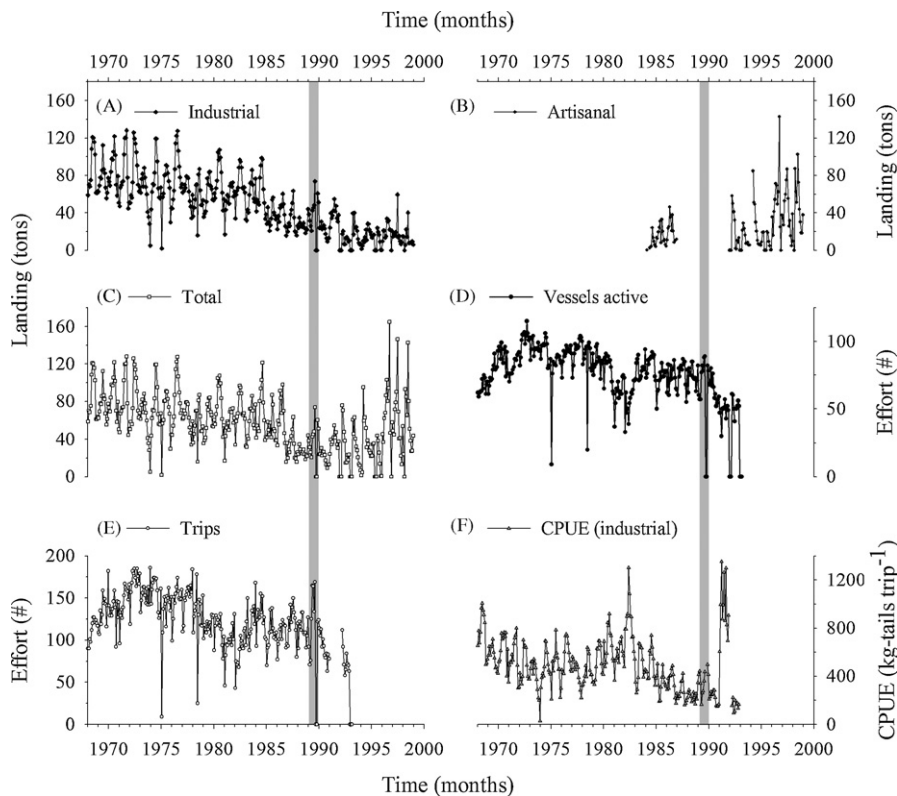


Fig. 2. Monthly time series from the white shrimp fishery off the Colombian Pacific: (A) industrial landing, (B) artisanal landing, (C) total landing, (D) number of trawling vessels active, (E) number of fishing trips, and (F) CPUE. The vertical gray area symbolizes the transition period for data collection by the Instituto Nacional del los Recursos Naturales (INDERENA) and the Instituto Nacional de Pesca y Acuicultura (INPA).

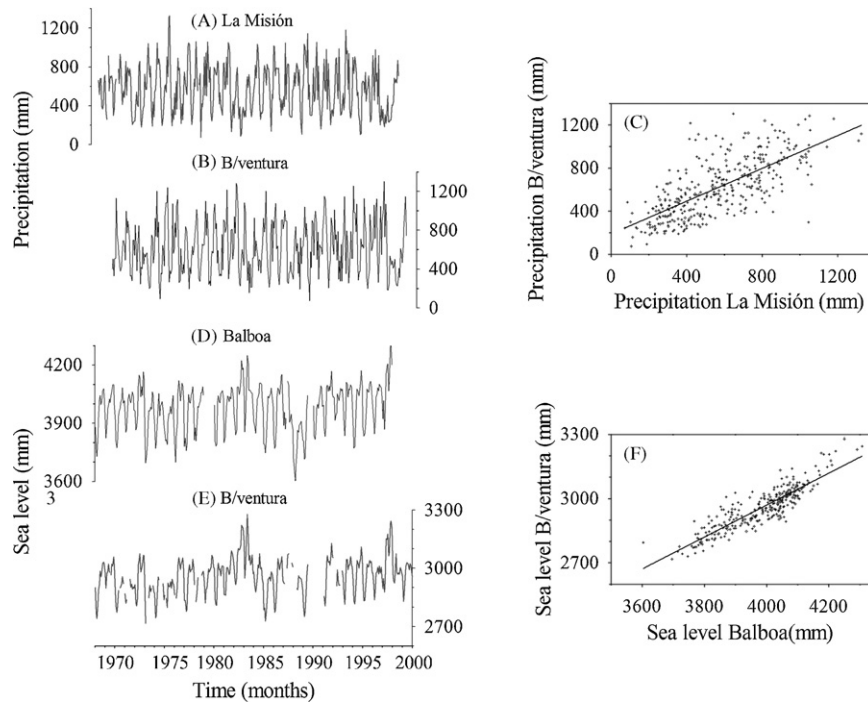


Fig. 3. Monthly time series of (A) precipitation at the San Juan River (station “La Misión”), (B) precipitation at Buenaventura, (C) the relationship between time series (A) and (B), (D) sea level height at Balboa (Panamá), (E) sea level at Buenaventura, and (F) the relationship between the sea level at (D) and (E).

of the surrounding observations) with notable cases in January 1975 and June 1980 (Fig. 2A, C–E). Although extreme, such values were not removed from the analysis because they showed a consistent pattern of low fishing effort corresponding to low landings (Fig. 2D and E). Regarding the other landing and effort minima, they are all explained by the closed seasons imposed by the fisheries administration in an attempt to protect spawning (September–October 1989) and spawning and recruitment (December–February 1991–1992, 1992–1993,

1993–1994, 1997–1998), and by two closed seasons negotiated with fishing communities in April–June 1995 and November 1996 (Fig. 2).

In contrast, the CPUE time series assembled with landings and trips showed minimal values in 1974–1975 and the early 1990, whereas maximum values were observed between 1980 and 1982. In addition, it is evident that extremely high CPUE values also occurred during a few months in 1982 and 1991 (Fig. 2F).

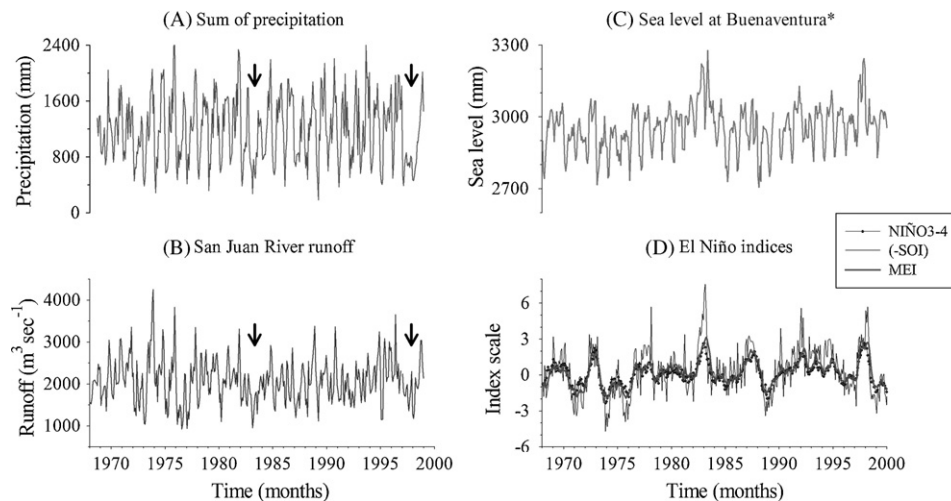


Fig. 4. Abiotic variables used to test environment–resource associations in the white shrimp fishery. (A) Sum of precipitation at Buenaventura and the San Juan River, (B) San Juan River runoff, (C) sea level at Buenaventura (*indicates that missing data were estimated by linear regression with sea level at Balboa), and (D) three indices of the El Niño events, Niño 3–4 (the temperature anomalies at the El Niño 3–4 region of the Central Equatorial Pacific), the southern oscillation index, SOI (note that we plotted the negative values for simplifying visualization), and the Multivariate El Niño Index (MEI). The occurrence of the 1982–1983 and 1997–1998 strong El Niño events is represented with arrows.

3.1.2. Abiotic variables

Time series of monthly precipitation at Buenaventura and the San Juan River (Fig. 3A and B) were highly variable with averages of 619 ± 265 mm and 567 ± 247 mm, respectively, and were significantly correlated ($r=0.71$, $p \ll 0.01$; C). An even stronger relationship was observed between sea level height at Balboa ($\bar{X} = 3980 \pm 118$ mm; D) and Buenaventura ($\bar{X} = 2960 \pm 95$; E); the regression line showed less dispersion ($r=0.89$, $p \ll 0.01$; F).

After estimating the missing data for the precipitation and sea level height time series, it is evident that the first variable exhibited several extended periods of “dryer” conditions concomitant with lower runoff ($r=0.66$, $p \ll 0.01$; also note the arrows in Fig. 4A and B). On the other hand, the sea level at Buenaventura had less high frequency variability than rainfall and runoff, and was characterized by a bimodal pattern of annual maxima as well as a long-term increasing trend (Fig. 4C). It is also remarkable that the sea level at Buenaventura seems to follow, to some extent, the same pattern as the CPUE (Figs. 2F and 4C). In addition, the lowest values of precipitation and runoff (Fig. 4A and B) as well as the highest sea levels (Fig. 4C) clearly coincided with the occurrence of the strong El Niño events of 1982–1983 and 1997–1998 (Fig. 4D).

3.2. Seasonal cycles

Regarding the abiotic variables, two annual peaks were observed in both the sum of precipitation and the San Juan River runoff (Fig. 5A and B). The first maximum, for both variables, was observed in May–June whereas the second (which

was quantitatively the most important) occurred in September for the sum of precipitation and in October–November for runoff (A and B). Sea level heights, on the other hand, were minimal between January and February with mean values between 3800 mm and 3900 mm (C).

Fishing effort, expressed as the number of trips, showed the lowest values in September–October whereas the maximum was observed in December and the minimum in January (Fig. 5D). Such behavior was similar to that observed for the number of active vessels (data not shown). On the other hand, the CPUE peaked in May–August and was lowest between October and January (E), whereas, the considerably shorter time series of artisanal landings showed quarterly pulses with maximum yields in March, June, September, and December (F).

3.3. ARIMA models

Fishing effort and the CPUE were strongly autocorrelated and reflected the seasonal pattern of the CPUE as well as the relatively homogeneous distribution of fishing effort throughout the year (Fig. 6A and B). On the other hand, autocorrelation functions of the abiotic variables were dominated by the annual cycle (C–E). All the time series used in the analysis required consecutive and seasonal differencing to make them stationary. After the estimation phase, all the models included significant parameters on monthly and seasonal scales, with the last set of parameters numerically greater than the former (Table 1). In addition, when the ARIMA models were used for prewhitening the CPUE, the negative effects of fishing effort on the CPUE were apparent with lags of 0, 3 and 17 months (F). In turn, for

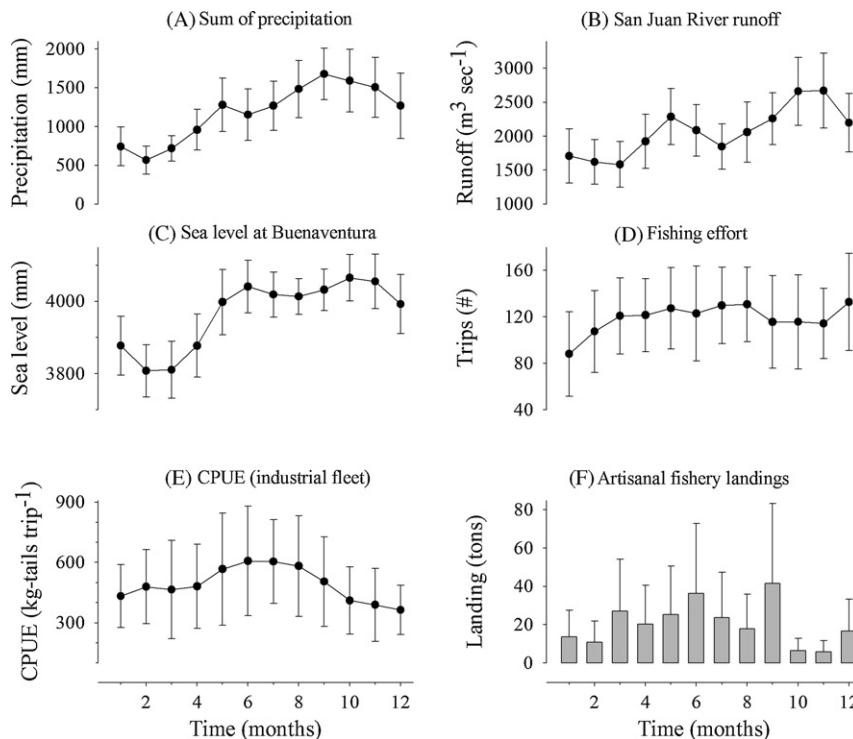


Fig. 5. Seasonal cycles of (A) sum of precipitations, (B) San Juan River runoff, (C) sea level height at Buenaventura, (D) fishing effort as the number of fishing trips, (E) the corresponding CPUE, and (F) artisanal white shrimp landings at Buenaventura. Error bars correspond to one standard deviation.

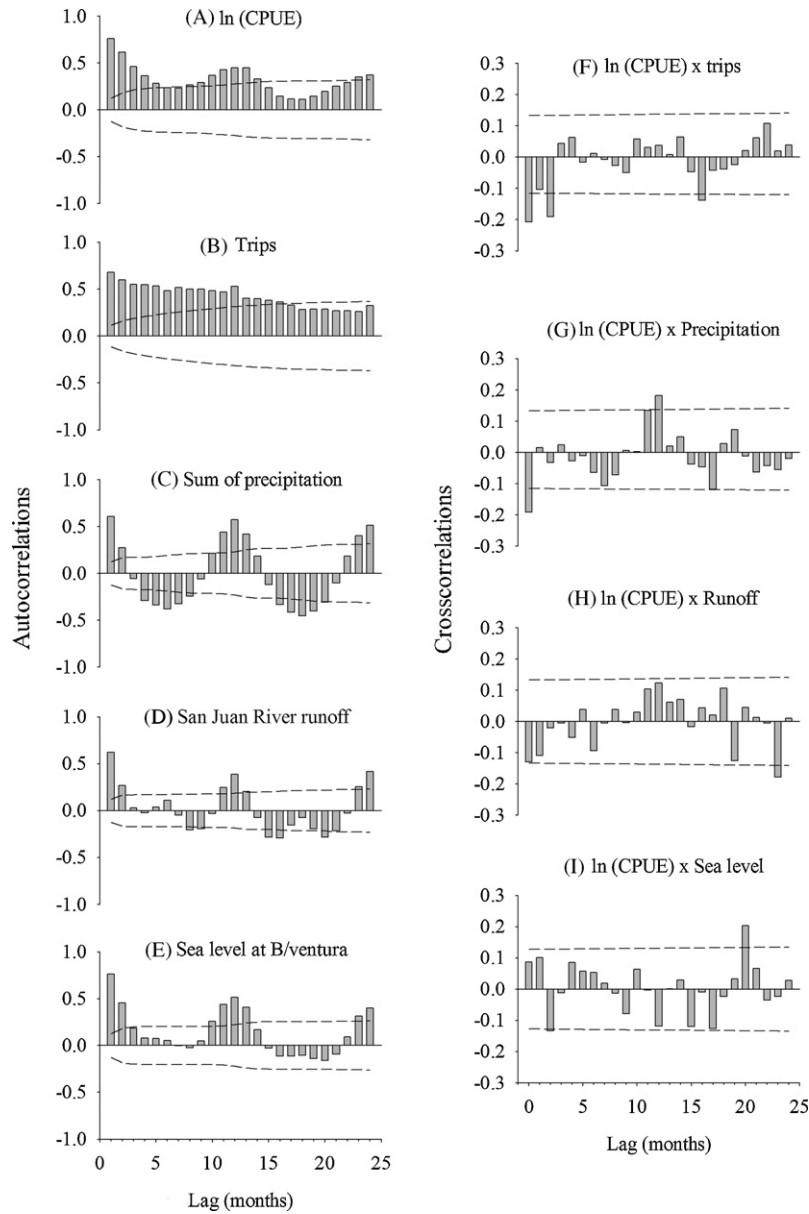


Fig. 6. Autocorrelation functions for (A) natural logarithm of the CPUE, (B) number of fishing trips, (C) sum of precipitation, (D) San Juan River runoff, (E) sea level at Buenaventura. Also presented are the crosscorrelations of the natural logarithm of the CPUE with (F) number of fishing trips, (G) sum of precipitation, (H) San Juan River runoff, and (I) sea level height at Buenaventura. Dashed lines represent 95% confidence intervals.

Table 1
Models estimated for monthly time series of white shrimp CPUE and environmental variables in Buenaventura (1968–1989)

Variables	Model type	Expression	AIC
Runoff (Y)		$Y_t^* = ((1 - 0.50B)(1 - 0.84B^{12})) / ((1 + 0.20B^2)a_t)$	3608
Sum of precipitation (Y)		$Y_t^* = (1 - 0.61B)(1 - 0.71B^{12})a_t$	3466
Sea level	ARIMA	$Y_t^* = (1 - 0.33B)(1 - 0.87B^{12})a_t$	2621
Trips		$Y_t^* = (1 - 0.60B - 0.13B^3)(1 - 0.88B^{12})a_t$	
CPUE (Y)		$\ln Y_t^* = (1 - 0.51B - 0.21B^3)(1 - 0.90B^{12})a_t$	73.09
CPUE (Y), sum of precipitation (X)	Transfer function	$\ln Y_t^* = 0.0002X_{t-12}^* + (1 - 0.48B)(1 - 0.87B^{12})a_t$	84.57

The backshift operator (B) is defined as $B^k(X_t) = X_{t-k}$. All parameters were significant with $p < 0.05$. *These time series were differenced with the operator $(1 - B)(1 - B^{12})$. AIC: Akaike information criterion (The SAS Institute Inc., 2002).

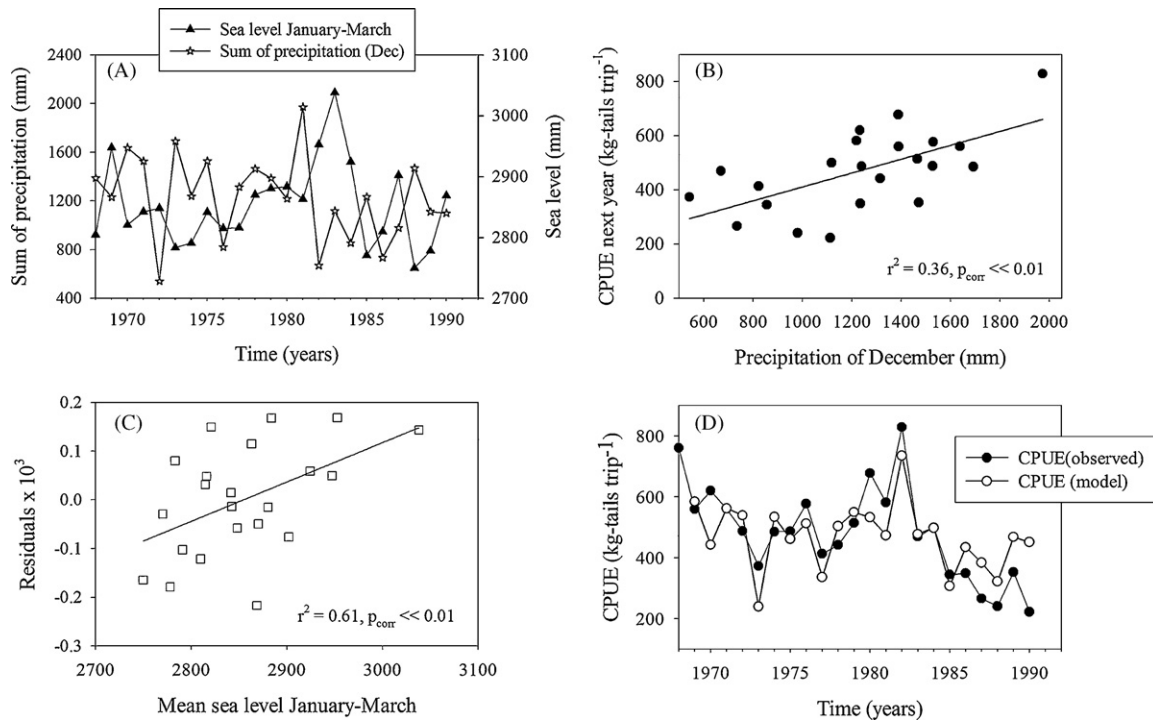


Fig. 7. Annual time series of (A) sea level during January–March and sum of precipitation of last December, (B) correlation between precipitation of December (Dec) and the mean CPUE of the following year, (C) correlation between the mean sea level at Buenaventura during January–March and the residuals of the regression in (B), and (D) a comparison between the actual mean annual CPUE and the estimations from a multiple linear regression of CPUE as a function of precipitation during last December and sea level during the first trimester. P_{corr} = p -value corrected for autocorrelation (Pyper and Peterman, 1998).

the sum of precipitation, the most significant effects were found at 0 (negative) as well as at 11–12 months (positive) (G). Most of the crosscorrelations between runoff and the CPUE were not statistically significant; however, the crosscorrelation function, like precipitation, showed positive values at lags of 0 and 11–12 months (H). On the other hand, and in contrast with precipitation, the runoff presented a significant correlation with CPUE at a lag of 24 months (H).

Most of the correlations between sea level and the CPUE were not significant. However, the crosscorrelation function suggested negative effects of this variable over shrimp abundance with lags of 3, 12, 15, and 17 months whereas a positive and significant effect was observed at 22 months (Fig. 6I).

3.3.1. Transfer function models

Because the relationship between the CPUE and precipitation was the only one that presented significant crosscorrelations with lags ≤ 1 calendar year, transfer function modeling was conducted exclusively in this case. Table 1 presents the results of transfer function modeling, which assigned more importance to the autoregressive structure of the error than to the environmental variable, which exerted its influence on the CPUE with a dead time of 12 months (Table 1).

3.4. Interannual scale

As observed on the monthly scale, annual precipitation and river runoff were strongly correlated ($r=0.71$, $p<0.01$). In addition, the MEI and the Niño 3–4 indices were negatively

correlated with the sum of precipitation ($r>-0.55$, $p<0.01$) and runoff ($r=-0.60$, $p<0.01$) whereas the SOI was positively correlated to them ($r=0.55$ and 0.60 , respectively, $p<0.01$). In addition, it was observed that total annual precipitation, mean river runoff, and sea level were not correlated with total annual CPUE ($p>0.05$). However, when we looked for associations guided by *a priori* hypotheses based on the knowledge of the white shrimp life cycle, we found that rainfall fell in December (Fig. 7A), during the critical period of postlarvae settling in the nurseries was positively regressed with the mean CPUE in the industrial fishery throughout the following year ($r=0.60$, $p_{\text{corr}} \ll 1$; B). Furthermore, the residuals of this simple linear regression model were significantly associated ($r=0.78$, $p_{\text{corr}} \ll 0.01$) with the mean sea level measured in Buenaventura during the first trimester, within the most important period of postlarval settling and when upwelling is active in the Panama Bight (C). The inclusion of precipitation from last December as well as the sea level height from the first trimester in a multiple linear regression model explained as much as 54% ($r^2=0.54$) of the total observed annual CPUE variance (D). The inclusion of last December's river runoff did not improve the predictive power of the regression model at all, nor did the inclusion of fishing effort.

With respect to the occurrence of El Niño events, we noted that the precipitation that fell in December was also correlated with the mean annual Niño 3–4 index ($r=-0.42$, $p<0.05$) but not with the SOI ($r=0.35$, $p>0.05$) or the MEI ($r=-0.31$, $p>0.05$). On the other hand, river runoff from December was correlated with all three indices: Niño 3–4 ($r=-0.47$, $p<0.05$),

SOI ($r=0.38$, $p<0.01$), and MEI ($r=-0.39$, $p<0.01$). Moreover, the mean sea level between January and March was closely associated with all the El Niño indices so that the correlation with the Niño 3–4 index was 0.63 ($p<0.01$) with the SOI -0.64 ($p<0.01$) and with the MEI 0.69 ($p<0.05$). However, when correlated directly, the CPUE was not correlated with any of the El Niño indices ($p \gg 0.1$).

4. Discussion

In this work, we present a time series analysis based on a relatively long dataset of monthly observations corresponding to the western white shrimp fishery off the Colombian Pacific. These data were drawn directly from the fishing companies at Buenaventura and consisted of industrial and, to a lesser extent, artisanal landings as well as records corresponding to the activity of the industrial fleet. Although the methods used for data collection may have changed with time due to the reassignment of functions to several government agencies, the CPUE values used for estimating the ARIMA models and testing statistical associations with the environment were based exclusively on the dataset from INDERENA which, basically, followed the same methodology from 1968 to the late 1980s (“Proyecto para el Desarrollo de la Pesca Marítima”, Barona, 1972; FAO, 1973). In contrast with the CPUE, we covered a longer time interval using landing data alone. This strategy introduced more uncertainty but offered us a longer time series to better understand the interannual response of white shrimp populations to important ocean atmosphere processes such as the ENSO cycle (see Section 4.2.3).

4.1. Landings and fishing effort

Strictly speaking, for using the CPUE as a proxy of abundance, it is necessary to operate with standardized measurements of fishing effort. However, when we look at the curves of fishing trips and the number of vessels active per month (Fig. 2D and E), it is evident that fishing effort experienced strong fluctuations between 1968 and 1992 (Fig. 2D and E) that were negatively correlated with the CPUE with lags of 0–3 months (Figs. 2F and 6F). The sharp decline experienced by fishing effort between ~1980 and 1982 has been attributed to economic causes such as a pronounced increment in fuel prices and the low prices paid per pound of shrimp on the U.S.A. market during the recession of the late 1970s (Rubio, 1994). In addition, for the study area, it was demonstrated that shrimp catches are significantly dependent on trawling speed which, in turn, is a function of engine power (Pineda, 1992). As a consequence, the use of non-standardized fishing effort in this study may have, to some extent, overestimated the actual CPUE (abundance). Nevertheless, as is inferred from our data (Figs. 2D–F and 6F), the CPUE derived from fishing trips still reflects the abundance of shrimp. In fact, during the late 1970s, there were concerns that the trawling fleet was losing efficiency since >75% of the vessels were older than 10 years (Herazo, 1981). In addition, to counteract the increased costs of fuel, fishermen opted for reducing the effective trawling hours by eliminating nighttime trawling (Herazo, 1981). As a

consequence, it is likely that economic factors compensated, in some way, the increase of the trawling fleet fishing power.

4.1.1. Artisanal fishery

The collection of artisanal white shrimp fishery data has been limited principally to landing statistics. It is also evident that the task of monitoring this fishery was affected by the instability in government politics regarding its administration (as reflected by the change of the agencies responsible for fisheries administration) as inferred from the lack of data between 1987 and 1992 (Fig. 2B). The artisanal shrimp fishery takes place along all the estuarine areas in the Colombian Pacific and is conducted with fishing units equipped with gillnets of 6 and 7 cm mesh opening, the first operated on non-mechanized boats and the second on boats equipped with a 25–40 HP engine (e.g. Díaz-Ochoa et al., 1997). To the best of our knowledge, there are no studies in the Colombian Pacific dealing with a quantification of fishing effort for the artisanal fishery. However, we hypothesize that because of the low level of technological improvements involved in this activity, landings have the potential to be used as a measurement of relative abundance. If that were correct, the increase of total landings observed throughout the 1990s (A–D) would indicate a restoration of white shrimp abundance to levels similar to those observed in the early 1970s (A and C). This is consistent with the abrupt jump observed in the industrial CPUE in the early 1990s (F).

4.2. The role of the abiotic environment

4.2.1. Sea level height and the upwelling influence

The area of the Panama Bight was described by Forsbergh (1969) as environmentally affected by oceanographic processes such as upwelling during January–March which, in turn, is closely related to the atmospheric dynamics determined by the seasonal changes in the Trade Winds direction associated with the latitudinal migrations of the ITCZ (e.g. Strub et al., 1998; Tchantsev and Cabrera, 1998). Therefore, Northeast Trades are associated with a generalized increase of primary production at the beginning of the year (e.g. Forsbergh, 1969; Rodríguez and Stuardo, 2002). In Panama, the upwelling intensity (inferred from variations in sea level) has been linked to white shrimp production based on landing statistics lagged 3 months (Forsbergh, 1969; D’Croz et al., 1979) and a similar relationship was also proposed for the Colombian shrimp fishery, but lagged 4–6 months (Forsbergh, 1969). It should be noted, however, that Forsbergh (1969) did not consider the interferences of autocorrelation in his correlation analysis. On a monthly scale, our results show that the sea level at Buenaventura was only slightly negatively correlated with the CPUE with a lag of 2 months, within the time interval considered with biological significance for the white shrimp life cycle; we lack a clear explanation for the positive correlation observed at 21 months (Fig. 6I). Therefore, we suggest that, in contrast to the Panamanian populations of the white shrimp that live closer to the upwelling centers at ~6–7°N (Forsbergh, 1969), in the Colombian Pacific, shrimp are not as strongly affected by the increased biological productivity associated with upwelling.

From the plot of the linear regression between the sea level height at Buenaventura and Balboa, we note that the dispersion of data from the regression line (Fig. 3F) is considerably lower compared with a similar plot for the rainfall observations at La Misión station (San Juan River) and Buenaventura (Fig. 3C). This comparison suggests that sea level height has a “more regional” signal than other variables such as rainfall. In this case, rainfall was more variable than sea level although the former was measured at much closer stations than the latter (Fig. 1). This regional character might explain why the relationship between the mean sea level during the upwelling season and the residuals of the regression between the CPUE and the sum of precipitation during December are significantly correlated on the interannual scale (Fig. 7B). We postulate that the sea level height at Buenaventura responds to the seasonal cycle of the ITCZ concomitant with Trade Winds variability, so that higher sea levels correspond to weaker Northeastern Trades and, therefore, less advection of surface waters offshore during the critical period of shrimp postlarvae settlement.

4.2.2. Precipitation and runoff

The lag of ~ 1 calendar year observed in the crosscorrelation function between the sum of precipitation and the CPUE indicates that the entry of freshwater through precipitation and, also possibly river runoff, significantly influence shrimp abundance in the fishing areas (Fig. 6G and H). The entry of juvenile shrimp into the adult areas begins 4–6 months after spawning in October–November (Pineda, 1992) in the open sea and its principal pulse is observed between January and May (Herazo, 1981; Pineda, 1992). Nonetheless, spawning could occur continuously, so that the year-round entry of postlarvae into the nursery areas is also possible. According to the lag estimated with the transfer function (Table 1), it took almost 1 year for the effects of the entry of freshwater on the first developmental stages of the shrimp to become evident in the fishing areas. This lag time seems to be due to the pattern of extended recruitment (*sensu* Wang and Somers, 1996) observed in the fishing areas (Herazo, 1981 and references within) as well as the growth process, which determines the time required for the recruited cohorts to reach their maximum biomass. From a statistical point of view, however, the modeling of the CPUE, considering only the autoregressive structure, was adequate and the inclusion of an environmental variable did not improve the predictive capacity of the model as can be inferred from the lower Akaike information criterion (AIC) for the ARIMA model compared with the TF model (Table 1).

On an annual scale, the CPUE was significantly associated with precipitation in December of the previous year (Fig. 7B). December corresponds to the end of the season with maximum precipitation (Fig. 5A) and, simultaneously, with the main spawning and postlarvae settling season (Pineda, 1992; Ramírez, 1994). On a monthly scale, the recruitment pattern within the fishing areas possibly “diluted” the influence of the precipitation over the course of the year, limiting the ability of the TF model to explain the higher percentages of variance associated with the CPUE. In turn, the “integration” of the CPUE signal on this annual scale revealed a stronger association with precipitation at the beginning of the main season when postlarvae enter

the nursery areas (January–May; Pineda, 1992). Consequently, rainfall in December explained approximately 36% ($r^2 = 0.36$; Fig. 7B) of the total variance of the CPUE attained the following year (B). This fact suggests that the *Litopenaeus occidentalis* life cycle in the Buenaventura area is importantly dependent on freshwater inputs, taking place during a relatively brief period at the end of the year, when the success of a major part of the juvenile recruitment to the adult stock areas is determined. Although reliable information is lacking as to the fishing effort for calculating the CPUE of the trawling fleet after 1992, we have found that, consistent with our results, the landings of *Litopenaeus occidentalis* in Buenaventura between 1990 and 1998 (data not available after 1998) are also associated with precipitation in December ($r = 0.8$, $p < 0.05$).

4.2.3. ENSO cycles and shrimp abundance

An analysis of the tendencies followed by precipitation in December also showed that this variable had substantially higher levels in the years preceding the 1982–1983 El Niño event than after it (Fig. 7A). A similar behavior was followed by the annual CPUE, but with a time lag of ~ 1 year, suggesting an important role of the precipitation in December for determining shrimp abundance during the following year (Fig. 7D). Alternatively, since the white shrimp is a short-lived species, one could argue that the drop of the annual CPUE after 1982 could be due to the restoration of fishing effort after the industrial fishery crisis of the late 1970s (Fig. 2D and E). However, an inspection of the cross-correlation function between the CPUE and fishing effort shows that the most important effects occurred in the short term, with a time lag of 0–3 months, whereas on longer time scales, there was only a weak association between these variables (Fig. 6F). In addition, although the fishing effort recovered after 1982, it never attained the levels observed before 1980 but the CPUE was substantially lower than that observed before 1980 (Fig. 7D).

The tendency of the precipitation at the end of the year was correlated with the Niño 3–4 index but not with either the MEI or the SOI. These results suggest that, although the ENSO cycle may have certain influence on the behavior of freshwater inputs in December, other signals such as those on the interdecadal scale, can be very important as well. The ENSO indices were not correlated with the CPUE, indicating that these events may have a dramatic effect on short time scales, as was the case in 1982, 1992, and 1997 (Fig. 2), but that they do not exert a long-term direct influence on shrimp populations.

On the interannual time scale, the multiple regression model fitted with the sum of precipitation in December and the mean sea level during the first trimester as predictor variables allowed us to explain an important proportion of the mean CPUE obtained during the following year ($r^2 = 0.54$; Fig. 7D). Because this statistical association was obtained using *a priori* hypotheses taking into the account the knowledge of the white shrimp life cycle and the characteristics of its abiotic habitat, we conclude that an important part of the decline of white shrimp fishery observed since the mid-1980s in the Colombian Pacific was associated with environmental changes affecting shrimp survival through habitat quality (e.g. availability of less saline habitat during settling in the estuaries) and the advection of early development

stages to the open sea during the main settlement season at the beginning of the year (higher sea levels in January–March would mean less advection of postlarvae offshore; Fig. 7C).

On the other hand, the decreased yields of the industrial fishing fleet in the study period were exacerbated by the exponential growth of the artisanal fishing catches (Fig. 2B), especially after the proliferated use of nets with 6-cm mesh size in the 1990s. Hauls with such nets are able to catch a large proportion of the juvenile stock. Therefore, control of the artisanal fishing effort, especially in terms of inadequate fishing gear, should remain a priority for the sustainable management of the *Litopenaeus occidentalis* fishery in the Buenaventura area.

From a regional perspective, we note that, for the El Niño event of 1982–1983, it has been postulated that shrimp catches diminished to great extent in Colombia (e.g. Pineda, 1992) presumably because the suitable habitat of this species extended southward favoring spawning off Ecuador and reducing the concentration of shrimp populations off Colombia (Pineda, 1992). However, the idea that the important fisheries of *Litopenaeus occidentalis* to the south are limited to Colombia (e.g. Hendrickx, 1995) seems to be erroneous. In fact, the system of collecting statistical information in Ecuador has, for years, pooled both the data from the most economically important aquaculture industry with data from the marine fisheries dominated by *Litopenaeus occidentalis* (e.g. Klima, 1989). In addition, Mendo and Tam (1993) noted that shrimp (*Litopenaeus vannamei*) populations off northern Peru undergo non-equilibrium conditions associated with the ENSO cycles, so that during the El Niño events of 1965, 1969, 1972, and 1976 the penaeid fishery populations seem to have doubled their maximum sustainable yield relative to non-El Niño years (Mendo and Tam, 1993). Despite the rather low landings in Buenaventura during 1982 (Fig. 2; Pineda et al., 1992), the CPUE attained maximum values during the El Niño 1982–1983, as occurred off Ecuador during the same event or off northern Peru in the 1965, 1969, 1972, and 1976 El Niños. This similar response suggests that shrimp populations in the eastern tropical Pacific may be connected in some way which is still poorly investigated and deserves more attention in future studies.

4.2.4. Comparison with other commercial penaeid shrimps

Several studies have analyzed the association between precipitation and the recruitment of other penaeid shrimp. For example, in the tropical area of the Philippines (Guimaras Islands), various penaeid species responded differently to changes in salinity in the nursery areas located in the mangrove swamps that border the rivers. These differences were attributed to the improved adaptation of some species to low salinity (i.e. *Metapenaeus ensis*, *Litopenaeus merguensis*) compared with other species that prefer saltier water (e.g. *Metapenaeus anchistus*) (Primavera, 1998). Another study carried out to the west of the Malaysia peninsula revealed that the annual shrimp landings (mostly *Litopenaeus merguensis*) over the last two decades were associated positively with the availability of shallow areas (<5 m) and with the coverage of mangrove forests, whereas they were negatively correlated with precipitation (Loneragan et al., 2005). In the southeastern United States, once they enter the estuaries, penaeid

Litopenaeus setiferus juveniles tend to remain in rather reduced areas, where they are exposed to the influence of local conditions such as salinity/precipitation, temperature, tidal influx, substrate type, and trophic interactions (Webb and Kneib, 2004 and references therein). Between 1969 and 1994 in the south of the Gulf of Mexico (Campeche Sound), the migration of the shrimp *Farfantepenaeus duorarum* towards the nursery areas was correlated with the rainy season, primary productivity, and oceanic circulation patterns, whereas periods with peak juvenile recruitment in the fishing areas were affected by rain, river runoff, and winds from the north (Ramírez-Rodríguez et al., 2003 and references therein). This kind of environmental association was also described in the coastal lagoon Mar Muerto (Mexican Pacific) for the shrimp *Litopenaeus vannamei* revealing that the juvenile growth rate was notably increased during the rainy season, whereas the continuous emigration toward the open sea was correlated negatively with salinity (Medina-Reyna, 2001). In another study, Haas et al. (2001) evaluated the associations of various environmental factors with abundance series from different developmental stages of the shrimp *Litopenaeus aztecus* in the southern U.S. (Louisiana) for 1970–1997. These authors found that temperature was positively correlated with juvenile abundance but not with postlarval abundance, whereas salinity was correlated positively with adult abundance. Due to the strong association between juveniles and adults, no correlation was found between early stages and spawning stock whereas a notable influence of the environmental variables on juvenile abundance was determined so that these authors concluded that the prevailing conditions in estuaries are critical for determining the strength of the annual cohorts recruited.

The pattern of the environment–penaeid shrimp relationship that emerges from the few studies cited above seems to be consistent with the behavior found for *Litopenaeus occidentalis* in the Buenaventura area. White shrimp development seems to be favored by high contributions of freshwater (low salinity) precisely in the period when postlarval settlement occurs in the mangrove swamps and estuaries.

Contrary to our expectations, the runoff from the San Juan River had very little predictive power for the CPUE on a monthly scale (Fig. 6H) and, furthermore, its correlation with the CPUE practically disappeared on an annual scale. In this study, the series of the San Juan River runoff was considered because it is the longest available record and because this river represents a large contribution of water and sediments in the coastal area of the Colombian Pacific (Restrepo and Kjerfve, 2000). Nonetheless, and in spite of its location within the area where the *Litopenaeus occidentalis* shrimp fishery is developed, the mouths of the San Juan River are relatively far from the nursery areas located to the south of Buenaventura (e.g. Tortugas Gulf, the Guapi sector). Even when the coastal ocean associated with the San Juan delta shows high productivity, the circulation there is characterized by scarce stratification of the water column and net transport of salt offshore (Restrepo and Kjerfve, 2002), conditions that are not very favorable for postlarval development. As a consequence, it is likely that the association of the CPUE with the river runoff in the study area reflects the close correlation between precipitation and river runoff (e.g. Poveda et al., 2001).

This way, the entry of freshwater mainly produces changes in salinity in the habitat, and these changes contribute to determining the availability of shelter for postlarvae and juveniles (e.g. Primavera, 1998; Haas et al., 2001). Future research on the influence of this runoff in the areas to the south of Buenaventura is expected to allow descriptions of associations between recruitment and environmental factors such as nutrient contributions, turbidity, transport, and the formation of frontal zones (Grimes and Kingsford, 1996 and references therein). An especially interesting factor to keep in mind for future studies is the transport of the surface currents associated with Trade Winds dynamics as well as the role of the tidal currents, which, in other areas, have been shown to play a crucial role in postlarval transport towards the nursery areas (e.g. Criales et al., 2005, 2006).

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