Abstract—The reproductive activity and recruitment of white mullet (*Mugil curema*) was determined by observations of gonad development and coastal juvenile abundance from March 1992 to July 1993. Adults were collected from commercial catches at three sites in northeastern Venezuelan waters. Spawning time was determined from the observation of macroscopic gonadal stages. Coastal recruitment was determined from fish samples collected biweekly by seining in La Restinga Lagoon, Margarita Island, Venezuela. The examination of daily growth rings on the otoliths of coastal recruits was used to determine their birth date and estimate the period of successful spawning. Fish with mature gonads were present throughout the year but were less frequent between September and January when spawning individuals migrated offshore. In both years, juvenile recruitment to the lagoon was highest between March and June when high densities of 25–35 mm juveniles were observed. Back-calculated hatching-date frequency distributions revealed maximum levels of successful spawning in December–January that were significantly correlated with periods of enhanced upwelling. The relation between the timing of successful spawning and the intensity of coastal recruitment in white mullet was likely due to variations in food availability for first-feeding larvae as well as to variations in the duration of the transport of larvae shoreward as a result of varying current conditions associated with upwelling.

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Reproduction and recruitment of white mullet (*Mugil curema*) to a tropical lagoon (Margarita Island, Venezuela) as revealed by otolith microstructure*

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White mullet (*Mugil curema*) is a widespread coastal pelagic fish occurring from Massachussetts to southern Brazil. Considered to be catadromous, the juvenile fish recruit to lagoons and estuaries following a period of offshore spawning (Blaber, 1987; Ibañez-Aguirre, 1993; Ditty and Shaw, 1996). White mullet is an important economic resource supporting many small communities through both fishing and aquaculture (Alvarez-Lajonchere, 1982; Gómez and Cervigón, 1987). Small schools of mullet are captured with gill and "atarraya" nets near the coast and in neritic waters and between 300 and 400 metric tons are sold annually on Margarita Island, Venezuela.

Reproductive periodicity in white mullet varies over its geographic distribution. Several authors have reported protracted or continuous reproduction in tropical waters and generally two spawning peaks per year (Jacot, 1920; Anderson, 1957; Angell, 1973; Moore, 1974; Alvarez-Lajonchere, 1976, 1980; Yañez-Arancibia, 1976; Rodriguez and Nascimento, 1980; Garcia and Bustamente, 1981; Franco, 1986; Ibanez-Aguirre, 1993). Figure 1 summarizes previous work describing the spawning periods of *M. curema* based on gonad development and estimated according to the arrival of juveniles in the coastal zones. The spawning period is quite variable. Angell (1973) suggested that schooling occurs in coastal areas just prior to the offshore spawning migration and that the departure of individuals for the spawning grounds causes a reduction of the gonadosomatic index in the nearshore populations. Moore (1974) also reported that during the spawning period fully ripe fish are rare in coastal collections. Despite these studies, little is known of the factors influencing reproductive patterns of the white mullet. Ibanez-Aguirre (1993) suggested that the timing of reproduction in *M. curema* in Tamiahua Lagoon, Mexico, is an adaptation to avoid competition with juveniles of the conspecific *Mugil cephalus*. In areas of favorable thermal regimes, *M. curema* may penetrate a wider range of salinities and competitively exclude *M. cephalus* (Moore, 1974).

The periodicity of white mullet reproduction may be related to environmental variability that signals periods of optimal early growth and survival. Stability of the water column and suit-

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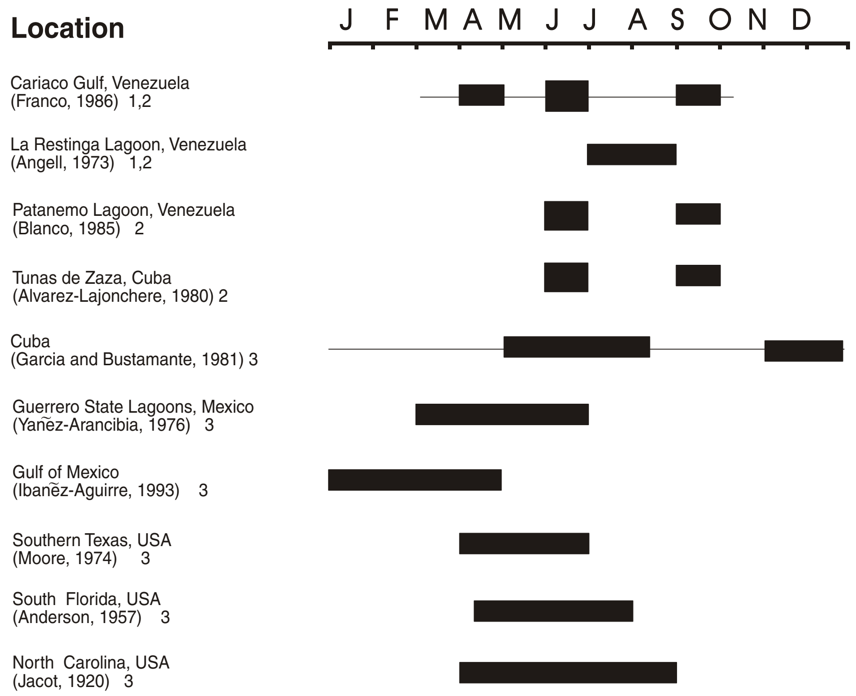

Figure 1

Spawning periods for white mullet (*Mugil curema*) in tropical waters, based on the histological observations of gonads (1), macroscopic observations of gonads (2), and estimated from the arrival of juveniles in coastal areas (3). Thin horizontal lines indicate periods of continuous but minor spawning between periods of peak spawning.

able food in coastal lagoons, river deltas, and estuarine mangrove areas have been identified as important factors influencing the recruitment of juvenile Mugilidae (Yañez-Arancibia, 1976; Blaber and Blaber, 1980; Blaber, 1987; Vieira, 1991). Based on macroscopic gonad observations of schools of white mullet captured offshore, Etchevers (1974) proposed that the spawning of white mullet recruiting along the southern coast of Margarita Island, Venezuela, occurs between La Tortuga Island and Margarita Island in the vicinity of the 1000-m deep Cariaco trench (Fig. 2). Seasonal environmental variability in this area is mainly generated by the alternation between upwelling during the dry season and freshwater discharge during the wet season (Gómez, 1983; Müller-Karger et al., 1989). The rainy season strongly influences the eastern Caribbean as freshwater plumes from the Amazon and Orinoco Rivers lower salinities throughout the region. Both upwelling and freshwater runoff produce intense peaks in coastal primary production (Gines 1972; Ferraz-Reyes et al., 1987; Müller-Karger et al., 1989), which could influence spawning periodicity and recruitment success. The purpose of this study was to document the periodicity of reproduction and recruitment of *M. curema* along the southern coast of Margarita Island and to examine their relationship with environmental signals, particularly those associated with upwelling.

Methodological advances in counting daily growth increments in otoliths of marine fishes (Pannella, 1971; Campana and Nielsen, 1985) have greatly aided studies of the age, growth, and recruitment of larval and juvenile fishes (Wilson and Larkin, 1980; McBride and Conover, 1991; Jenkins and May, 1994; Sirois and Dodson, 2000). For the striped mullet (*M. cephalus*), a close relative of the white mullet, Radtke (1984) showed that the first increment is formed one day after hatching and that additional increments are formed daily thereafter. Daily growth rings have also been demonstrated in laboratory studies for *M. so-iuy* by Li et al. (1993). In the present study, we examined the microstructure of the otoliths of juveniles recruiting to a coastal lagoon in order to back-calculate the date of hatching and hence the time of successful spawning. We first validated that otolith growth increments of juvenile *M. curema* were formed daily.

Material and methods

Reproductive periodicity was documented from samples of adult fish taken monthly from commercial catches in three fishery zones in Venezuela: 1) the Chacopata zone, located between Chacopata lagoon and Coche and Cubagua Islands; 2) the Cariaco Gulf zone; and 3) the Margarita zone located along the southern coast of Margarita Island and the northern coast of Cubagua Island (Fig. 2). Measurements of water temperature, salinity, and rainfall were

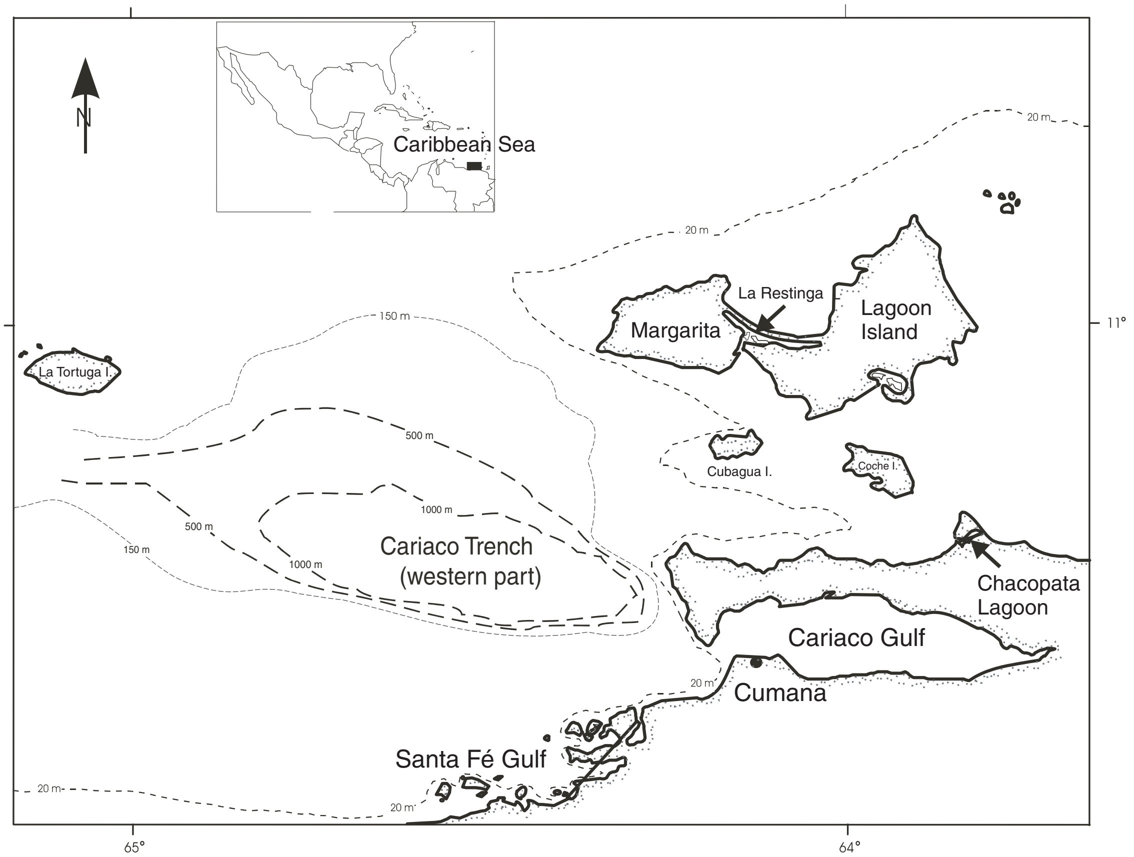

Figure 2

Map of the northeastern coast of Venezuela showing locations mentioned in the text.

collected periodically throughout the entire study period at the La Salle meteorological station, next to La Restinga Lagoon on Margarita Island.

Total (TL) and standard (SL) lengths of adult mullet were measured to the nearest 0.5 cm and total and gutted body mass were recorded to the nearest 0.1 g. Sexual maturity was determined by observation of the gonads and gonadal stages were classified as follows:

Stage I	Ovaries transparent and inconspicuous, whitish-yellow in color and rounded with a small diameter. Testes longer than ovaries and ribbonlike in form.
Stage II	Ovaries rounder and wider than in stage I, and yellow in color. Testes thinner, and wider than stage I, but still with thin edges and a ribbon-like form; white in color.
Stage III	Ovaries large, pale yellow, smooth in appearance, turgid, and round. Ovocytes easily distinguished macroscopically (as granular). Testes milky-white in color (bright), turgid, and wider in appearance and having thicker edges than in stage II.
Stage IV	Spawned (spent) ovaries purple and wrinkled in appearance. Testes whitish, or transparent with white patches, and wrinkled in appearance.

Recruitment periodicity was documented from samples of juveniles seined at semimonthly intervals at the mouth of La Restinga Lagoon (Fig. 2). The 2-cm mesh beach seine measured 1.5 m deep and 50 m long. Juvenile white mullet were distinguished from other juvenile mullets according to the descriptions of Alvarez-Lajonchere et al. (1976). White mullet juveniles were characterized by a scaly gray appearance as opposed to the shiny metallic gray appearance of a sympatric mullet species (*Mugil incilis*). For white mullet, recruitment is defined as the appearance of juveniles in coastal areas (Vieira, 1991). We calculated catch per unit of effort (CPUE) as the number of juveniles per seine haul. For all samples, standard length of fish was measured to the nearest 1 mm. Otolith analysis was restricted to one sampling period per month. After examining size-frequency distributions of juveniles captured in the lagoon, the otoliths of approximately 20 individuals representing all cohorts collected on a given sampling date were analyzed. The otoliths (sagittae) were removed with needles, rinsed in water, and then attached to strips of masking tape. The otolith was then sanded to obtain a transversal section (Fig. 3) with a thickness of approximately 20 μm by using the technique described by Secor et al. (1992) and a metallurgic jig adapted from Neilson and Geen (1986). Readings of the number of increments were made along the curvilinear surface running from the nucleus to the edge of the otolith (Fig. 3). Because daily growth increments were

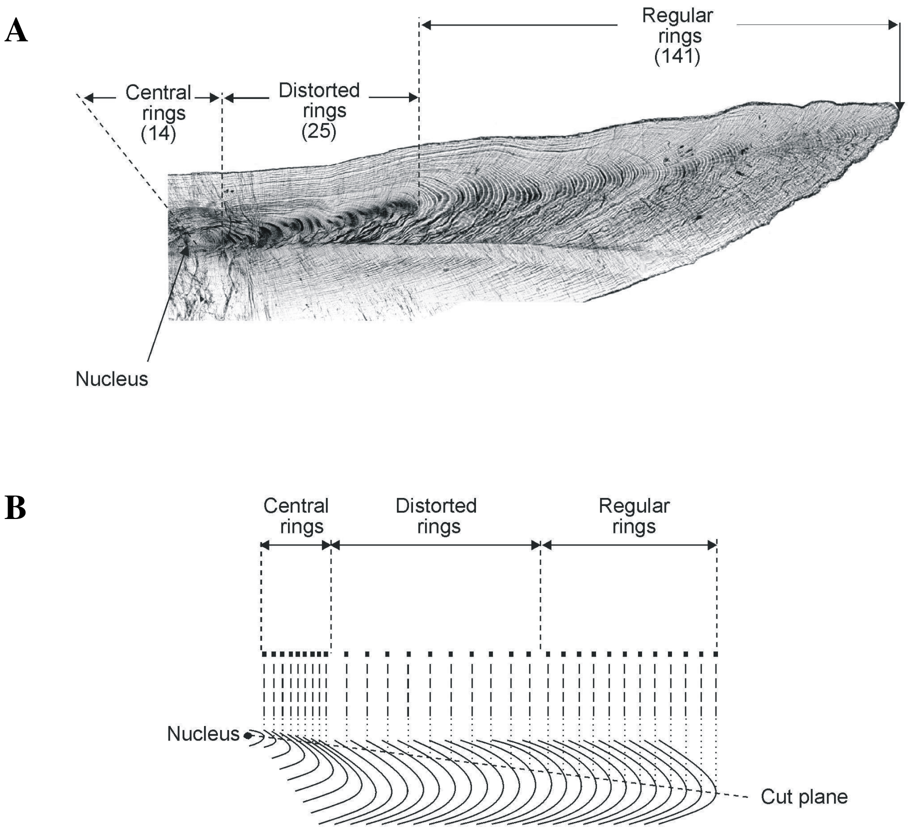

Figure 3

(**A**) Photomicrograph in optical microscopy of the posterior radius of a polished otolith from a 180-day-old juvenile white mullet (*Mugil curema*). Different sequences of rings are indicated which result from a horizontal plane not aligned with the changing growth plane of the otolith. Numbers of rings in each sequence are shown in parentheses. (**B**) Schematic presentation of the changing growth plane of the otolith, the cut plane, and the resultant increment distortion (black rectangles represent the distance between adjacent rings).

less consistent in the anterior field, otolith counts were always made along the posterior radius of the sagittae. We also measured the area of the nucleus, which represents the prehatch zone. All measurements were made under a microscope which was connected to an image analyzer and computer.

To evaluate the error in counting growth increments on otoliths, one reader made 7 independent counts of the number of growth increments on otoliths obtained from 11 juveniles representing the size-range of sampled fish. The number of growth increments ranged from 63 to 289 (mean=147) and the mean coefficient of variation was 8.71% (SD=2.13%) (Fig.4). We therefore considered an error of approximately 10% for the counts of growth increments. In applying the technique to the subsamples of the different cohorts sampled in the lagoon, at least two counts were made for each otolith. All counts were made by the same person.

To evaluate if otolith growth increments were formed daily, we read the otoliths of juveniles sampled on successive sampling dates and compared the average increase in the number of otolith increments to the number of days between samplings (Struhsaker and Uchiyama, 1976; Jordan, 1993; Jenkins and May, 1994). Birthdate was obtained by subtracting the number of daily growth rings on otoliths from the date of capture. We used the hatching mark as defined for *M. cephalus* (Radtke, 1984) and *M. iso-iuy* (Li et al., 1993) to locate the hatching mark on the otoliths of the white mullet.

Knowing that white mullet embryos hatch from 24 to 40 hours after fertilization (Anderson, 1957; Houde et al., 1976), we back-calculated hatching dates of recruits to estimate when successful spawning occurred. We examined the relationship between the spawning dates of recruits and an index of the intensity of upwelling. In calculating this index, we determined wind stress based on data from Fundación La Salle, Margarita Island, and Cumaná Airport meteorological stations. The upwelling index (UI) was based on Bowden's (1983) theoretical calculations as follows:

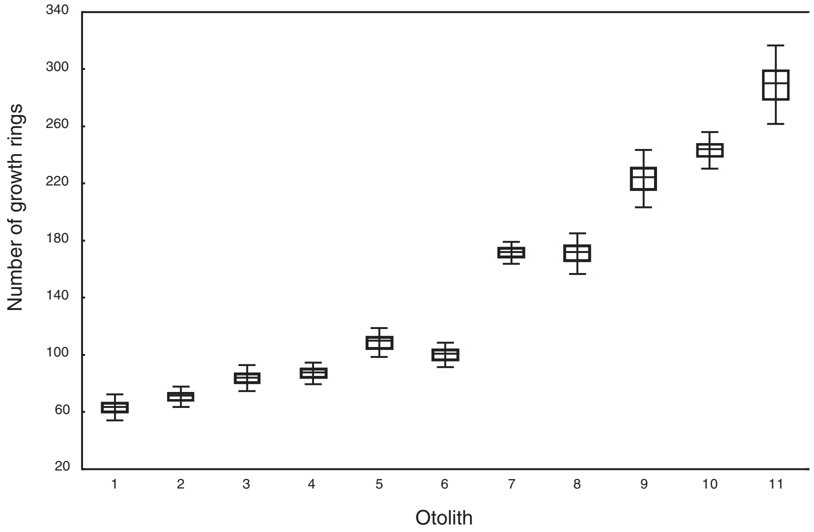

Figure 4

Number of growth increments (counted on seven independent occasions) on otoliths from 11 juvenile white mullet of varying size. Means, standard errors, and standard deviations are illustrated.

$$\mathrm{UI} = \frac{\tau_{sx}.100}{\rho_w.f},$$

where f = Coriolis parameter;
τ_{sx} = surface wind stress; and
ρ_w = average density of the water (1025 kg/m^3).

The term f was calculated as

$$f = 2\ \omega \sin (f_i),$$

where ω = angular velocity of rotation of the earth (7.29×10^{-5} s [seconds]): and
f_i = latitudinal position at the place i.

The term τ_{sx} represents surface wind stress measured in the x-axis perpendicular to the coast (Bowden, 1983), often considered in terms of the empirical equation

$$\tau_{sx} = k \times \rho_a \times W^2,$$

where k = empirical drag coefficient (1.11 to 3.25, as a function of wind velocity; Bowden 1983);
ρ_a = mean density of the air (1.25 kg/m^3); and
W = wind velocity.

The drag coefficient, *k,* changes as a function of wind velocity and gives values equivalent to those of Bakun et al. (1974).

The relationship between upwelling and the birth dates of successful recruits (captured in La Restinga Lagoon) was determined in two steps. First, we calculated the birth dates of juveniles captured during one monthly sampling period during each of the 18 months of the study by applying the frequency distribution of birth dates of aged juveniles to the total catch for that date. A total of 398 juveniles were aged by otolith analysis. If x% of aged fish captured on a given date were hatched on Julian Day y, this percentage was applied to the total catch of juveniles for that sampling date. Secondly, all fish hatched on a given day were summed across the 18 monthly sampling dates. This frequency distribution was then correlated with the distribution of UI estimates over the same period of time as that of the birth dates.

Before proceeding with correlation, trends in birth date and UI data series were described by using a smoothing spline. The spline fit uses a set of smoothly spliced 3rd degree polynomial segments (Simonoff, 1996; JMP® software, version 3.2.1, SAS Institute, Cary, North Carolina). Predicted values were correlated with the raw data points in order to optimize the value of lambda used to fit the smoothing spline. Increasing the value of lambda increases the degree of smoothing but weakens the correlation between predicted and raw data. Pearson correlation and cross-correlation functions were used to describe the temporal relationship between upwelling and the date of hatching of fish recruited to the coastal lagoon.

Results

The white mullet surveyed in the commercial catches measured from 4 to 36 cm SL. The largest fish were from the Chacopata zone where the most abundant sizes classes were those from 22 to 30 cm. The most abundant sizes in the Cariaco Gulf and Margarita Island zones were 20 to

26 cm and 18 to 26 cm, respectively. The mullet from the Margarita zone were mainly juveniles and small adults (Fig. 5).

Maturity and reproductive periodicity

An examination of gonad maturity revealed that 90% of the male and female mullet in the Margarita zone were immature or at developing stages (I and II) and only 10% in developed and spawning stages (III and IV). In contrast, 53.8% of females and 42.8% of males of the population of generally larger mullet sampled at Chacopata were in developed and spawning stages. Finally in the Cariaco Gulf zone, where the fish were of intermediate size, compared to fish at Margarita and Chacopata, 41.2% of females and 32.7% of males were in developed and spawning stages.

Throughout our study, sexually mature (stage-III) fish were present in the samples from the Chacopata fishery (Fig. 6), and their abundance showed a marked seasonal pattern. Mature and spent fish were least abundant (<25% of the population) between September and January and most abundant from April to August 1992 and May to June 1993. In contrast, in the Margarita fishery, immature (stage-I) fish dominated the samples and mature fish only occurred sporadically (Fig. 6). Finally, in the Cariaco Gulf zone, immature and maturing fish (stage-I, and stage-II) generally dominated the population, except in July when mature fish became abundant.

Otolith microstructure

The otolith of *M. curema* had a round nucleus with a mean radius of 9.26 µm (95% confidence interval (CI)=0.54, *n*=8), and the dark area in the center had a mean diameter of 4.97 µm (CI=0.82, *n*=8). The otolith was round during the larval period and became ovoid when mullet reached 10–12 mm (SL). In the early juvenile stage (18–20 mm SL), the otolith was strongly elongated and the anterior end was arrow-like. In juveniles (>20 mm SL), the otolith was always thin, concave, and umbrella shaped in form (Fig. 3).

Validation of otolith increment lines

The otolith increments counted for the first strong cohort present in the lagoon during March and April 1992 demonstrated that the average number of increments added during the 14-day interval between sampling collections was close to 14 days (Table 1). This indicated that otolith increments were formed daily, as observed in other species of mullet.

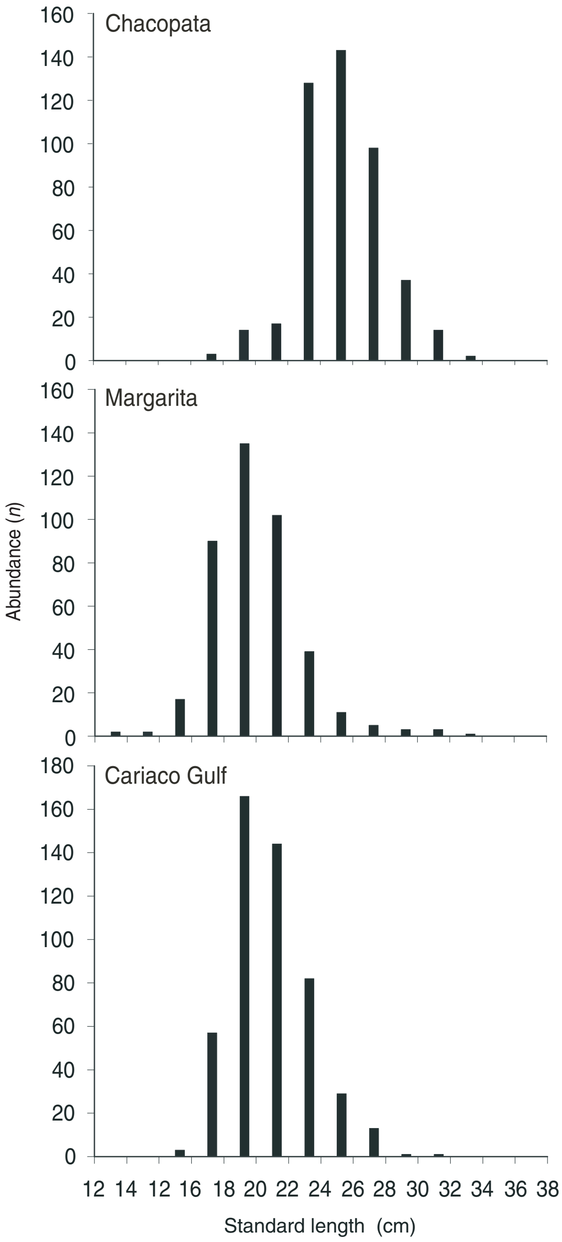

Figure 5

Length-frequency distributions of white mullet surveyed in the commercial catches from the three fishery zones of northeast Venezuela.

Juvenile recruitment

The catch-per-unit-of-effort measurements for juveniles captured in La Restinga Lagoon demonstrated a seasonal pattern and high recruitment from March to early July 1992 and from late March to May 1993, and low recruitment during the remaining months (Fig. 7). The recruitment peak in 1992 was more than twice that in 1993. The periods of strong recruitment were associated with the rainy season in northeastern Venezuela (Fig. 7), as previously reported by Okuda et al. (1978), Gómez (1983), and Ferraz-Reyes (1989).

The discontinuous length-frequency distributions of juveniles sampled biweekly suggested the presence of four cohorts in the lagoon during the study period (Fig. 8). Two cohorts were present on 5 March 1992, the first sampling date. The cohort of smaller juveniles, referred to as the first cohort, had a mean length of 29.8 mm (range of 18 to

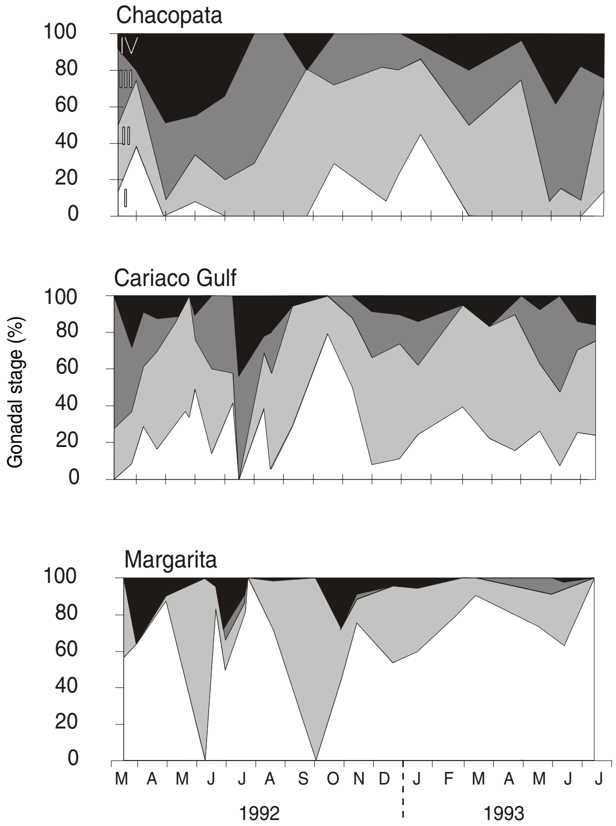

Figure 6

Percent composition of four maturity stages (I to IV, see text for definitions) of *Mugil curema* (males and females combined) captured from Margarita, the Cariaco Gulf, and the Chacopata fishery zones of northeast Venezuela.

36 mm) and varied in age from 50 to 70 days (Fig. 9). The cohort of larger juveniles, referred to as the second cohort, had a mean length of 105 mm (range of 90 to 130 mm), and otolith analysis indicated an age of 160 to 240 days (Fig. 8). This cohort was present until May 1992 and was largely absent thereafter (Fig. 7). A third cohort was first observed in mid October 1992. It measured from 50 to 100 mm in length, overlapping the length distribution of cohort 1. As such, no clear distinction could be made between these two cohorts on these dates. The third cohort became more distinct in December 1992 and January 1993 as individuals from the first cohort left the lagoon. These individuals were aged from 95 to 200 days old in December. This cohort was present until approximately April 1993 and disappeared thereafter (Fig. 9). Finally, a fourth cohort first appeared in March 1993 and consisted of fish of similar size and age as the first cohort observed in March of the previous year.

The back-calculated hatching dates showed that the second, older cohort observed in the lagoon in March 1992 was composed of mullet that had hatched between August and October 1991 (Fig. 10). The younger cohort in the March 1992 sample originated from continuous hatching from late December 1991 to late March 1992. The back-calculated hatching dates indicated that larval production of successful recruits was almost absent during April and May 1992 but small increases were observed in June and July 1992. The third cohort, which first appeared in September 1992, was

Table 1

Validation of daily increment formation in the otoliths of juvenile white mullet (*Mugil curema*) sampled at 14-day intervals in March and April 1992. *n*= number of otoliths in sample, mean age (standard deviation) is given in days on date of capture, and "difference" is the difference in mean age between successive sampling dates.

Sampling dates	5 March 1992	19 March 1992	2 April 2 1992
n	15	20	19
Mean age (SD)	56.46 (4.81)	70.85 (9.88)	84.3 (11.24)
Difference		14.39	13.45

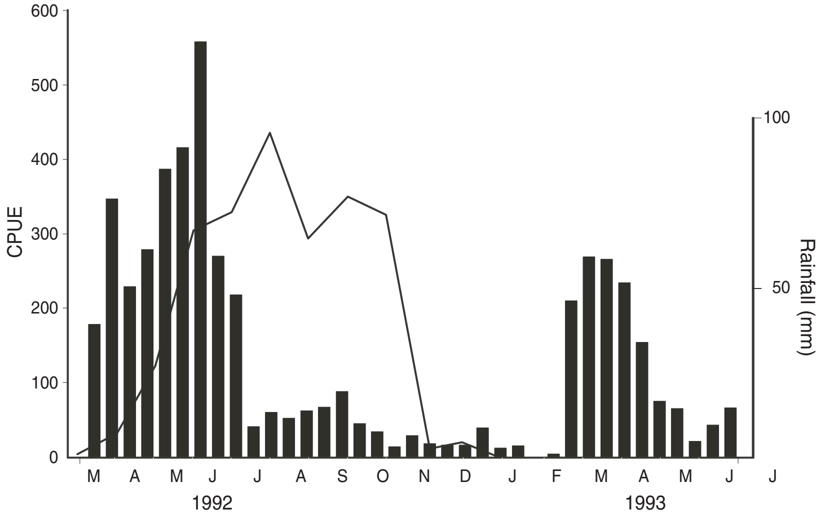

Figure 7

Histogram of monthly abundance of juvenile white mullet as indicated by catch per unit of effort (CPUE) from semimonthly sampling in La Restinga lagoon from March 1992 to July 1993. The continuous black line presented in the first annual cycle represents the mean monthly rainfall averaged over the period 1985–93.

Table 2

Correlation analyses of hatching date and upwelling index data series. Increasing lambda values used to fit the smoothing spline weakens the r^2 values between observed and predicted values of birth date and upwelling index over time (columns 2 and 3). In contrast, increasing lambda values strengthen the correlation (Pearson's correlation) between the two data series (column 4). BD = birth date, UI = upwelling index

Data series	Hatching dates (r^2, P)	Upwelling index (r^2, P)	BD versus UI (r, P)
Raw data	—	—	0.28, <0.05
Smoothing spline $\lambda = 1$	0.82, <0.000	0.86, <0.000	0.36, <0.000
Smoothing spline $\lambda = 10$	0.73, <0.000	0.74, <0.000	0.41, <0.000
Smoothing spline $\lambda = 100$	0.67, <0.000	0.63, <0.000	0.45, <0.000
Smoothing spline $\lambda = 1000$	0.64, <0.000	0.54, <0.000	0.52, <0.000
Smoothing spline $\lambda = 10{,}000$	0.56, <0.000	0.45, <0.000	0.57, <0.000
Smoothing spline $\lambda = 100{,}000$	0.48, <0.000	0.40, <0.000	0.64, <0.000

composed of individuals that had hatched between June and August 1992. Finally, individuals in the fourth cohort, which first appeared in the lagoon in March 1993, were fish that had hatched in January and February 1993.

The hatching dates of recruits coincided with periods of increasing upwelling, particularly during January and February of 1992 and 1993 (Fig. 10). The use of increasing levels of lambda to fit the smoothing spline increasingly weakened the correlations between predicted and observed values of birth dates and UI index and strengthened the correlations between birth dates and the upwelling index (Table 2). Choosing a lambda value of 10 resulted in r^2 values greater than 0.70 ($P<0.000$) between the raw and predicted data series and in an r value of 0.41 ($P<0.000$) between birth date and the upwelling index. Cross-correlation analysis between these two series revealed that the strongest correlation ($r=0.52$, $P<0.000$) occurred when the upwelling index lagged behind birth dates by 8 days and by 46 days. These lag periods reflect the coincidence of the major peak of upwelling with the two peaks of birth dates that are separated by approximately 35 days. Given the estimated 10-day error associated with aging otoliths, the 8-day lag cannot be interpreted.

Discussion

Our sampling of white mullet in the coastal waters of northeastern Venezuela revealed the presence of mature fish throughout the year, but abundance was lowest between August and January. Mullet from the Margarita zone were small (4 to 36 cm in SL) and mostly immature (>80%). Because size at maturity of white mullet is 24 cm (Marin and Dodson, unpubl. data), most of the adults in the lagoon were probably in their first spawning cycle. Similarly, mullet from the Cariaco Gulf zone also appeared to be young adults in their first spawning cycle. In contrast, mullet from the Chacopata zone were larger and generally in more advanced stages of gonadal development. This finding suggests that the Chacopata mullet were part of a prespawning aggregation, and the location of the aggregation agrees with the more offshore location of the Chacopata fishery.

Because white mullet spawn offshore (Jacot, 1920; Anderson, 1957; Ditty and Shaw, 1996), the small proportion of mature fish in the coastal fisheries from July to April is likely explained by the migration of adults to the offshore spawning grounds. If this is so, reproduction is not indicated by an increase in the frequency of fish in advanced stages, but rather is associated with the disappearance of maturing and mature fish from coastal areas. The disappearance of fish in advanced stages from coastal areas as the spawning season approaches was also reported by Angell (1973) and Moore (1974). The analysis of birth dates of juveniles sampled in the La Restinga Lagoon indicates that successful spawnings are concentrated in the periods of increased upwelling and also coincide with the end of the rainy season. The spawning season may or may not be concentrated at these times but larvae that hatch during upwelling events are most likely to successfully recruit to the lagoon.

Although reproduction in tropical fishes is often protracted, peaks in successful spawning may nevertheless be initiated by environmental cues (Redding and Patiño, 1993). The white mullet possibly uses temperature or other signals associated with upwelling to synchronize its spawning with upwelling events. The variations in the timing of recruitment of white mullet in different geographical regions may be the result of variation in the timing of favorable conditions that enhance survival. Such conditions may include increased primary production (Ferraz-Reyes, 1983; Müller-Karger et al., 1989) or hydrographic mechanisms likely to facilitate transport of larvae to coastal nursery areas (Blaber, 1987), so that survival is increased. Populations likely have adequate time to adapt to environmental conditions in particular areas because local hydrographic patterns develop over geological time scales (Bakun, 1986; Sinclair, 1988; Heath, 1992).

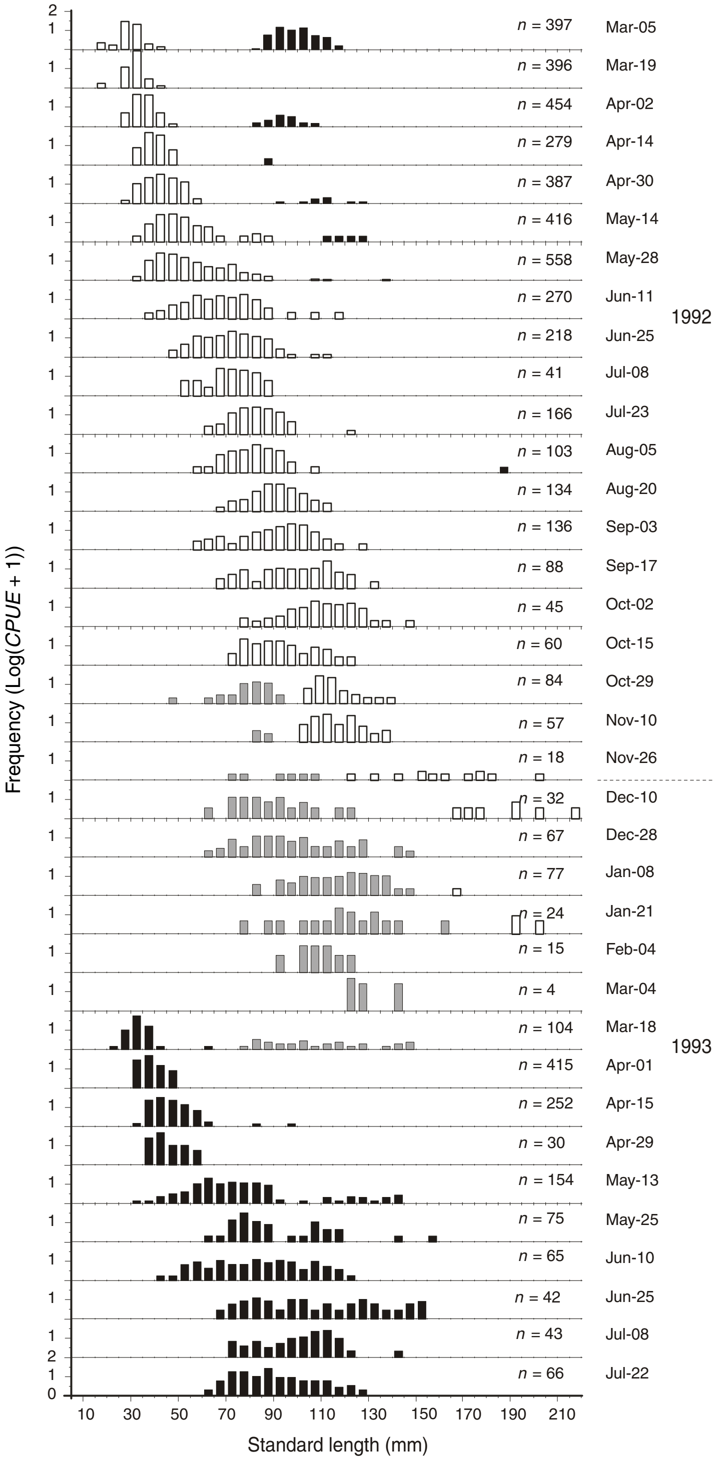

Figure 8

Semimonthly size distributions of juvenile white mullet from March 1992 to July 1993 in La Restinga Lagoon. The abundance for each size class is presented as the Log CPUE + 1. From top to bottom, open bars represent cohort 1, black bars represent cohort 2, gray bars represent cohort 3, and black bars represent cohort 4. Cohorts were identified by discontinuities in size distributions of juveniles. *n* = number of fish sampled.

Strong offshore transport of surface waters occurs during upwelling events, so that a rapid metamorphosis to the demersal stage may be critical for the coastal recruitment of white mullet. This rapid metamorphosis is suggested for several offshore spawning fishes with pelagic larvae that subsequently recruit to estuaries (Creutzberg et al., 1978; Heath, 1992) or that remain near the bottom during ebb flow, once close to the coast, thereby reducing offshore transport (Bartsch and Knust, 1994). White mullet undergo metamorphosis to the demersal stage 14 days after hatching (Houde et al., 1976) at which time they would be entrained in the inshore transported water that occurs at depths greater than 50 m in the coastal zone of northeastern Venezuela (Quintero, unpubl. data). Several studies suggest that increased mortality is caused by increased predation associated with the change to bottom habitat (Johannes, 1978; Bakun, 1986). Heath (1992) suggested that mortality from predation is particularly high during migration to nursery areas. Given the time to metamorphosis (14 days) and the age of white mullet when they enter the lagoon (50 to 70 days for the first cohort), metamorphosis to the demersal stage most probably occurs at least one month before entry into the lagoon (Anderson, 1957; Caldwell and Anderson, 1959; Yañez-Arancibia, 1976; Vieira, 1991).

During the demersal period at sea, white mullet may be exposed to considerable mortality due to benthic predators. Variation in the abundance of recruitment pulses into La Restinga Lagoon may reflect the interplay between spawning time and the mortality during transport to the coastal area. At some point between metamorphosis and lagoon entry, juvenile mullet also develop active swimming behavior to facilitate passive transport. We observed intensive recruitment of small mullet into the lagoon between March and June by individuals that had hatched the previous December to February. The timing of their hatching means that their return to the lagoon was likely facilitated by prevailing currents. In contrast, recruitment of mullet to the lagoon over the remainder of the year was weak and sporadic, and fish were much larger and older. At its first appearance in the lagoon, the third cohort was twice the age of the first cohort. These fish were not produced during a period when currents would likely have facilitated larval transport to the lagoon (little upwelling) and their lower densities may partially reflect increased mortality during the more prolonged return to the lagoon. We propose that spawning during periods of weak upwelling causes a delay in transport to coastal nursery areas and consequently decreased survival.

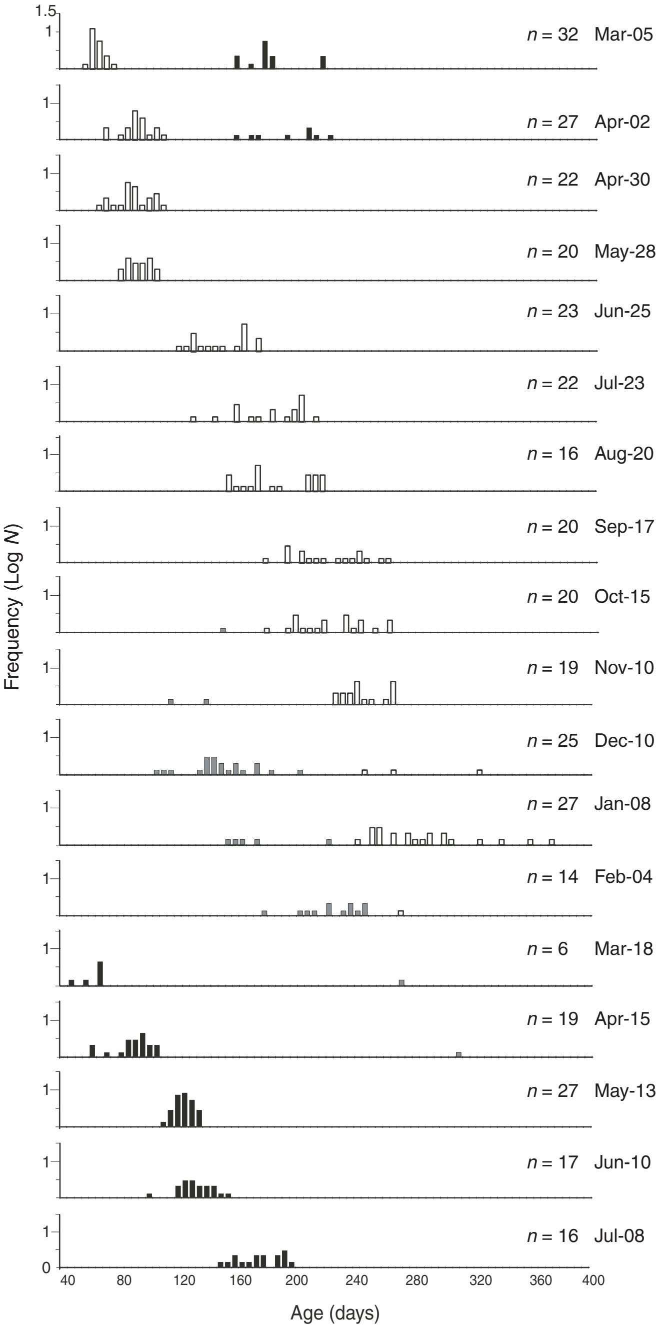

Figure 9

Monthly age distributions of juvenile white mullet from March 1992 to July 1993. Age was calculated by counting daily growth rings starting with the hatch mark. From top to bottom, open bars represent cohort 1, black bars represent cohort 2, gray bars represent cohort 3 and black bars represent cohort 4. *n* = number of otoliths examined.

Periods of hatching leading to successful recruitment, from late December to March, coincided with moderate peaks in the upwelling index. This successful recruitment may be the result of moderate levels of wind speed (<6 m/s^2), that promote moderate upwelling and yield optimal trophic conditions for fish larvae (Cury and Roy, 1989). Coastal upwellings in northeast Venezuelan waters are caused by

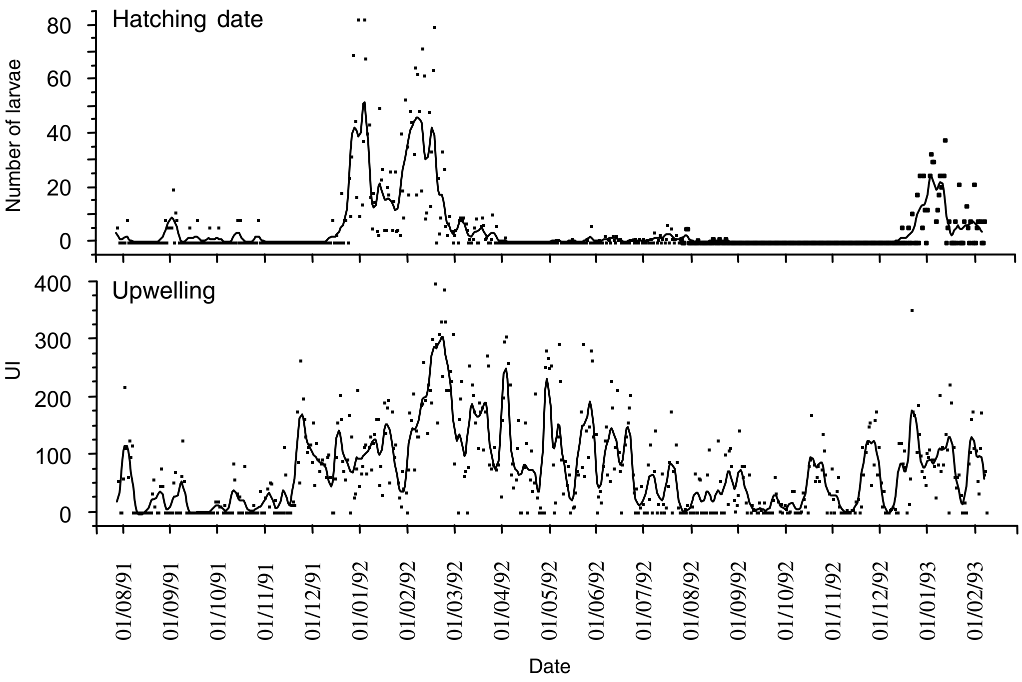

Figure 10

(**Upper panel**) Frequency distribution of hatching dates for juvenile white mullet recruits caught in 1992 and 1993 in La Restinga lagoon. Points represent raw data. Continuous black line represents the trend line generated after application of a smoothing spline (lambda=10). (**Lower panel**) Upwelling index (UI) for northeastern Venezuela calculated from August 1991 to March 1993. See text for description of calculation. Points represent raw data. Continuous black line represents the trend line generated following application of a smoothing spline (lambda=10).

moderate levels of wind stress and this differs from the strong upwellings observed in such places as Peru and Senegal. The relation between the timing of successful spawning and the intensity of coastal recruitment in white mullet is likely due to variations in the duration of the transport of larvae and juveniles to the shore as a result of varying current conditions as well as variations in food availability for first-feeding larvae.

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