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Unexpected reproductive strategy of *Sardinella aurita* off the coast of Venezuela

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Abstract Biological sampling of Spanish sardine (*Sardinella aurita* Valenciennes, 1847) off the coast of Venezuela from 1956 to 1989 was used to study the reproductive strategy and migration pattern of the population. Whereas in many pelagic fishes the energy re-allocation necessary for reproduction usually occurs optimally at the end of the upwelling season when planktonic production reaches a maximum, in the present study a 5 mo delay was observed. This suggests that energy was stored as lipids early in the season and released later via metabolism for gamete production. Major reproduction did not occur in an area and at a time when offshore transport and turbulence were low, which is also unusual for a pelagic fish species. These results are discussed in terms of the life cycle of the Spanish sardine and its possible migratory patterns. The reproductive strategy of this population apparently gives priority to optimising food availability for the offspring and not to preventing eggs and larvae being transported offshore. The presence of "retention" areas could explain this unexpected strategy.

Introduction

The Spanish sardine (*Sardinella aurita* Valenciennes, 1847) fishery of northeastern Venezuela is strictly manual, using small boats and seines. Fishing operations are restricted to a narrow belt, rarely exceeding five nautical miles, that covers a small area based on known stock distribution and mainly over grounds <50 m (Fig. 1). During recent years, the total catch has been ~50 000 t (Guzmán et al. 1997). The shelf is oriented east–west along the southeastern boundary of the Caribbean Sea. This orientation, the trade-wind regime, and the complex shelf topography (capes, submarine valleys and offshore banks) favour the occurrence of upwelling events from January to June (Herrera and Febres 1975). There is a high input of water from the Orinoco discharge, estimated at 36 000 $m^3 s^{-1}$ (Monente 1990), with maximum levels during August and September. The combined effect of wind-induced coastal upwelling in the dry season and river runoff in the rainy season generates relatively high levels of primary production, that are highly variable in space and time, ranging from 3 g C $m^2 d^{-1}$ in coastal upwelling areas to 0.2 g C $m^2 d^{-1}$ offshore from main upwelling sources (Varela et al. 1997).

Even though the major biological traits of *Sardinella aurita* in eastern Venezuela are relatively well known, a review by Huq (1997) demonstrated the lack of knowledge of some important aspects of the species' life history in this area. Although data on its growth and feeding habits are available (Huq 1997), its reproductive strategy, interannual variability in relation to environmental changes, and its migration cycle are poorly known; these are investigated in the present paper. There is general agreement that nurseries exist in the southern part of the distribution area (Cariaco Gulf and Santa Fe region) which also serve as "retention" areas. However, according to various conflicting studies reviewed by Huq, major spawning occurs not only in such areas but also in the northernmost part of the distribution area that is exposed to trade winds and offshore transport. This contrasts with the studies of Parrish et al. (1983) and Bakun and Parrish (1990) on the reproductive ecology in coastal pelagic species which demonstrated that reproduction takes place at times and in areas where turbulence and offshore transport are low, i.e. conditions that favour larval survival. Their data were based on different cases con-

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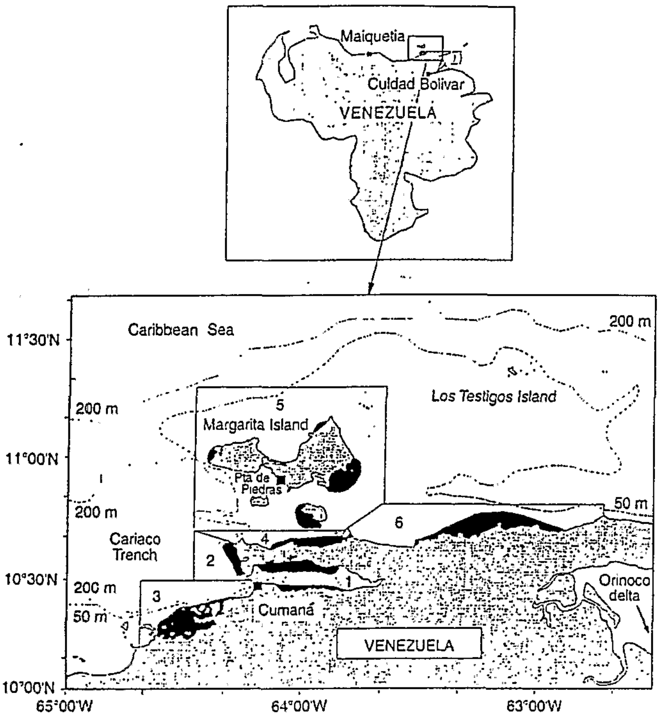

Fig. 1 *Sardinella aurita*. Locations of fishing grounds (*black areas*) in six fishing sectors (*1* Cariaco Gulf; *2* West Araya; *3* Santa Fé; *4* North Araya; *5* Margarita; *6* Carúpano) situated in main area of distribution of Venezuelan population (< 50 m depth)

nected with eastern-boundary major upwellings and in one case, a western-boundary area (southern Brazil – data on *S. aurita*). Are the characteristics of this species in northeastern Venezuela described by Huq compatible with the findings of Parrish et al. and Bakun and Parrish and with those of Roy et al. (1992) on the optimal environmental window for reproduction ($5\ \mathrm{m\ s^{-1}}$ < wind speed $< 6\ \mathrm{m\ s^{-1}}$)?

The reproductive period of *Sardinella aurita* is also a subject of some controversy, although most reports (reviewed by Huq 1997) indicate major spawning activity between November and February, i.e. ~ 6 mo after the end of the upwelling season. In fishes, gonad maturation requires a large amount of energy, and therefore usually occurs during or just after that period of the year favourable for feeding (Woodhead 1960; Hoar 1969; Potts and Wootton 1984; Wootton 1992). How then does *S. aurita* balance its energy budget if it reproduces mainly in the less-productive season in eastern Venezuela? Can this be explained by nutrient input from the Orinoco river during the rainy season (from July to October)? In small pelagic fishes, gonad development is usually responsible for an increase in condition. In Senegal and in the Côte d'Ivoire, for instance, Camarena (1986) and Le Loeuff et al. (1993) found a positive relationship, with no lag time between changes in the gonadosomatic index and condition factor, respectively, of *S. aurita*. Morimoto (1991) reported the same for the Japanese sardine *Sardinops melanostictus*. Does *Sardinella aurita* in eastern Venezuela, store fat during the upwelling season, enabling it to reproduce at a later date?

In this paper, we try to answer the above questions using a combination of biometric and environmental data. Numerous examples from the literature have shown that analysis of sexual maturity stage, length-frequency distributions and condition factor reveals important aspects on reproduction and some information on migration. An unusually large amount of available data combined with multivariate analysis techniques have enabled us propose some answers to some of the above questions.

Materials and methods

Biological data

Data of the National Fund for Agriculture and Husbandry Research (FONAIAP) of the Venezuelan Ministry of Agriculture and Husbandry from July 1956 to September 1989 were used in this study. Samples of 60 to 100 *Sardinella aurita* Valenciennes, 1847 from the same seine set were obtained monthly during landing operations at canning factories. A total of 96 346 individual observations, irregularly distributed over the study period, were recorded (average number of observations per year = 2 950; range = 440 to 8 229), with more observations being available during the latter part of the sampling period (after 1973). Sampling came to a halt in a few years (1960, 1970, 1974 and 1980), due to lack of personnel or to the absence of fishing activities. Six geographic sectors were monitored: Cariaco Gulf, west Araya, Santa Fé, north Araya, Margarita and Carúpano (Fig. 1, Table 1).

The data recorded for each individual fish were: date and sector of catch, total length (to nearest 1 mm), weight (to nearest 1 g), sex and maturity stage. However, weight data were available for only 88 514 fishes (92% of total observations). Macroscopic observation of the gonads enabled the separation of individuals into males, females and unsexed individuals (classed as immature), and defined eight sexual maturity stages for males and females (after Simpson and González 1967). In summary, Stages 0 to 3 correspond to juveniles or early maturing individuals, Stages 4, 5 and 6 are near the beginning or end of reproduction, and Stage 7 corresponds to egg resorption[1].

Linear regressions between the logarithmic-transformed values of length and weight were estimated for each 3 mo period. Individuals which lay outside the 99% confidence intervals in each 3 mo period were removed from the data set under the assumption that a transcription or measurement error of weight occurred. After this empirical filtering, 88 364 weight observations remained in the data set.

Condition factor

The individual condition factor (CF_i) proposed by Le Cren (1951) and recommended for calculating allometric growth (see Fréon 1986 for literature review), was used:

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[1] According to Simpson and González (1967): "stage 0 = translucent, elongated, cylindrical ovaries about 2 mm in width; 1 = more vascularised and of width 2.5 to 3 mm; 2 = ovaries are still mostly translucent, have an orange-red coloration and occupy about half of the unoccupied body cavity and contain some small opaque eggs; 3 = ovaries occupy almost two-third of the unoccupied body cavity and contain many opaque eggs; 4 = ovaries occupy all of the unoccupied body cavity; 5 = running-ripe: the eggs are transparent and are easily extruded by light pressure; 6 = recently spent; 7 = the ovary is flaccid, and the remaining eggs are being resorbed."

Table 1 *Sardinella aurita*. Number of monthly observations for all variables except weight, by sex and fishing sector

	Month												
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	(Total)
Sex													
Male	2838	3471	4284	3280	4802	5248	4533	4686	5233	4200	3645	1838	(48058)
Female	2804	3381	4016	3289	4865	4686	4636	4782	5426	4373	3712	1868	(47838)
Immature[a]	0	37	94	0	49	42	0	0	0	28	85	117	(452)
Sector													
1	995	1855	2377	1841	3280	3939	2781	2472	2661	1842	1770	1096	(26909)
2	1069	998	1103	867	1179	413	735	606	1644	885	723	771	(10993)
3	2294	2113	2979	1101	702	1071	1682	1189	1093	811	1120	601	(16756)
4	199	300	244	119	660	340	660	1588	1406	1334	892	480	(8222)
5	824	1445	1518	2451	3739	3627	3142	3128	3403	3025	2347	785	(29434)
6	259	178	173	190	156	586	169	485	452	704	590	90	(4032)
(Total):	(5640)	(6889)	(8394)	(6569)	(9716)	(9976)	(9169)	(9468)	(10659)	(8601)	(7442)	(3823)	(96346)

[a] Young fish: sex could not be determined

$$CF_i = 100\, W_i/Wst_i = 100\, W_i/aL_i^b \; . \quad (1)$$

where W_i = observed individual total weight and Wst_i = theoretical individual total weight; $Wst_i = aL_i^b$, where L_i = individual length and a and b are constants resulting from length–weight relationship $W = aL^b$ fitted by functional regression.

Unequal sampling over space and time limits the use of a time-series analysis. In such case, unbiased estimates of means per sector, month or year may be obtained by using the general linear model (GLM, McCullag and Nelder 1989; SAS Institute Inc. 1989). The corrected mean ("expected population mean" or "LSmeans") estimated by the least-squares method represents an unbiased estimator of the condition factor for a given area and time. The equation of the model is:

$$CF_{i,j,k,l} = m + a_i + b_j + c_k + d_{j,k} + e_{i,j} + f_{i,k} + gL_{i,j,k,l} + \varepsilon_{i,j,k,l} \; , \quad (2)$$

where m is a constant, $a \ldots f$ are parameters depending on "main effects" related to variables of Year$_i$, Month$_j$, Sector$_k$ (class variables), respectively, and their interactions; g = parameter related to covariate L observed in Year i, Month j, Sector k with l repetitions, and ε is the residual. In a first analysis, the individuals were separated by sex, but in view of the similarity of the results of this analysis, the sexes were subsequently grouped.

Sexual maturity stages

Because of a paucity of observations on gonads at Maturity Stages 5 and 6 (1 and 0.6%, respectively), which occur only during and just after spawning, we combined Maturity Stages 4, 5 and 6 to describe mature male and female sardines. (Also, Stages 5 and 6 follow the same seasonal pattern as Stage 4, although the latter is more abundant: 7.3%.) The proportion of these three (combined) stages in the length-frequency distributions (number of individuals per 1 cm class interval) permitted the estimation of length at the first stage of maturity (L_{00}) and average length at sexual maturity (L_{50}).

A reproductive index (Reprod) was estimated only for individuals longer than L_{00} (92 834 individuals). Reprod is the ratio of individuals in reproductive stages to the total number of individuals larger than L_{00}. The two sexes were regrouped in view of the similarity of results. As Reprod is a proportion, we intended to fit a logistic model, since the theoretical distribution is binomial, using the link-function logit (McCullag and Nelder 1989; GENMOD procedure: SAS Institute Inc. 1993). The model initially retained included the same interactions as Eq. (2); however, the SAS software was not able to allocate sufficient memory to fit this model because of the many interactions. It was only possible to fit a model without interactions relative to the year:

$$E(\mathrm{Reprod}_{i,j,k,l}) = f(x) = f(m + a_i + b_j + c_k + d_{j,k} + e.L_{i,j,k,l}) \; , \quad (3)$$

where $f(x) = \exp(x)/(1 + \exp(x))$, the logistic function; m is a constant; $a \ldots d$ are parameters depending respectively on main effects B-year$_i$ ("biological year", i.e. 12 mo period between August of current year and July of following year), Month$_j$, Sector$_k$ and their interactions; e = parameter related to covariate L observed in Year i, Month j, Sector k, with l repetitions. We also adjusted a generalised model of the same form as Eq. (2) by approximating the binomial distribution by a normal distribution:

$$\mathrm{Reprod}_{i,j,k,l} = m + a_i + b_j + c_k + d_{j,k} + e_{i,j} + f_{i,k} + gL_{i,j,k,l} + \varepsilon_{i,j,k,l} \; . \quad (4)$$

Environmental variables

Coastal meteorological station data of wind speed and direction from Cumaná (period 1969 to 1989) and Punta de Piedras on Margarita Island (period 1972 to 1989) were taken from Aparicio and Contreras (1997) for the first station and Campos and Velasquez (1991) for the second. We first considered using the Ekman-transport estimated by Aparicio and Contreras as an upwelling index. However, satellite imagery shows phytoplankton blooms not only on that part of the coastline that is oriented along the wind axis (in accordance with the Ekman theory), but also in other regions (Müller-Karger and Varela 1990). This is related to the complex submarine topography (islands and banks) in these regions, and to the existence of a particular mechanism in the Cariaco Gulf whereby surface water is transported away by prevailing winds and subsequently replaced by cold nutrient-rich water from the neighbouring Cariaco Trench (Richards 1960; Okuda et al. 1978). We therefore estimated a second upwelling index independent of wind direction. For this, the average monthly wind speed at each coastal meteorological station was calculated. The station at Cumaná is more influenced by the effect of the continental land mass than the Margarita Island station, especially as regards the dominant northeast trade winds (Fig. 1). The mean annual wind speed is thus 2 m s^{-1} weaker than that obtained at Margarita Island (Aparicio and Contreras 1997). This second, computed, upwelling index is the yearly mean of positive anomalies from both stations, assuming the simplifying hypothesis that average winds do not intervene significantly in the enrichment process. This index revealed temporal changes similar to those of Ekman transport (because stronger-than-average winds are generally from the east), except for the year 1972 at Cumaná (Aparicio and Contreras 1997). Finally a wind-speed data set from the remote meteorological station of Maiquetia (Fig. 1) was also used because it covered a longer period (1956 to 1989) than those for the other regions.

We used records of the monthly river level at Ciudad Bolivar station as a monitor of Orinoco river runoff. This has been recorded since the beginning of the century and was available from Aparicio (1997).

Results

Sex ratio and length at first maturity

The sex ratio for all samples of *Sardinella aurita* was not statistically different from unity (s = no of females:no of males $= 0.995; \chi^2 = 0.50; p = 0.48$).

The cumulative frequency curve of individuals which had reached or passed Maturity Stage 4 indicated that reproduction begins at 15 cm (L_{00}) and that nearly 50% of individuals are mature at 20 cm ($L_{50} = 19.7$ cm)

Spatial and temporal variability in length

Length distributions as a function of geographical sector followed a north–south gradient (Fig. 2). In the southern area (Cariaco, west Araya and Santa Fé sectors) modal lengths were between 16 and 18 cm, in the northern area (north Araya, Margarita and Carúpano sectors) they were between 19 and 21 cm. However, the range of distributions was large in all sectors (10 cm < L < 24 cm), and certain sectors in the northern area (North Araya and Carúpano) displayed bimodal frequencies in which the secondary mode (13 to 16 cm) included length classes that were smaller or equal to primary modes in the southern area.

There was seasonality in the relative abundance of individuals > 19 cm in the south, with a minimum in May to June and a maximum in December (Fig. 3). This seasonality was strong, as exemplified by the occurrence of a mode at 22 cm in December, suggesting immigration rather than growth – which is relatively slow in sardine of this length (0.5 cm mo^{-1}). Nevertheless, no compensatory trend in the relative abundance of individuals > 19 cm was obvious in the length-frequency distribution in the northern area (data not shown).

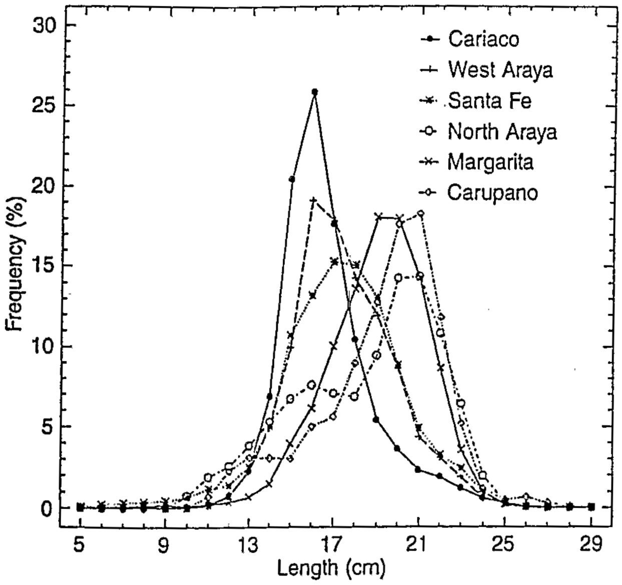

Fig. 2 *Sardinella aurita*. Length-frequency distribution in each fishing sector (combined data for 1956 to 1989)

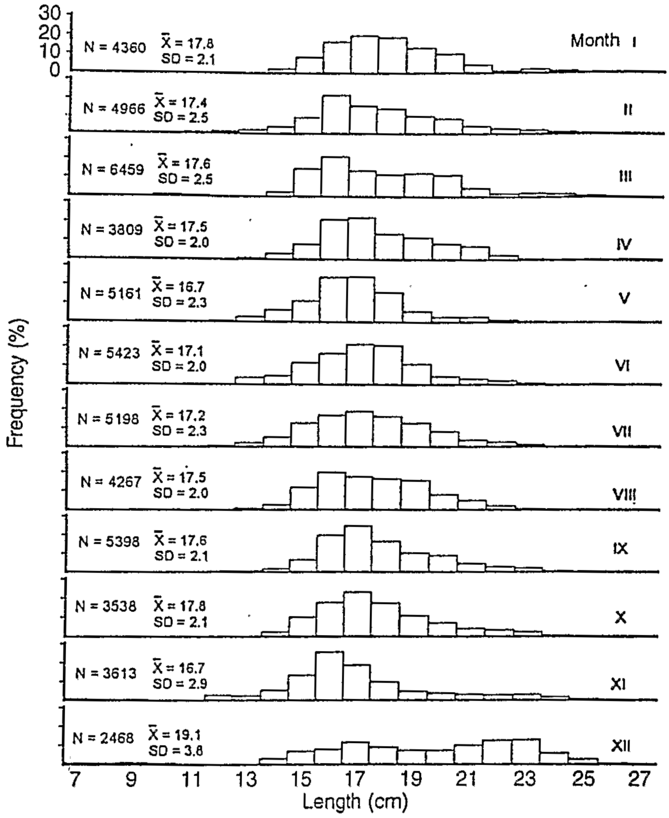

Fig. 3 *Sardinella aurita*. Monthly changes in length–frequency distribution in southern area of fishing grounds (combined data for 1956 to 1989)

Spatial variability in condition factor and reproductive index

A functional regression gave the following values for the length–weight relationship, where b is significantly greater than 3 ($p < 0.001$): $W = (1.0377\ 10^{-6})\ L^{3.399}$, $r = 0.98$.

General linear models (Eqs. 2 and 4) explained 49% of the total variance in the condition factor and 32% of that in the reproductive index, all effects and interactions being significant ($p < 0.0001$; Tables 2 and 3). In both cases, the interaction between year and month contributed most to the sum of squares (SS), but due to the corresponding large number of degrees of freedom (df), its mean-square value was relatively small and similar to those of the other interactions. The highest mean square

Table 2 *Sardinella aurita.* Sources of condition factor variability between 1956 and 1989 resulting from fit of general linear model (Eq. 2) (*SS* sum of squares; *MS* mean square: *F* Fisher's test; $^{\bullet}p < 0.001$)

Source of variation	(*df*)	SS	MS	*F*
Model	(422)	522.4	1.2380	198.6*
Error	(87939)	548.3	0.0062	–
Corrected total	(88361)	1070.7	–	–
Sector	(5)	11.75	2.3499	376.9*
Year	(29)	54.86	1.8916	303.4*
Month	(11)	7.45	0.6777	108.7*
Month × sector	(53)	19.25	0.3633	58.3*
Year × month	(247)	122.18	0.4947	79.3*
Year × sector	(71)	67.28	0.9476	152.0*
Length	(1)	27.1	27.1082	4347.7*

Table 3 *Sardinella aurita.* Sources of variability in reproductive index between 1956 and 1989 resulting from fit of general linear model (Eq. 4) (*B-year* biological year, i.e. 12 mo period between August of current year and July of following year: $^{\bullet}p < 10^{-3}$)

Source	(*df*)	SS	MS	F
Model	(439)	25005563	56960	98*
Error	(92395)	53483522	579	–
Corrected total	(92834)	78489085	–	–
Sector	(5)	105932	21186	37*
B-year	(34)	2041177	60035	104*
Month	(11)	936850	85168	147*
Month × sector	(55)	990458	18688	32*
B-year × month	(246)	6087250	24745	43*
B-year × sector	(83)	1882520	22681	39*
Length	(1)	1955555	1955555	3378*

was, in both cases, related to length (the only quantitative variable; therefore, $df = 1$), followed by year and sector for condition factor, and year and month for reproductive index. The sampling scheme was unfortunately too unbalanced to account for all interactions in the estimation of LSmeans. We therefore adjusted the following models, which permitted us to estimate LSmeans per sector, year and month, but did not allow us to study in detail the interactions related to year:

$$CF_{i,j,k,l} = m + a_i + b_j + c_k + d_{j,k} + f\,L_{i,j,k,l} + \varepsilon_{i,j,k,l} \,, \tag{2a}$$

Table 4 *Sardinella aurita.* Main statistics of logistic regression applied to Eq. (3) relative to reproductive index between 1956 and 1989 (*B-year* biological year, i.e. 12 mo period between August of current year and July of following year; $^{\bullet}p < 0.0001$)

Criteria for assessing goodness-of-fit (df = 92 834)		
Criterion	Value	(*df*)
Deviance	39152.5	(0.4062)
Pearson χ^2	75329.3	(0.7816)
Log likelihood	−19576.2	(–)
Likelihood statistics		
Source	(*df*)	χ^2
Sector	(5)	319.4*
B-year	(33)	5518.9*
Month	(11)	1147.9*
Month × sector	(55)	2605.9*
Length	(1)	5792.9*

$$\text{Reprod}_{i,j,k,l} = m + a_i + b_j + c_k + d_{j,k} + f\,L_{i,j,k,l} + \varepsilon_{i,j,k,l} \,, \tag{4a}$$

where the notation is identical to that in Eqs. (2) and (4), respectively. These two general models explain 29 and 21% of the total variance, respectively. In the logistic regression (Eq. 3) all criteria for assessing goodness-of-fit are significantly different from 1 ($p < 0.001$), and all effects are significant according to their χ^2 values (Table 4). The relative contribution of independent variables and predicted means by sector, B-year and month of Eqs. (4a) (data not shown in table) and (3) are similar. As for mean lengths, the corrected means of the condition factor distinguish the southern area, where values do not exceed 1.0, from the northern area, where they are >1.0 (Fig. 4). There is no such distinction for the reproductive index, where the two extreme values both correspond to sectors in the northern area: 18% for north Araya and 10% for Margarita.

Temporal variability in condition factor and upwelling

Despite its small amplitude (0.97 to 1.07), the condition factor exhibited a clear seasonal variability, with a maximum in August and a minimum in December to January (Fig. 5). We tried to relate this variability to two sources of production in the area: coastal upwelling and Orinoco river discharge. The increase in the condition factor in February began just after the initiation of

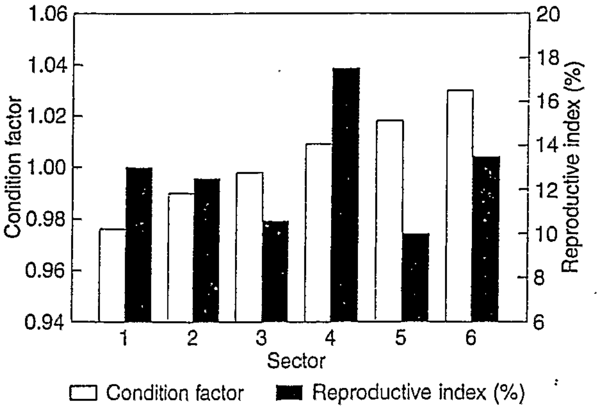

Fig. 4 *Sardinella aurita.* Condition factor and reproductive index as a function of fishing sector ["expected population mean" (or "LSmeans") of combined data for 1956 to 1989]

coastal upwelling and, as expected, a series of high winds accounted for this increase until June. But it was after this period that the condition factor attained its highest values, from July to October, corresponding to the rainy season and maximum Orinoco river discharge (Aparicio 1997).

Since most biological and environmental phenomena are seasonal, we searched for confirmation of a relationship between sources of production and the condition factor by analysing annual trends. The interannual variability in the condition factor (0.91 to 1.08) was higher than the seasonal range of variation (Fig. 6). Note that the decreasing trend observed from 1977 occurred when sampling was regular and intensive (except for the years 1979 and 1980). This trend is similar to those observed for the two upwelling indices from the coastal stations in the area ($r = 0.52$ and 0.49; $p < 0.05$). The longer wind series from the Maiquetia meteorological station, which is located 300 km westwards, exhibits an even greater trend, and is therefore highly correlated with the condition-factor series ($r = 0.85$; $p < 0.001$). Nevertheless, the significant values of r arise merely from similar trends in the series of condition factor and upwelling index, but do not reflect the fact that both local maxima and minima of the two series do not fit. We found no linear or non-linear relationships between condition factor and level of the Orinoco river.

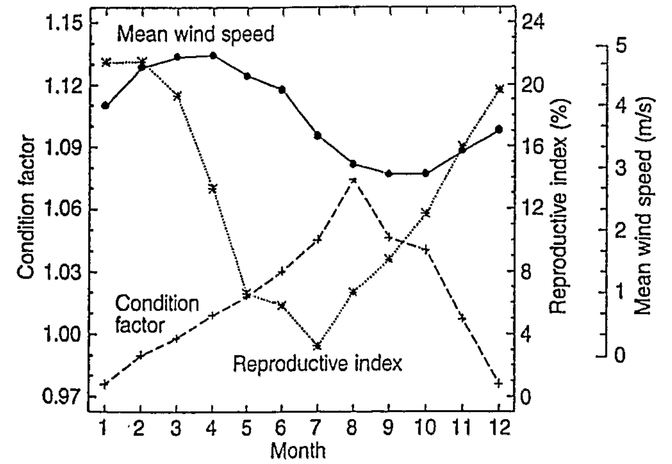

Fig. 5 *Sardinella aurita.* Monthly changes in mean wind speed in Cumaná and Punta de Piedras (see Fig. 1) from 1972 to 1989, and in condition factor and reproductive index for 1956 to 1989 (LSmeans of yearly data combined)

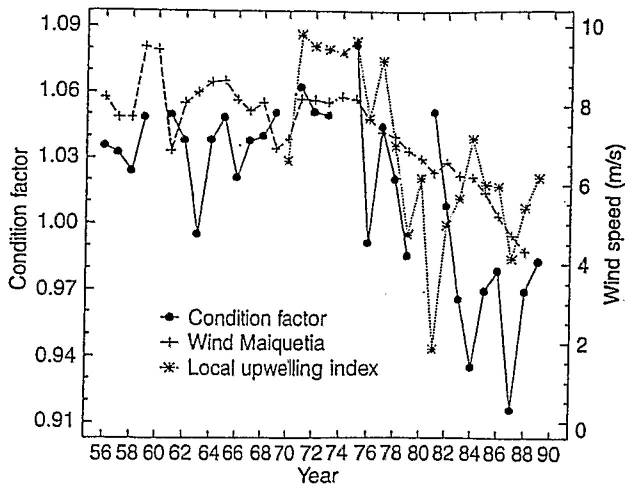

Fig. 6 *Sardinella aurita.* Changes in average condition factor (LS means 1956 to 1989), wind speed at Maiquetia (1956 to 1989), and second local upwelling index (see "Materials and methods" – "Environmental variables") for northeastern Venezuela (1975 to 1989)

Temporal variability in reproductive and upwelling indexes

The reproductive period of *Sardinella aurita* displayed strong seasonality. It extended from November to March, i.e. 5 to 6 mo after the peak in the condition factor, when >16% of those individuals >15 cm were at Maturity Stages 4, 5 or 6 (Fig. 5). A detailed analysis, by geographical sector, revealed considerable spatial and temporal variability. The December to January peak was essentially due to individuals from the southern area. On the other hand, reproduction in the northern area dropped steeply in December (Fig. 7). Furthermore, the apparently extended reproductive season actually masks large interannual variability [although for specific analysis of the LSmeans of the B-year × month interaction, we had to regroup the six sectors, initially used in Eq. (4), in the two southern and northern areas to avoid an unbalanced model – results not shown]. The duration of the reproductive period varies as a function of year, and may be early or late. We have tried unsuccessfully to characterise early or late years by parallel variations in the condition factor, upwelling index and/or Orinoco output. Even though a significant correlation was found between the condition factor and the annual reproductive index (Fig. 8; $r = 0.56$; $p < 0.002$), this

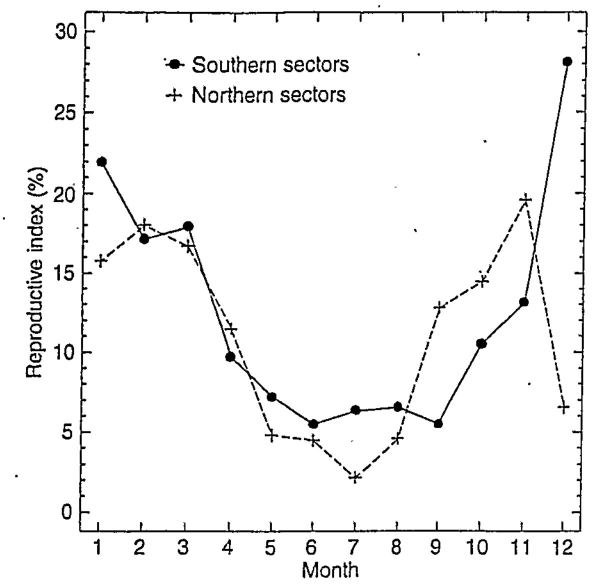

Fig. 7 *Sardinella aurita.* Monthly changes in reproductive index in southern (Cariaco, west Araya and Santa Fé sectors) and northern (north Araya, Carúpano and Margarita sectors) areas of fishing grounds (LSmeans of combined data for 1956 to 1989)

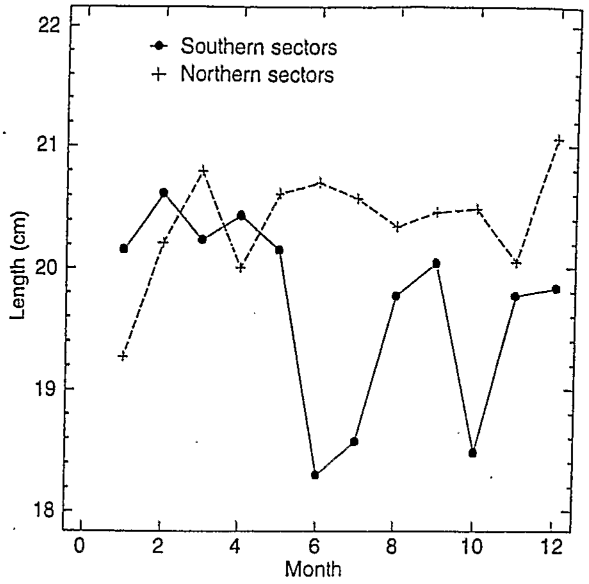

Fig. 9 *Sardinella aurita.* Monthly changes in mean length of Maturity Stages 4, 5 and 6 between January and December in southern (Cariaco, west Araya and Santa Fé sectors) and northern (north Araya, Carúpano and Margarita sectors) areas (LSmeans of combined data for 1956 to 1989)

mainly reflects the similarity between trends in the two corresponding series and not short-term relationships. As for the previously mentioned relationship between condition factor and wind speed in Maiquetia, the reproductive index and the wind speed at Maiquetia also seem to be related, but here the correlation coefficient is smaller ($r = 0.47$; $p < 0.01$).

Seasonal changes in average length during the reproductive period differed between sectors. For individuals at Maturity Stages 4, 5 and 6 (Fig. 9) there were significant differences between individuals from the southern and those northern areas only during the months of June to July (when reproduction is minimum) and in October. During the reproductive period, average lengths differed by only 1 cm between the south and north. This result contrasts with the large differences in mean length observed between the sectors when the whole population is considered (Fig. 2).

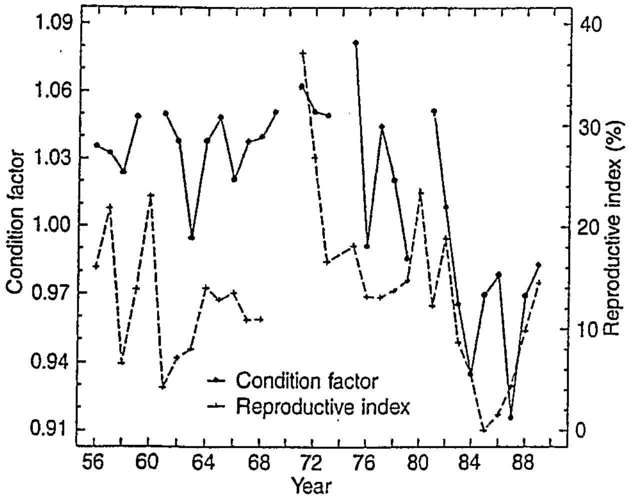

Fig. 8 *Sardinella aurita.* Comparison of changes in mean condition factor (January to December) and mean reproductive index (over the "biological year"; see legend to Table 3) from 1956 to 1989 (LSmeans)

Discussion

Life cycle

The wide distribution of young recruits (Fig. 2) and mature individuals (Fig. 4) indicates that *Sardinella aurita* nurseries off Venezuela are not restricted to the southern area, in contrast to the prevailing hypothesis reported by (but not supported by) Huq (1997). However, individuals >19 cm were abundant in the southern area only during the reproductive period (Fig. 3), which strongly suggests the occurrence of a spawning migration from north to south during December to January. This is confirmed by the similarity between the mean length of reproductive individuals over the whole area during the main reproductive season (Fig. 9). We therefore propose the following life cycle: reproduction takes place mainly from November through March. In the southern area, the reproductive season is short with a peak usually in December, and involves young individuals that have developed in the same area during their first year of life and older adults which have migrated rapidly from the northern area [a similar pattern was described by Boëly et al. (1982) for the same species in Senegal]. In the northern area, reproduction is more protracted, and averaged data reveal two close peaks (November and February).

In the southern area, the irregularity of spawning in combination with the relative abundance of young individuals strongly suggests that there is significant recruitment from reproduction in the northern area. We do not know by which mechanisms (passive transport of eggs and larvae or active migration of juveniles) and at what age recruitment to these southern nurseries occurs.

The main limitation of our analysis lies in the unbalanced nature of the sampling design and the presence of spatial and temporal interactions in condition factor and reproductive index (this limitation has been partially corrected by LSmeans estimates). As far as the life cycle of *Sardinella aurita* is concerned, the main limitation arises from the use of a single type of commercial fishing gear which under-sampled small length classes, particularly those <14 cm. Moreover, spatial coverage was limited to certain coastal fishing areas, whereas hydroacoustical cruises (Cárdenas 1997) and egg surveys (López 1972) have shown that during certain years an important fraction of the population, especially large individuals, may be located in the northern and eastern limits of the distribution area

Reproductive strategy

Sardinella aurita in this area exhibit a strong positive allometry and a balanced sex ratio, as previously reported for this species (Fontana and Pianet 1973; Boëly 1978; Fontana 1981; Huq 1997).

A large increase in the gonadosomatic index during the reproductive period would be expected to increase the value of the condition factor. Curiously, in the study area, the reproductive peak did not coincide with the condition factor maximum which occurred 5 mo earlier, but instead with its minimum. The steady increase in the condition factor from January to June may have been related to an accumulation of energetic reserves associated with the high productivity connected with the upwelling. The persistence in the high values of the condition factor until October is difficult to explain in the context of a balanced energy budget, especially the sharp increase from July to August. It is probably related to nutrient enrichment from the Orinoco river which attains maximum runoff during this period (Aparicio 1997). In their study of the lipid content of this species between September 1968 and May 1971, Tornes et al. (1971) confirmed the storage of fat at the end of the upwelling period, especially at body lengths >17 cm (minimum value = 3% in March; maximum value = 14% in August to September). We therefore conclude that the energy available during the period of maximum planktonic production was not immediately used for reproduction, but stored as fat and metabolised for reproduction several months later. This storage strategy is energetically costly (Wootton 1979), and may be reflected in the small maximum total length of this species in this area: 27 cm compared to 39 cm in the Mauritania–Senegal area where productivity is similar or slightly higher (Fréon 1986), or 31 cm off the Côte d'Ivoire and Ghana where productivity is lower (Le Loeuff et al. 1993). In the literature, we found only one example of a similar strategy in a clupeid – in *Sardina pilchardus* off the coast of Algeria. (Tomasini et al.1989). Usually, *Sardinella aurita* is considered to be an opportunistic species which spawns under many different spatial and temporal conditions as soon as necessary energetic requirements are met, but whose main spawning period corresponds to the end of the upwelling season when plankton is still abundant (Fréon 1986; Cury and Fontana 1988).

Using a comparative approach, Bakun (1996) defined three requirements (a "triad") that are necessary in order that a habitat be suitable for the reproduction of pelagic fishes: enrichment (upwelling, mixing, etc.); concentration processes (water-column stability, convergence, frontal formation); and retention of ichtyoplankton within an appropriate habitat. This ideal combination is achieved when the monthly coastal wind speed is ~5 to 6 m s^{-1} in eastern boundary currents (Roy et al. 1992). This speed is above the maximum monthly average for the two continental stations in the present study, but corresponds to the maximum value recorded for Punta de Piedras (Margarita Island) in April. In Venezuela, mass spawning at the time of maximum upwelling (which occurs only in certain years) could be controlled by the amount of energy available for gonad maturation in the preceding months. Massive spawning at the time of maximum condition factor (around August) would benefit from the combined advantage of low turbulence, which would minimize the dispersal of food and larvae swarms (Lasker 1981; Peterman and Bradford 1987), as well as from weak offshore transport for the larvae; but it would have the disadvantage of taking place at the beginning of a protracted period of prey shortage. This disadvantage is apparently overcome by the storage of energy as lipids, allowing a reproductive lag of several months and enabling spawning to take place at a period preceding maximum biological production. In addition, moderate turbulence during this period increases the encounter rate between plankton particles and larvae (Rothschild and Osborn 1988; MacKenzie and Leggett 1991). Undesirable transport of larvae out of the area may be limited by the moderate intensity of the upwelling compared to that in eastern boundary currents, and by the complex topographical features of the shelf and coastline (Fig. 1). These factors in combination with a relatively wide shelf (Bakun et al. 1991) may allow the existence of numerous retention zones [e.g. island- and cape-effects, double-cell circulation similar to those described by Jacques and Tréguer (1986)], although we lack current data to explore this hypothesis.

The actual influence of annual environmental variability (wind speed or Orinoco runoff) on the biology of *Sardinella aurita* was not obvious in our results. It can be only suspected from the possibly spurious correlation observed between average wind speed recorded at a distant meteorological station and the condition factor of a population over 30 yr. Although interannual variations in the condition factor were correlated with variations in the reproductive index, our attempt to establish a relationship between the latter and upwelling indexes was unsuccessful. This type of relationship has been established in other instances, e.g. in the southern Benguela ecosystem (Schülein et al. 1995). It would appear that in Venezuelan waters interannual reproductive variability may depend on other factors such as river runoffs, unless the data available were insufficient.

In conclusion, our main result is the observation of a particular reproductive strategy of *Sardinella aurita* as a function of specific environmental and topographical conditions that are distinct from those observed in the eastern boundary upwelling areas. This strategy consists of mass spawning in an area and at a time that would not seem optimal, and is effected by a pattern of energy translocation that is unusual in this species. In certain years, the unusual strategy of energy storage was replaced or concurrent with a more normal pattern of immediate energy utilization, suggesting some opportunism in the reproductive strategy of this species. The lag time between spawning and local upwelling events permits larvae and juveniles to grow at a period when prey is most abundant.

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