SARDINE AND ANCHOVY SPAWNING AS RELATED TO TEMPERATURE AND UPWELLING IN THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

Sardine and anchovy spawning was analyzed regarding its relation to sea-surface temperature and upwelling, using CalCOFI cruise data and Bakun's upwelling indices.

Previous reports of temperature ranges for sardine and anchovy spawning have not taken into account the distribution of SST and have mostly referenced the cooler spawning area of the species. By obtaining the proportion of positive stations to total sampled stations for each tenth of a degree Celsius in the SST distribution, we were able to discriminate the ranges of preferred temperatures of spawning for both species. Sardines spawn in a much wider temperature range (13°–25°C) than anchovy (11.5°–16.5°C). Two maxima of spawning occur in the California Current: at 15°C and 23°C. An additional peak is present in the Gulf of California at about 19°C. Only one maximum is evident for anchovy spawning, at about 14°C.

The distribution of spawning as a function of upwelling was also analyzed for both species. There is a maximum for sardines at intermediate values of upwelling. There are two maxima for anchovy: a minor one at low levels of upwelling and a major one at the maximum values of upwelling. We conclude that sardines are eurythermic as compared to anchovies, but spawn only at intermediate values of upwelling, whereas anchovies are stenothermic but spawn at much wider ranges of upwelling, particularly at low and high values. The differences suggest exclusive competition, but more detailed analyses are needed.

RESUMEN

Se analizó el desove de sardina y anchoveta con respecto a su relación con la temperatura superficial del mar y las surgencias, utilizando los datos de los cruceros CalCOFI y los índices de surgencia desarrollados por Bakun.

Los intervalos de temperaturas de desove de sardina y anchoveta que se habían señalado anteriormente no tuvieron en cuenta la distribución de la temperatura superficial; además, se habían referido mayormente al área más fría de la distribución del desove. Mediante la obtención de la proporción de las estaciones positivas a las totales por cada décima de grado en la distribución de frecuencias de la temperatura superficial, fué posible discriminar los intervalos de temperaturas preferentes para el desove de ambas especies. Las sardinas desovan en un intervalo de temperatura mucho más amplio (13° a 25°C) que el de anchoveta (11.5° a 16.5°C). Se presentan dos máximos de desove de sardina en la Corriente de California: uno a 15°C y otro a 23°C. Otro máximo adicional se presenta en el Golfo de California a 19°C. Sólo se registró un máximo de desove en la anchoveta, alrededor de 14°C.

La existencia de tres máximos no es, proponemos, un fenómeno inherente de la especie, sino una característica inducida ambientalmente. Creemos que algún factor relacionado con las surgencias puede ser el responsable de esta desusual distribución.

Se analizó también la distribución del desove de ambas especies en función de las surgencias; hay un máximo para la sardina a niveles intermedios de surgencia. Hay dos máximos para la anchoveta: uno menor que se localiza a niveles bajos de surgencia, y el más importante, que ocurre a niveles máximos de surgencia.

Concluimos que las sardinas son euritérmicas en comparación con las anchovetas, pero que desovan a niveles intermedios de surgencia, mientras que las anchovetas son estenotérmicas pero desovan en una amplitud mayor de valores de surgencia, particularmente a valores bajos y altos. Los resultados sugieren exclusión competitiva, pero se necesitan análisis más detallados.

INTRODUCTION

Environmental temperature has long been considered the most important factor affecting marine organisms; their geographical distribution is closely associated with the latitudinal temperature gradient. Temperature affects the rate of metabolic processes. Cold winter temperatures can depress the activity of

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poikilotherms to a point where there is no possibility for acclimation. Conversely, summer temperatures can increase oxygen consumption to an extent that metabolic demands exceed energy reserves. Thus, tolerance to temperature is an important factor regulating the distribution of fishes (Levinton 1982).

Massive stocks of pelagic fishes are possible only in areas where productivity is high. Upwelling areas (including the California–Baja California coast) are among the most productive in the world, with upwelling being recognized as a fundamental cause (Nelson 1979).

Sardines (*Sardinops*) and anchovies (*Engraulis*) are both subtropical species, coexisting particularly in areas of subarctic and tropical mixing, where they constitute some of the most voluminous fisheries species in the world. Recent papers have emphasized their ample and synchronous fluctuations of abundance and geographical extension (Lluch et al. 1989; Parrish et al. 1989). The connection of these changes to temperatures has been hypothesized (Crawford et al., in press; Lluch et al., in press). In this paper, we analyze temperature ranges associated with the spawning of both species off the west coast of North America.

Adult sardines' tolerance for temperature seems to be very wide. On the cold side, Smith (1978) states that sardines feeding during the summer off British Columbia may have been at temperatures "far colder" than 13°C. On the other hand, temperatures higher than 25°C are commonly associated with sardine catches in Magdalena Bay (Casas 1987), and there are unpublished reports of 28° temperatures associated with sardine catches. Parrish et al. (1989) state the range of 7° to 27° as the temperature tolerance of adult *Sardinops*.

Regarding spawning temperatures, Tibby (1937) concluded that the optimum for sardines lies between 15° and 18°, with an implied peak at 16°. Ahlstrom (1965) found similar temperature limits, with peaks between 14.7° during the 1951–56 season and 15.3° in 1958. Earlier, Ahlstrom (1954) had found that the relation between temperature and spawning was complex, pointing to a 3-degree temperature range of 13.5° to 16.5° during the season, but higher than 19° during the "off-season." He also pointed out that the minimum spawning temperature for sardines is 13°. This temperature was confirmed in his 1965 paper and by Smith (1978). Parrish et al. (1989) stated that most spawning occurs within the 13°–17° range, following Ahlstrom (1965). At the warm-water limits, Saldierna et al. (1987) reported a minimal temperature of 16.1° and a maximum of 25.6° associated with eggs and larvae in Magdalena Bay.

Hammann (in press) analyzed the temperatures associated with positive stations for sardine eggs in the Gulf of California. He found that the average SST was 19.9°, and stated that 50% of the positive stations were between 17.75° and 20°.

Data on anchovy tolerance to environmental temperature are scarce. Smith and Lasker (1978) pointed out that temperatures representative for anchovies commonly vary 4° to 6°C. Ahlstrom (1966), however, reported temperature ranges for anchovy eggs from 9.9° to 23.3°, and pointed out that most anchovy eggs were taken within a 7° range, from 12° to 18.9°; indeed, the adult limits of tolerance for temperature should be wider.

The relationship between sardine abundance and upwelling is controversial. Although the high productivity induced by nutrient-rich subsurface waters is a fundamental component of the system, many authors have pointed to the lack of relation between abundance of sardines and productivity (Ahlstrom 1965) or even to upwelling's deleterious effects on sardine abundance, operating either through offshore transport of larvae (Parrish et al. 1981) or increased water turbulence (Lasker and MacCall 1983).

DATA AND METHODS

We used data from CalCOFI cruises from 1951 through 1989, which comprise some 19,500 samples from stations shown in figure 1. Data for each sample include surface or 10-meter temperatures (as available), and number of sardine and anchovy eggs and larvae. Positive samples are those containing eggs or larvae of these species. Averaged upwelling indices were taken from Mason and Bakun (1986) and updated with data supplied by them for the points marked in figure 1.

Sardine and anchovy eggs and larvae percent frequency distributions were each divided by the corresponding overall percent SST frequency distribution.

Average upwelling indices were estimated for all of the SST range. To obtain them, we used Bakun's monthly averaged upwelling indices. We then estimated the average SSTs for the subareas shown in figure 1, compared the monthly index with the average SST in that month, and finally estimated the average for all the indices in each SST interval (0.1°C).

Average sardine egg abundance as a function of upwelling was estimated with the same monthly averaged indices mentioned above, and relating to

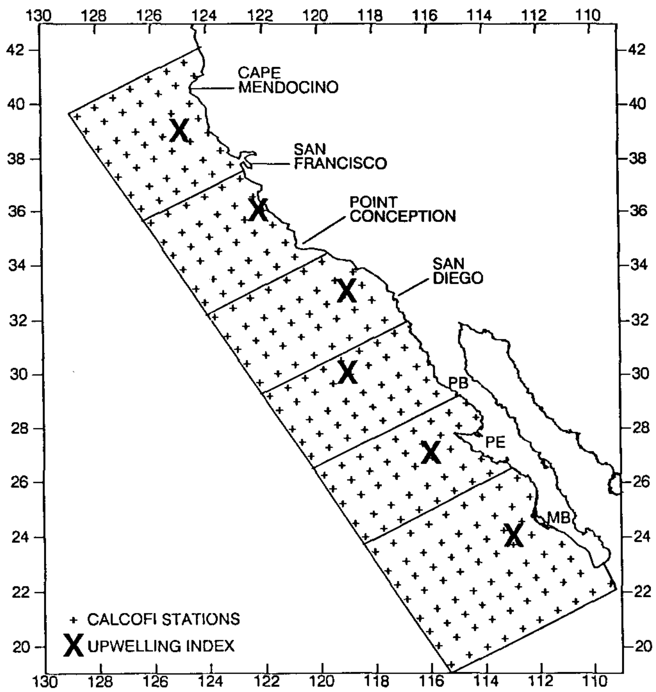

Figure 1. Area of study. The CalCOFI grid is shown as small crosses for the principal stations sampled. Large X's are locations of monthly averaged upwelling indices. Subareas were used to average SST measurements to relate them to upwelling indices. PB = Punta Baja; PE = Punta Eugenia; MB = Bahía Magdalena.

them (in intervals of 10 units) the average number of positive stations. The overall average number was estimated for each upwelling interval.

All of the series were smoothed for improved presentation, since there is high interpoint variability. We mostly used 11-term running averages centered in the sixth datum. However, we used Spencer's method (in a commercial statistical software) to smooth the upwelling indices series because of the need to preserve the extreme points. We also estimated the percent distribution of each of the series to avoid scaling problems when showing them in the same graph.

RESULTS

The percent frequency distribution of SST is shown in figure 2, together with eggs-associated percent temperature distribution (i.e., the frequency distribution of the temperature of positive stations) for both sardines and anchovy.

Figures 3 and 4 show the quotients of the percent distribution of sardine and anchovy eggs and larvae divided by the percent distribution of SST. Points above 1.0 (the baseline) are preferred temperatures for spawning, since their frequency is larger than the one expected as a function of overall SST distribution; values less than one are less frequent than the overall SST distribution.

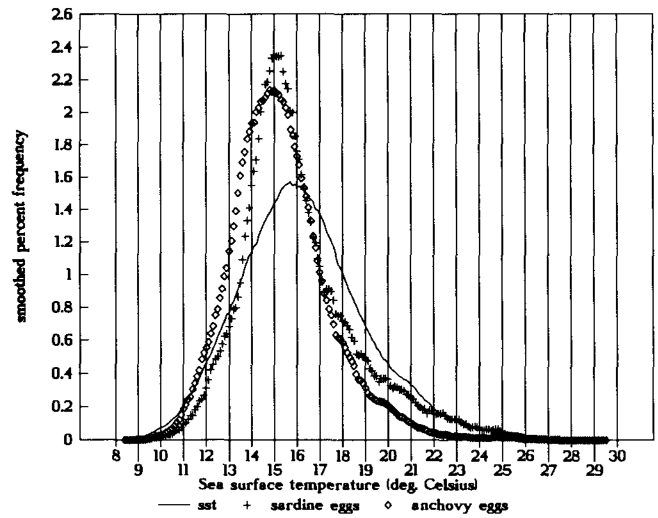

Figure 2. Percent frequency distribution of overall sea-surface temperature measurements, percent number of positive stations for sardine eggs, and percent number of positive stations of anchovy eggs. Series smoothed by 11-term running means, centered on the sixth datum.

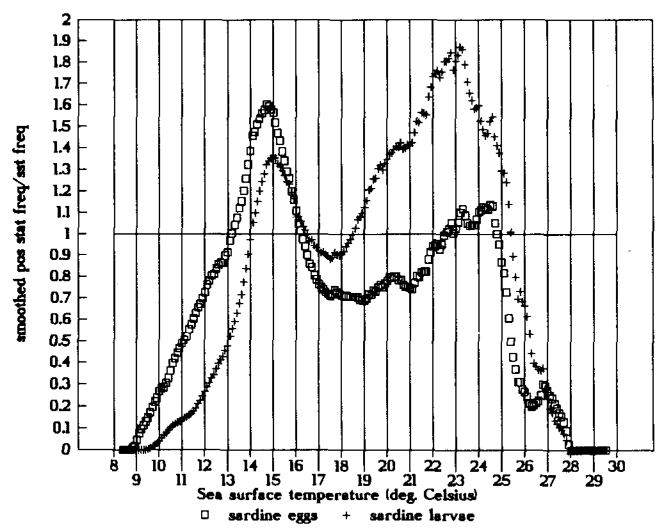

Figure 3. Quotients of the percent frequency distribution of positive stations for sardine eggs and larvae and the general SST percent frequency distribution. Series smoothed by 11-term running means, centered on the sixth datum. Horizontal line denotes baseline.

With this transformation, differences between species become very apparent. First, the sardines' preferred spawning range is much wider, from roughly 13.5° to 25°, whereas that of anchovies is restricted to 11.5° to 16.5°. Second, sardine spawning shows two different peaks, the first at 15° and the second at 23°, whereas there is only one peak (14°) for anchovies.

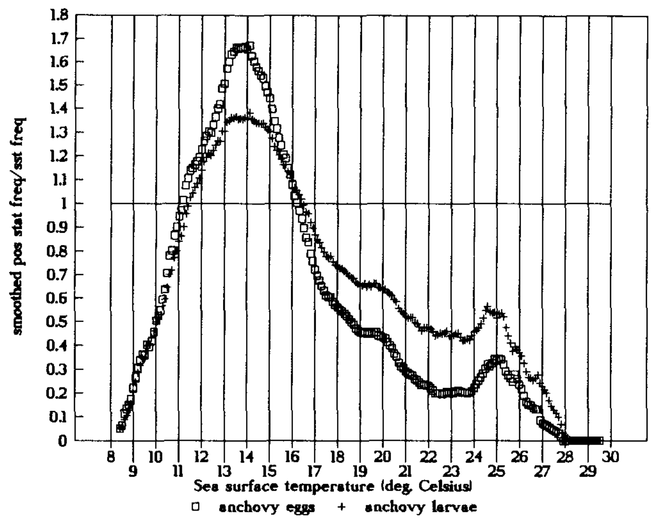

Figure 4. Quotients of the percent frequency distribution of positive stations for anchovy eggs and larvae and the general SST percent frequency distribution. Series smoothed by 11-term running means, centered on the sixth datum. Horizontal line denotes baseline.

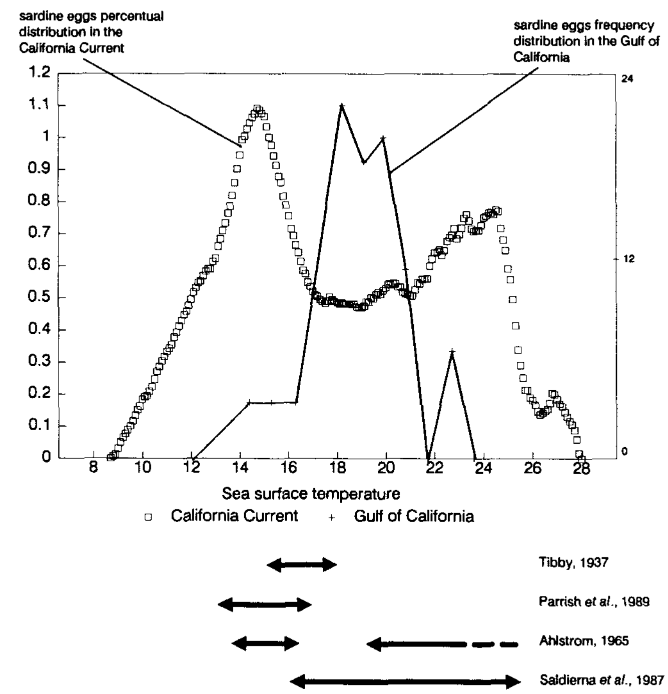

Figure 5. Summary of sardine spawning temperature ranges as reported by several authors. *Upper section*, sardine spawning in the California Current (this paper) and in the Gulf of California (from Hammann, in press). *Lower section*, temperature ranges of sardine spawning as reported by several authors.

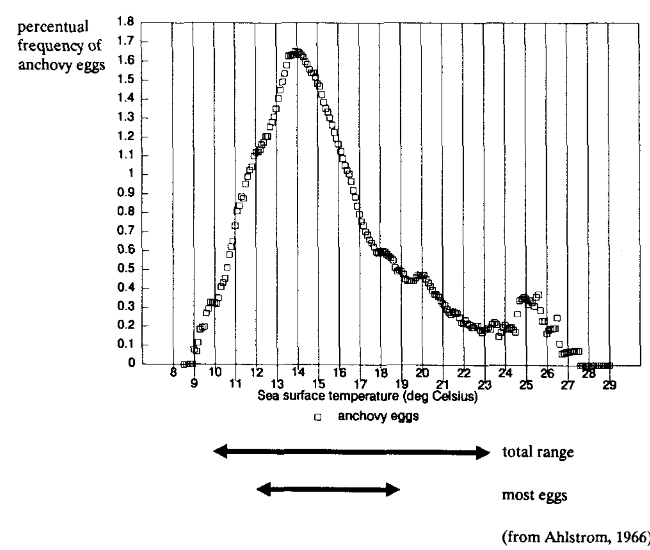

Figure 6. Summary of anchovy spawning temperature ranges. *Upper section*, anchovy spawning percent frequency distribution (this paper). *Lower section*, temperature ranges as reported previously.

Regarding the differences between egg and larval distributions for both sardines and anchovies, it seems evident that sardine eggs spawned below 14.5° have a diminished rate of survival. Even though there is spawning from 9° up, there seems to be a great loss under 14°. The peak distribution for this range is 14.6° for eggs, but 15° for larvae. On the contrary, anchovy eggs and larvae seem to match very closely at this cooler limit, with similar peaks for both.

Figure 5 shows the percent distribution of sardine spawning as a function of SST in the California Current and the Gulf of California (after Hamman, in press), as well as ranges as mentioned by Tibby (1937), Ahlstrom (1954, 1965), Parrish et al. (1989) and Saldierna et al. (1987).

Although there is very little information on anchovy spawning temperatures, the available reports are summarized in figure 6.

Average upwelling indices as a function of SST are shown in figure 7, both as the scatter diagram and the smoothed series. The major peak occurs at 12.5°C, but the 16° peak is the most extended. High upwelling indices are associated with the 15°–18.5° range. The decline in upwelling intensity also shows the north-south gradual decline in productivity, as temperatures rise.

Spawning of both sardine and anchovy as a function of upwelling are presented in figure 8; spawning is represented by the proportion of positive to total stations associated with each of the upwelling indices. The differences are striking. There is a clear maximum for sardine spawning at intermediate values, below or above which spawning declines markedly, but there are two peaks for anchovy — a minor one at very low levels of upwelling and a major one at the higher indices.

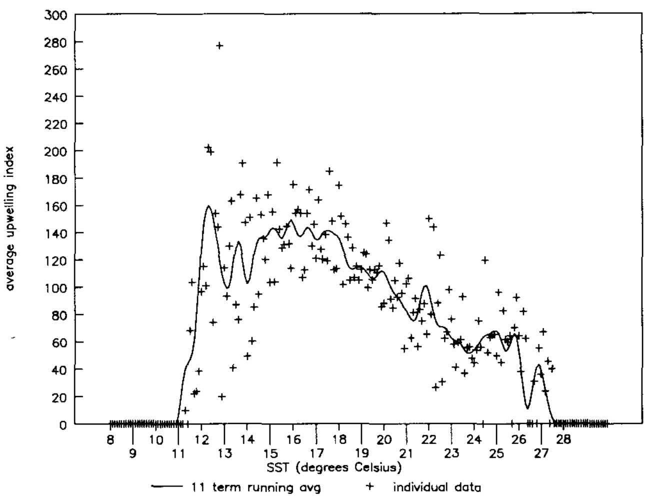

Figure 7. Average upwelling indices in the temperature domain (+) and smoothed series by Spencer's method.

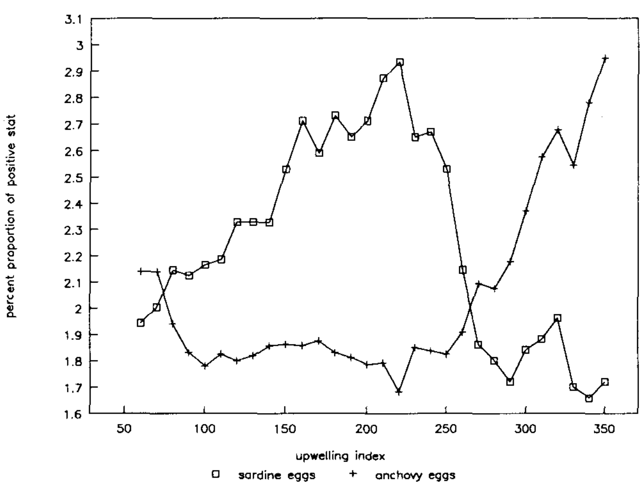

Figure 8. Percent proportion of positive stations for sardine and anchovy eggs as a function of upwelling index intervals. Series smoothed by 11-term running means, centered on the sixth datum.

One point should be stressed concerning figures 7 and 8: whereas figure 7 shows average upwelling indices as a function of temperature, figure 8 plots percent frequency of positive stations for sardine and anchovy eggs as a function of upwelling. As a result, the upwelling indices scales are quite different, and the graphs only indicate general trends within their total amplitude. No comparison between them would be meaningful.

DISCUSSION

It is always difficult to define absolute temperature limits for organisms, whether breeding or not, since in nature there tends to be an ample variation. It is evident that sardines and anchovies spawn through a very wide temperature range: there are positive stations from less than 10°C to more than 28°C for both sardines and anchovies (figure 2). There are no clear-cut limits within these distributions.

On the other hand, the maxima for both species appear very close (15° for anchovy and 15.3° for sardine), and are very much the same as the general SST distribution, whose peak is around 15.5°. However, the general SST distribution has a definitive influence on the apparent distribution of sardine and anchovy spawning: the absolute number of positive stations depends on the total number of stations at a particular temperature. Thus it is the proportion of positive stations at each temperature that interests us; that is, the quotient between the relative temperature distribution of eggs and larvae and the general SST frequency distribution (figures 3 and 4).

The relative proportion of larvae to eggs increases from north to south for both species. This could mean either that survival of larvae increases toward the warm side of the ranges or that the higher proportion is an effect of the shorter development time of the egg as a function of higher temperatures. Another possibility (suggested by one of our reviewers) is that larvae grow slower in the south. Existing data are not sufficient to indicate which of these options — alone or combined — apply.

Most previous authors have worked with sardine spawning in the cooler temperature range. Tibby (1937), Ahlstrom (1954, 1965), Smith (1978), and Parrish et al. (1989) refer to temperature ranges that closely agree with the first peak reported in this paper. The warmer temperature range has seldom been reported, and only at its southern end, around Magdalena Bay (Saldierna et al. 1987). However, Ahlstrom (1954) referred to this second range as the "off-season" and reported temperatures "higher than 19°C."

The results reported by Hammann (in press) show that in the Gulf of California the temperature range for sardine spawning (14°–23°) is located between the two peaks reported in this paper for the California Current. It is unusual that there may be three different temperature ranges for sardine spawning, as presented here. Normally, the optimum spawning temperature would be expected around the midpoint between the extremes. The spawning temperatures in the Gulf of California are around this midpoint of the total range. Thus, we believe that the hiatus found between the two major peaks in the California Current is not an inherent phenomenon, but a different, environmentally caused feature.

We believe that the environmental factor responsible for the gap in the sardine spawning range is somehow related to upwelling. Low upwelling (and induced productivity) limit the abundance of sardines, as is evident from the fact that there are no sardines where there is no upwelling — as in the area between Ensenada and Bahía Sebastián Vizcaíno, except during the upwelling season. On the other hand, limits to sardine spawning at high upwelling indices can be assumed from the reports of several authors: Ahlstrom (1965) reported that no clear relation existed between productivity and sardine abundance; Lasker (as summarized by Lasker and MacCall 1983) proposed that intense upwelling could negatively affect the survival of larvae because of turbulence and instability of the water column. Another way in which intense upwelling could negatively influence sardine abundance is by the offshore transport of larvae (Parrish et al. 1981).

Both mechanisms — egg and larvae loss from turbulence, and offshore transport of larvae — would operate after spawning. We find that spawning itself is influenced by upwelling. It is clear from figure 8 that there is a maximum of spawning at intermediate values of upwelling; at lower and higher values, spawning decreases considerably. There must be some way for sardines to select appropriate upwelling conditions for spawning.

We suggest that sardines spawn preferably at (1) the range of temperatures with intermediate upwelling values (figure 7: temperatures between 14° and 15°C) that is found between the lower temperature range with high values of upwelling (12°–13°) and the warmer temperature range with high values of upwelling (15°–18°); and (2) at temperatures higher than 18.5°, as average upwelling indices decline to intermediate values. These two ranges correspond to the two peaks of spawning as a function of temperature shown in figure 3. The gap between the two peaks corresponds to the high upwelling values and a temperature range between 15° and 18°.

SST is a good indicator of spawning only at the limits, particularly at the lower one; otherwise, it is a poor indicator, since there is a very wide range of appropriate temperatures. However, the combination of temperature and upwelling appears to determine time and space of sardine spawning.

Anchovies, on the other hand, seem to behave the opposite way: a narrow range of spawning (figure 4) combines with the capability of spawning at low or high upwelling indices (figure 8). We suggest that the peak of anchovy spawning is somehow related to the high values of upwelling that occur at the low temperature range (12° to 13°) as shown in figure 7.

Figure 8 suggests competitive interaction between both species, with sardines showing ecological dominance. However, other factors may determine anchovies' preference for upwelling, and further analysis of this possible relationship is required.

We conclude that sardines may be considered as eurithermic and preferring warmer temperatures for spawning than anchovies, which are stenothermic and prefer cooler temperatures, as indicated in the formerly reported observations. Anchovies seem much more adapted for cooler spawning than sardines. This point is supported further by the importance of the warmer peak for sardines.

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