

# Production and Mortality of Anchoveta (*Engraulis ringens*) Eggs off Peru\*

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PAULY, D. and M. SORIANO. 1989. Production and mortality of anchoveta (*Engraulis ringens*) eggs off Peru, p. 155-167. In D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

## Abstract

The egg production of anchoveta was estimated by month from 1953 to 1985 based on estimates of mature female biomass batch fecundity and related factors for the period 1953-1985 off Peru (4-14°S). These theoretical estimates of production were related to empirical estimates derived from egg surveys conducted from 1964 to 1985. This yielded estimates of egg mortality; a multiple regression model including parent stock size, sardine biomass, SST and SST anomaly explained a large fraction of the variance of these egg mortality estimates. However, how results suggest parent *concentration* (rather than parent stock size) to be the key parameter affecting anchoveta egg mortality, a hypotheses which will have to be tested in a future contribution.

## Resumen

Se estimó la producción de huevos mensual de la anchoveta peruana (4-14°S) de 1953 a 1985 basado en estimaciones de la fecundidad biomasa de hembras maduras y factores relacionados para el período 1953-1985 frente a Perú (4-14°S). Estas estimaciones de producción teóricas fueron relacionadas con estimaciones empíricas obtenidas de cruceros de evaluación de huevos realizados de 1964 a 1985. Esto proporcionó estimaciones de mortalidad de huevos; un modelo de regresión múltiple que incluye el tamaño del stock de padres, biomasa de sardina, TSM y anomalías de TSM, explicó una gran parte de la varianza de estos estimados de mortalidad de huevos. Sin embargo, como los resultados lo sugieren, la concentración de padres (más que el tamaño del stock de padres) es el parámetro clave que afecta la mortalidad de huevos, una hipótesis que deberá ser probada en una contribución futura.

## Introduction

Recruitment to a stock depends on (i) the size of the spawning stock and (ii) the survival of the eggs and larvae. Within fishery biology, an immense literature exists on how to forecast the recruitment of fish stock given a knowledge of spawning stock size, i.e., from the "top-down" (reviews in Ricker 1954; Cushing 1988). There have also been numerous attempts to approach the recruitment problem from the "bottom-up", i.e., through detailed analyses of the factors controlling the survival of eggs and larvae (see, e.g., papers in Sharp 1980 and Rothschild 1986).

While generally, "bottom-up" approaches have been more costly, more data intensive, yet less successful than "top-down" approaches in providing management advice, it is nevertheless clear that management of important fish resource species should be based on an understanding of all aspects of their life history, including the early stages.

In the case of the Peruvian anchoveta, sufficient data are available on the dynamics of the parent stock, and on the distribution and density of the eggs to justify an attempt to identify the major causes of anchoveta egg mortality.

\*ICLARM Contribution No. 507.

## Materials and Methods

Two sources of data were tapped for this contribution:

- i) length-structured biomass estimates obtained by VPA (Pauly and Palomares, this vol.) and which were used to estimate parent biomass, mature female biomass and egg production, by month, for the period January 1953 to July 1985, using a model to be briefly described further below; and
- ii) Ninety maps of anchoveta egg distribution based on egg surveys conducted from 1964 to 1985, and which were published and subjected to preliminary analyses by Santander (1987) and Senocak et al. (this vol.).

The model used here to estimate the monthly reproductive output (RO), i.e., egg production, of anchoveta has the form:

$$RO_i = \sum_{j=1}^n B_{ij} \cdot P_{ij} \cdot A_j \cdot S_k \cdot PF_j \cdot RF \quad \dots 1)$$

where  $j$  is the number of length classes for which, in a given month  $i$ , anchoveta biomass estimates are available (see Table 1 for the definition of the other terms).

Fig. 1 gives an example of the type of maps published by Santander (1987) and the first five columns of Table 2 summarize the key information pertaining to or extracted from these maps. Most important here is the fifth column, i.e., the estimates of egg standing stock, derived by planimetry (Santander 1987). [Some of these maps represented surveys which had covered less than the 4-14°S stretch of the Peruvian coast used here as reference. The estimated egg standing stocks for these maps have been, in these cases, extrapolated to the whole reference area using a procedure documented in Santander (1987). The detailed planimetry of Senocak et al. (this vol.), which did not involve any large-scale extrapolation, shows that no detectable bias was introduced by Santander's extrapolation procedure.]

Table 1. Specifications of the multiplicative model used by Pauly and Soriano (1987) to estimate the egg production of Peruvian anchoveta (equation 1), by month ( $i$ ), based on biomass data by length class ( $j$ )<sup>a</sup>.

Tabla 1. Especificaciones del modelo multiplicativo usado por Pauly y Soriano (1987) para estimar la producción de huevos de anchoveta (ecuación 1) por meses ( $i$ ) basado en datos de biomasa por clase de longitud ( $j$ ).<sup>a</sup>

| Variable or constant | Definition  | (units)         | Remarks and/or source of estimate   |
|----------------------|---|-----------------|---|
| $B_{ij}$             | Biomass of male and female anchoveta  | (tonnes)        | From VPA III output of Pauly and Palomares (this vol.)  |
| $P_{ij}$             | Fraction of mature fish   | (dimensionless) | Derived from logistic curve with shape and position varying with SST (see Pauly and Soriano 1987)           |
| $A_j$                | Size-specific factor relating anchoveta fecundity per unit weight to length | (dimensionless) | See Tables 2 and 3 in Pauly and Soriano (1987)  |
| $S_k$                | No. of spawnings per month, $k=1$ (January); $k=12$ (December)              | (1/t)           | From Table 3 in Pauly and Soriano (1987), based on Jordan (1980)  |
| $PF_j$               | Fraction of females in parent stock   | (dimensionless) | From Fig. 4 and Table 3 in Pauly and Soriano (1987), based on Clark (1954), Miñano (1958) and Jordan (1959) |
| $RF$                 | Relative batch fecundity  | (eggs/g)        | Value of 596/g female taken from Santander et al. (1984)  |
| $10^9$               | Factor for adjusting gram to tonne  | (dimensionless) | Used, but not given in Equation (1)   |
| $n$                  | Number of length classes used in month ( $i$ )                              | (dimensionless) | Variable between months   |

<sup>a</sup> See Pauly and Soriano (1987) for further details on model derivation and specification and on data sources.

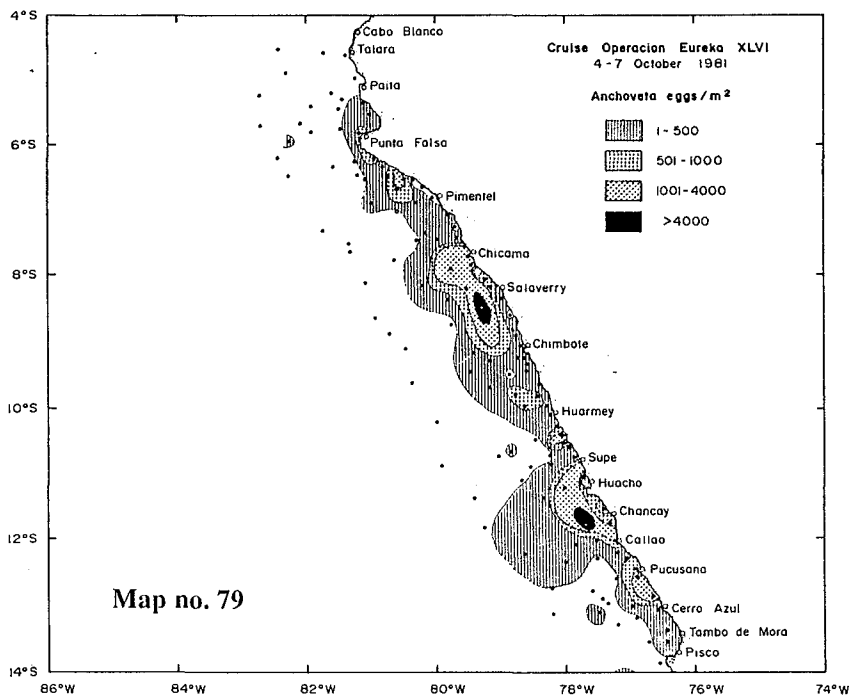


Fig. 1. Anchoveta egg distribution off Peru (4-14°S), in early October 1981. Details on this map (No. 79 in Santander 1987), given here as an example, are provided in Table 2.

*Fig. 1. Distribución de huevos de anchoveta frente al Perú (4-14°S) a comienzos de Octubre 1981. Detalles de éste mapa (No. 79 en Santander 1987), presentado aquí como un ejemplo, se dan en la Tabla 2.*

Pauly (1987) had attempted to estimate anchoveta egg mortality by relating theoretical egg production (as estimated via equation 1), to the egg standing stock in Santander's maps. However, the model he used to calculate egg mortality (his equation 4) produced biased estimates when egg mortality was low (J.A. Gulland, pers. comm. to D. Pauly, December 1987), and his whole section on "the cannibalization of anchoveta eggs" (inclusive of his Table 2 and Fig. 4) is thus erroneous.

We used instead an approach suggested by J.A. Gulland (pers. comm.). Defining  $N_d$  as the egg standing stock at the end of period  $D$ , and  $R$  as the initial size of a "cohort" of anchoveta eggs, it follows for that cohort, that:

$$N_d = R e^{-ZD} \quad \dots 2)$$

where  $Z$  is the egg mortality from spawning/fertilization to hatching and  $D$  (days) is the egg development time. The parameter  $D$  can be estimated from:

$$\log_{10} D = 6.953 - 4.09 \log_{10}(T+26) \quad \dots 3)$$

where  $T$  is the sea surface temperature (SST, in °C) and which was derived by Pauly (1987) based on data in Santander and Sandoval de Castillo (1973) and equation (5) in Pauly and Pullin (1988).

Under steady-state condition (assumed here to prevail shortly before, during and after a given egg survey was conducted and/or during a period of one month), equation (2) implies a mean standing stock ( $\bar{N}$ ) whose value can be estimated from:

$$\bar{N} = \frac{1}{D} \int_0^D R e^{-ZD} \quad \dots 4)$$

or

$$\bar{N} = \frac{R}{ZD} (1 - e^{-ZD}) \quad \dots 5)$$

Table 2. Summary of data on anchoveta egg surveys conducted from 1964 to 1985 off Peru (4-14°S)<sup>a</sup>, with added ancillary information and some derived statistics.

Tabla 2. Resumen de los datos de los cruceros de evaluación de huevos de anchoveta llevados a cabo de 1964 a 1985 frente al Perú (4-14°S) con alguna información adicional y estadísticas derivadas.

| Running no. | Map no. | Year | Month | Map standing stock (egg x 10 <sup>12</sup> ) <sup>a</sup> | Daily reproductive output (egg x 10 <sup>12</sup> ) <sup>b</sup> | Anchoveta parent stock (t x 10 <sup>6</sup> ) <sup>b</sup> | Sardine biomass <sup>c</sup> (t x 10 <sup>6</sup> ) | Egg development time (day) <sup>d</sup> | Z (day <sup>-1</sup> ) <sup>e</sup> | Estimated Z (day <sup>-1</sup> ) <sup>f</sup> |
|-------------|---------|------|-------|---|--|--|---|---|-------------------------------------|---|
| 1           | 1       | 1964 | Mar   | 27.4  | 16.8   | 5.01   | 0.32  | 1.53                                    | -                                   | 0.238   |
| 2           | 2       |      | Apr   | 17.0  | 3.35   | 3.19   | 0.31  | 1.74                                    | -                                   | 0.251   |
| 3           | 3       |      | Jun   | 12.9  | 4.71   | 1.04   | 0.30  | 2.02                                    | -                                   | 0.076   |
| 4           | 4       |      | Sep   | 137.0   | 68.8   | 1.54   | 0.31  | 2.10                                    | 0.049                               | 0.555   |
| 5           | 5       |      | Dec   | 60.3  | ( 1.89 )   | (0.532)  | 0.34  | 2.02                                    | -                                   | 0.138   |
| 6           | 6       | 1965 | Mar   | 51.4  | 35.8   | 7.36   | 0.36  | 1.37                                    | -                                   | 0.248   |
| 7           | 7       |      | Apr   | 8.03  | 7.20   | 8.26   | 0.37  | 1.27                                    | 0.206                               | 0.373   |
| 8           | 8       |      | Jul   | 53.3  | 20.7   | 3.30   | 0.38  | 1.55                                    | -                                   | 3.457   |
| 9           | 9       |      | Nov   | 44.0  | 60.3   | 3.07   | 0.35  | 1.72                                    | 1.212                               | 3.396   |
| 10          | 10      | 1966 | Feb   | 16.2  | 19.7   | 6.55   | 0.33  | 1.37                                    | 0.822                               | 0.249   |
| 11          | 11      |      | May   | 4.94  | 1.19   | 3.10   | 0.31  | 1.78                                    | -                                   | 0.428   |
| 12          | 12      |      | Sep   | 418.0   | 74.4   | 1.44   | 0.30  | 2.14                                    | -                                   | 0.407   |
| 13          | 13      |      | Nov   | 97.4  | 123.0  | 2.50   | 0.30  | 1.96                                    | 1.139                               | 1.001   |
| 14          | 14      | 1967 | May   | 6.36  | 0.704  | 1.33   | 0.30  | 1.89                                    | -                                   | 0.162   |
| 15          | 15      |      | Sep   | 292.0   | 49.1   | 0.998  | 0.30  | 2.19                                    | -                                   | 0.250   |
| 16          | 16      |      | Nov   | 116.0   | 52.4   | 1.09   | 0.30  | 2.25                                    | 0.018                               | 0.108   |
| 17          | 17      | 1968 | Feb   | 50.2  | 32.0   | 2.70   | 0.30  | 1.77                                    | 0.134                               | 0.100   |
| 18          | 18      |      | Sep   | 169.0   | 185.0  | 2.74   | 0.30  | 1.98                                    | 0.921                               | 1.524   |
| 19          | 19      |      | Dec   | 15.5  | 127.0  | 2.16   | 0.31  | 1.85                                    | 7.722                               | 0.723   |
| 20          | 20      | 1969 | Jan   | 22.0  | 16.5   | 2.35   | 0.31  | 1.60                                    | 0.225                               | 0.462   |
| 21          | 21      |      | Jul   | 9.42  | 19.5   | 1.72   | 0.32  | 1.80                                    | 2.002                               | 1.155   |
| 22          | 22      |      | Sep   | 82.3  | 69.4   | 1.77   | 0.32  | 1.84                                    | 0.527                               | 2.422   |
| 23          | 23      | 1970 | May   | 22.1  | 53.8   | 14.10  | 0.30  | 1.61                                    | 2.330                               | 1.741   |
| 24          | 24      |      | Sep   | 82.0  | (259.0)  | (3.60)   | 0.30  | 1.89                                    | 3.104                               | 2.866   |
| 25          | 25      |      | Oct   | 22.6  | (253.0)  | (3.60)   | 0.30  | 1.82                                    | 10.989                              | 3.581   |
| 26          | 26      |      | Nov   | 9.05  | (135.0)  | (3.60)   | 0.30  | 1.87                                    | 13.369                              | 1.956   |
| 27          | 27      | 1971 | May   | 107.0   | 1.24   | 3.02   | 0.30  | 1.60                                    | -                                   | 0.697   |
| 28          | 28      |      | Aug   | 12.7  | 95.4   | 3.83   | 0.47  | 1.70                                    | 7.353                               | 5.493   |
| 29          | 29      |      | Nov   | 29.3  | 178.0  | 3.72   | 0.98  | 1.85                                    | 6.006                               | 3.385   |
| 30          | 30      | 1972 | Feb   | 2.08  | ( 44.3 )   | (2.59)   | 1.50  | 2.21                                    | 20.661g                             | 0.233   |
| 31          | 31/32   |      | Jul   | 13.2  | ( 33.1 )   | (1.77)   | 2.18  | 1.29                                    | 2.385                               | 2.755   |
| 32          | 33      |      | Aug   | 23.8  | ( 79.8 )   | (1.38)   | 2.18  | 1.42                                    | 3.324                               | 6.717   |
| 33          | 34/35   |      | Sep   | 7.19  | (120.0)  | (1.12)   | 2.18  | 1.57                                    | 15.924                              | 8.129   |
| 34          | 36      |      | Oct   | 5.47  | (106.0)  | (0.946)  | 2.18  | 1.55                                    | 21.505                              | 6.810   |
| 35          | 37      |      | Dec   | 62.3  | 9.70   | 2.34   | 2.18  | 1.26                                    | -                                   | 0.347   |
| 36          | 38      | 1973 | Jan   | 35.2  | ( 5.06 )   | (3.05)   | 2.18  | 1.08                                    | -                                   | 0.094   |
| 37          | 39      |      | Mar   | 41.3  | (10.7)   | (3.07)   | 2.18  | 1.27                                    | -                                   | 0.181   |
| 38          | 40/41   |      | Jun   | 19.8  | ( 2.75 )   | (4.71)   | 2.18  | 1.94                                    | -                                   | 1.244   |
| 39          | 42      |      | Jul   | 18.9  | ( 20.4 )   | (9.53)   | 2.18  | 2.06                                    | 0.915                               | 1.880   |
| 40          | 43      |      | Aug   | 109.0   | ( 23.5 )   | (4.44)   | 2.18  | 2.16                                    | -                                   | 1.139   |
| 41          | 44      |      | Sep   | 60.9  | (52.4)   | (6.70)   | 2.17  | 2.12                                    | 0.634                               | 0.616   |
| 42          | 45      |      | Nov   | 70.7  | (170.0)  | (2.28)   | 2.17  | 1.85                                    | 2.43                                | 3.395   |
| 43          | 46      | 1974 | Feb   | 86.4  | (69.5)   | (2.27)   | 2.15  | 1.67                                    | 0.381                               | 0.257   |
| 44          | 47      |      | May   | 3.44  | ( 2.79 )   | (1.55)   | 2.13  | 1.61                                    | 0.34                                | 0.954   |
| 45          | 48      |      | Aug   | 85.2  | (173.0)  | (1.58)   | 2.14  | 1.91                                    | 1.967                               | 2.540   |
| 46          | 49      |      | Sep   | 64.7  | (116.0)  | (0.864)  | 2.15  | 2.04                                    | 1.766                               | 1.155   |
| 47          | 50      |      | Nov   | 29.6  | (93.7)   | (0.941)  | 2.17  | 1.85                                    | 3.183                               | 1.169   |
| 48          | 51      | 1975 | Feb   | 40.7  | (29.3)   | (1.73)   | 2.20  | 1.69                                    | 0.243                               | 0.210   |
| 49          | 52      |      | Aug   | 56.0  | (105.0)  | (1.37)   | 2.20  | 2.04                                    | 1.841                               | 1.167   |
| 50          | 53      |      | Sep   | 55.6  | (196.0)  | (1.78)   | 2.19  | 2.06                                    | 3.465                               | 1.610   |
| 51          | 54      |      | Dec   | 67.4  | 40.5   | 1.71   | 2.12  | 1.98                                    | 0.182                               | 0.694   |
| 52          | 55      | 1976 | Jan   | 17.0  | (50.8)   | (2.22)   | 2.10  | 1.84                                    | 3.007                               | 0.447   |
| 53          | 56      |      | Jul   | 53.8  | 22.8   | 1.93   | 1.98  | 1.50                                    | -                                   | 4.768   |
| 54          | 57      |      | Aug   | 53.6  | 57.3   | 2.06   | 2.03  | 1.54                                    | 0.705                               | 8.885   |
| 55          | 58      |      | Nov   | 19.2  | 81.2   | 2.16   | 2.18  | 1.64                                    | 4.352                               | 6.748   |
| 56          | 59      | 1977 | Mar   | 45.9  | ( 9.30 )   | (1.68)   | 2.37  | 1.35                                    | -                                   | 0.191   |
| 57          | 60      |      | Apr   | -313  | ( 2.70 )   | (1.53)   | 2.42  | 1.35                                    | -                                   | 0.402   |
| 58          | 61      |      | Jul   | 28.0  | (23.9)   | (0.821)  | 2.52  | 1.77                                    | 0.507                               | 1.832   |
| 59          | 62/63   |      | Aug   | 25.4  | (49.0)   | (0.632)  | 2.48  | 1.87                                    | 1.85                                | 1.823   |
| 60          | 64/65   | 1977 | Oct   | 17.1  | 42.5   | 3.13   | 2.39  | 1.94                                    | 2.433                               | 0.997   |
| 61          | 66      | 1978 | Apr   | 2.67  | ( 0.901 )  | (1.19)   | 2.42  | 1.54                                    | -                                   | 0.448   |
| 62          | 67      |      | Jul   | 64.7  | ( 4.83 )   | (0.394)  | 2.52  | 1.94                                    | -                                   | 0.538   |
| 63          | 68      |      | Oct   | 6.44  | (22.2)   | (0.377)  | 2.39  | 1.94                                    | 3.432                               | 1.116   |
| 64          | 69      |      | Dec   | 25.5  | ( 5.54 )   | (0.621)  | 2.24  | 1.82                                    | -                                   | 0.833   |
| 65          | 70      | 1979 | Feb   | 21.6  | 13.5   | 1.14   | 2.32  | 1.63                                    | 0.025                               | 0.193   |
| 66          | 71      |      | Jul   | 30.1  | 10.2   | 0.492  | 2.49  | 1.80                                    | -                                   | 1.175   |
| 67          | 72      |      | Sep   | 66.2  | 26.7   | 0.385  | 2.50  | 1.87                                    | -                                   | 1.786   |
| 68          | 73      |      | Nov   | 69.8  | 15.8   | 0.283  | 2.52  | 1.66                                    | -                                   | 1.256   |
| 69          | 74      | 1980 | Jan   | 21.8  | 3.72   | 0.461  | 2.53  | 1.58                                    | -                                   | 0.372   |
| 70          | 75      |      | Sep   | 68.2  | 28.9   | 0.360  | 2.57  | 1.94                                    | -                                   | 1.219   |
| 71          | 76      | 1981 | Feb   | 27.3  | 21.2   | 1.63   | 2.57  | 1.58                                    | 0.277                               | 0.268   |
| 72          | 77      |      | Apr   | 10.3  | 4.39   | 1.80   | 2.57  | 1.66                                    | -                                   | 0.494   |
| 73          | 78      |      | Sep   | 18.1  | 111.0  | 1.16   | 2.57  | 2.02                                    | 6.188                               | 1.651   |
| 74          | 79      |      | Oct   | 74.5  | 158.0  | 1.59   | 2.57  | 1.87                                    | 2.097                               | 3.915   |
| 75          | 80      | 1982 | Feb   | 86.4  | 69.7   | 2.36   | 2.57  | 1.58                                    | 0.329                               | 0.336   |
| 76          | 81      |      | Sep   | 31.6  | 127.0  | 0.782  | 2.98  | 1.78                                    | 4.01                                | 4.220   |
| 77          | 82/83   |      | Dec   | 9.79  | 9.96   | 0.412  | 3.60  | 1.03                                    | 0.10                                | 0.060   |
| 78          | 84      | 1984 | Sep   | 49.6  | 2.71   | 0.0394   | 3.76  | 2.08                                    | -                                   | 0.174   |
| 79          | 85      |      | Dec   | 85.6  | 1.06   | 0.114  | 3.21  | 1.96                                    | -                                   | 0.173   |
| 80          | 86      | 1985 | Feb   | 96.2  | 3.66   | 0.269  | 2.84  | 1.93                                    | -                                   | 0.029   |
| 81          | 87      |      | Mar   | 7.76  | 4.33   | 0.603  | 2.65  | 1.78                                    | -                                   | 0.076   |
| 82          | 88      |      | Aug   | 47.4  | 30.1   | 0.602  | 2.12  | 2.10                                    | 0.289                               | 0.491   |
| 83          | 89      |      | Sep   | 38.0  | (12.9)   | (0.187)  | 2.15  | 2.08                                    | -                                   | 0.361   |
| 84          | 90      | 1986 | May   | 10.8  | ( 0.163 )  | (0.327)  | 2.34  | 1.91                                    | -                                   | 0.174   |

<sup>a</sup> Adapted from Santander (1987, Table 3).

<sup>b</sup> From (part of) equation (1) and biomasses estimated by Pauly and Palomares (this vol.).

<sup>c</sup> From Table 1 in Muck (this vol.), with monthly values interpolated between annual means (used from June/July); these estimates are very crude and need refinement, based on future VPA estimates of sardine biomasses.

<sup>d</sup> From equation (3) and SST in Pauly and Tsukuyama (1987) for 1953 to 1982, and from Senocak et al. (this vol.) from 1983 to 1985.

<sup>e</sup> From equation (6).

<sup>f</sup> From equation (9).

<sup>g</sup> Outlier, not used for estimates of parameters of equations (6) and (9).

Both N and R can be turned into egg production rates through division by D, i.e.,

$$\frac{N/D}{R/D} = \frac{1 - e^{-ZD}}{ZD} \quad \dots 6)$$

N/D then corresponds to the above-mentioned map standing stock estimates divided by egg development time (see also Senocak, this vol.), while R/D corresponds to the output of equation (1), reexpressed on a daily basis.

Various plausible multiple regression models were then applied to the data of Table 2, our aim being to identify biologically acceptable factors explaining the observed variability in egg survival. The Rojas/Alamo database on anchoveta food and feeding habits (see Rojas de Mendiola, this vol.; Alamo, this vol.; and Pauly et al., this vol.) was also tapped for data on anchoveta egg cannibalism and the results were used to help interpret the output of our egg mortality models.

## Results and Discussion

### Parental Biomass and Egg Production, 1953 to 1985

Fig. 2 and Tables 3, 4 and 5 present the results obtained by applying equation (1) to the biomass data generated by Pauly and Palomares (this vol.). The estimates of parental biomass in Fig. 2 resemble those published earlier by Pauly and Soriano (1987). As was the case earlier, the lone independent estimate of parental biomass obtained for August/September 1981 using the egg production method (Santander et al. 1984) is very close to our estimates of parental biomass for that period (see also Table 3, footnote).

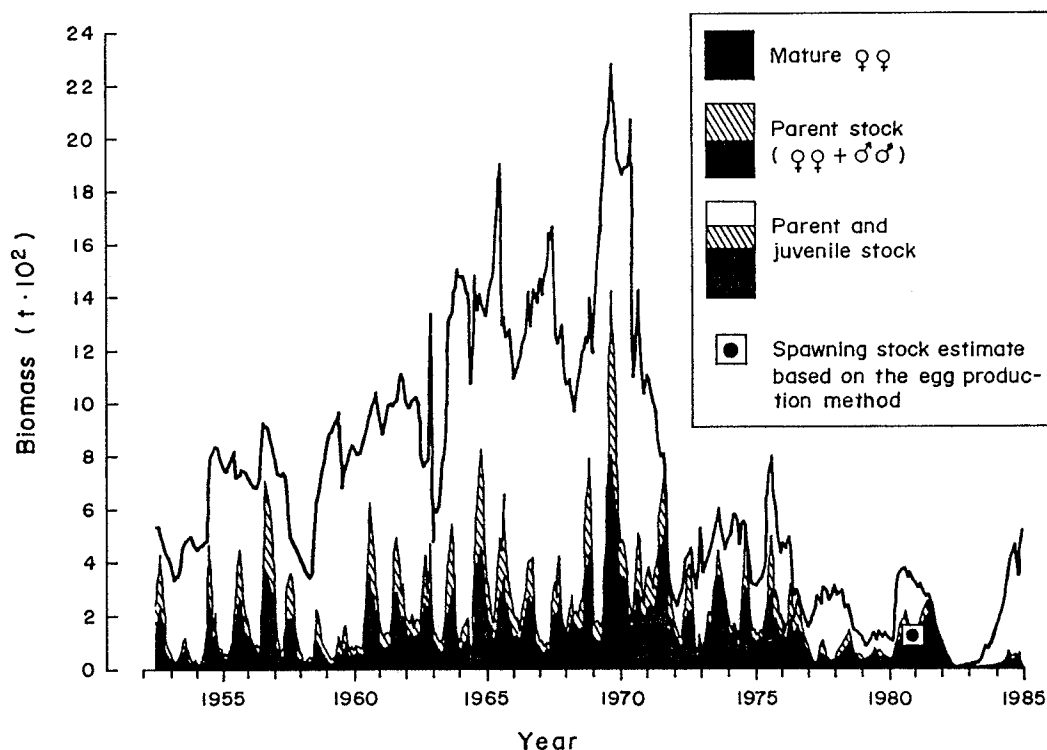


Fig. 2. Total biomass, parent (=mature) stock and biomass of mature female anchoveta off Peru (4-14°S), January 1953 to July 1985. Note strong, regular seasonal oscillations and very good match with independent spawning stock estimate in August/September 1981 by Santander et al. (1984).

Fig. 2. Biomasa total, stock de padres (=maduros) y biomasa de anchovetas hembras maduras frente al Perú (4-14°S), Enero 1953 a Julio 1985. Notar la fuerte y regular oscilación estacional y una muy buena concordancia con la estimación independiente del stock desovante en Agosto/Septiembre 1981 de Santander et al. (1984).

Table 3. Estimated biomass of mature female and male anchoveta (*Engraulis ringens*) off Peru (4-14°S), January 1953 to July 1985 (in tonnes). Note that estimates for the early/mid-1970s tend to be biased upward (see text).<sup>a</sup>

Tabla 3. Biomasa estimada de anchovetas maduras (*Engraulis ringens*) hembras y machos frente al Perú (4-14°S), Enero 1953 a Julio 1985 (en toneladas). Notar que los valores para comienzos y mediados de 1970 tienden a estar sobreestimados (ver texto).

| Year | Jan       | Feb        | Mar        | Apr        | May       | Jun       | Jul       | Aug       | Sep       | Oct       | Nov       | Dec       |
|------|-----------|------------|------------|------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| 1953 | 2,324,629 | 3,687,629  | 4,255,910  | 3,354,697  | 1,780,670 | 759,621   | 675,923   | 444,380   | 322,403   | 192,221   | 236,800   | 325,083   |
| 1954 | 778,346   | 1,190,877  | 958,377    | 470,370    | 306,811   | 214,251   | 343,315   | 130,482   | 150,946   | 163,288   | 306,942   | 1,397,974 |
| 1955 | 4,628,339 | 3,299,281  | 1,448,142  | 2,109,215  | 862,341   | 784,263   | 705,329   | 466,236   | 584,753   | 421,088   | 670,558   | 1,086,364 |
| 1956 | 2,511,945 | 4,049,643  | 4,450,385  | 2,986,737  | 2,341,447 | 1,952,697 | 1,820,396 | 1,424,517 | 973,275   | 780,623   | 884,357   | 773,870   |
| 1957 | 1,407,115 | 7,022,473  | 6,651,020  | 6,078,912  | 5,823,122 | 4,335,316 | 2,842,668 | 1,079,831 | 547,811   | 707,394   | 752,574   | 3,120,840 |
| 1958 | 3,280,197 | 3,526,073  | 3,371,224  | 1,882,582  | 1,072,449 | 699,824   | 624,921   | 195,383   | 227,089   | 286,092   | 432,654   | 276,946   |
| 1959 | 606,482   | 2,214,714  | 1,807,238  | 1,372,257  | 869,253   | 604,095   | 422,105   | 383,747   | 334,340   | 376,378   | 519,242   | 1,166,015 |
| 1960 | 698,823   | 1,402,145  | 1,602,622  | 1,021,144  | 699,377   | 840,562   | 702,882   | 869,485   | 838,234   | 802,908   | 811,071   | 1,797,878 |
| 1961 | 4,050,912 | 6,233,816  | 4,684,939  | 4,031,832  | 3,236,062 | 1,977,297 | 1,307,135 | 1,285,905 | 1,260,206 | 1,342,832 | 1,348,396 | 1,685,565 |
| 1962 | 4,776,121 | 4,918,827  | 3,830,377  | 2,923,596  | 3,214,620 | 2,279,411 | 1,895,947 | 1,781,146 | 2,094,791 | 1,494,146 | 1,863,795 | 1,777,456 |
| 1963 | 2,136,645 | 3,503,178  | 4,254,088  | 2,913,276  | 4,657,700 | 1,355,650 | 1,478,852 | 1,184,660 | 1,131,397 | 1,059,453 | 1,182,109 | 1,909,215 |
| 1964 | 3,845,888 | 4,974,556  | 5,426,498  | 3,193,788  | 1,384,392 | 1,041,711 | 971,146   | 1,462,987 | 1,542,929 | 1,852,280 | 525,536   | 703,178   |
| 1965 | 4,154,754 | 6,281,776  | 7,360,888  | 8,261,310  | 6,437,582 | 4,036,225 | 3,297,160 | 2,580,483 | 1,687,431 | 2,063,787 | 3,068,186 | 4,878,389 |
| 1966 | 4,440,739 | 6,549,658  | 4,728,831  | 3,409,429  | 3,102,499 | 2,081,105 | 1,899,162 | 1,929,042 | 1,435,945 | 2,241,601 | 2,504,874 | 2,933,097 |
| 1967 | 4,057,425 | 4,122,205  | 4,176,276  | 2,099,257  | 1,334,167 | 1,031,783 | 1,123,584 | 836,175   | 997,957   | 961,965   | 1,089,122 | 2,658,287 |
| 1968 | 3,197,645 | 2,702,713  | 4,174,045  | 2,097,710  | 1,860,501 | 1,145,809 | 1,632,899 | 2,107,437 | 2,744,281 | 2,007,215 | 2,155,906 | 1,964,527 |
| 1969 | 2,345,165 | 2,769,932  | 6,324,308  | 6,935,128  | 7,895,689 | 4,133,864 | 1,715,978 | 1,760,900 | 1,771,295 | 1,660,915 | 1,582,342 | 2,133,276 |
| 1970 | 6,310,369 | 10,787,530 | 14,137,810 | 11,135,920 | 9,698,282 | 7130761   | 4,779,425 | 4,848,070 | 4773541   | 4,473,689 | 3,000,746 | 2,543,317 |
| 1971 | 1,895,066 | 3,194,843  | 5,098,249  | 4,817,334  | 3,015,614 | 2,350,503 | 3,121,872 | 3,827,084 | 3466583   | 3,018,701 | 3,724,288 | 3,800,192 |
| 1972 | 5,886,226 | 6,889,323  | 7,445,824  | 4,767,073  | 3,136,134 | 2,713,880 | 2,138,707 | 1,690,730 | 1,348,869 | 1,227,993 | 1,140,384 | 2,337,956 |
| 1973 | 3,768,454 | 3,882,752  | 3,840,114  | 1,524,991  | 815,748   | 582,377   | 1,175,937 | 541,483   | 816,565   | 1,341,442 | 2,163,379 | 1,972,436 |
| 1974 | 2,597,888 | 3,543,061  | 4,410,033  | 4,155,136  | 3,360,099 | 3,040,496 | 2,408,332 | 1,971,782 | 1,441,163 | 1,611,421 | 1,676,850 | 1,126,649 |
| 1975 | 1,010,533 | 2,187,394  | 5,053,889  | 4,045,153  | 2,830,089 | 1,514,035 | 1,496,137 | 1,264,570 | 1,304,127 | 1,410,340 | 1,279,203 | 1,710,247 |
| 1976 | 2,127,963 | 4,190,732  | 5,050,645  | 2,679,496  | 2,930,559 | 2,578,082 | 1,934,089 | 2,059,849 | 1,234,449 | 1,582,157 | 2,160,741 | 3,214,625 |
| 1977 | 1,918,159 | 2,460,301  | 2,663,668  | 2,557,887  | 1,853,953 | 1,374,297 | 1,053,084 | 752,210   | 506,851   | 313,111   | 128,175   | 195,377   |
| 1978 | 245,908   | 806,537    | 1,063,143  | 833,071    | 425,599   | 207,846   | 273,494   | 247,411   | 332,788   | 505,281   | 734,338   | 869,859   |
| 1979 | 1,002,829 | 1,138,779  | 1,388,163  | 1,118,577  | 618,940   | 463,546   | 491,525   | 480,336   | 384,936   | 330,773   | 283,047   | 363,351   |
| 1980 | 461,452   | 523,174    | 705,087    | 545,491    | 635,123   | 518,556   | 528,168   | 419,273   | 360,454   | 356,880   | 382,628   | 480,753   |
| 1981 | 929,657   | 1,630,146  | 1,708,486  | 1,804,618  | 2,128,345 | 1,604,501 | 1,382,503 | 1,434,416 | 1,160,744 | 1,590,016 | 1,568,468 | 1,849,099 |
| 1982 | 2,031,170 | 2,363,049  | 2,525,817  | 2,195,488  | 2,184,578 | 1,476,403 | 1,481,406 | 838,298   | 781,703   | 790,185   | 670,058   | 412,029   |
| 1983 | 120,318   | 23,904     | 5,454      | 7,087      | 17,376    | 21,052    | 8,318     | 3,638     | 3,271     | 4,106     | 5,000     | 6,446     |
| 1984 | 9,966     | 14,545     | 29,025     | 42,545     | 62,900    | 35,087    | 41,590    | 42,797    | 39,407    | 65,037    | 96,077    | 113,573   |
| 1985 | 197,855   | 268,764    | 603,246    | 406,172    | 445,338   | 498,387   | 391,979   | -         | -         | -         | -         | -         |

<sup>a</sup>The mean of the values for August and September is  $(1434416 + 1160744)/2 = 1.297580$ , or  $1.3 \times 10^6$  tonnes, very close to the independent estimate of  $1.2 \times 10^6$  tonnes of Santander et al. (1984).

Table 4. Estimated biomass of mature female anchoveta (*Engraulis ringens*) off Peru (4-14°S), January 1953 to July 1985 (in tonnes). Note that estimates for the early/mid-1970s tend to be biased upward (see Table 3 and text).

Tabla 4. Biomasa estimada de anchovetas (*Engraulis ringens*) hembras maduras frente al Perú (4-14°S), Enero 1953 a Julio 1985 (en toneladas). Notar que los valores para comienzos y mediados de 1970 tienden a estar sobreestimados (ver Tabla 3 y texto).

| Year | Jan       | Feb       | Mar       | Apr       | May       | Jun       | Jul       | Aug       | Sep       | Oct       | Nov       | Dec       |
|------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| 1953 | 1,321,212 | 2,014,939 | 2,275,717 | 1,801,389 | 965,765   | 426,267   | 389,939   | 265,458   | 185,938   | 110,709   | 139,214   | 184,368   |
| 1954 | 429,495   | 650,656   | 536,331   | 276,803   | 189,279   | 139,294   | 219,618   | 85,966    | 94,424    | 101,666   | 189,623   | 828,052   |
| 1955 | 2,522,634 | 1,819,346 | 829,857   | 1,193,904 | 503,620   | 464,845   | 426,699   | 289,324   | 365,414   | 272,767   | 443,084   | 707,374   |
| 1956 | 1,526,926 | 2,352,075 | 2,572,280 | 1,817,512 | 1,450,474 | 1,251,817 | 1,203,284 | 986,455   | 662,526   | 550,157   | 623,856   | 559,713   |
| 1957 | 818,338   | 3,698,823 | 3,510,480 | 3,232,838 | 3,049,771 | 2,288,889 | 1,502,866 | 585,645   | 299,382   | 289,275   | 414,063   | 1,630,828 |
| 1958 | 1,896,764 | 1,902,070 | 1,817,655 | 984,118   | 592,998   | 391,414   | 355,133   | 118,092   | 138,124   | 174,493   | 262,950   | 161,936   |
| 1959 | 333,331   | 1,156,546 | 959,565   | 753,630   | 484,261   | 370,056   | 253,737   | 234,677   | 193,313   | 217,767   | 300,051   | 651,279   |
| 1960 | 365,556   | 736,150   | 861,472   | 580,851   | 419,607   | 515,849   | 450,584   | 564,575   | 552,077   | 531,202   | 526,773   | 1,115,724 |
| 1961 | 2,373,017 | 3,538,035 | 2,700,905 | 2,368,130 | 1,928,769 | 1,224,675 | 828,860   | 823,744   | 815,505   | 872,371   | 869,044   | 1,064,992 |
| 1962 | 2,832,774 | 2,896,403 | 2,348,297 | 1,840,781 | 2,015,436 | 1,469,378 | 1,252,760 | 1,198,712 | 1,411,393 | 1,034,031 | 1,268,713 | 1,204,870 |
| 1963 | 1,375,350 | 2,123,551 | 2,511,024 | 1,795,522 | 2,939,777 | 841,235   | 913,842   | 735,298   | 696,602   | 652,689   | 744,581   | 1,158,849 |
| 1964 | 2,146,985 | 2,715,533 | 2,997,359 | 1,850,239 | 848,986   | 659,378   | 630,918   | 960,219   | 1,015,379 | 1,227,516 | 294,556   | 403,778   |
| 1965 | 2,676,725 | 3,818,796 | 4,353,884 | 4,648,581 | 3,580,680 | 2,269,759 | 1,850,283 | 1,469,941 | 977,384   | 1,207,745 | 1,776,023 | 2,762,433 |
| 1966 | 2,406,010 | 3,478,431 | 2,574,854 | 1,930,134 | 1,836,428 | 1,290,514 | 1,215,856 | 1,268,462 | 977,172   | 1,536,607 | 1,754,989 | 2,092,552 |
| 1967 | 2,759,539 | 2,538,842 | 2,559,680 | 1,327,411 | 822,522   | 643,145   | 710,856   | 545,855   | 661,927   | 656,376   | 752,256   | 1,813,840 |
| 1968 | 2,090,197 | 1,756,402 | 2,580,961 | 1,419,964 | 1,257,604 | 801,035   | 1,147,133 | 1,496,569 | 1,959,417 | 1,466,828 | 1,570,893 | 1,404,380 |
| 1969 | 1,516,585 | 1,627,485 | 3,472,801 | 3,839,018 | 4,309,745 | 2,339,228 | 1,054,600 | 1,097,834 | 1,122,922 | 1,057,294 | 1,012,820 | 1,299,171 |
| 1970 | 3,555,944 | 6,043,169 | 8,022,568 | 6,647,045 | 6,075,676 | 4,744,813 | 3,377,803 | 3,478,003 | 3,479,941 | 3,216,208 | 2,171,110 | 1,795,029 |
| 1971 | 1,265,653 | 1,964,446 | 2,971,928 | 2,685,583 | 1,758,190 | 1,401,111 | 1,872,242 | 2,334,073 | 2,227,656 | 2,056,919 | 2,555,923 | 2,618,777 |
| 1972 | 4,050,227 | 4,809,750 | 5,271,819 | 3,316,578 | 1,981,685 | 1,692,488 | 1,387,116 | 1,174,567 | 1,027,277 | 924,213   | 787,335   | 1,341,532 |
| 1973 | 1,990,209 | 2,110,506 | 2,155,432 | 923,170   | 514,383   | 386,946   | 851,625   | 391,547   | 606,030   | 1,018,524 | 1,650,892 | 1,583,212 |
| 1974 | 2,099,287 | 2,792,510 | 3,459,558 | 3,257,313 | 2,653,672 | 2,363,980 | 1,955,769 | 1,632,632 | 1,186,710 | 1,354,742 | 1,342,611 | 877,815   |
| 1975 | 775,308   | 1,464,269 | 3,113,251 | 2,593,830 | 1,923,235 | 1,118,888 | 1,129,588 | 989,220   | 1,039,252 | 1,148,818 | 1,077,513 | 1,451,570 |
| 1976 | 1,811,819 | 2,795,350 | 2,998,613 | 1,700,991 | 1,801,625 | 1,530,117 | 1,145,651 | 1,234,141 | 792,898   | 1,012,637 | 1,390,817 | 1,920,117 |
| 1977 | 1,110,230 | 1,402,801 | 1,574,778 | 1,605,820 | 1,253,189 | 1,002,394 | 806,196   | 600,132   | 416,590   | 260,225   | 95,584    | 124,228   |
| 1978 | 146,899   | 431,767   | 569,676   | 458,174   | 250,568   | 171,093   | 341,778   | 62,729    | 222,000   | 341,871   | 499,929   | 589,929   |
| 1979 | 637,459   | 731,523   | 895,537   | 731,496   | 406,464   | 321,374   | 341,140   | 335,095   | 275,129   | 236,665   | 201,065   | 241,088   |
| 1980 | 308,531   | 343,108   | 446,921   | 347,099   | 411,600   | 344,778   | 364,262   | 303,403   | 266,986   | 268,496   | 288,103   | 355,013   |
| 1981 | 652,317   | 1,051,476 | 1,112,970 | 1,196,661 | 1,420,186 | 1,124,657 | 1,015,496 | 1,068,897 | 896,331   | 1,210,731 | 1,217,515 | 1,457,802 |
| 1982 | 1,606,276 | 1,851,687 | 2,006,827 | 1,771,793 | 1,762,474 | 1,206,989 | 1,215,206 | 713,321   | 676,012   | 672,629   | 565,089   | 339,891   |
| 1983 | 88,086    | 17,161    | 2,987     | 3,630     | 9,161     | 11,052    | 4,735     | 2,420     | 2,304     | 2,804     | 3,370     | 4,269     |
| 1984 | 6,246     | 9,086     | 18,053    | 25,778    | 41,675    | 24,282    | 28,511    | 30,013    | 27,958    | 45,221    | 64,723    | 75,672    |
| 1985 | 128,788   | 175,265   | 376,325   | 269,785   | 301,652   | 342,614   | 273,543   | -         | -         | -         | -         | -         |

Table 5. Estimated monthly reproductive output by the anchoveta stock off Peru (4-14°S), January 1953 to July 1985, in billion eggs (i.e.,  $\times 10^9$ ). The values for the early/mid-1970s are overestimates (see Tables 3, 4 and text).

Tabla 5. Estimación mensual de la producción de huevos del stock de anchoveta frente al Perú (4-14°S), Enero 1953 a Julio 1985, en billones de huevos (es decir  $\times 10^9$ ). Los valores para comienzos y mediados de 1970 están sobreestimados (ver Tablas 3, 4 y texto).

| Year | Jan       | Feb       | Mar       | Apr     | May     | Jun       | Jul       | Aug       | Sep        | Oct        | Nov       | Dec       |
|------|-----------|-----------|-----------|---------|---------|-----------|-----------|-----------|------------|------------|-----------|-----------|
| 1953 | 223,001   | 417,595   | 277,665   | 56,483  | 11,271  | 50,263    | 151,742   | 279,131   | 217,516    | 149,058    | 156,856   | 34,823    |
| 1954 | 60,900    | 137,709   | 102,567   | 17,793  | 5,183   | 37,383    | 140,422   | 148,742   | 163,292    | 194,956    | 259,386   | 191,144   |
| 1955 | 315,471   | 403,509   | 174,539   | 56,349  | 9,335   | 73,434    | 208,382   | 361,279   | 618,567    | 603,340    | 792,571   | 250,866   |
| 1956 | 374,074   | 758,040   | 607,044   | 135,692 | 37,093  | 296,722   | 904,731   | 1,981,312 | 1,561,567  | 1,632,756  | 1,381,554 | 280,881   |
| 1957 | 155,591   | 517,390   | 381,124   | 94,086  | 23,095  | 156,332   | 300,852   | 357,408   | 244,835    | 380,447    | 299,984   | 141,887   |
| 1958 | 518,700   | 445,033   | 339,109   | 23,393  | 8,296   | 49,545    | 142,436   | 163,321   | 253,806    | 361,256    | 384,722   | 34,239    |
| 1959 | 44,404    | 146,000   | 114,313   | 30,434  | 6,993   | 54,097    | 128,467   | 294,425   | 226,750    | 295,232    | 305,874   | 110,823   |
| 1960 | 29,557    | 101,636   | 115,909   | 29,071  | 9,226   | 101,566   | 301,887   | 910,650   | 1,241,628  | 1,422,102  | 1,076,289 | 388,551   |
| 1961 | 528,572   | 1,079,356 | 597,202   | 139,173 | 40,253  | 239,320   | 502,711   | 1,185,258 | 1,589,138  | 1,954,018  | 1,402,278 | 324,524   |
| 1962 | 608,424   | 969,642   | 693,496   | 145,039 | 52,135  | 336,026   | 882,237   | 2,065,840 | 3,172,399  | 2,892,567  | 2,501,054 | 480,932   |
| 1963 | 420,475   | 835,661   | 634,301   | 131,410 | 77,738  | 168,788   | 506,827   | 952,468   | 1,125,873  | 1,206,342  | 1,110,459 | 305,934   |
| 1964 | 323,521   | 561,300   | 501,471   | 100,526 | 20,036  | 141,186   | 418,582   | 1,499,760 | 2,063,507  | 2,895,659  | 242,803   | 77,668    |
| 1965 | 794,962   | 1,487,000 | 1,110,642 | 216,088 | 51,141  | 281,229   | 640,907   | 1,279,788 | 1,186,701  | 1,750,467  | 1,810,299 | 505,548   |
| 1966 | 288,570   | 551,604   | 385,616   | 91,841  | 36,815  | 252,329   | 756,715   | 1,982,197 | 2,232,726  | 4,068,163  | 3,710,504 | 953,446   |
| 1967 | 1,016,306 | 1,120,565 | 832,521   | 118,315 | 21,812  | 138,367   | 452,102   | 897,621   | 1,471,914  | 1,814,239  | 1,571,817 | 731,381   |
| 1968 | 662,502   | 894,911   | 834,520   | 154,923 | 45,590  | 258,750   | 1,050,496 | 3,229,639 | 5,549,850  | 5,038,703  | 3,950,467 | 665,776   |
| 1969 | 510,700   | 606,165   | 616,716   | 174,754 | 56,303  | 312,715   | 603,249   | 1,494,839 | 2,081,500  | 2,217,373  | 1,627,657 | 357,585   |
| 1970 | 594,626   | 1,577,838 | 1,666,492 | 436,584 | 163,688 | 1,269,115 | 3,088,409 | 7,588,246 | 10,352,370 | 10,445,460 | 5,413,273 | 875,599   |
| 1971 | 481,033   | 961,559   | 855,984   | 134,621 | 38,304  | 259,789   | 982,472   | 2,958,945 | 4,479,487  | 5,702,904  | 5,347,169 | 1,133,995 |
| 1972 | 1,602,956 | 3,296,360 | 2,867,123 | 428,504 | 64,603  | 443,638   | 1,236,406 | 3,015,993 | 4,355,195  | 4,285,281  | 1,942,809 | 300,584   |
| 1973 | 193,709   | 429,375   | 416,083   | 63,714  | 13,875  | 101,969   | 779,360   | 886,931   | 1,915,416  | 3,897,503  | 4,827,496 | 1,115,445 |
| 1974 | 1,412,494 | 3,040,711 | 2,869,610 | 679,645 | 188,187 | 1,325,342 | 3,395,300 | 6,711,189 | 5,785,994  | 7,996,861  | 5,022,691 | 631,701   |
| 1975 | 499,349   | 1,039,876 | 1,202,590 | 273,601 | 79,166  | 461,409   | 1,373,710 | 3,009,560 | 4,306,292  | 5,679,465  | 4,381,157 | 1,254,503 |
| 1976 | 1,506,248 | 2,362,314 | 1,217,878 | 219,638 | 64,788  | 354,618   | 706,656   | 1,775,937 | 1,755,170  | 2,376,781  | 2,434,723 | 512,852   |
| 1977 | 230,978   | 422,197   | 424,027   | 134,950 | 45,766  | 368,202   | 952,937   | 1,808,994 | 1,769,965  | 1,316,274  | 296,443   | 49,160    |
| 1978 | 40,253    | 82,948    | 78,159    | 18,911  | 5,278   | 25,020    | 104,061   | 275,860   | 508,464    | 923,167    | 1,030,519 | 245,475   |
| 1979 | 195,182   | 376,880   | 351,158   | 74,649  | 14,198  | 106,376   | 317,198   | 709,652   | 801,274    | 767,934    | 473,503   | 93,963    |
| 1980 | 115,443   | 196,023   | 168,802   | 32,054  | 13,022  | 94,896    | 319,551   | 706,241   | 867,625    | 1,040,662  | 841,643   | 203,865   |
| 1981 | 295,708   | 594,822   | 478,298   | 131,578 | 52,624  | 381,288   | 1,106,638 | 2,774,401 | 3,323,482  | 4,888,765  | 3,874,244 | 997,701   |
| 1982 | 1,030,399 | 1,951,983 | 1,644,554 | 366,554 | 120,343 | 679,860   | 1,926,211 | 2,943,836 | 3,818,172  | 4,282,944  | 2,659,675 | 308,748   |
| 1983 | 46,929    | 14,002    | 527       | 43      | 75      | 708       | 2,161     | 4,972     | 7,098      | 9,153      | 8,319     | 2,066     |
| 1984 | 2,177     | 4,870     | 6,674     | 1,986   | 1,427   | 7,769     | 25,091    | 65,242    | 81,401     | 143,562    | 141,249   | 32,941    |
| 1985 | 46,425    | 102,543   | 134,229   | 29,575  | 11,480  | 108,643   | 255,221   | -         | -          | -          | -         | -         |

However, the parental biomass estimates, and hence, the estimates of reproductive output for some months (especially during the early 1970s), are different from the values than would have been estimated based on available independent estimates of biomass (Pauly and Palomares, this vol.). Thus, in order for our estimates of egg mortality to be as accurate as possible, we have replaced, in Table 6, the VPA-based estimates of parental biomass (and reproductive output) by proportionally adjusted independent biomass estimates (and by the corresponding estimate of the reproductive output, respectively) in all cases when two biomass estimates for the same month differed by more than 5%. The adjusted estimates are given in brackets in Table 2.

### The Evidence for Egg Cannibalism in Anchoveta

Fig. 3A presents a plot of  $\ln(N/(D \cdot P))$  vs. parental stock size ( $P$ ) for the period 1964 to 1985. As might be seen, there is a strong negative correlation between the egg survival index ( $\ln(N/(D \cdot P))$ ) and parent stock, suggesting a strong impact of parental stock on egg mortality rate. This confirms an earlier plot of Santander (1987) based on maps covering the period 1964 to 1982 and on the parental biomass estimates of Pauly and Soriano (1987).

However, parental biomass is not the only factor affecting anchoveta egg survival, and we have derived, to illustrate this, the model:

$$\ln(N/(D \cdot P)) = 33.23 - 2.15 \log_{10} P - 2.50T + 0.063T^2 \quad \dots 7)$$

where  $T$  is the SST in  $^{\circ}\text{C}$  and where  $R^2 = 0.594$  (see also Fig 3B and Table 6). Fig. 4 shows that the residuals of this model lack structure, as required for multiple linear regression. Equation (7), it must be realized, is only one of the many possible models, and should not be taken as representing final identification of factors affecting anchoveta egg survival.

Interesting here is Fig. 5 which shows the dependent variable of equation (7) as a function of temperature. As might be seen, some curvature is apparent, as implied by the significant squared term in equation (7).

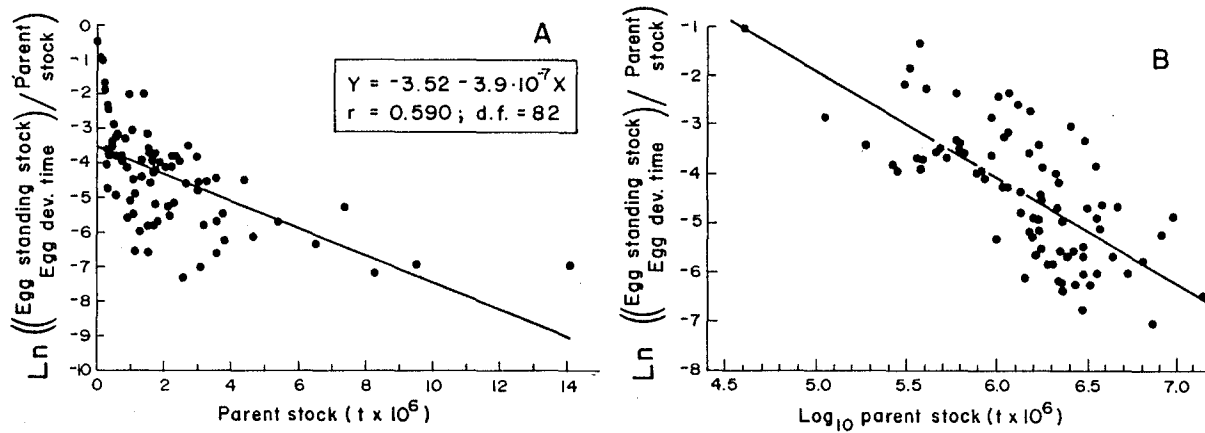


Fig. 3. Evidence of density-dependence in anchoveta egg survival.

A. Bivariate plot, as used to derive Ricker-type stock-recruitment relationships.

B. Plot of the residuals of equation (7) vs. the line linking the index of egg survival (Y-axis) and parental stock. Note markedly improved fit over Plot A, resulting from the inclusion of SST and SST<sup>2</sup> as variables (see text).

Fig. 3. Evidencia de la densodependencia en la sobrevivencia de huevos de anchoveta.

A. Ploteo bivariable, tal como es usado para derivar la relación stock-reclutamiento de Ricker.

B. Ploteo de residuales de la ecuación (7) vs la línea que relaciona el índice de sobrevivencia de huevos (eje Y) y el stock de padres. Notar el mejor ajuste en relación al ploteo A, a consecuencia de la inclusión de TSM y TSM<sup>2</sup> como variables (ver texto).

Table 6. Statistics of multiple regression linking anchoveta egg survival index and its predictor variables (equation 7; degrees of freedom = 80, R = 0.771).

Tabla 6. Datos estadísticos de la regresión múltiple que relaciona el índice de sobrevivencia de huevos de anchoveta y sus variables predictoras (ecuación 7; grados de libertad = 80; R = 0.771).

| Variables                | (Units)                                | Estimates              | Standard errors <sup>a</sup> |
|--------------------------|--|------------------------|------------------------------|
| $\ln (N/(D \cdot P))$    | (eggs 10 <sup>9</sup> / days · tonnes) | (independent variable) | 0.952                        |
| $\log_{10}$ parent stock | (tonnes)                               | -2.147                 | 0.257                        |
| Sea surface temp (SST)   | (°C)                                   | -0.250                 | 0.942                        |
| (SST) <sup>2</sup>       | (°C) <sup>2</sup>                      | 0.0627                 | 0.0245                       |

<sup>a</sup> Standard error of Y-estimate

Taking the partial derivative of equation (7) with respect to temperature:

$$\frac{\delta \ln (N/(D \cdot P))}{\delta T} = 2 (0.0663)T - 2.50 \quad \dots 8)$$

and setting it equal to zero allows estimation of the temperature ( $T_{\min}$ ) at which  $\ln (N/(D \cdot P))$  is minimum, i.e.,  $T_{\min} = 19.8^\circ\text{C}$ .

Thus, our analysis of Santander's maps provides evidence for:

- i) parental cannibalism on anchoveta eggs; and
- ii) a parabolic relationship between egg mortality and SST, with maximum close to the upper limit of the optimal temperature range of anchoveta (about 15-20°C).

One multiple regression model we derived, using the data in Table 2, to explain variability of our estimates of egg mortality, is:

$$\log_{10} Z_{\text{egg}} = -23.7 + 0.608 \log_{10} P + 0.379 \log_{10} S + 0.505 A_T + 2.4T - 0.0751T^2 \quad \dots 9)$$

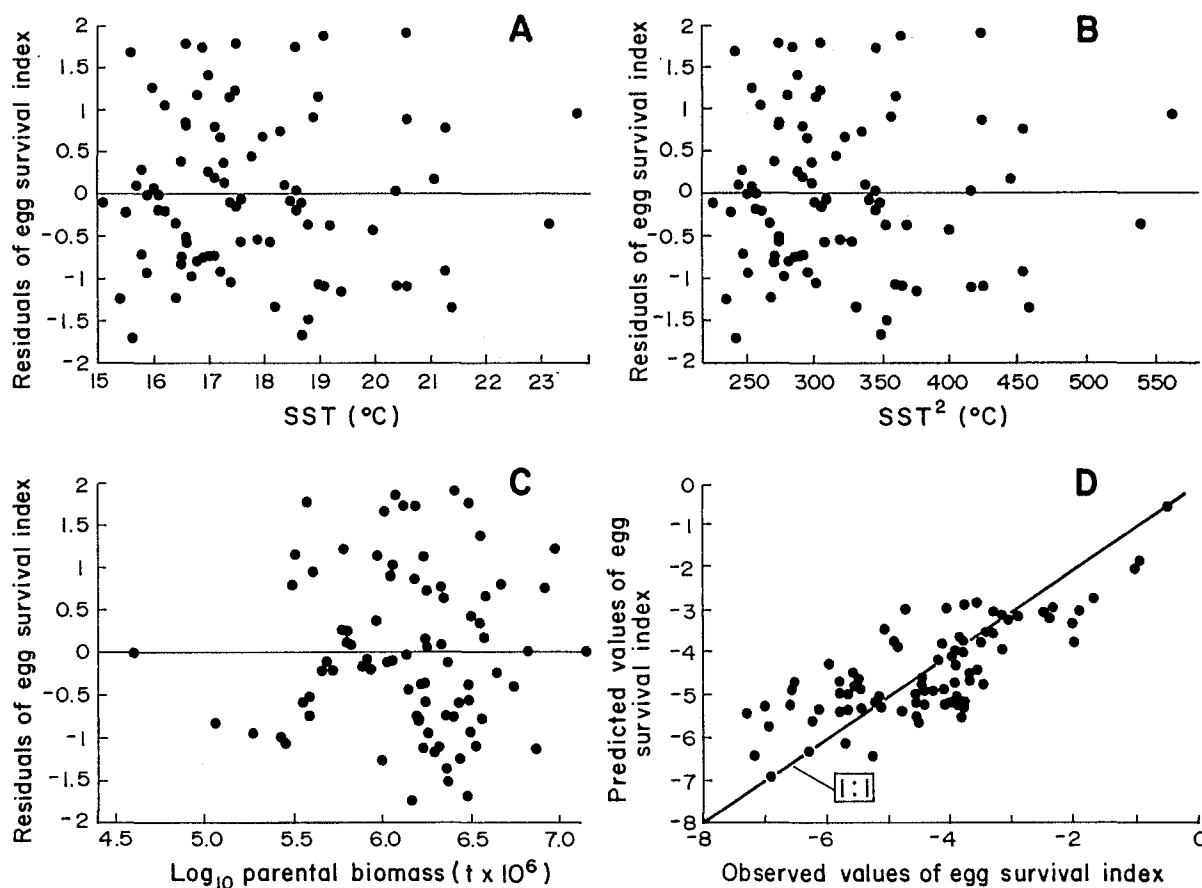


Fig. 4. Selected features of model represented by equation (7). A-C: residuals of equation (7) linking egg survival index and its predictor variables. Note absence of structure. D: plot of observed vs predicted values of the egg survival index.

Fig. 4. Características seleccionadas del modelo representado por la ecuación (7). A-C: residuales de ecuación (7) relacionando el índice de sobrevivencia de huevos y sus variables predictoras. Notar la ausencia de estructura. D: ploteo de valores observados vs valores predictivos del índice de sobrevivencia de larvas.

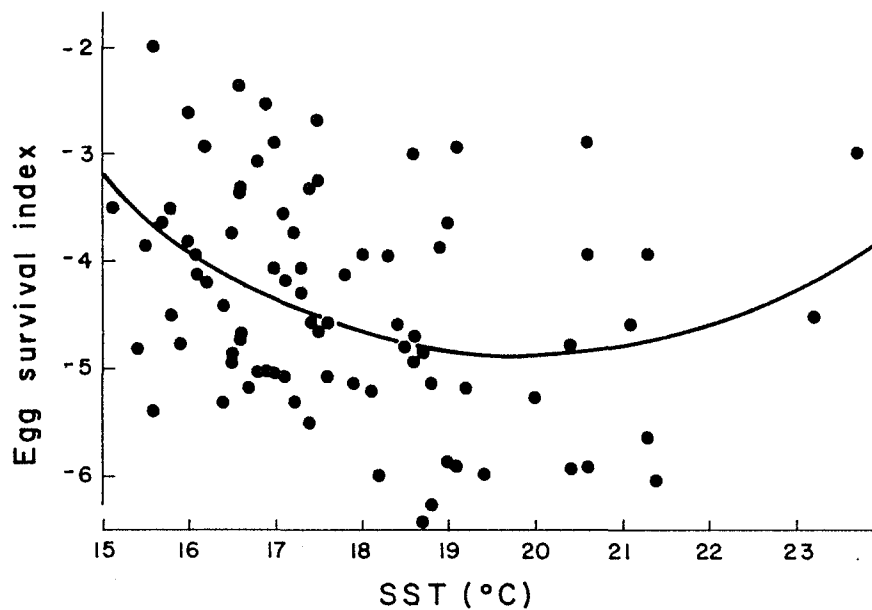


Fig. 5. Relationship of egg survival index and SST; note curvature, suggesting a minimum at 19.8°C.

Fig. 5. Relación entre el índice de sobrevivencia de huevos y TSM; notar curvatura, sugiriendo un mínimo a 19.8°C.

which has an  $R^2 = 0.562$  and whose statistics are given in Table 7. Fig. 6 shows that this model gives a particularly good fit to SST and SST anomaly, and a lesser fit to the biological variables (parent stock and sardine stock). Again, SST has a parabolic relationship with egg mortality. Taking the partial derivative of equation (9) with respect to T gives:

$$\frac{\delta \log_{10} Z_{egg}}{\delta T} = 2.4 - 2(0.0751) T \quad \dots 10)$$

which set equal to zero and solved for T gives  $T_{max} = 16.0^\circ\text{C}$ .

Thus, we find again that anchoveta egg mortality has a peak within the range of temperature that is optimal for anchoveta.

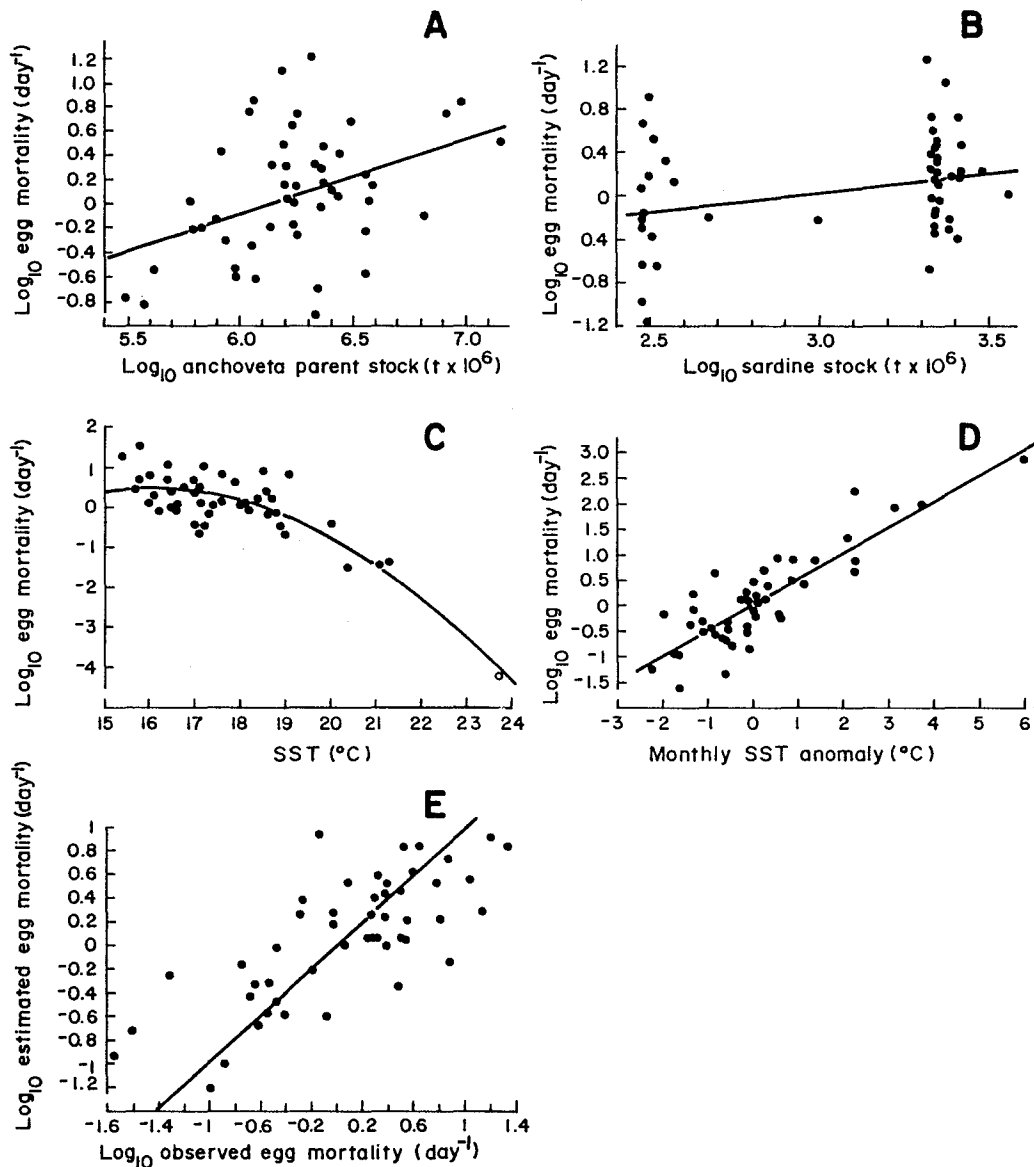


Fig. 6. Relationship between anchoveta egg mortality and its predictor variables. The solid lines of Plots A-D represent the axes of equation (9), with intercepts set at the mean of all other variables; the dots represent the residuals, plotted from the solid lines. Plot E shows the predicted vs. the observed mortalities. Note overall good fit of equation (9) to the data, the absence of structure in the residuals, and the strong relationship between mortality, SST and SST anomaly.

Fig. 6. Relación entre la mortalidad de huevos de anchoveta y sus variables predictoras. Las líneas sólidas de los ploteos A-D representan el eje de la ecuación (9), con interceptos fijados al promedio de todas las otras variables; los puntos representan los residuos, ploteados de las líneas sólidas. El Ploteo E muestra la mortalidad estimada vs la observada. Notar el buen ajuste general de la ecuación (9) a los datos, la ausencia de estructura en los residuos y la fuerte relación entre mortalidad, TSM y la anomalía de TSM.

Table 7. Statistics of equation (9), relating anchoveta egg mortality and its predictor variables (degrees of freedom = 43;  $R = 0.751$ ).

Tabla 7. Datos estadísticos de la ecuación (9), que relaciona la mortalidad de huevos de anchoveta y sus variables predictoras (grados de libertad = 43;  $R = 0.751$ ).

| Variables                 | (Units)              | Estimates         | Standard errors <sup>a</sup> |
|---------------------------|----------------------|-------------------|------------------------------|
| $\log_{10}$ egg mortality | (day <sup>-1</sup> ) | (indep. variable) | 0.4937                       |
| $\log_{10}$ parent stock  | (tonnes)             | 0.6078            | 0.2851                       |
| $\log_{10}$ sardine stock | (tonnes)             | 0.3788            | 0.2160                       |
| SST anomaly (AT)          | (°C)                 | 0.5049            | 0.0758                       |
| Sea surface temp. (SST)   | (°C)                 | 2.4007            | 0.6881                       |
| (SST) <sup>2</sup>        | (°C) <sup>2</sup>    | -0.0751           | 0.0185                       |

<sup>a</sup> Standard error of Y-estimate.

Fig. 6D, which shows the *positive* partial correlation between anchoveta egg mortality and SST anomaly, suggests, however, that the observed parabolic relationship between SST and egg mortality do not reflect a causal linkage. Rather, SST, which fluctuates seasonally, is lowest in September-October (see Fig. 8 and Bakun 1987), during a period when anchoveta concentrate under the coast for spawning (Jordán 1971; FAO 1981; Csirke, this vol.).

Anchoveta feed during the spawning season and hence, the peak consumption of anchoveta eggs by adult anchoveta occurs in September-October (Fig. 7; Table 8). This could explain the apparent relationships between SST and egg mortality. As for SST anomaly, we assume that it is linked with anchoveta egg mortality via two mechanisms: (1) increased predation on anchoveta eggs by zooplankton and other predators not included in our models, and whose metabolic rate and hence, food consumption, can be expected to increase when the SST anomaly increases and (2) increased concentration of anchoveta within the small inshore patches of low SST waters that remain during high SST anomalies (Muck et al., this vol.).

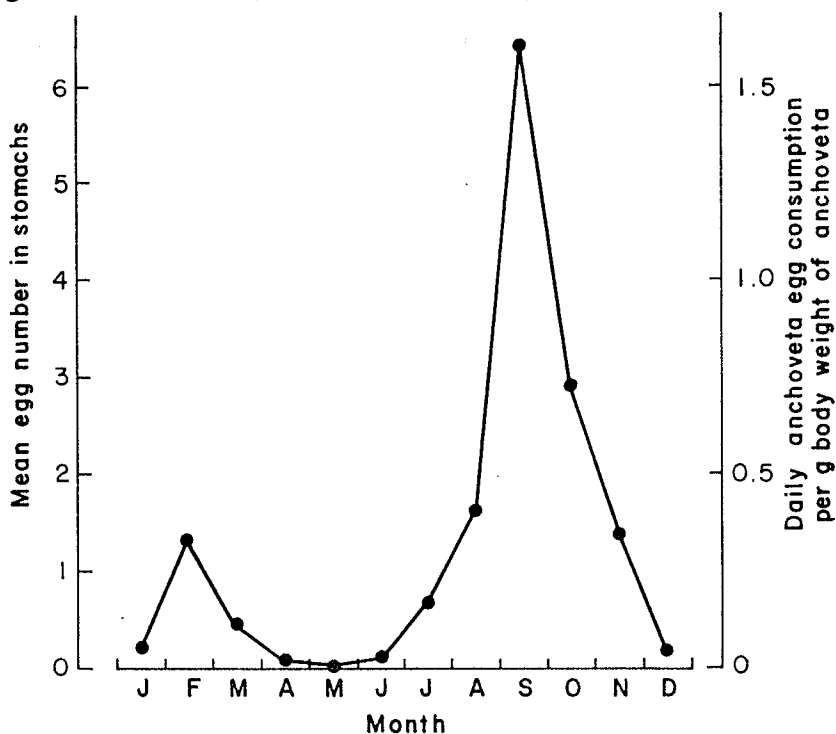


Fig. 7. Mean number of anchoveta eggs in the stomach of anchoveta sampled from 1953 to 1982 by Rojas de Mendiola (this vol.) and Alamo (this vol.), as extracted from their database (see Table 8 for details). Note strong seasonality, with a major peak during the major spawning season (September/ October) and a minor peak during the minor spawning season (February/March). The scale on the right side provides an approximate conversion to egg consumption rate (see Table 8).

Fig. 7. Número promedio de huevos de anchoveta en el estómago de anchoveta muestreada de 1953 a 1982 por Rojas de Mendiola (este vol.) y Alamo (este vol.), extraído de su base de datos (ver tabla 8 para detalles). Notar la fuerte estacionalidad, con un pico mayor durante la estación de desove principal (Septiembre/Octubre) y un pico menor durante la estación de menor desove (Febrero/Marzo). La escala del lado derecho proporciona una conversión aproximada de la tasa de consumo de huevos (ver Tabla 8).

Equation (9) predicts, for anchoveta eggs in August/September 1987, a value of  $Z = 2.13 \text{ day}^{-1}$ ; this is much higher than the value of  $0.91 \text{ day}^{-1}$  presented by Santander et al. (1984).

Data are available which might allow resolving this discrepancy, and testing of the hypotheses presented above. Notably, a detailed analysis of the Rojas/Alamo database on anchoveta stomach contents emphasizing seasonal and interyear variations of egg cannibalism (i.e., going beyond the mean seasonal cycle in Fig. 8), and combined with corresponding estimates of anchoveta concentration, could contribute toward elucidating the role of egg cannibalism in anchoveta population dynamics.

Table 8. Data for quantification of egg cannibalism in anchoveta, as extracted from the Rojas/Alamo database (see Rojas de Mendiola, this vol.; Alamo, this vol.; Pauly et al., this vol.).

Tabla 8. Datos para la cuantificación del canibalismo de huevos de anchoveta, extraídos de la base de datos de Rojas/Alamo (ver Rojas de Mendiola, este vol.; Alamo, este vol.; Pauly et al., este vol.).

| Month     | No. of anchoveta with sampling month and record for eggs | No. of anchoveta with eggs in the stomach | Total no. of eggs in stomach | Mean eggs per anchoveta stomach | Daily Anchoveta egg consumption <sup>a</sup> |
|-----------|--|---|------------------------------|---------------------------------|--|
| January   | 616  | 38  | 126                          | 0.205                           | 0.051  |
| February  | 769  | 77  | 1000                         | 1.300                           | 0.325  |
| March     | 852  | 22  | 379                          | 0.445                           | 0.111  |
| April     | 633  | 17  | 60                           | 0.095                           | 0.024  |
| May       | 409  | 7   | 17                           | 0.042                           | 0.010  |
| June      | 266  | 6   | 34                           | 0.128                           | 0.032  |
| July      | 589  | 23  | 401                          | 0.681                           | 1.170  |
| August    | 996  | 204                                       | 1632                         | 1.639                           | 0.410  |
| September | 1698   | 520                                       | 10935                        | 6.440                           | 1.610  |
| October   | 869  | 99  | 1664                         | 1.915                           | 0.479  |
| November  | 1057   | 112                                       | 1469                         | 1.390                           | 0.348  |
| December  | 971  | 53  | 188                          | 0.194                           | 0.048  |

<sup>a</sup> Approximate daily anchoveta egg consumption per g body weight of anchoveta (see also Fig. 7), as computed from the daily ration of 0.448 g estimated by Pauly et al. (this vol.) for anchoveta of about 20 g live weight, and a mean stomach content of 0.122 g. The quotient of mean stomach content over ration is  $\approx 3.7$ , but this estimate of turnover rate was increased to 5 to account for the facts that (1) most stomachs with eggs were sampled early mornings, when stomach contents are less than average and (2) that eggs are more rapidly digested than other food items.

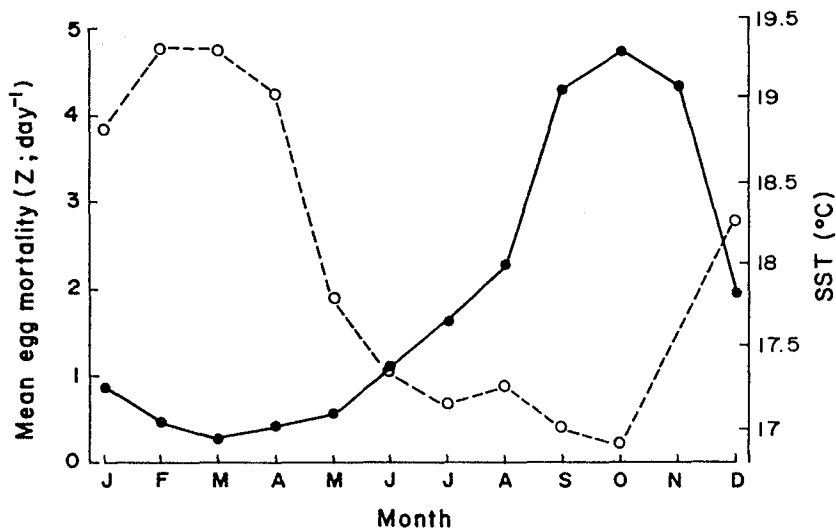


Fig. 8. Solid line: annual cycle of mean monthly anchoveta egg mortality, 1964 to 1985, based on map-specific  $Z$  values in Table 2, or on estimates from equation (9) when these could not be computed via equation (6); monthly means were smoothed over 3 months. Note strong summer peak, coincident with peak occurrence of eggs in anchoveta stomachs (see Fig. 7). Dotted line: mean seasonal cycle of sea surface temperature, as derived using only SST values for the months represented in Table 2, and smoothing over 3 months.

Fig. 8. Línea sólida: ciclo anual del promedio mensual de la mortalidad de huevos de anchoveta, 1964 a 1985, basado en valores de  $Z$  obtenidos de mapas específicos de la Tabla 2, o en estimaciones de la ecuación (9) cuando éstos no pudieron ser computados por la ecuación (6); los promedios mensuales fueron suavizados mediante promedio corrido de 3 meses. Notar el fuerte pico de verano, coincidente con la ocurrencia del pico de huevos en los estómagos de anchoveta (ver Fig. 7). Línea interrumpida: ciclo estacional promedio de la temperatura superficial derivado usando solo valores de TSM para los meses presentados en la Tabla 2, y suavizados con promedios corridos de 3 meses.

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