

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

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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.

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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)^a.

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).^a

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

^a See Pauly and Soriano (1987) for further details on model derivation and specification and on data sources.

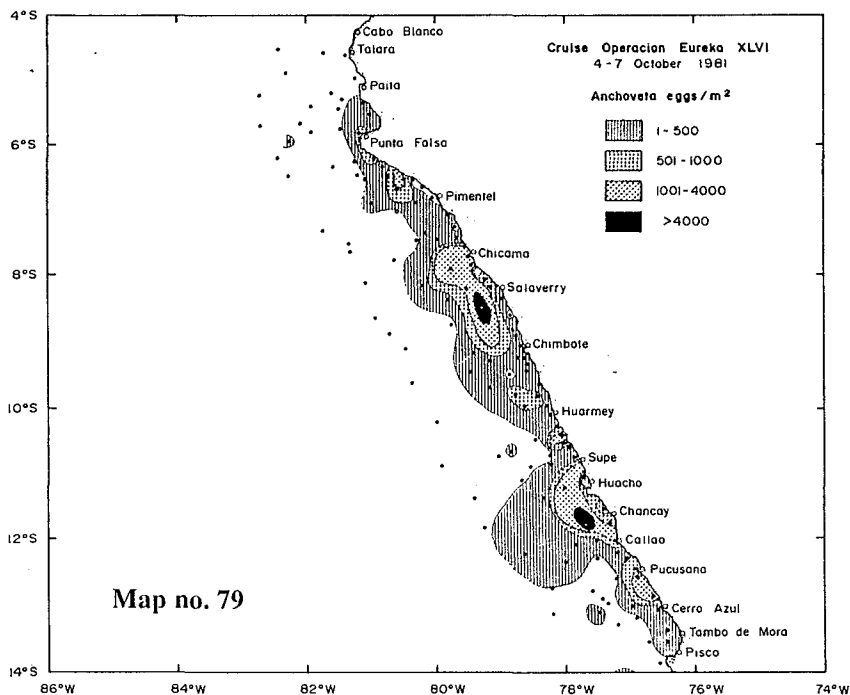


Fig. 1. Anchoveta egg distribution off Peru (4-14°S), in early October 1981. Details on this map (No. 79 in Santander 1987), given here as an example, are provided in Table 2.

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:

$$N_d = R e^{-ZD} \tag{... 2}$$

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:

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

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:

$$\bar{N} = \frac{1}{D} \int_0^D R e^{-ZD} \tag{... 4}$$

or

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

Table 2. Summary of data on anchoveta egg surveys conducted from 1964 to 1985 off Peru (4-14°S)^a, 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 ¹²) ^a	Daily reproductive output (egg x 10 ¹²) ^b	Anchoveta parent stock (t x 10 ⁶) ^b	Sardine biomass ^c (t x 10 ⁶)	Egg development time (day) ^d	Z (day ⁻¹) ^e	Estimated Z (day ⁻¹) ^f
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	1.21	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	-	-	(1.53)	2.42	1.35	-	0.402
58	61		Jul	28.0	(2.70)	(0.821)	2.52	1.77	0.507	1.832
59	62/63		Aug	25.4	(23.9)	(4.90)	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

^a Adapted from Santander (1987, Table 3).

^b From (part of) equation (1) and biomasses estimated by Pauly and Palomares (this vol.).

^c 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.

^d 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.

^e From equation (6).

^f From equation (9).

^g 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).

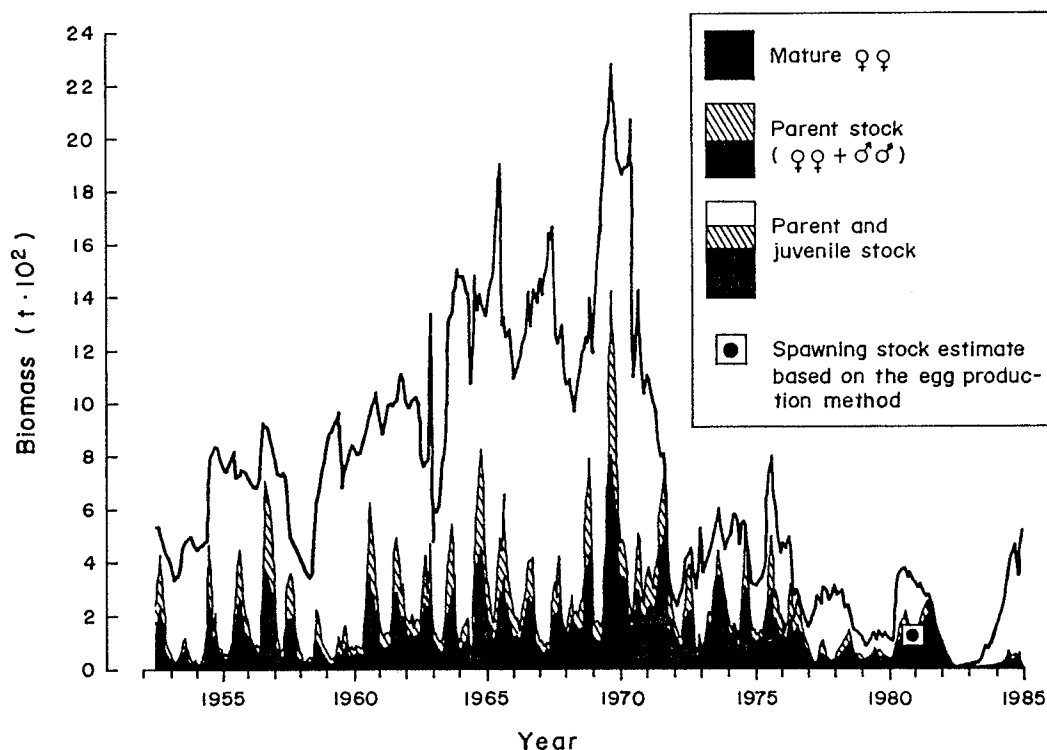


Fig. 2. Total biomass, parent (=mature) stock and biomass of mature female anchoveta off Peru (4-14°S), January 1953 to July 1985. Note strong, regular seasonal oscillations and very good match with independent spawning stock estimate in August/September 1981 by Santander et al. (1984).

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).^a

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	-	-	-	-	-

^aThe mean of the values for August and September is $(1434416 + 1160744)/2 = 1.297580$, or 1.3×10^6 tonnes, very close to the independent estimate of 1.2×10^6 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	4,287,944	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).

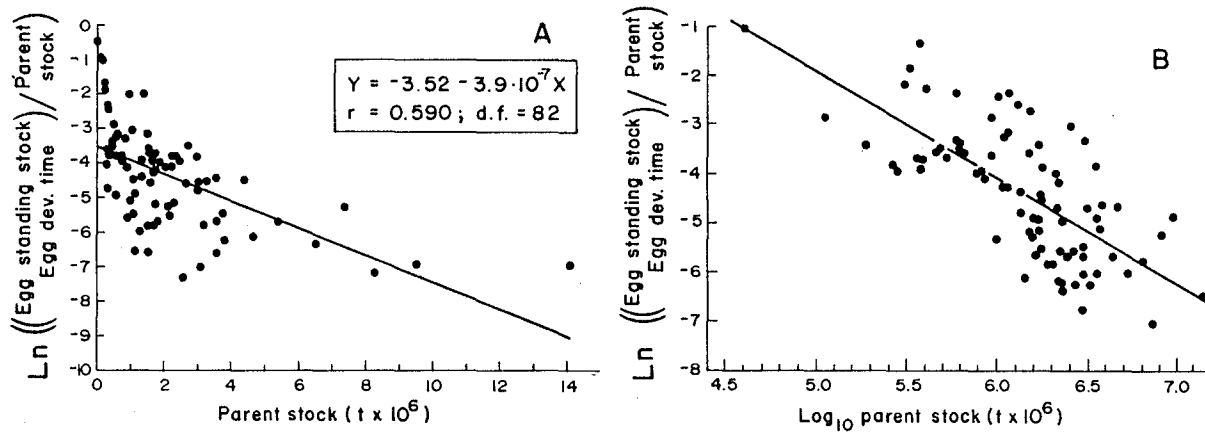


Fig. 3. Evidence of density-dependence in anchoveta egg survival.

- 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 SST² 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 TSM² 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 ^a
$\ln (N/(D \cdot P))$	(eggs 10 ⁹ / 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) ²	(°C) ²	0.0627	0.0245

^a 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:

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

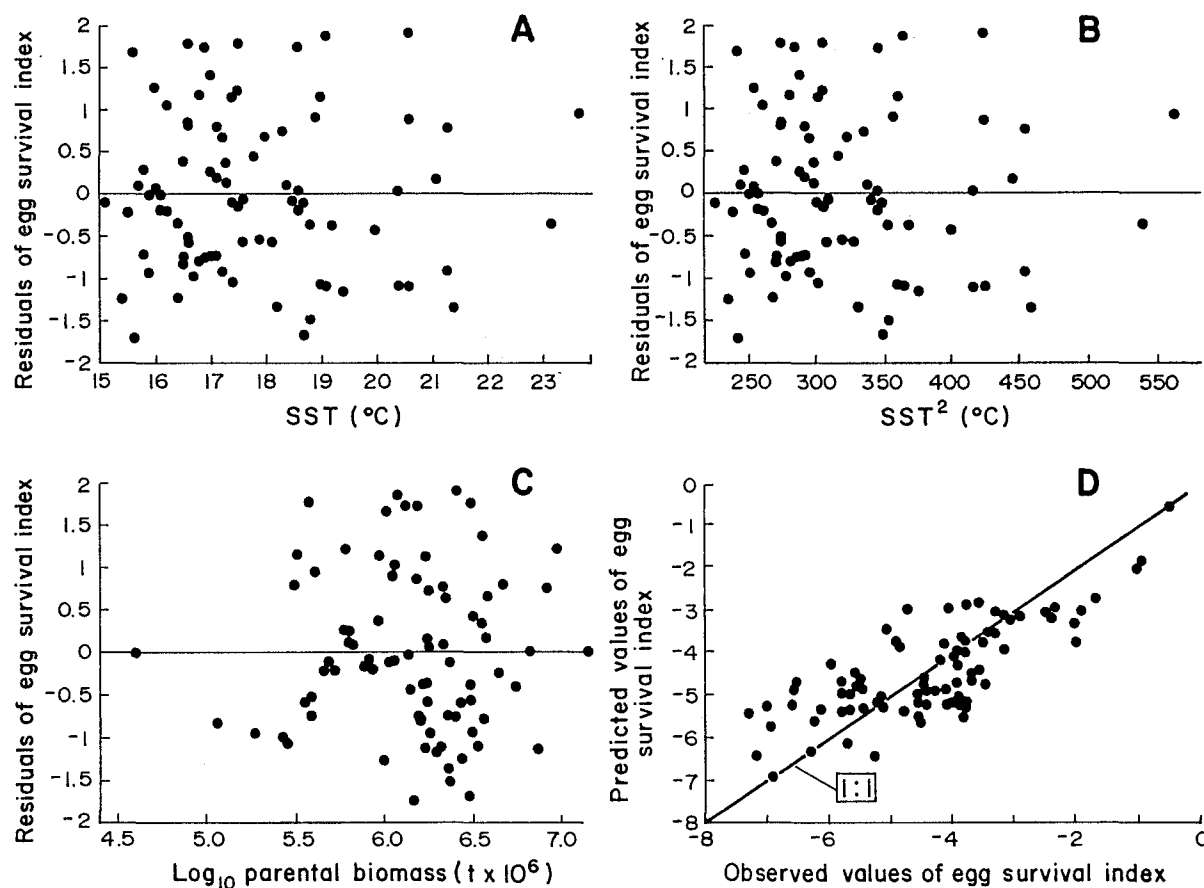


Fig. 4. Selected features of model represented by equation (7). A-C: residuals of equation (7) linking egg survival index and its predictor variables. Note absence of structure. D: plot of observed vs predicted values of the egg survival index.

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.

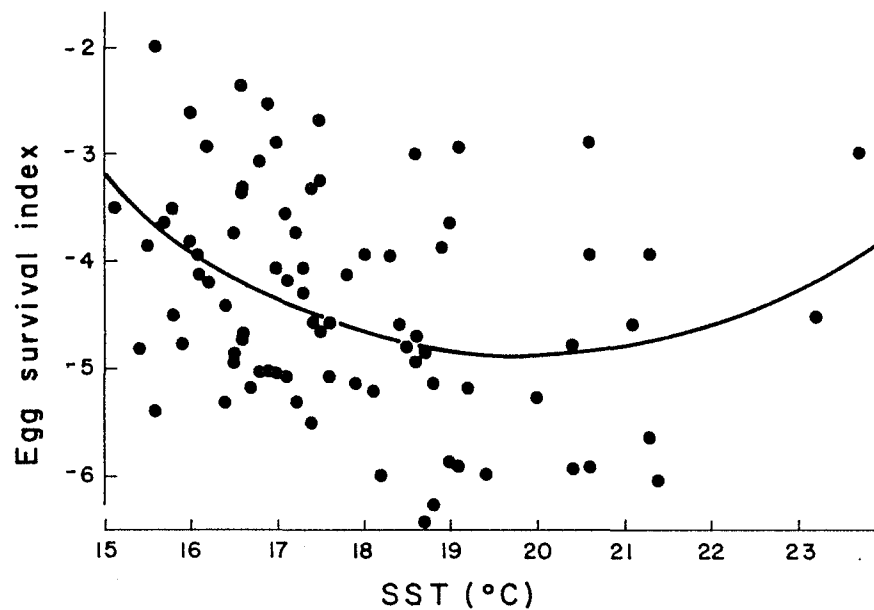


Fig. 5. Relationship of egg survival index and SST; note curvature, suggesting a minimum at 19.8°C.

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.

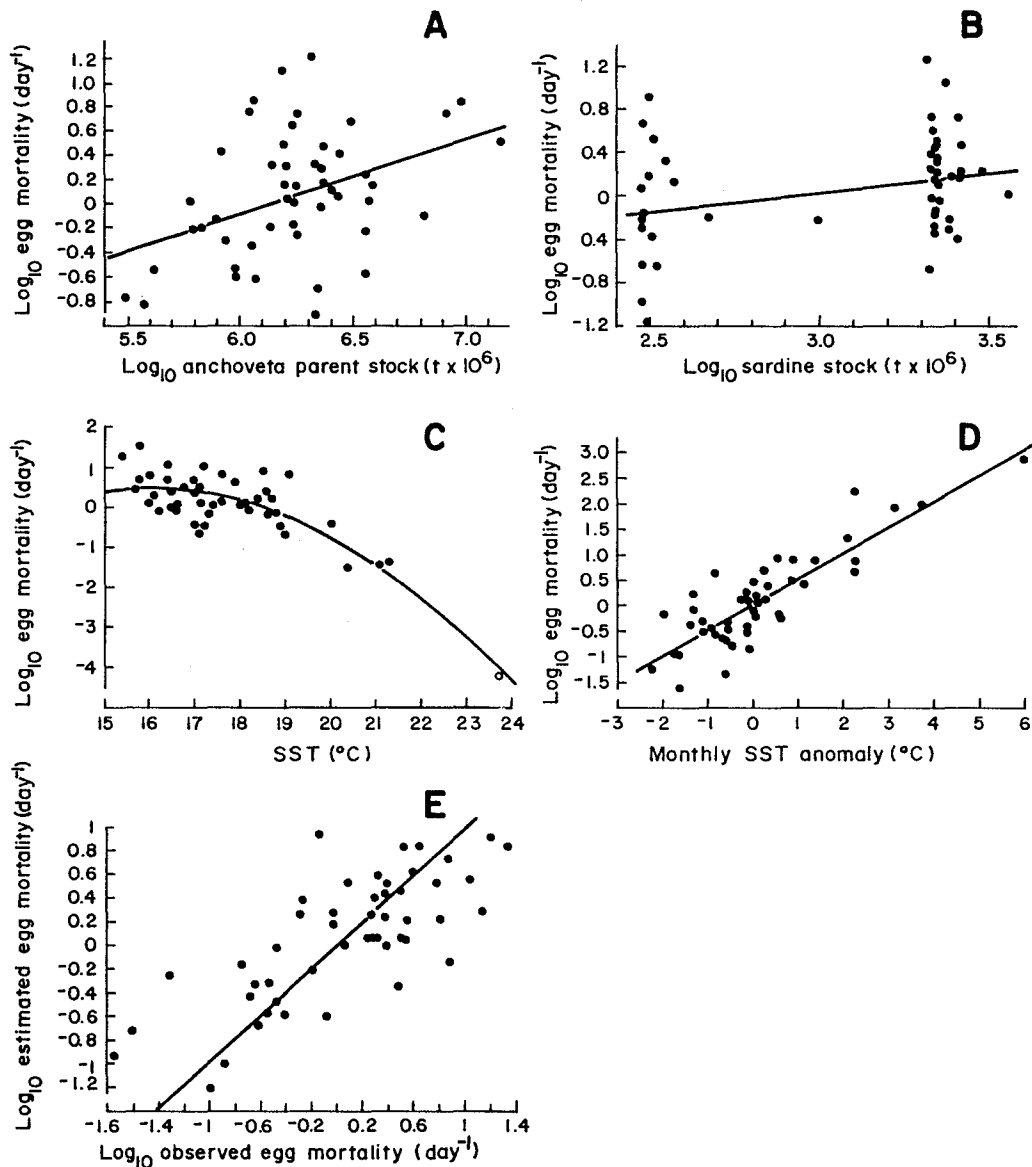


Fig. 6. Relationship between anchoveta egg mortality and its predictor variables. The solid lines of Plots A-D represent the axes of equation (9), with intercepts set at the mean of all other variables; the dots represent the residuals, plotted from the solid lines. Plot E shows the predicted vs. the 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 ^a
\log_{10} egg mortality	(day ⁻¹)	(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) ²	(°C) ²	-0.0751	0.0185

^a 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.).

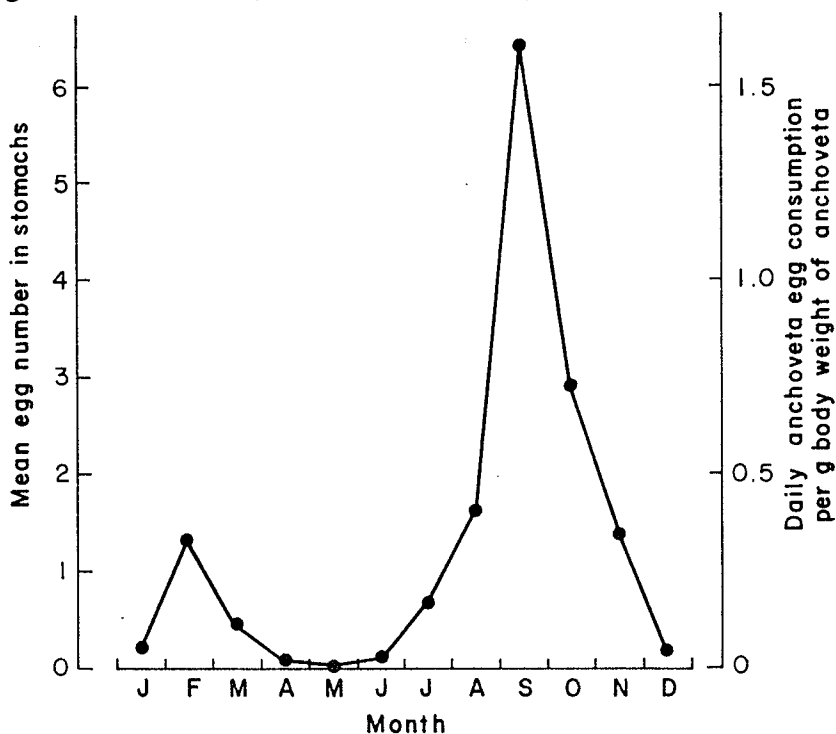


Fig. 7. Mean number of anchoveta eggs in the stomach of anchoveta sampled from 1953 to 1982 by Rojas de Mendiola (this vol.) and Alamo (this vol.), as extracted from their database (see Table 8 for details). Note strong seasonality, with a major peak during the major spawning season (September/October) 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 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 ^a
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

^a 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 ≈ 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.

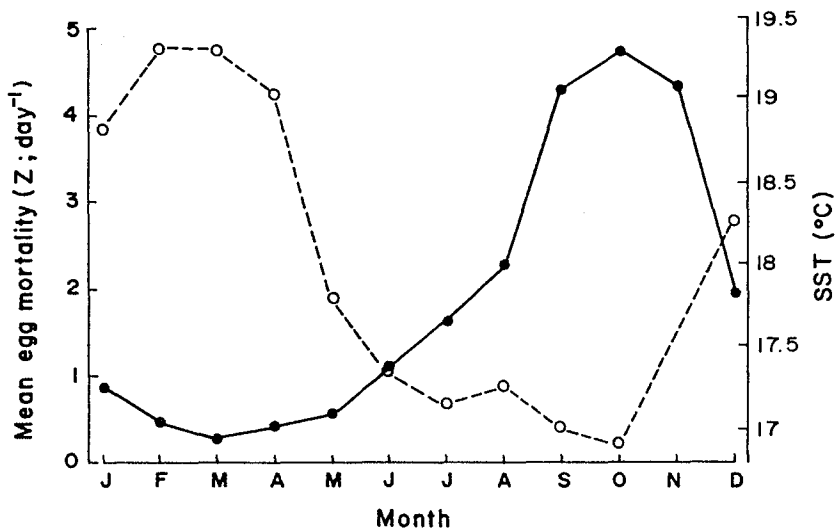


Fig. 8. Solid line: annual cycle of mean monthly anchoveta egg mortality, 1964 to 1985, based on map-specific Z values in Table 2, or on estimates from equation (9) when these could not be computed via equation (6); monthly means were smoothed over 3 months. Note strong summer peak, coincident with peak 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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