EGG MORTALITY OF THE PERUVIAN ANCHOVY (*Engraulis ringens*) CAUSED BY CANNIBALISM AND PREDATION BY SARDINES (*Sardinops sagax*)[*]

by

H. Santander[1], J. Alheit[2], A.D. MacCall[3] and A. Alamo[1]

[1] Instituto del Mar del Peru, Apartado 22, Callao-Peru
[2]Programa Cooperative Peruano-Alemán de Investigación Pesquera (PROCOPA), IMARPE, Apartado 22, Callao-Peru
[3] Southwest Fisheries Center, P.O. Box 271, La Jolla- CA. 92038, U.S.A.

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Resumen

En Agosto-Septiembre 1981, se colectaron 925 muestras de ichthyoplancton, y estómagos de I 500 anchovetas (*Engaulis ringens*) y 578 sardinas (*Sardinops sagax sagax*); estas muestras fueron colectadas de una extensión de 600 millas a lo largo de la costa peruana entre los 6°S y 14°S. Los análisis de las mues- tras de plancton revelaron que los huevos de anchoveta estaban concentrados en una franga relativamente angosta, de alrededor de 9 millas de ancho, pararela a la costa y a una distancia de 8 a 17 millas de ésta. Los huevos no parecen ser transportados muy lejos de las áreas de desove. La tasa diaria de mortali- dad de los huevos de anchoveta es extremadamente alta: 60% (z = 0.91). Las anchovetas consumen más huevos en las áreas donde la densidad de huevos es alta y se alimentan menos de estos cuando la densidad de huevos es baja. El 61.1% de los estómagos de anchoveta y el 62.4% de los estómagos de sardina contenían huevos de anchoveta. El número promedio de huevos de anchoveta en los estómagos de anchoveta fue de 5.5, y en los estómagos de sardina fue de 16.4. Los huevos de edades diferentes parecen ser digeridos a ritmos diferentes. La predación de sardinas sobre huevos de ancnhoveta puede ser particularmente peligrosa ahora que el stock peruano de anchoveta ha alcanzado el nivel más bajo que jamás se haya registrado. Una comparación entre la anchoveta peruana y la anchoveta del norte frente a California (*E. mordax*) muestra que la contribución del canibalis- mo de huevos a la mortalidad total de los huevos es mayor en la anchoveta del norte.

INTRODUCTION

Predation on eggs either by cannibalism or by other species might regulate the size of fish stocks. Recently, egg cannibalism in the northern anchovy, *Engraulis mordax*, was the subject of a detailed investigation (Hunter and Kimbrell, 1980; MacCall, 1980). It was concluded that cannibalism on eggs and larvae is sufficiently intense to be a regulatory mechanism.

Egg cannibalism in the Peruvian anchovy, *E. ringens*, has been recorded several times (Rojas de Mendiola and Ochoa, 1973; Rojas de Mendiola, 1980). However, sample sizes were too small to draw firm conclusions. Furthermore, important parameters, e.g., egg mortality, batch fecundity, spawning rate, etc., were not known and, consequently, the impact of egg cannibalism could not be estimated.

In 1981, the Instituto del Mar del Perú, carried out a cruise to estimate the spawning biomass of the central and northern anchovy stock. The samples and data obtained from this cruise gave the opportunity to estimate the extent of egg cannibalism in the Peruvian anchovy and to determine the effect of predation on anchovy eggs by sardines, *Sardinops sagax sagax*. Further details on biological parameters used in this study on egg cannibalism are given in Santander et al. (in prep.) and Alheit et al. (in prep.). This investigation was a cooperative effort of IMARPE and the Peruvian-German Fisheries Research Project which was financed by the German Agency of Technical Cooperation (GTZ).

METHODS

In August/September 1981, 925 ichthyoplankton samples were collected by the R/V 'Humboldt' along the Peruvian coast from Pisco in the south to Punta Falsa in the north. Vertical hauls from 70 m. were carried out with the Calvet net. The area under investigation was divided up into three regions: Region 1, from Punta Falsa to Salaverry, Region 2, from Salaverry to Puerto Supe and Region 3, from Puerto Supe to Pisco. More details on the egg samples from the sea are given in Santander et al. (in prep.).

With a delay of one to two weeks, 50 collections of anchovies and 16 collections of sardines, each one consisting of about 30 fish, were taken in the same area by a purse- seiner. The body cavity of the fish was opened and they were preserved in 10% formalin.

Anchovy eggs were assigned to three different age phases according to their embryonic development. Phase 1 corresponds to stages 1–2 of Santander and O.S. de Castillo (1973), phase 2 corresponds to stage 3–11 and phase 3 corresponds to stage 12–18.

RESULTS

Comparison of the abundances of eggs in the sea and of eggs encountered in stomachs. Anchovy eggs occurred along the whole Peruvian coastline from the north, about midway between Punta Falsa and Pimentel, down to the south, to Tambo de Mora (Figure 1). High densities (more than 100 eggs per sample = 0.05 m^2) were recorded opposite Chicama, Salaverry, Chimbote, Huarmey, Puerto Supe, Huacho, Ancón, Callao and Tambo de Mora. The highest densities were around 1,000 eggs per sample, i.e., 20,000 eggs per m^2. The mean numbers of anchovy eggs per anchovy stomach are included in Figure 1.

There is good agreement between the positions of collections with high numbers of eggs per stomach and the high densities of anchovy eggs in the sea, particularly opposite Chicama, Salaverry, Huacho, Ancón and Callao. Only one collection out of 50 did not have any anchovy with anchovy eggs in the stomach, and this collection was taken outside of the distribution area of the anchovy eggs in the sea. The distribution of the sardine eggs along the coast was not continuous, as it was in the case of the anchovy, but rather patchy (Figure 2). Again, the correspondence of occurrence of sardine eggs in the sea with the occurrence of sardine eggs in anchovy stomachs was fairly good, apart from the northern area. However, it has to be taken into account that the stomach samples were collected about one to two weeks later than the egg samples. This explains why there is not much correspondence in some areas and it demonstrates that some spawning areas are rather stable over a period of one to two weeks.

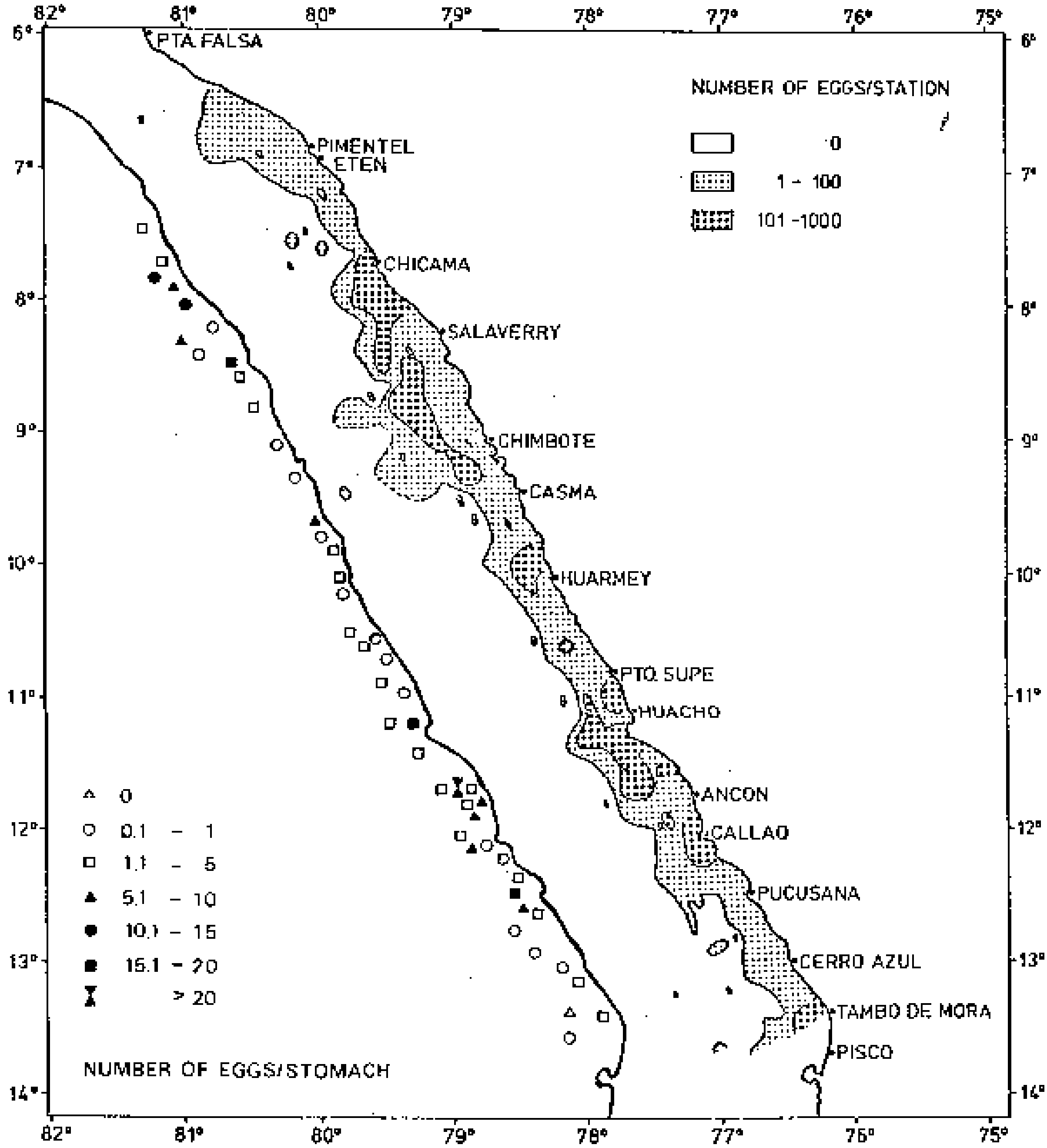

Fig. 1. Distribution and densities of anchovy eggs in the sea and in anchovy stomachs.

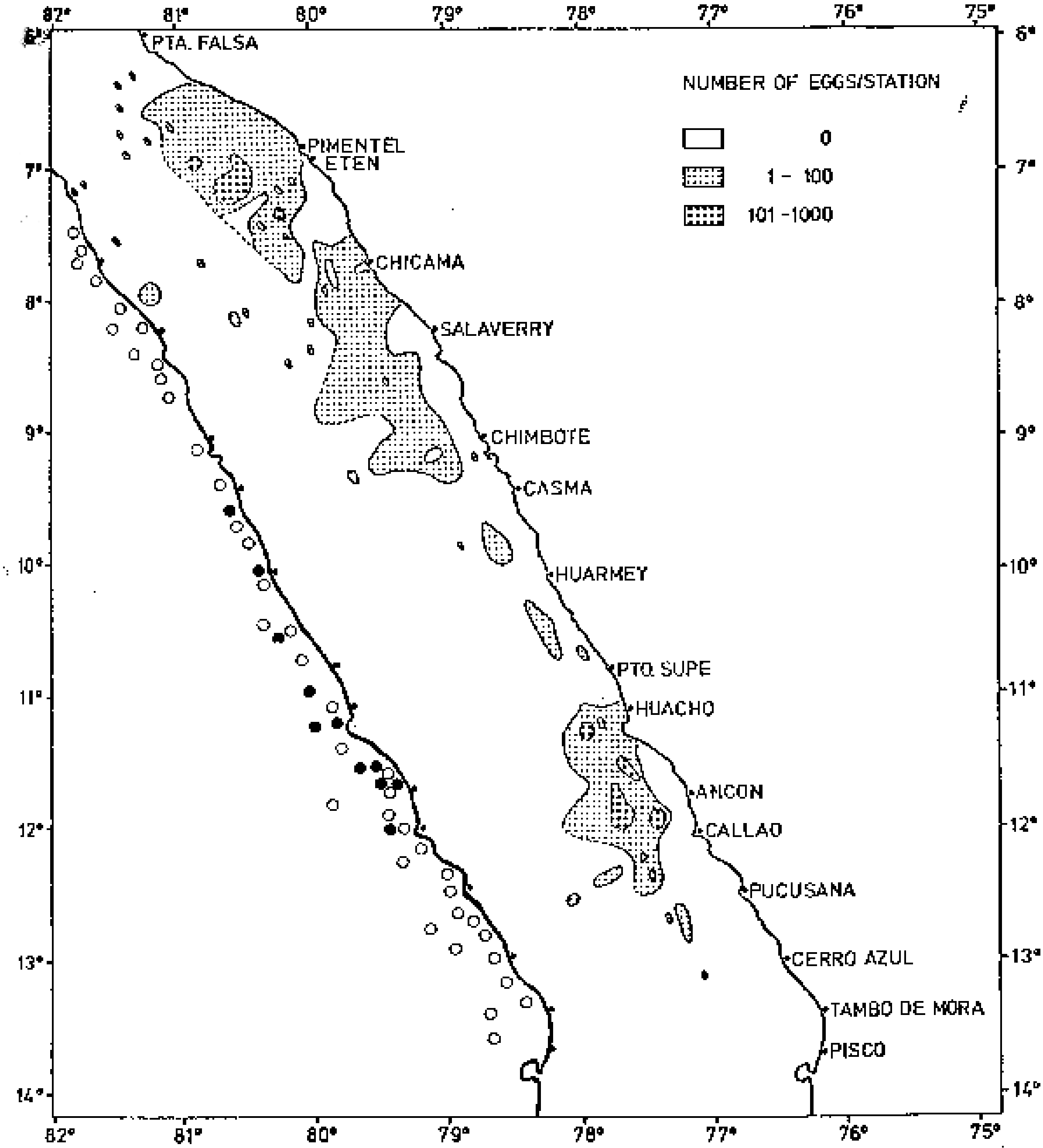

Fig. 2. Distribution of sardine eggs in the sea and in anchovy stomachs. • = sardine eggs found in stomachs, O = no sardine eggs found in stomachs.

Maximum densities of anchovy egg distribution. The density peaks of anchovy eggs were encountered at different distances off the coast in the three regions (Figure 3). In Region 1, in the north, the highest densities were between 8 and 14 miles off the coast. In Region 3, in the south, the highest densities were between 11 and 17 miles off the coast. However, in the middle, in Region 2, high densities were encountered over a large area, from 8 to 29 miles off the coast. When the data of the three regions are combined, it becomes evident that the highest densities were encountered from 11 to 14 miles off the coast, and that still fairly high densities were at 8 and 17 miles. The sites of the collections with high numbers of eggs per stomach partly overlap with the sites of high densities of anchovy eggs in the sea (Figure 4). With one exception, all collections with a mean value of more than 4 eggs per stomach were collected between 5.2 and 15.6 miles off the coast. This demonstrates that the anchovies take up more eggs in areas of high egg densities and eat less eggs in areas of lower densities.

Distribution of eggs in different phases of embryonic development. From Figure 3, it was assumed that the eggs are spawned by the anchovies mainly between 8 and 17 miles off the coast and that the eggs are then transported offshore and inshore. The decrease of egg densities offshore and inshore was supposed to be caused by a dilution effect due to transportation by water movements and due to a high egg mortality. The period from the spawning of the egg to the hatching of the larva is temperature dependent and lasts in the Peruvian anchovy about 2 to 2.5 days (Santander et al., in prep.). It was expected to find young newly spawned eggs mainly in the areas of high egg densities, whereas older eggs should be encountered further inshore and, particularly, further offshore.

To study these processes, the eggs collected from the sea and from the stomachs were assigned to three phases according to the state of their embryonic development (Table 1). The distribution of the three age phases was studied separately for the three regions. In doing that, one has to be aware of the fact that the duration of the three age phases is very different. Thus, e.g. the number of eggs in phase 1 should be relatively low, because this phase lasts only about 2.4 hours at 16.5°C. In Region 1 (Figure 5) the peak of phase 1 eggs was at 17 miles off the coast. Phase 2 peaked further inshore, at 11 and 14 miles. Phase 3 had its peak at 17 miles as phase 1.

Table 1: Duration of egg phases at 16.5°C, modified after P.E. Smith (MS, 1982).

Phase	**Duration (h)**
1	2.4
2	28.5
3	25.3

This demonstrates that the majority of the eggs is not transported away very far from the site of their spawning. However, with increasing age of the eggs the density peaks are less pronounced and older eggs seem to be spread more evenly over the area under investigation. Similar distributional movements of eggs in different phases took place in Region 2 (Figure 6) and Region 3 (Figure 7). In all three regions, the density peaks of phase 1 and phase 3 correspond with each other exactly, whereas the peak of phase 2 is always further inshore or offshore.

For the area between 5 and 23 miles offshore, the percentages of the eggs in the three phases were calculated (Table 2). 7.2% to 19.4% of the eggs were in phase 1, 68.6% to 86.8% in phase 2 and 6.0% to 12.0% in phase 3. On average, 13.4% of the eggs were in phase 1, 78.5% in phase 2 and 8% in phase 3. The same procedure was carried out with the eggs obtained from the stomachs. However, in this case, 39% of the eggs were in phase 1. 37% in phase 2 and 23.7% in phase 3. That means, about three times as many eggs as supposed were in phase 1 and 3, whereas only about the half of that what was expected was in phase 2.

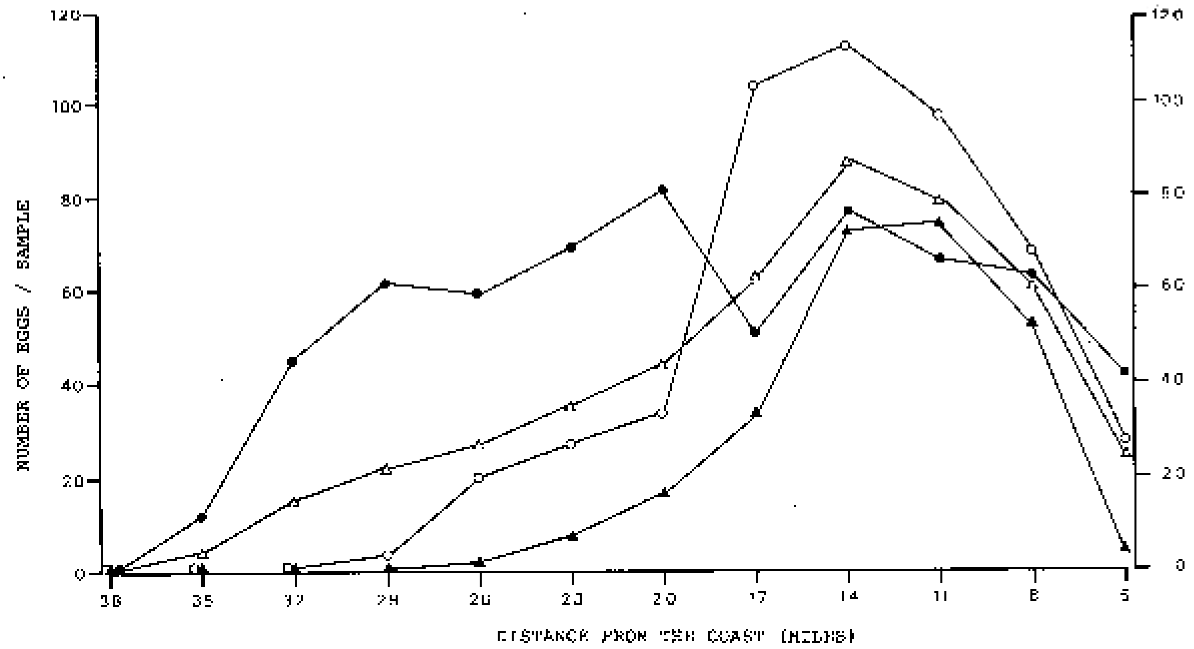

Fig. 3. Anchovy egg densities and their distance from the coast. Δ = Total area, ▲ = Region 2, O = Region 3.

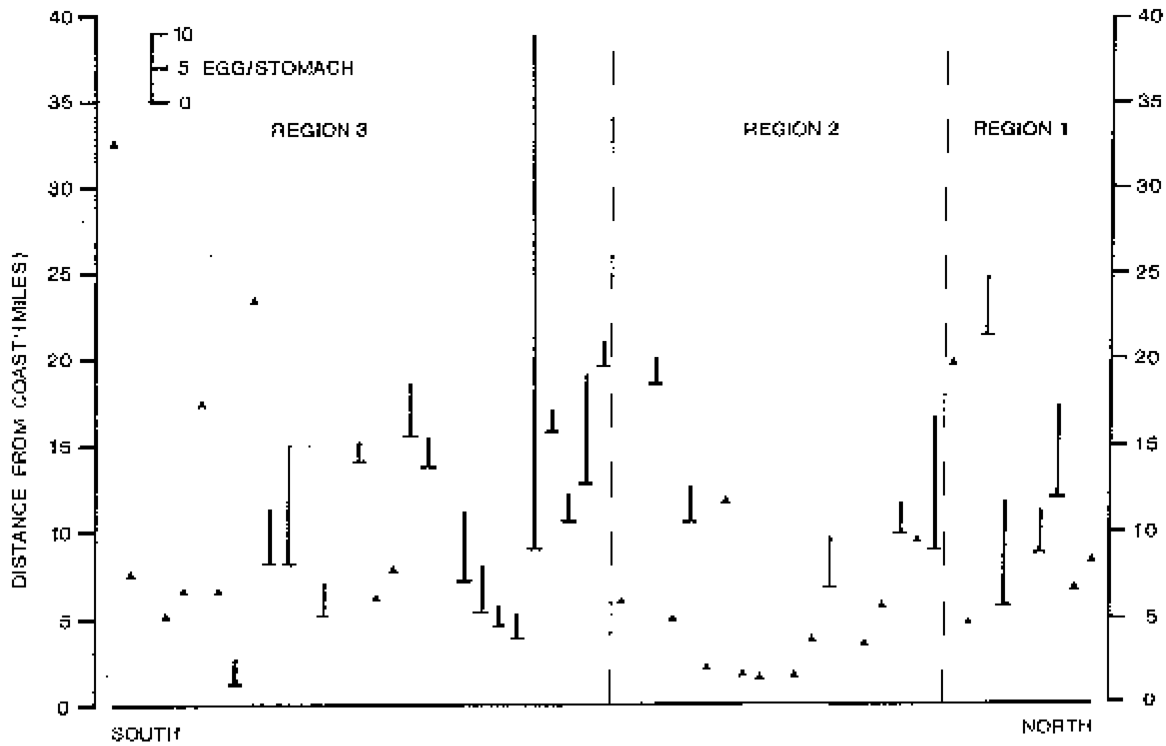

Fig. 4. Distance of anchovy collections from coast and mean number of eggs in anchovy stomachs per collection. ⊥ = indicates in which distance from the coast the collection was taken, ▲ = less than four eggs per stomach.

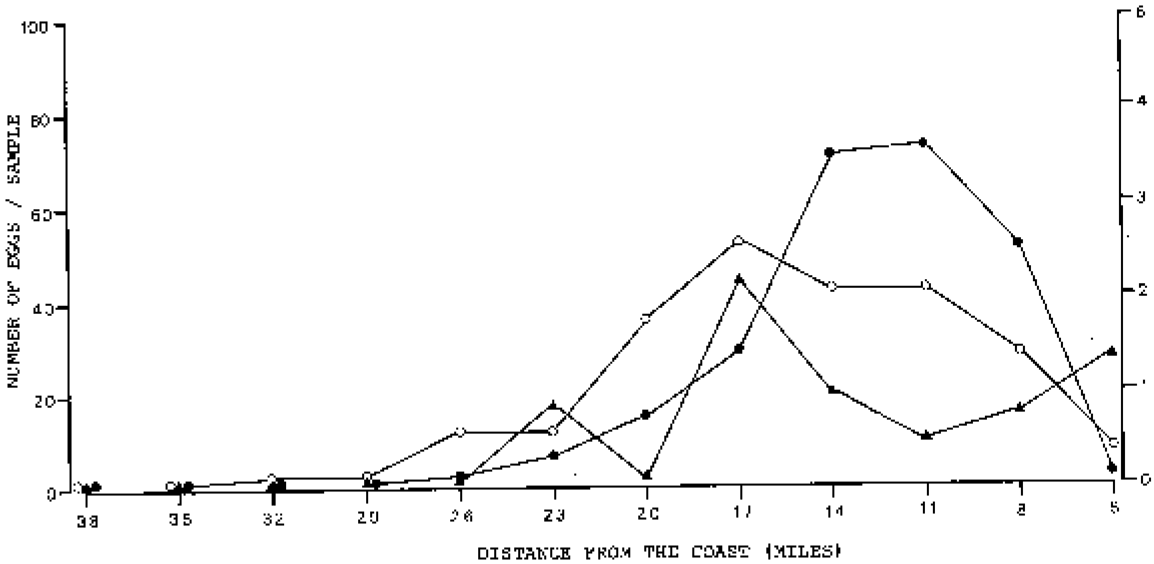

Fig. 5. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 1. ▲ = Phase 1, • = Phase 2, O = Phase 3.

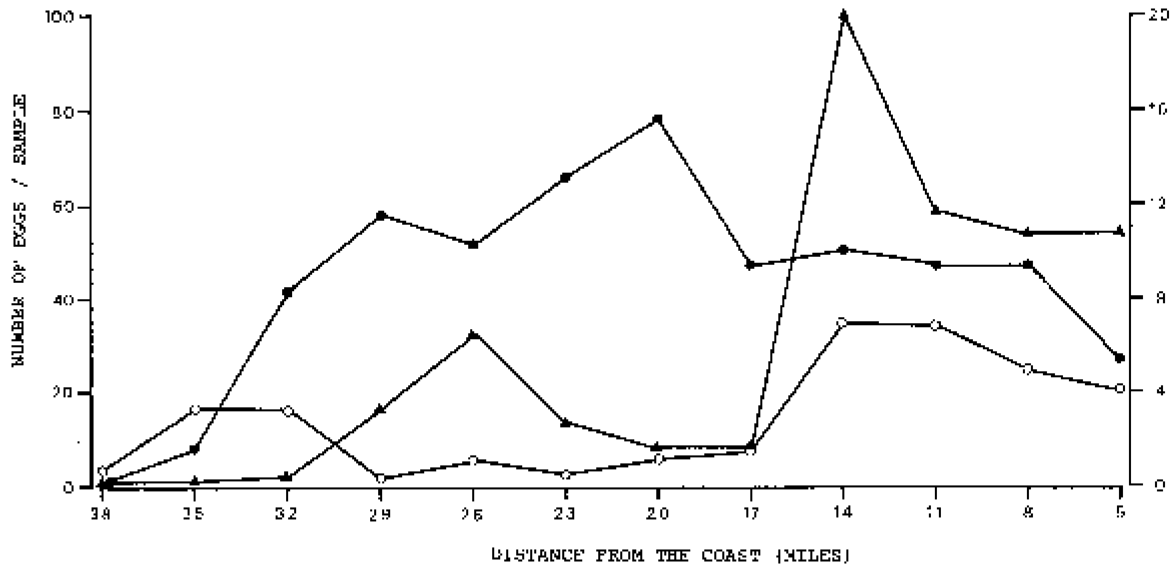

Fig. 6. Distribution of anchovy eggs, which are indifferent phases of embryonic development, in Region 2.

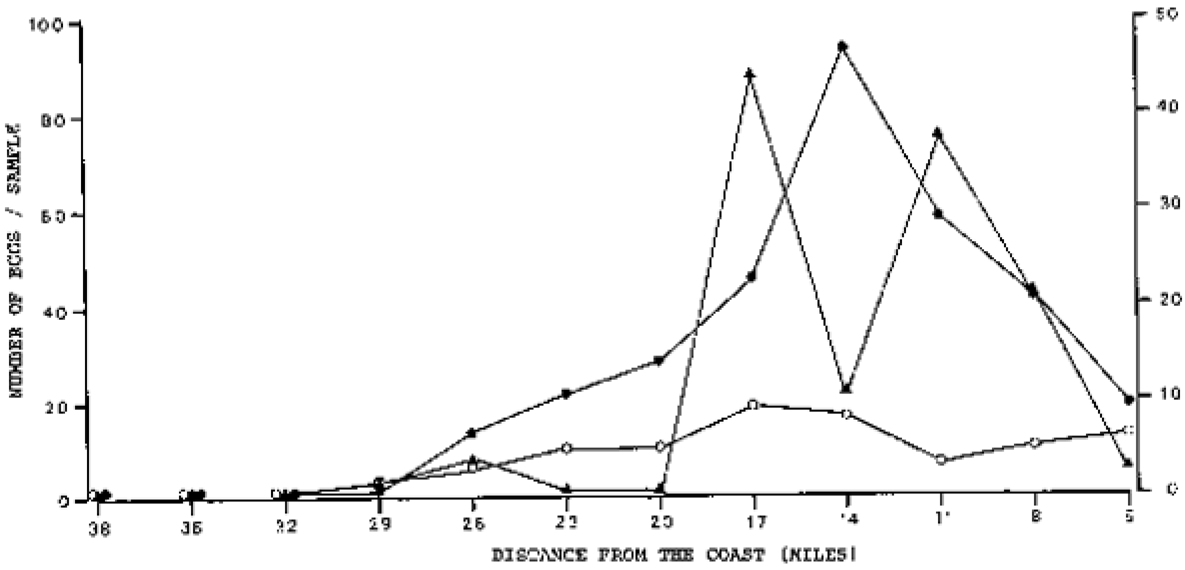

Fig. 7. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 3.

Table 2: Percentages of eggs in phase 1, 2, and 3. For the eggs collected from the sea, only the area between 5 – 23 miles offshore was considered. The total percentage of the eggs in the stomachs was calculated from all collections of stomachs.

Region	**Phase 1**		**Phase 2**		**Phase 3**	
	Sea	**Stomach**	**Sea**	**Stomach**	**Sea**	**Stomach**
Region 1	7.2	69.2	86.8	17.8	6.0	13.0
Region 2	13.7	13.6	80.2	53.3	6.1	33.1
Region 3	19.4	39.2	68.6	37.2	12.0	23.7
TOTAL	13.4	39.3	78.5	37.0	8.0	23.7

Phase 1, which lasts only about 2.4 hours at a temperature of 16.5°C, is not only overrepresented in the stomach contents, but it is encountered as well in stomachs which were collected a long time after phase 1 had disappeared from the sea. The daily spawning period starts usually at 18.00 hours at night and lasts until 02.00 hours in the morning (Santander et al., in prep.). After 05.00 hours in the morning, phase 1 eggs should not be anymore in the sea. However, phase 1 eggs were obtained from stomach samples which were taken at any time over the daily 24 hours cycle (Table 3). The percentages of phase 1 eggs in stomachs were particularly high in the morning hours and they dropped towards the late afternoon, but phase 1 eggs did not disappear totally from the stomachs at any time of day.

Table 3: Percentages of eggs in phase 1, 2, and 3. Recovered from stomachs which were collected at different times of day. Each collection had 30 anchovies.

Time of day (hours)	**Number of Collections**	**% of eggs**		
		Phase 1	**Phase 2**	**Phase 3**
07.00–10.59	11	58.5	24.5	17.0
11.00–14.59	7	53.1	32.1	14.7
15.00–18.59	9	14.8	53.9	31.3
19.00–22.59	10	30.7	38.9	30.4

Comparison of mean numbers of anchovy eggs in anchovy and sardine stomachs. A total of 1,500 anchovy stomachs from 50 collections each one containing 30 fish were analysed for numbers of anchovy eggs. Mean numbers of eggs per stomach in these 50 collections ranged from 0 to 79.4 eggs. The total mean was 5.5 anchovy eggs per anchovy stomach (Table 4). A total of 578 sardine stomachs from 16 collections each one containing on average 36 fish were analysed, too. Mean number of anchovy eggs per stomach in these 16 collections ranged from 0 to 120.0 per sardine stomach. The total mean was 16.4 anchovy eggs per sardine stomach (Table 4). According to these data, an individual sardine had about three times as many anchovy eggs in its stomach than an anchovy.

Table 4: Number of collections, total number of stomachs analysed, percent of stomachs with eggs and mean number of eggs per stomach in anchovies and sardines.

	Anchovies	**Sardines**
Number of collections	50	16
Total number of stomachs	1,500	578
Stomachs with anchovy eggs, %	61.1	62.4
Mean number of eggs per stomach	5.5	16.4

Calculation of percentage natural egg mortality from egg cannibalism. Hunter and Kimbrell (1980) calculated how much natural mortality is due to egg cannibalism. Their method was slightly modified by MacCall (1980) who used the catch equation to determine the coefficient of mortality due to cannibalism:

$$F_c = \frac{C_c}{E_o} \times \frac{Z}{1-e^{-Zt}}$$

Where:

C_c = daily egg consumption per gram of adults

E_o = daily egg production per gram of adults

F_c = coefficient of mortality due to cannibalism

Z = coefficient of total mortality

t = length of time eggs are subject to mortality (i.e., time from spawning to hatching).

Using Hunter and Kimbrell's (1980) method and including MacCall's (1980) modification, the percentage of mortality due to egg cannibalism was calculated for the Peruvian anchovy and compared to that of the northern anchovy (Table 5). Whereas in Peru, egg cannibalism was responsible for 10% of the total egg mortality, this value was 28% for the northern anchovy.

Table 5: Estimation of the percentage of natural egg mortality due to egg cannibalism in Peruvian and northern anchovy. The sources of the data for the Peruvian anchovy are Santander et al. (in prep.) and for the northern anchovy Hunter and Kimbrell (1980) and MacCall (1980). The variables B, C and H in the estimation for the Peruvian anchovy come from Hunter and Kimbrell (1980).

Variable	Peruvian	Northern
	Anchovy	Anchovy
A Mean eggs/stomach	5.5	5.1
B Rate of gastric evacuation	.701	.701
C Duration of feeding (h)	24	24
D Ration, eggs/fish	92.53	85.80
E Mean fish weight (g)	25.8	16.8
F Ration, eggs/grams wet weight = C_c	3.6	5.1
G Eggs spawned/grams ovary-free female weight	581	389
H Ratio of ovary-free weight to total female weight	.954	.954
I Eggs spawned/grams total female weight	554	371
J Ratio of females spawning/night	.16	.16
K Ration of females/school	.5	.5
L Eggs/gram school weight = E_o	44.4	29.7
M Coefficient of natural egg mortality = Z	.91	.39
N Length of time eggs are subject to mortality = t	2.0	2.5

DISCUSSION

At the present state of knowledge, it is difficult to explain why eggs of phase 1 and 3 are overrepresented in anchovy stomachs. Misidentification is clearly not the reason, as eggs of the three phases cannot be confused with each other. All eggs which could not be identified were labelled as ‘disintegrated’ and not included in the calculations. However, it might be that eggs of phase 2 are particularly vulnerable to ‘disintegration’ in anchovy stomachs. Furthermore, as not much is known about the vertical distribution of anchovy eggs in different stages of embryonic development, it could be argued that phase 2 eggs are in depths in which the anchovies feed less. However, that does not seem very probable.

Another puzzle is the occurrence of phase 1 eggs in fish stomachs collected in the late afternoon. The analysis of the egg samples from the field demonstrated clearly that spawning is terminated at 02.00 hours and that no spawning takes place in daytime. The only explanation is that phase 1 eggs encountered in fish stomachs collected in the late afternoon must have been fed upon a long time before the fish were collected. That means, they must have spent several hours in the fish stomachs without being affected much by digestive processes. Hunter and Kimbrell (1980) report that identifiable parts of eggs may remain in the stomachs up to 8 hours, but the contents of the eggs (embryo and yolk) are digested after 2 hours. As the content of phase 1 eggs from stomachs collected in the afternoon was not damaged, one may conclude that phase 1 eggs are particularly resistant towards digestive processes. This supports the above mentioned hypothesis of differential vulnerability to ‘disintegration’ of eggs in different age phases.

The data in Table 5, give the impression that egg cannibalism in anchovies plays a less important role in the Peruvian anchovy. This would be surprising as the egg densities in the Peruvian ecosystem are higher than in the Californian system (Santander et al., 1982). However, it has to be considered that different methods were applied to collect the fish. Whereas, in California, the fish were caught with a trawl, in Peru, the anchovies were sampled with a purse-seiner. A purse-seine haul lasts usually 2 to 3 hours. If the fish stop feeding when the haul begins, a high number of eggs might already be digested by the time the fish are fixed in formalin. According to the gut evacuation rate determined in the laboratory by Hunter and Kimbrell (1980), the mean residence time of eggs in the stomach is only 1.4 hours. The 10% contribution of cannibalism to the total egg mortality estimated for the Peruvian anchovy (Table 5) has therefore, to be considered only as a minimum estimate.

For a long time, it has been speculated that exploited clupeoid species might be suppressed by competitors feeding on eggs and larvae (e.g. Murphy, 1977). The data on sardines predating on anchovy eggs which are presented here support this hypothesis. The mean number of anchovy eggs in sardine stomachs is more than three times higher than in anchovy stomachs (Table 4). However, it is not possible yet to estimate the consumption of anchovy eggs by sardines, as the stock size of the sardines in the spawning area of the anchovy is not known. Predation on anchovy eggs by sardines might be particularly dangerous to the central and northern Peruvian anchovy stock now, as the sardine stock seems to have been increasing over the last years (J. Valdivia, pers. comm.) whereas the anchovy stock has reached its lowest level ever recorded (Santander et al., in prep.).

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