Development of the Larvae and Variations in the Size of the Eggs of the Argentine Anchovy, *Engraulis anchoita* Hubbs and Marini*

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Some problems regarding the spawning of the Argentine anchovy *Engraulis anchoita* have been investigated. They are: (a) problems regarding the relationship between egg size and the size of the female, (b) variations in the dimensions of the eggs found in the plankton throughout the reproduction season and (c) the influence of the size of the eggs upon the development of the larvae.

There is a positive ($r = 0{\cdot}4$) correlation between egg diameter and the length of the female anchovy. There is great variation in egg size within the ovary of a single female. The most frequent differences (calculated from egg volume) lie between 1:1·5 and 1:1·6. The mean major diameter of the eggs for the females is 1·19–1·25 mm during the first year of life, 1·25–1·29 mm in the second year, and 1·29–1·32 mm in the third year.

The differences in the size of the eggs found in the plankton within a single area, and during the same period of time, are considerable. They reach the ratio 1:2. The percentage values of the classes of egg sizes show little variation during the most intensive spawning, but there appears to be a tendency towards a decrease in egg size during the latter months of the reproductive period. This tendency seems to be independent of changes in the temperature.

The size of the eggs has little influence upon the survival capacity of the larvae when there is a lack of food supply in the external environment. Larger eggs produce longer larvae with bulkier yolk sacs, but they consume more yolk. Under experimental conditions, where there is a lack of food, the larvae are able to live for up to eight days, and a very few, up to nine days. Disregarding any differences in fecundity, no significant difference appears to exist between spawning contributions of different age-groups of anchovies.

Introduction

The fluctuations in the annual classes of fishes, especially of those fishes which are of commercial value, have been an object of concern for scientists of several countries for a long time. Most authors agree in that the fate of an annual class is dependent upon factors related to the production of eggs by the spawn-

* This paper has been prepared through the sponsorship of Consejo Nacional de Investigaciones Cientificas y Tecnicas de la Republica Argentina.

ing stock, and the conditions under which embryonic and larval developmetn takes place.

One of the problems which has been considered by several workers, especially during recent years, is the influence exerted by the size of the eggs upon the survival of the larvae. Most authors (Blaxter and Hempel, 1963; Rannak, 1958) concluded that the conditions affecting the larvae are closely connected to the food supply of the embryo, represented by the yolk-sac, its amount being dependent upon the size of the eggs. The larvae born from larger eggs and from those eggs which have a larger yolk-sac appear to be stronger and more resistant to unfavourable environmental conditions.

The present paper deals with the problem of the variations of the dimensions of the eggs in the Argentine anchovy, *Engraulis anchoita* Hubbs and Marini, and with the influence that the size of the eggs might exert upon the larvae. This problem arose from the observation that the size of anchovy eggs found in the plankton within a single area showed striking variations, up to the point where, in certain cases, the volume of one egg was twice the volume of another.

The work was planned so as to provide answers to the following questions:

1. Which cause bears greater weight upon the variations of egg sizes: the size of the female, or individual variations?
2. How do these variations appear in the plankton throughout the spawning season?
3. What influence do the dimensions of the eggs have upon the conditions of the larvae?

The spawning season of the Argentine anchovy is quite long. Starting at the beginning of the spring, in September, at a seawater temperature of about 10°C, it reaches its peak in October, at a seawater temperature of about 11–14°C. From mid-November onwards the anchovy continues its reproduction with a not too intensive rhythm, until June at least. In the following period the intensity of the spawning increases at the end of summer and at the beginning of autumn, during the months of February and March, at a seawater temperature of about 20°C.

Two different populations of anchovy are believed to exist, one of them reproducing in spring and the other in autumn.

The eggs in the ovary of an individual female do not mature at the same time and are not spawned at once. According to the egg size, there exist in the ovary three different egg groups at differing degrees of maturity. During spawning the female spawns first the eggs of the group of larger and more mature eggs, then after a certain time interval spawns the eggs of the second group, and finally it may be that after another period of time the eggs of the third group are spawned.

Materials and Methods

All of the material was obtained during the 1964–65 reproduction season of the anchovy from coastal fishing grounds some three to twelve sea miles off Mar del Plata. Plankton samples containing anchovy eggs were collected at weekly intervals starting with the commencement of the spawning period, which took place *en masse* from 22. September onwards.

Samples were obtained regularly over a period of 10 weeks, until 24. November. On this date the anchovy left the coastal region, a circumstance which, for practical reasons, made further collection of material very difficult.

A sample which was taken in February, the time at which the anchovy reappears in the coastal region, although in smaller quantities, contained only 6 eggs. At the end of May, 14 eggs were obtained in plankton samples taken near the coast.

The temperature of the seawater was taken during each collection. Samples were taken to the laboratory as soon as possible, where the eggs were separated and measured. Measurements of approximately 100 eggs were made from each sample, a total of 1,060 eggs being measured throughout the entire study. Each egg was measured (major and minor axes) under a microscope with a micrometer eyepiece. Eggs were classified, according to their size, in three classes: large eggs (major axis $>$ 1·40 mm); medium eggs (major axis between 1·30 and 1·40 mm) and small eggs (major axis $<$ 1·30 mm).

Every week 10 eggs were taken from each of the three classes and were placed in three glass aquaria, each with a capacity of 8 l. They were all kept under similar conditions for observations regarding the survival of the larvae. The salinity of the water was 34·4‰ and its temperature, 16–18°C. No use was made either of aerators or artificial illumination. The aquaria were shaded from direct sunlight. The remaining eggs were also kept in separate aquaria in order to obtain larvae, for the purpose of determining their length and calculating the volume of their yolk-sac.

As soon as the larvae hatched, measurements were taken to determine the total length of the larvae and the volume of the yolk-sacs. In order to calculate the volume of the yolk-sacs, the live larvae were placed on a slide. Water was removed with a fine pipette to stop the movements of the larvae and to keep them lying in a fixed position. A sketch of the yolk-sac was then made under the microscope by means of a camara clara, always using the same magnification. This procedure of measuring the total length of the larvae and sketching the yolk-sacs was repeated 36 hours after hatching. The mean volume of 100 yolk-sacs which were previously sketched and separated was determined by means of a micro-burette. With this information, and the calculation of the surface of the greatest section of the yolk-sacs, it was possible to estimate the volume of each of the yolk-sacs. The surface of the sections of the yolk-sacs was calculated on the basis of their sketches, which were made on millimetric graph paper. For each calculation of a particular mean volume, 20 sketches of yolk-sacs were taken into account.

The larvae from each of the classes of eggs which were kept aside for observations regarding survival were kept in aquaria without food supply. The time taken for the re-absorption of the yolk-sac, and the period during which the larvae remained alive while using their own food supply was observed.

To determine the relationship between the size of the eggs and the length of the females, mature ovarial eggs were used.

To measure the mature eggs in the ovary of females of different sizes, only individuals which were completely sexually mature were used, so that the eggs were set free simply by exerting a slight pressure on the body. It is difficult to find females in this state of maturation (CIECHOMSKI, 1965) and only twenty-five individuals were available. The eggs were extracted directly from the

Table 1

Size, in mm, of the major axis of eggs taken from female anchovies of different lengths. One hundred eggs from each female were measured

Fish length groups: 120–130 mm			131–150 mm			151–170 mm			175 mm		
Fish length mm	Mean egg size	Egg size limits	Fish length mm	Mean egg size	Egg size limits	Fish length mm	Mean egg size	Egg size limits	Fish length mm	Mean egg size	Egg size limits
120	1·24	1·11–1·30	131	1·26	1·17–1·35	155	1·33	1·21–1·39	175	1·32	1·21–139
125	1·15	1·11–1·21	131	1·26	1·17–1·37	160	1·28	1·21–1·35	–	–	–
128	1·22	1·11–1·30	134	1·27	1·17–1·39	161	1·31	1·08–1·39	–	–	–
129	1·19	1·14–1·26	137	1·23	1·17–1·35	163	1·30	1·21–1·44	–	–	–
130	1·16	1·08–1·21	137	1·20	1·17–1·26	168	1·29	1·21–1·35	–	–	–
130	1·19	1·11–1·26	140	1·25	1·17–1·35	168	1·26	1·17–1·35	–	–	–
–	–	–	140	1·26	1·21–1·30	–	–	–	–	–	–
–	–	–	140	1·27	1·21–1·30	–	–	–	–	–	–
–	–	–	145	1·31	1·21–1·39	–	–	–	–	–	–
–	–	–	147	1·26	1·21–1·35	–	–	–	–	–	–
–	–	–	147	1·24	1·17–1·35	–	–	–	–	–	–
–	–	–	150	1·26	1·14–1·35	–	–	–	–	–	–
mean 1·19 mm			mean 1·25 mm			mean 1·29 mm			mean 1·32 mm		

females before measuring, and were placed on a slide together with a small amount of seawater. Measurements were taken under a microscope with a micrometer eyepiece. One hundred eggs were measured from each female.

Results

Dimensions of the eggs in the ovary

Among fishes the size of the eggs is usually related to the size of the female. The correlation is positive: the larger the female, the larger are the eggs. Several authors have shown this relationship in different species of fishes. Nevertheless, this rule is not strictly followed by all species. For instance, BLAXTER and HEMPEL (1963) have shown that within the same species of herring (*Clupea harengus*) this relationship is significant for one spawning group, while in another group the mean values (dry weight) of the eggs of females of different size appear to be more uniform.

In the case of the Argentine anchovy, FUSTER DE PLAZA (1964) observes that the correlation between the diameter of the more mature group of eggs and the total length of the females gives the value of $r = 0{\cdot}96$. FUSTER DE PLAZA used mature individuals which were approaching spawning, but not running fish. In the present work care has been taken to observe this correlation in greater detail, using fresh material and eggs from running females in the belief that only the comparison of completely mature sexual products can lead to precise results. The results of these observations are shown in Table 1 and Figure 1, respectively.

As has been mentioned above, only twenty-five females were available and there were none of a length greater than 175 mm. The relationship between egg size and the length of the female is clear, but the value of the correlation coefficient, $r = 0{\cdot}4$, is lower than that obtained by FUSTER DE PLAZA. The discrepancy of the results might be attributable to a difference in the state of

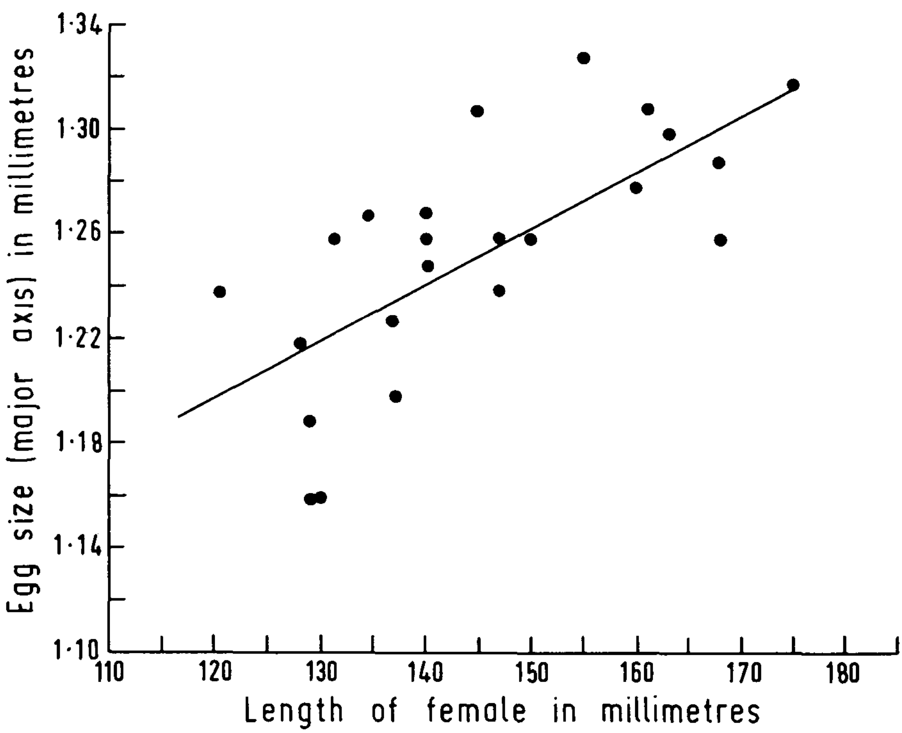

Figure 1. Mean egg sizes produced by anchovies of different lengths. Regression lines fitted by least squares. $Y = 0.9363 + 0.002214\ k$.

maturity of the eggs used in the two studies. Since the present results are based on rather sparse material, it will not be safe to venture a definite conclusion on this point.

Another interesting point was brought out by inspection of the data; there is a considerable variation in the size of mature eggs within a single female. The most frequent variations in egg volume within a single female, calculated with the usual formula for an elipsoid, (calculated from major and minor axes) was in the order of 1:1·5 to 1:1·6.

The perivitelline space in an anchovy egg developing in water is very small, and the measurements of the mature eggs in the ovarium are not very different from those of the eggs found in the sea.

The anchovy begins to reproduce in its first year of life. According to the data given by Fuster de Plaza (1964), (Petersen's method) the anchovy of the spring population reaches 130 mm in its first year, 150 mm in the second, 175 mm in the third and 185 mm in its fourth year of life. From Table 1 it follows that the mean major diameter of the eggs is 1·19–1·25 mm during the first year of life, 1·25–1·29 mm in the second year, and 1·29–1·32 mm in the third year. No data are available for the females in their fourth year. In all the calculations, the great individual variations in the size of the eggs in the ovary of a single female should be borne in mind. Mature eggs of 1·19 mm in diameter

Table 2

Percentage distribution of anchovy eggs of different size (major axis measurement) throughout the most intensive reproduction period

Date 1964	t°C	Egg size groups Small eggs (< 1·30 mm)	Medium eggs (1·30–1·40 mm)	Large eggs (> 1·40 mm)
22. September	10·0	28·5	51·0	20·8
29. September	10·8	34·8	45·5	19·7
6. October	11·0	23·8	54·2	22·0
13. October	11·8	26·0	56·0	18·0
20. October	11·0	18·0	50·0	32·0
27. October	12·5	10·0	70·0	20·0
4. November	13·8	28·3	61·3	10·4
10. November	12·8	18·7	68·8	12·5
18. November	13·0	28·0	51·3	20·7
24. November	13·5	28·5	49·3	22·2
Mean		24·5	55·7	19·8

can be found in a three-year-old female, while 1·29 mm eggs are to be found in a one-year-old female. The variations in the size of the eggs in a single ovary appear to be similar in all of the females, but with a tendency to become sharper in the larger individuals.

Variations in the size of the eggs from the plankton

The dimensions of the eggs of the anchovy found in the plankton are quite variable. The values obtained can be summarized in the following manner:—

Egg size	Major axis mm	Minor axis mm	Mean volume mm^3
small	1·17	0·65	0·285
medium	1·37	0·72	0·378
large	1·57	0·87	0·556

The medium-sized eggs are the most abundant and it can be seen that the volume of the smallest eggs is about half the volume of the largest ones.

Although there exist some differences in the shape of the eggs, which can be either circular or more ovoid, these differences are in general slight, and in most cases, the highest value for the minor axis corresponds to the lowest value for the major axis and vice versa. For this reason, in order to simplify the calculations, the values for the major axis have been taken as a basis.

Table 2 shows the results of the observations upon the size of anchovy eggs found in the sea throughout the months when spawning is most intensive. The most usual length for the major axis is 1·30–1·40 mm. The most uncommon eggs are those whose major axis exceeds 1·40 mm. The percentage values of the three egg groups are similar throughout the 10 weeks of most intensive spawning. The temperature of the water during this time varies by as much as 3°C.

At the beginning of February only six eggs could be obtained when there was a small second peak in the spawning of anchovy. The water temperature was 20°C. Four of these eggs belonged to the small egg class, and the remaining two, to the medium egg class. At the end of May when the water temperature had decreased to 14·6°C, fourteen anchovy eggs were obtained from the plankton.

Twelve of them belonged to the small size class and two to the medium size class. While the number of eggs is too few to permit any definite conclusion, their size may be smaller towards the end of the spawning season.

Variation in egg size has been studied by several authors throughout the spawning season for several species. In the case of the *Engraulis encrasicholus* in the Black Sea, LUGOWAIA (1963) has shown that the size of the eggs in the plankton decreases towards the end of the spawning season. Larger eggs were found in June than in July. For the same species, in the Gulf of Marseille in the Mediterranean, ABOUSSOUAN (1964) found the largest eggs in the plankton during the months of May and June, and the smallest during August and September. For the mackerel of the Atlantic waters of Canada, DANNEVIG (1919) found that the size of the eggs found in the plankton decreased as the spawning season advanced. These authors did not give any explanation for these observations. FISH (1928) believed that the decrease in the size of cod eggs in Massachusetts Bay towards the end of the spawning season was due to an increase in the temperature of the seawater.

In the case of the Argentine anchovy, during the two months of most intense spawning from mid-September to mid-November, no tendency towards a decrease in egg size was observed, and there was a 3°C increase in the temperature of the water. Eggs of various sizes were found in the plankton which suggests that several year-classes were spawning together. This is confirmed by the fact that mature spawners of different sizes are found throughout this period. If the dimensions of the anchovy eggs found in the plankton decrease during the summer and autumn months, it may be assumed that the younger and smaller individuals are then predominant in the spawning population. This would agree in part with data obtained by FUSTER DE PLAZA (1964), who found that the autumn anchovy reaches its first sexual maturity at a length somewhat less than that of the spring anchovy. It might also be assumed that the decrease in size of the anchovy eggs in the plankton could be related to the spawning of the second, or even the third group of ovarial eggs which will reach their mature stage sometime later in the season. The influence of the temperature of the water appears to be less important since the decrease in egg size which takes place as the spawning season advances can be related to the increase (to 20·0°C) as well as to the decrease (to 14·6°C) in the temperature.

Relationship between size of eggs and conditions of the larvae

Observations were made of the larvae from eggs of the three size groups. The results are shown in Table 3. No difference in incubation time was observed between the embryos from eggs of different sizes. At a temperature of 16–18°C the incubation time for the anchovy embryo is about 60 hours. As may be seen in Table 3, smaller larvae with smaller yolk-sac volumes are born from smaller eggs, and longer larvae with greater yolk-sac volumes from larger eggs. The larvae were very active in the aquaria and were nearly always swimming. Some 36 hours after hatching, at a temperature of 16–18°C, the larvae had consumed more than half their yolk. The analysis of the data regarding the volume of the remaining yolk and that consumed, showed that the larger the larvae, the more rapidly they consumed their supply. The smaller larvae consumed 0·0425 mm^3 in 36 hours, and in the same time the medium-sized larvae consumed 0·0620 mm^3 and the larger larvae 0·0765 mm^3 so the volume of the remaining yolk after

Table 3

Yolk-sac consumption by anchovy larvae hatched from eggs of different size. The figures in parentheses represent limit values. The mean yolk-sac volume is calculated on the basis of 20 larvae, the survival time from one hundred larvae

	Small eggs (< 1.30 mm)	Medium eggs (1.30–1.40 mm)	Large eggs (> 1.40 mm)
Mean length of larvae at hatching (in mm)	3·08 (2·85–3·28)	3·14 (2·80–3·45)	3·38 (3·15–3·60)
Mean yolk-sac volume of larvae at hatching (in mm)	0·0795 (0·0706–0·1021)	0·1024 (0·0961–0·1125)	0·1220 (0·1066–0·1403)
Mean length of larvae 36 hours after hatching (in mm)	3·75 (3·60–4·15)	3·78 (3·60–4·16)	4·02 (3·96–4·18)
Mean yolk-sac volume of larvae 36 hours after hatching (in mm^3)	0·0370	0·0404	0·0455
Mean yolk-sac volume consumed during the first 36 hours after hatching (in mm^3)	0·0425	0·0620	0·0765
Mean yolk-sac volume consumed during the first 36 hours after hatching by anomalous larvae (in mm^3)	–	–	0·0571
Duration of yolk-sac stage in hours	70–80	70–80	80–90
Duration of survival time of larvae in days without food supply	7–8	7–8	7–9

36 hours is not very different among the larvae of the three classes. During this period the increase in body length of the larvae of the three classes is approximately the same. The yolk is completely consumed in 70–80 hours by the smaller larvae and the difference in time for the complete consumption of the yolk is very small among the larvae of the three classes. At this stage of their development the eyes of the larvae were highly pigmented and their jaws were functional.

Determinations have not yet been made regarding the protein, lipid and carbohydrate contents of the yolk. These data would make possible a determination of the organic matter available to the larvae of the anchovy.

The consumption of the yolk appears to be largely due to catabolic processes. This conclusion is based upon observations made on abnormal larvae which were unable to perform locomotory movements as intensive and frequent as those of normal larvae. These abnormal larvae consumed about three-quarters of the yolk used by normal larvae. The influence of the movements of the larvae upon the consumption of their food supplies has been pointed out by Lasker (1962) in the case of the sardine (*Sardinops caerulea*), by Holliday, Blaxter and Lasker (1964) for the herring (*Clupea harengus*) and by other authors for other species of fishes.

When the yolk has been used up, the larvae of the anchovy are able to live for a certain time without feeding, through the exclusive use of the alimentary supplies of their own bodies. In these circumstances there is a slight decrease in body length. This phenomenon has also been observed by other authors working on other species of fishes (Blaxter and Hempel, 1963; Lasker, 1962 and 1964).

Under these conditions, where there is a lack of food, the larvae can live for up to eight days, and a very few up to nine days.

Survival appears to be the same for the larvae of all three classes. The few larvae able to live for nine days came from the larger eggs.

Discussion

On the basis of the experiments and observations described, it may be concluded that the size of the eggs of the Argentine anchovy has no noticeable influence upon the possibilities of survival of the larvae deprived of an environmental supply of food. The larger larvae, having greater alimentary needs, consume more yolk. Although they are hatched from larger eggs and thus have a greater yolk supply, as a result of more intense consumption, they are, at the end, in conditions similar to those larvae derived from the smaller eggs, so far as survival in poor feeding conditions is concerned.

The results of these observations, so far as they demonstrate the small influence of the size of the eggs upon the conditions of the larvae, do not agree with the findings of certain other workers. For example, BLAXTER and HEMPEL (1963) have shown experimentally that herring larvae born from eggs of different sizes and from different spawning groups, showed differences that can be reflected later on the survival of the larvae. BLAXTER and HEMPEL (1963) did not work with the size of the eggs, but rather with their dry weight. Their experiments show clearly that the time required for the reabsorption of the yolk is longer for herring larvae born from heavier eggs. Their survival time in poor feeding conditions is also longer, and their growth is more rapid than that of larvae born from lighter eggs. Similar findings have not been observed in the case of the Argentine anchovy. It should be remarked that the herring eggs used by BLAXTER and HEMPEL showed greater size differences than the eggs of the anchovy, and that they came from geographically separated spawning groups. Within a single spawning group, the differences were not so sharp. The problem of the relationship between the size of the eggs and the survival of the larvae is relevant to studies of population dynamics. The basis of the problem is that, if larvae with a lower viability are born from smaller eggs, and if smaller eggs come from younger individuals, the renewal of the stock will depend principally upon the older year-classes. BRIDGER (1959) and MARTY (1959), cited by HEMPEL and BLAXTER (1963), believe that in the case of the herring, older individuals produce greater eggs and therefore, stronger larvae, with a greater yolk supply. If this is the case, the abundance of herring larvae will depend more upon the relative spawning potential of the older fish than on the total spawning potential of all the spawners.

As was shown in the case of the Argentine anchovy, it appears that larvae from larger eggs do not possess a higher survival potential than the larvae hatched from smaller eggs. As a result, the reproductive potential of spawners of different sizes would be similar, and no significant difference should exist in the contribution of the spawners of different year-classes, to the renewal of the anchovy population. (Differences in the fecundity of the various lengths are not taken into account). This is further supported by the fact that individuals of all ages participate when spawning is at its greatest intensity so that there would be no differences in the environmental food supply available to larvae produced by the different year-classes.

Acknowledgement

It is a great satisfaction for the present author to acknowledge here her gratitude to Dr. Mariano Pizarro for his valuable help in the volume determination of 100 yolk-sacs, which provided the basis for the succeeding calculations.

Summary

The correlation coefficient between egg diameters and the length of the females has the value $r = 0{\cdot}4$. There is a great variation in egg size within the ovary of a single female. These variations have the tendency to become more marked in the larger individuals.

There is a two-fold difference in the size of the eggs found in the plankton within a single area. There appears to be a tendency towards a decrease in egg size during the latter month of the reproductive period.

It has been shown that the size of the eggs does not have much influence upon the survival of the larvae when there is a lack of food in the external environment.

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