REPORT

ON

MACKEREL INVESTIGATIONS IN 1897.

BY

J. PERCY MOORE.

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INTRODUCTION.

The almost unparalleled scarcity of mackerel in our waters during the last decade, and the consequent loss to our fishermen, having given rise to the fear of a permanent decrease in numbers of this excellent fish, it has become incumbent upon the United States Fish Commission to determine the cause of the decrease and, if possible, to augment the supply. Similar periods of scarcity, but of shorter duration, are recorded from time to time in the history of the mackerel fishery, and have hitherto been followed by times of greater plenty. This well-known fact should lead us to hope that the present conditions are only temporary, but it is none the less important to determine, and if possible to overcome, the disturbing cause, to the end that a constant and certain supply of this capricious wanderer may be had.

Why the mackerel supply is thus subject to periodical wax and wane is unknown. There are no certain data upon which to venture a solution of the problem. Are their numbers depleted by disease? There is no evidence that the mackerel is subject to any serious infectious disease. Is the decrease due to a period of lowered fertility, of less or greater duration? Here again we lack facts. We know but little to what extent the biological and physical conditions of the sea have varied, nor yet how variations in these factors affect the vitality and habits of the mackerel. There may have been no actual diminution in the propagating capacity of the fish, but some condition peculiarly detrimental to the development of the eggs and embryos may have existed, causing their consequent destruction on a large scale. Has there been a real or only an apparent decrease due to migrations of the fish from our waters to other parts of the ocean? This view, most frequently accepted as explaining the fact, has little to support it, and is a mere guess founded on the known wandering habits of the mackerel.

For several years past the Fish Commission has attempted to overcome the deficiency by propagating the mackerel artificially. So far as any practical results are concerned, the attempt has been unsuccessful. Briefly stated, the difficulties have been two, namely, the number of eggs obtained has been entirely inadequate, and the proportion hatched in most cases has been low.

The present report contains a statement of the results attained in the course of a brief study of this work of mackerel propagation during the season of 1897. The investigation was begun in early June at

Woods Hole, and was continued from June 25 to July 27 on board the steamer *Fish Hawk*, in Casco Bay, Maine. During August the material and data gathered were worked over at Woods Hole. At Woods Hole the local fisheries were watched closely in order to determine the advent of spawning schools, and numerous samples of male and female fish were examined in order to secure material for a study of the maturing ova and spermatozoa. Two small lots of eggs, aggregating 110,000, were brought to the station and kept under observation during their whole period of development.

At Casco Bay the season proved peculiarly unfavorable for the investigation, which could not be brought to completion with the limited time and facilities at our disposal. Only a few over 1,000,000 eggs were taken, the first on June 25, the last on July 8. Although this number was sufficient to permit a study of the general history of development and the preservation of material for a more complete review of the embryology, it proved to be entirely inadequate for purposes of experimentation, which, in order to yield conclusive results and eliminate all doubtful factors, requires extensive checks. The impossibility of applying these, and the necessity of limiting the experiments to but one series of those proposed, render this part of the work less valuable than it otherwise might have proved.

For a discussion of the sources of supply of eggs and the conditions under which they were taken, I refer to the reports of Mr. Locke for Woods Hole, and Lieutenant Swift for operations of the *Fish Hawk*.

The results of the investigations may best be considered under the three heads or groups into which they were organized, namely, (1) embryology, (2) surface towings, and (3) experiments.

1. RESULTS OF EMBRYOLOGICAL STUDIES.

Under this head will be considered the morphology of the reproductive organs, the general history of development, and observations on the conditions which affect it. In the present connection only a general account showing the similarity in development of the mackerel to other fishes producing similar pelagic eggs (the cod, Spanish mackerel, sea bass, etc.) need be given, prominence being given to only those features which are of most interest to fish-culturists.

A careful study of the rate of growth of the mackerel leads to the conclusion that maturity is reached at the age of three years, at which time the female is 12 to 14 inches long and the male somewhat smaller. In the region included between Cape Cod and Block Island the spawning season extends from the middle of May to about the 1st of July; but few spawning fish are taken after June 15. At Casco Bay the season probably begins and ends, respectively, about two weeks later, the majority of the fish spawning before the 25th of June. From the time of our arrival a systematic record was kept of the condition of ovaries and testes of as many fish as could be obtained for examination. Very nearly all were partly or entirely spent, and the proportion of fully spent fish increased toward the end of the season, though occasionally a spawning or even immature ovary was met with. It is worthy of remark that, even in the same run, fish in very different conditions of maturity were found. Most of them were nearly or quite through spawning; a smaller number might be immature, and for some unknown reason would probably fail to ripen their eggs this season, while a still smaller number would be spawning fish. In nearly all cases the number of males was greater than the number of females. The fishermen were almost unanimous in stating that a run of spawning fish much more productive than any which we encountered had passed into Casco Bay about two weeks previous to our arrival.

If an ovary of a mackerel be examined just previous to the spawning season, it will be found to contain ova of three sizes or generations. Constituting the bulk of its lamellæ are large, opaque ova measuring from 0.35 mm. to 0.55 mm. (say about 0.02 inch) in diameter. These have large, ill-defined nuclei, well-developed egg-membranes and egg-follicles, protoplasm filled with yolk-spherules and a number of minute oil-droplets, which latter are scattered in the smaller, but more or less closely aggregated in the larger of these ova. The opaque ova just described are destined to produce the mature eggs of the approaching spawning season. Packed between them are smaller ova of two sizes. The larger ones measure about 0.12 mm. in diameter, are about as numerous as the large, opaque ova, and are destined to produce a crop of eggs a year hence. The smallest measure about 0.04 mm. in diameter, are very numerous, aggregated in clusters, have large and distinct nuclei, no follicles, and retain the character of simple cells. From these future crops of ova will arise.

As the spawning season approaches, part of the opaque ova increase rapidly in size. The yolk-corpuscles, to which the opacity was due, pass into solution, and as a consequence the yolk becomes more and more transparent and of a pale amber color. The oil-droplets coalesce into two or three larger drops and finally into a single sphere, which is free to move about in the now fluid yolk. The nucleus has, meantime, become invisible. Such ova are ready for extrusion and the final processes of maturation. Owing to these changes the ovary as a whole has increased greatly in bulk, and becomes spotted all over, both externally and on the internal laminæ, with translucent spots, due to aggregations of the clear eggs. Unlike some fishes (those generally of sluggish habit or bottom-livers) the mackerel matures only a portion of the generation of eggs at one time. Thus is obviated any undue enlargement of the ovary, which would cause the body walls to protrude and doubtless obstruct the movements of the fish, a result which might be particularly serious to an active pelagic species like the mackerel. The number of ova produced at one time is seldom more than 50,000 and is frequently much less, but the aggregate number matured in one season by a female of average size is several hundred thousands.

All of the evidence which could be gathered from examinations of the ovaries of numerous fishes captured at different hours of the day seems to indicate that the common mackerel, like the Spanish mackerel and many other fishes, is a night spawner. Although development of the ova proceeds in all parts of the ovary at once, the process is at first more rapid in the posterior (external) end, which consequently becomes spent while the ova production is still active at the anterior (internal) end. The transparent eggs, or more correctly "egg mother-cells," now rupture the follicular membranes which envelop them and are dehisced into the ovarian cavity, where they lie among the ova-bearing laminæ bathed in a small quantity of serous fluid. They are slightly smaller and more irregular in shape than the fertilized ova, owing to the somewhat flaccid, wrinkled state of the egg membrane and the mutual pressure to which they are subjected. When first dehisced into the ovarian cavity they are rather opaque, owing to the presence of numerous minute spherules in and beneath the protoplasmic layer which envelops the fluid yolk. As these spherules are gradually absorbed, the egg mother-cells become more and more transparent; but the last granules do not finally disappear until the egg is extruded from the oviduct and feels the stimulus of contact with sea water. Under these circumstances the least opaque eggs immediately assume a crystalline transparency; the more opaque and less mature ones clear up more slowly, but usually as completely, and the process is probably facilitated in this, as in the case of the Spanish mackerel, by the presence of spermatozoa. Immediately upon contact with the sea water, whether or not spermatozoa be present, the egg mother-cell absorbs water and assumes a perfectly spherical shape, the egg membrane becomes tense, while the processes attending maturation ensue.

The egg now resembles the well-known pelagic ova of the Spanish mackerel, sea bass, and other fishes. It is at first perfectly spherical and varies considerably in size. The average diameter of a large number of eggs from all sources procurable is 1.25 mm., but even from the same female they have varied from 1.16 to 1.29 mm., and it was also found that all of the eggs produced by a particular female were sometimes larger, sometimes smaller, than the average. Thus, all the eggs of the two lots studied at Woods Hole which were measured averaged 1.15 mm., and the individual eggs varied but slightly from this average. On the other hand, all of the Casco Bay females produced eggs of larger size, at the same time presenting a greater range of variation. The horny, transparent, vitelline membrane which surrounds the egg is of uniform thinness except at a small circular area which, perhaps owing to its greater weight, always gravitates to the lowermost pole of the floating egg. This is a micropylar thickening, a crater-like elevation projecting inward in contact with the vitellus. A funnel shaped depression exists in its outer surface and extends about half way through, from which point it is continued to the inner surface by an exceedingly narrow and perfectly straight canal, the micropyle, through which the spermatozoan finds its way to fertilize the ovum. Exceedingly delicate canals perforate the whole region of the micropylar thickening and doubtless afford a means of interchange of water bearing the respiratory gases. Similar but much smaller and less numerous perforations exist in all parts of the vitelline membrane, but are difficult to demonstrate until during the later stages of development, when the membrane becomes more brittle and the perforations perhaps larger.

The egg proper, or vitellus, consists of a vesicle-like skin of protoplasm, faintly granular, of a pale brown color and of uniform thickness throughout, distended by a perfectly fluid transparent yolk, in which there are no structural elements observable, except occasionally a few aggregations of spherical bodies attached here and there to the inner surface of the protoplasmic pellicle. Floating freely about within the protoplasmic skin and, because of its lower specific gravity, always rising to the highest point in the egg, is a beautifully clear and perfectly spherical oil-drop, by virtue of the presence of which the egg is buoyant. The oil-drop also is enveloped by a delicate protoplasmic sheath, which is at first of uniform thickness and always quite distinct from the protoplasm enveloping the yolk. The oil-drop is of unusually large size, but varies both absolutely and relatively to the size of the egg to a considerable degree. Its average size is 0.28 mm. Its color also varies. Sometimes it is perfectly colorless; sometimes, and more frequently, of a pale amber, or even of a pinkish tint. And this variation may be observed in eggs taken from the same female. The reason for this is not apparent, but it was noticed that colorless oil-drops occur most frequently in eggs of the smaller sizes. Perhaps both may indicate a condition of impaired vitality, though this could not be proved by the results of the further course of development.

Owing to the unfavorable circumstances under which the mackerel eggs were taken, I was unable to study the maturation processes in the living egg, but material was preserved for a future study of this phase of development. There is no reason to doubt, however, that the process is essentially similar in this and other pelagic eggs, and I refer to my report on the Spanish mackerel and to the papers of Agassiz and Whitman on the cunner, and of Ryder on the cod, for some observations on these phenomena. The process consists essentially in the elimination from the egg mother-cell of a part of its nuclear substance, without which it seems incapable of fertilization. Accomplishing this by two successive nuclear divisions, the surplus material is cast out within two minute cells, the so-called polar bodies, which appear at the micropylar pole of the egg within a few moments after it reaches the water, pass into the perivitelline space, and lose further significance in development. The maturation processes appear to be hastened by copulation (the contact of a spermatozoan, after entrance through the micropyle, with the vitellus), and indeed are largely coincident with this, but may take place quite independently of it, in which case the time required for the completion of the process is longer. Not until after the extrusion of the polar bodies is the egg mature and ready for the union of the egg, or female pronucleus, and the sperm, or male pronucleus, which constitutes the essential act of impregnation. When this union takes place there is constituted a cell fundamentally different in its properties from the egg mother-cell which left the ovary, in that it is now a germ capable of further development into a complete organism. This process also could not be studied in the living mackerel egg, but probably does not there differ from what has been observed in the Spanish mackerel egg.

The spermatozoan of the mackerel consists of a pear-shaped head about 0.002 mm. in length, with a short rod-like middle piece attached like a stem to the narrow end of the pear, and bearing an exceedingly delicate flagellum or tail which is about 20 to 25 times the length of the head. When fully ripe, the sperm is quite fluid and mixes readily with sea water, through which the spermatozoa, by their very active lashing, quickly become disseminated. Under such circumstances, a very small quantity of sperm will serve to impregnate a great many eggs, and it is of practical importance to use as small a quantity as will effect the purpose, to the end that the eggs do not become clogged with great numbers of spermatozoa, which will adhere to their membranes and interfere with free respiration. With fresh and perfectly ripe sperm, the egg of the mackerel is very easily fertilized, even those eggs which exhibit a considerable degree of opacity, and are hence supposed to be less mature, responding at once to the presence of spermatozoa. In fact, even when considerable numbers of eggs, several hundreds of thousands, were handled, scarcely any would be found to be unfertilized, and in no case, except when the sperm or ova were obviously immature, did as many as 1 per cent fail of impregnation. This ease of fertilization and the almost perfectly uniform way in which the eggs would subsequently develop, all of them passing into the same stage at nearly the same moment, seem to me to indicate their healthful state and the necessity of seeking the cause of the failure of the hatching operations in some condition subsequent to this.

It is, of course, impossible, from the study of a relatively small lot of material obtained under only one set of conditions, and with no means of checking results by making comparisons, to state positively that the eggs were in the best vital condition, but the uniformity and regularity of results and the comparative scarcity of abnormalities, except those mentioned later on, seem to lead to this conclusion. My experiments to test the length of time during which the spermatozoa retained their fertilizing powers failed, owing to the accidental impregnation of the entire lot of eggs reserved for this purpose, and subsequently no opportunity for repeating the experiment was found. Direct observation, however, on sperm placed in pails or jars of water showed that the spermatozoa lost their activity completely in 45 to 60 minutes, and this period must consequently be admitted to be the extreme limit of their vitality under the conditions of the experiment.

I would here point out the futility of hoping for any better results through the substitution of the so-called dry method for the wet method of fertilization. The former was invented to meet certain peculiar conditions, and is indicated in cases where the contact of water with unfertilized eggs causes either the formation of a coat impervious to the spermatozoa or the development around the vitellus of a water space which the spermatozoa can not traverse. Impregnation in the case of the mackerel is naturally and easily accomplished by the intimate mixture, in a small quantity of sea water, of the freshly stripped ova with a small amount of perfectly ripe sperm from a previously selected male. The objection to the adoption of the dry method lies in this: Owing to its greater weight the micropyle, which is the only point through which a spermatozoan can enter the egg, lies always at its lowermost pole. Now, when the eggs are only moist and the sperm is poured over them, a much greater quantity is needed, and more of it will adhere to the membranes than when the eggs are freely suspended and the micropyle exposed to the active swimming spermatozoa. The dry method may be just as effective as the wet, but it can not be more so, and has the slight disadvantage just mentioned.

Simultaneously with the progress of the internal act of fusion of the male and female pronuclei, other and more obvious external changes in the egg are taking place. The protoplasmic pellicle, which at first forms a layer of uniform thickness, begins to accumulate with a peculiar wave-like streaming at the lower or micropylar pole of the egg. At first the thickening thus produced is in the form of a scarcely evident meniscus, which passes off on all sides into the thin pellicle. Gradually it increases in thickness until nearly all of the protoplasm has accumulated in a sharply defined disc, the blastodisc, which, when completed, has a circular outline. Its outer surface is in contact with the egg-membrane and conforms very nearly to its curvature. The inner surface of the blastodisc has a strongly convex, almost conical, form and projects into the yolk. At its margins, which rise abruptly from the yolk, the blastodisc passes into continuity on all sides with the protoplasmic pellicle, which has now become reduced to an excessively thin and delicate, but perfectly intact, layer. The completed blastodisc becomes the seat of future developmental processes. The remainder of the protoplasmic pellicle takes but little part in these processes, and is known as the periblast layer. Oriented with reference to the micropyle, the blastodisc seems always to be a little eccentric, and the micropylar thickening is readily found just outside of its center. The perivitelline space, which is described above as an exceedingly shallow space between the egg-membrane and the mature vitellus, has now, owing to the change in form of the latter, altered its character. Owing to the contact of the greater part of the external surface of the yolk and of the blastodisc with the egg membrane, it is in these regions obliterated or so exceedingly shallow as to escape detection. But there is a deep ring-like space running all around the margin of the blastodisc and corresponding with a circular groove which forms the boundary between the yolk and disc.

The pellicle of protoplasm enveloping the oil-drop has, like that surrounding the yolk, collected in a bleb-like mass on the under surface of the oil. Its shape is similar to the blastodisc except that it is not constrained within a limiting membrane and has conformed to the character of the fluids between which it lies, like the drop of water which gravitates to the under side of a soap bubble. This smaller disc takes no important part in development and undergoes no change until it becomes fused with the surrounding blastodisc. It will not be further considered.

Although just described as accompanying and succeeding fertilization, these processes must not be considered wholly as a consequence and therefore as a test of fertilization, for even in the absence of spermatozoa, changes almost precisely similar and likewise resulting in the formation of a blastodisc ensue, but are much later in reaching their fulfillment. In this case development never, so far as I have observed, proceeds any further, and in the course of a day or two the vitellus contracts, turns opaque, and rapidly disintegrates, the egg usually sinking to the bottom soon after the contraction becomes evident.

The brief chronological index to the stages of embryological development which follows is founded upon the time record of a series of embryos which developed at a mean temperature of 12.9° C. After the blastodisc has attained its greatest thickness and internal convexity, which occurs 1 hour and 20 minutes after impregnation, the heaped-up protoplasm slowly subsides, flattens a little, becomes slightly elongated along one axis, and remains quiescent for a time in this condition.

At 1 hour and 40 minutes after impregnation, the first segmentation furrow begins to appear as a narrow transverse depression across the middle of the outer surface of the disc, while on the inner surface appears a button-like elevation which is quickly subdivided by an internal depression placed exactly opposite to the external one. The halves of the button then subside and diverge, and, moving with a wave-like motion outward on each side of the internal furrow, cause a pair of prominent elevations to appear on this surface of the blastodisc. The external furrow rapidly extends to the margins of the blastodisc and cuts deeper into the protoplasm, which thus becomes almost separated into two equal halves or blastomeres, in each of which the protoplasm becomes actively heaped up. At the same time each blastomere tends to become circular, so that the blastodisc elongates in the axis at right angles to the first furrow. The segmentation furrow never cuts quite through the disc, but spares a thin layer of protoplasm on its deeper surface, so that the otherwise separate blastomeres remain connected by a protoplasmic web in contact with the yolk. The active process of division is completed very quickly. The heaped-up blastomeres then subside and pass into a resting state, during which the segmentation furrow becomes much less conspicuous. This condition is of relatively long duration, and it is interesting to note here that the slower development of this species as compared with the Spanish mackerel is due almost entirely to the greater duration of the resting periods, the periods of activity in each being of almost equal duration.

The second furrow, formed at right angles to the first, is completed in 2 hours and 35 minutes after the mixing of the ova and the sperm, and the four blastomeres resulting will soon be found to have shifted around the polar axis of the egg from left to right, supposing one to be facing the external surface of the segmenting disk. Protoplasmic movements, followed by a long resting stage, characterize this as well as succeeding periods of development.

The third and fourth furrows, parallel respectively to the first and second, and resulting in the formation of 8 and 16 blastomeres, are completed in 4 hours. Already, at this stage, irregularities in segmentation begin to appear, and their frequency makes the mackerel somewhat remarkable among fishes having similar eggs and modes of development. Even in the 8-cell stage one of the blastomeres may be much smaller than the others, or pushed from its place to a deeper plane than its fellows. In the formation of the fourth cleavage one or two of the cells may fail to divide with the others, producing a stage with 15 or 14 cells, or the division may be unequal, and in nearly all cases it is unsymmetrical. In most teleostomous fishes such irregularities occur much less frequently and not so early in the developmental process. The Spanish mackerel, however, presents a similar case. Such irregularities may possibly indicate impaired vitality in the eggs studied, but, as they occur with such frequency in every lot of material examined, I am inclined to doubt this. In no case in which the future development of such eggs was followed did the normal growth of the blastodisc or embryo appear to be modified. The typical 16-cell stage forms a nearly square figure consisting of 12 marginal and 4 central cells, which latter have shifted spirally around the polar axis of the egg as mentioned above. Up to this time the segmentation has been perfectly rhythmical, occurring in all of the blastomeres at the same time, but, from now on, the central and marginal cells have a different history, which, however, soon becomes confused.

Following the 16-cell stage is one of 28 cells, resulting from the nearly simultaneous division of the 12 marginal cells; those at the angles of the square blastoderm dividing along planes approximately diagonal; those at the middle of the sides along planes parallel with the diameters. The central cells do not divide at this time, but soon follow with a horizontal division, thus making two layers of cells in the central part of the disk, while but one continues at its margin. Between 5 and 6 hours after the beginning of development the marginal cells divide again, resulting in a disk containing about 56 cells. From this time on the divisions occur in a more irregular way, though their rhythmic character is still apparent. The marginal cells are for a time smaller than the central ones, and begin to give rise to buds, in which lie the outer ends of the division spindles, which give rise to the periblastic nuclei. Succeeding the next division the cells of the entire blastoderm become of very irregular shape, horizontal as well as vertical cleavages are formed in all parts of the disk, and the marginal cells have their longer axes placed in radial directions preparatory to the rapid formation of the periblast nuclei and the superficial spread of the blastoderm which now begins.

After 12 hours of development the arc of the blastoderm occupies about one-fifth of the meridional circumference of the egg. Its inner surface is nearly flat, the outer slightly convex and the margins thin. In its central part the cells are 3 to 4 layers deep and, owing to the repeated horizontal divisions, now smaller than the marginal. The latter are surrounded by a wide periblastic wreath containing numerous nuclei.

At 16 hours the blastodermic rim is inflected and the embryonic thickening begins to appear.

At 20 hours the blastoderm occupies about 35 per cent of the surface of the ovum, and the embryonic shield has extended to its vertex.

At 30 hours the blastoderm has covered about 50 per cent of the surface of the ovum and the body of the embryo is distinctly outlined.

At 40 hours the blastopore is still about 0.5 mm. in diameter, and the embryo extends around about 35 per cent of the egg circumference. The notochord is distinctly differentiated. The eyes are just becoming defined as out-pushings. The embryonic body is deep and compressed below, but no myotomes are visible. No pigment has yet developed.

At 45 hours the blastopore has decreased in diameter to an average of 0.4 mm. The embryo extends nearly halfway around the egg. The eyes stand out from the head quite prominently as rounded masses. The first myotome is formed.

At 52 hours the embryo measures in total length 1.7 mm.; 5 myotomes, of which the first 2 are very distinct, may be counted in the middle region of the trunk. The head is clearly marked off. Pigment begins to appear and the chromatophores are arranged along the margins of the trunk of the embryo for its entire length. The nervous axis is very conspicuous.

At 60 hours the length of the embryo has increased to 1.9 mm. Pigment has become much more abundant and is aggregating on the head. There are 11 distinct myotomes. The crystalline lens is appearing as a thickened in-pushing of the epiblast. The blastopore is nearly closed.

At 70 hours the length of the extended embryo is 2 mm. The epiblastic involutions for the crystalline lens and the ear-sac are distinctly marked. The nasal involution is beginning to appear. The fourth ventricle of the brain is differentiated and the cerebellum is folding off. The lateral-line sense organs are apparent as epiblastic thickenings. There are 19 myotomes. The pigment cells have become more conspicuous and branching. No pigment is present anterior to the eyes. A small pointed caudal tubercle is forming as a preliminary to the outgrowth of the tail.

At 78 hours the embryo measures 2.1 mm.; 20 or 21 myotomes are present. The ear-sacs are now closed vesicles, just anterior to which appear the beginnings of a large sense-organ. The lens has sunken deep into the optic cup, its inner wall is thickened, and its orifice is closing. The olfactory vesicles also have their orifices much constricted.

At 88 hours after the beginning of development the embryo measures 2.3 mm. in length, and the tail has grown out free of the yolk to a length of 0.2 mm. The head has become broad and conspicuous, and measures 0.4 mm. across the eyes. The ear-sacs are still thick-walled, simple vesicles, measuring 0.1 mm. in length. The branchial sense organs are conspicuous. The pigment is now arranged principally in two lines along the margins of the body, a very few scattered cells appearing on its dorsal surface. Yellow pigment makes its first appearance behind the forming eyes.

At 102 hours the embryo measures 2.4 mm., the free tail 0.3 mm. The median fin ridge has begun to develop on the tail, which has now been deflected to the left side of the embryonic axis. The alimentary canal (mesenteron) is still an open groove for most, if not all, of its length. The mouth depression is appearing, with slightly marked maxillary and mandibular processes inclosing it. The branchial clefts appear as faintly defined furrows. The head is still very broad and flat. The heart pulsates actively, but somewhat spasmodically. The oil-sphere is closely applied against the base of the tail and is undergoing rapid absorption. Its protoplasmic sheath has fused with the blastoderm, and the pigment cells, which have now developed on its internal surface, have united by anastomosing processes to constitute a reticulum.

At 114 hours the embryo is 2.6 mm. in entire length; the free tail is 0.3 mm. The caudal fin-fold is quite prominent. The tail has now turned with its flat side toward the yolk. There are about 73 myotomes. The head has not yet begun to rise freely from the yolk-sac. A thickening near the anterior end of the alimentary canal indicates the outgrowth of the liver. The alimentary groove seems to be entirely closed.

Hatching usually takes place at 120 hours after impregnation. The newly hatched larva measures 3.3 mm. in length; the yolk-sac 1.3 mm. in length and 0.8 mm. in depth. The oil-drop has become much reduced and its inner surface flattened. It measures 0.28 by 0.15 mm. The head projects slightly beyond the yolk-sac. The mouth and gill slits are not yet opened, but there is a peculiar cleft beneath the edge of the yolk-sac, just over the branchial region. The cephalic sinus is small. Pigment is just beginning to appear in the retina. The yolk-sac is ovoid, and deepest toward its posterior end. The oil-drop is embedded in the posterior ventral part of the yolk-sac, having been pushed forward a short distance from the base of the tail, and at the same time has rotated so that the flattened pigmented surface is now outermost. Considerable individual variation was observed in the exact position of the oil-drop. There is no black pigment on the surface of the yolk-sac, of the median fin-fold, or on the ventral surface of the embryo, except where a few chromatophores sometimes migrate downward over the base of the tail. On the head the black pigment has now formed a conspicuous reticulum extending to the extremity of the snout. On the body and tail the pigment is more scattered, but is chiefly confined to two series of chromatophores located along the base of the dorsal fin and the lateral aspects of the tail. The individual pigment cells tend to arrange themselves along the lines of the intermuscular septa, along which they are produced in slender, branching processes. Pale, greenish-yellow pigment appears in heavy masses, of which there is one on each side of the head behind the eye, another behind the oil-drop, and another on each side of the tail. This latter tends to be produced from the muscular trunk of the tail onto the dorsal and ventral fin-folds. On the third day after hatching the fry measure 3.75 mm., the yolk-sac is almost entirely absorbed, the mouth and the opercular slits are open and functional, the eyes are fully pigmented, and the pectoral fins have assumed their vertical position and adult proportions. By the fifth day after hatching the yolk-sac is entirely gone, the mouth is large and conspicuous, and the skeletal cartilaginous arches of the head are fully formed.

CAUSES AND CONSEQUENCES OF VARIATIONS AND ALTERATIONS IN THE SPECIFIC GRAVITY OF THE EGGS.

The eggs, when received at the ship, between 2 and 3 hours after mixing of the ova and sperm, were in the 2-cell to the 4-cell stage of development. At this time all of those which were mature and intact floated in a compact layer at the surface of water of a density which varied from 1.021 to 1.0226. One entire lot of 425,000, however, of what seemed to be particularly fine eggs of large size, and all fertilized, sunk at once in a density of 1.0216. When the density was raised to 1.0225 they slowly rose and just floated at the surface. To determine the variations in this respect among individual eggs, 100 living eggs were taken, all in the same condition and stage of development, and placed successively in water of different densities, with the following result:

Temperature.	Density.	Number of eggs sunken.	Number suspended.	Number floating.
19° C.	1.022	99	0	1
19° C.	1.024	66	10	24
19° C.	1.025	14	8	78
19° C.	1.0252	0	0	100

A careful comparison of the lightest and the heaviest eggs in the foregoing experiment showed that, excluding from consideration those which were immature or otherwise imperfect, the sunken eggs were more variable in size than the floating. The smallest were, in all probability, the not fully mature and more opaque eggs mentioned above. The larger sank because the oil-drop was relatively of a smaller size than in the eggs of intermediate size.

For the first 48 hours, at a temperature of 12.9° C., at which most of our observations were made, the eggs undergo no marked change in specific gravity. Those which sink during this period, unless a marked fall in the density of the water occurs, are either structurally imperfect or have, for some reason, died during the course of development. A very serious mortality occurred in many of our lots of eggs at about 18 to 24 hours after impregnation, when embryological development had reached the late blastula and early gastrula stage. When, during the early part of the third day of development, the body of the embryo is well formed, with from 3 to 8 myotomes differentiated, there is a marked increase in the specific gravity of the eggs. They then begin to sink slowly toward the bottom, most of them remaining for a long time in suspension, and a few (the number of which varies with the batch of eggs and the density of the water) retain their position at the surface. The cause of this increase in weight becomes more apparent as development proceeds. In the first place, it is to be noted that at about this time the oil-drop has been inclosed by the spreading blastoderm, and already on the third day shows signs of absorption in a flattening of the inner surface of the sphere and a diminution in size, shown by careful measurements. The oil-sphere, which at first measures about 0.29 mm. in diameter, has by the time of hatching decreased in one diameter to 0.16 mm., the other remaining at about its original size. The absorption of the yolk and oil-drop and the building-up of the more compact body of the embryo has, in the meantime, resulted in a contraction of the vitellus and an increase in the size of the perivitelline water space. The egg-sphere, therefore, while undergoing no increase in size, has come to include relatively more solid matter, and is therefore heavier.

I have gone somewhat fully into this matter, as I desire to show that the increase in specific gravity at this time and subsequently is a perfectly normal process. Probably any egg, the specific gravity of which is so nearly that of the density of the water in which it is developed—as was the case with these mackerel eggs—would undergo a similar submergence during the later phases of development. The eggs are not dead when they sink to the bottom (though of course those which have died will also sink), but lie among the mass of débris and sooner or later succumb to the influence of the decaying organic matter. This subject, with its probable significance and practical bearings, is considered in a later part of this report.

2. RESULTS OF SURFACE TOWINGS.

It was early in the course of the investigation considered that important aid might be rendered toward the practical ends of the work if the distribution of mackerel eggs deposited naturally in these waters could be determined, together with the environmental conditions under which they were obtained. To secure this information, surface towings were begun on June 26 and continued daily, except during the progress of two heavy storms, until July 27. After the arrival of Mr. Brett on July 1, the collection of this material and full physical and meteorological data bearing upon it were placed in his charge. Extensive and systematic examinations were made of the waters, especially about the eastern entrance of the bay, and less fully elsewhere. The material was fully examined by me, with special regard to the number and condition of the mackerel eggs present. The results were in part quite unexpected, and in part probably confirmatory of conclusions stated in a previous part of this report.

The inshore waters of Casco Bay have been generally supposed to be one of the most important spawning-grounds of the mackerel on our coast. If this opinion be well grounded, one would expect to find large numbers of mackerel eggs on the surface, and I was consequently much surprised at the almost utter barrenness of the collections in this respect. Although other pelagic eggs of at least twelve species were found, some of them in very great abundance, most of the surface specimens yielded no mackerel eggs at all, or but two or three were detected among thousands of the eggs of other species. An unidentified species of egg, which in its early stages, could scarcely be distinguished from the mackerel, was found in some abundance, but, when developed, produced a larva having very different characteristics. The only occasions on which any considerable number of mackerel eggs were obtained was during the prevalence of south and southeast winds, which blew within the scope of our observations the offshore surface waters, a fact indicated by an increased density. One is, therefore, probably justified in concluding that during the season of 1897 only a very few mackerel spawned inshore in the vicinity of Casco Bay, and that spawning for the most part was accomplished at a greater or less distance out at sea. This conclusion, of course, does not necessarily invalidate former conclusions that the waters of Casco Bay constitute an important breeding-ground for this species, but simply establishes the fact that certain conditions, not at present definitely known, sometimes cause most of the mackerel to spawn farther off shore. It may be added that the literature of the mackerel contains much evidence confirmatory of this opinion.

Of the mackerel eggs obtained by surface towings, all were in early stages of development, the oldest containing embryos having 12 or 13 myotomes and extending about halfway around the egg; that is, they were in stages that are reached under the artificial conditions of propagation during the third day of development. Now, of the eggs of various other species of fishes, as of the cunner, sea bass, and scup, which habitually spawn inshore, those obtained under similar conditions exhibited many examples in later stages of development, and one would expect, if the mackerel egg remained similarly afloat until hatched, that among the 200 or 300 eggs collected at the surface some of the later stages would be sure to occur. The absence of such stages seems to confirm the observation that in water of the comparatively low density obtained here the eggs of this species will not float during the later stages of development. It is possible that the eggs of the mackerel are usually deposited so far out at sea that the density of the water to which they are subjected is sufficient to float them during the entire period of development. It may also be suggested that large numbers of them may be carried by winds or currents to the open ocean, and there find the conditions best suited to their welfare.

But suppose they do normally sink in the 20 or 30 fathoms of water found where they were collected, or in the still deeper water whence most of them in all probability came, what conditions do they meet?

First, a column of water many (several hundred) times as high as that in the boxes and jars in which artificial propagation has been attempted. For a body of but little lower specific gravity to pass through such a stratum of water would require, even were the water in a perfectly quiescent state, a very considerable length of time—perhaps quite sufficient to permit hatching before the bottom is reached. But the constant slight movement to which these waters are subject owing to their agitation by tide, winds, and constant currents would greatly prolong the time of descent.

Secondly, the density undergoes a constant and in deep water a frequently considerable increase toward the bottom, so that the egg in its progress downward would always pass through water of a density corresponding to its own increasing specific gravity, and would thus be constantly buoyed up by a nicely adjusted force, the result of which would be to further delay it.

It is probably safe to conclude, then, that under natural conditions the egg of the mackerel is always suspended in water of a density very nearly equal to or greater than its own, and that it does not normally settle to the bottom and rest there in a mass of filth, and subjected to conditions of imperfect oxygenation, etc., which is the case in the forms of artificial hatching apparatus, namely, the Chester and McDonald systems of tidal boxes which have hitherto been chiefly employed. Another consideration to be noted is that the parallel increase in density of the water and the specific gravity of the egg will result in the maintenance of a nice balance of osmotic pressure which may possibly be a requisite to a healthful development. Three other conditions of change relate to light, oxygenation, and temperature, all of which decrease toward the bottom.

3. RESULTS OF EXPERIMENTS.

When the results of biological investigations of the conditions of development were sufficiently advanced to have led to the conclusion just briefly outlined, several important lines of experimentation seemed to be indicated. Direct observation of the changes in the living egg and of the conditions affecting the distribution of the egg in nature having suggested the importance of an increasing water density, a series of experiments designed to test the influence of this condition was first planned. Indeed, owing to the paucity of material and the limited time in which to work, this series was the only one which was conducted in anything like a systematic manner, and even here the results of individual experiments, which could not be repeated and verified, are too meager to be conclusive.

A description of one or two of these experiments, with their results, will suffice to indicate the general character and bearing of all.

Lot *D* consisted of 109,000 eggs, yielded by two females taken in the trap net of Mr. Sennett, June 26. Sperm and ova mixed at 5.15 p. m. All of the eggs were fertilized and in the 4-cell stage when examined on board the ship shortly after 7 p. m. All were placed in a McDonald cod-box, in which they floated buoyantly in water of a density of 1.0221. The eggs were allowed to remain without change all through the next day and until the morning of June 28, when, at the age of 40 hours, they were approaching the period of development when, according to previous observations, they might be expected to pass into suspension. Up to this time the mortality had been very small, and was chiefly the result of eggs having adhered to the somewhat rough wooden sides or the corners of the McDonald boxes, when they were left high and dry by the receding water and killed.

At 11 a. m. on June 28, at which time the blastopore had just closed, three lots of eggs, estimated to contain 25,000 each, were removed from the McDonald box and subjected to the following conditions: One lot, designated as sublot *DA*, was placed in a second McDonald box under conditions precisely similar to the first, and was retained as a check on the other sublots.

A second sublot, designated as *DB*, was placed in an apparatus designed to imitate the Chester tidal boxes and jar, arranged by cutting the bottom out of a 2-quart Mason butter jar, tying cheesecloth over both ends, and placing this upright in a pail provided with a siphon hose. The eggs were placed within the glass cylinder in water which had been gradually increased in density, and the apparatus then supplied with water, the density of which had been raised by adding a solution of rock salt to 1.0252, this having been previously determined to be the density in which the eggs would just float at this period of their development. About 500 gallons of this density of water, sufficient to fill one of the large deck boxes, was made up to supply the apparatus. After the height and rate of the tidal flow had been adjusted to that customarily adopted for the McDonald boxes, the apparatus was left to itself, except that it was necessary to replace the water in the supply tank and aerate it about every 12 hours.

The third sublot, designated *DC*, was also passed gradually into the water of 1.0252 density, and then placed in a box provided with cheesecloth bottom, which was floated in the supply box of high-density water on deck.

The history of these three sublots briefly told is as follows: During the next 24 hours, those comprising *DA* had gradually settled, becoming distributed all through the water and on the bottom, although the density had increased to 1.0226. The eggs were alive and the oil-sphere had begun to be absorbed. In sublot *DB* the eggs all floated in a compact layer at the surface of the water. They were slightly more advanced in development than *DA* and the oil-drop was smaller. Of sublot *DC* many of the eggs had been killed by rupture of the membrane or other injury caused by striking or sticking to the sides of the box while washing to and fro in the tank.

During the fourth and fifth days of development, most of the eggs of sublot *DA* lay on the cheesecloth at the bottom of the box and the embryos gradually grew weaker until they finally succumbed. A very few, about several hundred, hatched, but all died within 24 hours. The eggs of *DC* were almost all destroyed by being injured or stranded on the side of the floating box. Those of *DB* continued to develop beautifully until the close of the fourth and béginning of the fifth day, up to which time they had continued to float with only a very small percentage of loss. At this time they were nearly ready to hatch, having developed at a higher temperature and more rapidly than *DA*, but now they began to die rapidly and within a few hours the entire lot succumbed. A heavy rain-storm occurred about this time, and the density of the supply of salter water was found to have dropped to 1.024. But I do not attribute the mortality to this, because many of the embryos were observed to die while floating at the surface, to contract, turn opaque, and sink just as they do when affected by some deleterious substance.

Results practically similar to these were obtained in all experiments with higher densities, the encouraging feature being that, by this means, a much larger proportion usually remained alive until late stages of development than when low-density waters were employed. In no case was a greater number hatched, and in no case did the fry thus reared appear to be more vigorous.

Another rather interesting result was obtained by taking eggs which had sunken to the bottom of the usual apparatus and placing them in a circulating current in the McDonald shad jar, the outflow being protected by cheesecloth cage. Under such circumstances the numbers hatched were always larger than in samples of the same eggs which were left undisturbed, and fry already hatched could be kept alive and vigorous for a much longer time. Some were thus kept for 5 days, when the yolk-sac was absorbed, and they were ready to begin feeding. Half of one lot (lot *G*) of over 400,000 eggs, all of which sunk at once after fertilization, were thus treated. The remaining half being placed in a McDonald cod-box, every one of the eggs which had lain at the bottom of the box was dead before 36 hours had passed. The eggs placed in the closed current jar continued to develop up to the last day and some of them hatched. Probably the proportion hatched would have been much greater could the eggs have been prevented from piling up on the outlet screen and injuring one another by the pressure. Numerous other experiments were carried out, but none were more conclusive or satisfactory than those just indicated. It was found impossible, with the limited facilities, to be sure that only one condition had been varied, and that some other factor had not arisen to vitiate the results. In view of the fact that in no case was a greater per cent than 50 hatched, and that only once attained, it seems useless to describe the results with further detail. It seems proper to add that Mr. Corliss, superintendent of Gloucester station, advises me that he has this year attained much more encouraging results, having hatched in some cases over 80 per cent of the eggs placed in the McDonald cod apparatus.

SUMMARY AND CONCLUSIONS.

Following is a brief summary of what seem to be the most important results of the summer's work, but I wish particularly to point out that the statements contained in this report, based upon the limited data of but one season's experience, have not the force of final conclusions, but are offered as suggestions only, which I hope may be useful to the next student who takes up the problem of mackerel propagation:

During the season of 1897 the common mackerel spawned only very sparingly within the limits of Casco Bay, but in greater numbers at some unknown distance off the coast. Those fish which entered Casco Bay after July 1 were in mixed schools, but most of the females were already spent, or partly so. The best run of spawning fish occurred in this region, according to the united testimony of the fishermen, during the first half of June.

For each individual mackerel the season of productiveness extends over several weeks, the eggs being produced in several batches, which mature in succession. Night spawning is probably the rule with the mackerel, but the eggs probably continue to be dehisced into the ovarian cavity during most of the day. I have collected an abundance of evidence bearing on this point.

There are indications that eggs produced by mackerel in different regions differ in size. This may result from the existence of quite different schools or races. During the course of its development the egg increases in specific gravity, owing to absorption of the oil-drop, and sinks beneath the surface, where it encounters higher densities and other changed conditions.

The morphology of development does not differ in essentials from that of the cod, Spanish mackerel, and sea bass, which has been well described in publications of the United States Fish Commission. Irregularities of segmentation occur with unusual frequency and at unusually early stages.

The eggs collected from trap nets in the latter part of the afternoon, though sometimes presenting evidence of being not quite mature, were very easily fertilized and seemed to be healthy.

Fertilization should be effected by the wet method and immediately, as the sperm retains its vitality for a short time only.

The fertilized eggs are best transported in vessels of water; cheesecloth and muslin trays have proved unsatisfactory. The eggs should be freed of surplus sperm and be prevented from overheating.

The indications are that the poor results attained on the *Fish Hawk* are due not so much to the poor quality of the eggs as to some defect in the apparatus, possibly to some deleterious substance introduced somewhere in the hydraulic system.

The results of experiments indicate no form of apparatus better for the first two days of development than the usual tidal boxes, provided the sides are smooth, preferably of glass or enamel, and provided that the screens are kept free of any deleterious substances. For the later days of development and for the fry after hatching a higher density and greater purity of water and a form of apparatus that insures a better circulation and keeps the ovum in suspension without undue agitation is indicated.

Being very delicate and sensitive to physical injury and the presence of deleterious substances, the eggs should be handled as little as possible. A relatively small number should be placed in one receptacle, not more than would form a single layer on the surface (Mr. Corliss's opinion on this point differs from mine, he claiming to have had equal success with large and small numbers), and especially the hatching apparatus should be kept as free as possible from decaying organic matter or other contaminating substances.

RECOMMENDATIONS.

The experience of the past few years seems to render it sufficiently obvious that unless some very different conditions obtain in future there is little to be hoped for from the methods of propagating the mackerel now in vogue. The few millions of eggs annually secured are so insignificant in comparison with the vast numbers which must be produced naturally that even if all were hatched the fry resulting would be a mere drop in the ocean.

It is well known that the purse-seine fishermen operating some miles offshore frequently secure whole schools of spawning mackerel, from which the eggs run so freely that decks of fishing vessels become literally covered with those which have accidentally escaped. This circumstance, coupled with the before-mentioned fact of the readiness with which fertilization can be accomplished, leads to the following suggestion, which I recommend as a guide toward a tentative policy of the Fish Commission during the progress of further investigations:

The captains of the fishing schooners should be asked to cooperate upon such terms as may be agreed upon, to the end that when such spawning schools of mackerel are met with the fish should be immediately stripped, the ova and sperm mixed, and, after permitting a few minutes to insure fertilization, turned overboard to undergo their development amid the natural surroundings from which they were taken. In this way, especially when such schools were taken in the late afternoon or at night, vast numbers of fertilized and healthy eggs could be liberated under conditions which have been previously indicated as those most favorable to their growth.

The work of stripping and impregnation can be accomplished so simply and quickly that it would not materially interfere with the regular duties of fishing, and I have no doubt that the more intelligent fishermen, particularly in view of some small consideration, could accomplish it successfully. Each schooner could be provided with a circular of instructions and such vessels (large, shallow pans) as would be needed to insure the intimate contact of spawn and sperm when mixed. It may even be deemed advisable, though this seems hardly necessary, to place experienced spawners on vessels which would make favorable terms, to conduct the operations.

In presenting this suggestion one additional factor needs to be emphasized. While the exact spawning habits of the mackerel are unknown, the probability is that this function is accomplished while the males and females are actively swimming about together at a greater or less depth below the surface. The spermatozoa are probably more or less widely disseminated through the water. The ova are squirted out in a stream, and, being at this time highly buoyant, immediately begin to rise toward the surface, the micropyle, through which alone the spermatozoan may enter, being downward. Under such circumstances many ova must escape fertilization. That such is the case is shown by the very considerable number of unfertilized eggs which were observed among those of the mackerel collected in the surface towings this summer, and still better by my observations on the eggs of the cunner, of which fully 30 per cent of those examined had failed of fertilization. This shows that one very considerable advantage of artificial over natural propagation of pelagic fish ova is derived from an increased effectiveness of the means of bringing the sexual elements into contact. No doubt much may be gained by continuing the care of the developing ova to a later stage, when the means for so doing, as in the case of the shad, is effective; but when, as is at present the case with the mackerel, there are lacking facilities for prosecuting the work further under such circumstances as will insure a profitable scope of operations, it seems best to adopt the merchant's dictum of "small profits and large sales." No doubt the time will come when the means will be provided for carrying the eggs collected in this way up to the time of hatching.

It needs also to be pointed out that most of the eggs which would be produced by spawning schools thus captured are now entirely lost, and that this fact alone, in the case of the lobster, has been regarded as sufficient to commend the present mode of propagating that species; although here what was said above of the advantage to be gained by artificial fertilization is not applicable.

The advantages of this plan are economy and the possibilities of extensive operations; the disadvantage is its probable uncertainty from year to year.