
**PERITONEAL MEMBRANES, OVARIES, AND OVIDUCTS OF
SALMONOID FISHES AND THEIR SIGNIFICANCE
IN FISH-CULTURAL PRACTICES**



By William Converse Kendall

Scientific Assistant, U. S. Bureau of Fisheries

CONTENTS.

	Page.
Introduction.....	185
Abdominal viscera.....	185
Alimentary tract.....	187
Liver.....	187
Kidneys.....	187
Pancreas.....	187
Spleen.....	187
Air bladder.....	187
Gonads.....	187
The peritoneum and supporting membranes of the viscera.....	187
Histological structure and embryonic development.....	187
The dorsal mesentery of Salmonidæ.....	188
The ventral mesentery.....	188
Structure and development of genital organs of fishes in general.....	188
Observations upon ovaries and ovarian membranes of Salmonidæ.....	191
Oviducts of Salmonidæ.....	194
Peritoneal membranes, ovaries, and oviducts of Coregonidæ.....	197
Ovaries, ovarian membranes, and oviducts of smelts.....	197
Summary.....	200
Relationship of salmonoid fishes, ganoids, and elasmobranchs as indicated by the oviducts.....	200
Relation of the anatomical facts to fish-cultural practices.....	203
List of works consulted.....	206

PERITONEAL MEMBRANES, OVARIES, AND OVIDUCTS OF SALMONOID FISHES AND THEIR SIGNIFICANCE IN FISH-CULTURAL PRACTICES.

By WILLIAM CONVERSE KENDALL,
Scientific Assistant, U. S. Bureau of Fisheries.

INTRODUCTION.

The observations embodied in the present discussion were begun several years ago and have been carried on intermittently to the present time. The study has been attended by various difficulties. It has been almost impossible to obtain perfectly preserved specimens in which the internal organs had not been more or less deranged or mutilated. The membranes in question, being very delicate, are easily torn or broken in handling prior to or during dissection and are liable to disintegrate unless well preserved. These facts and others, together with erroneous ideas derived from published references to these structures, have occasioned many uncertainties which have taken a long time to clear up. Since the ovaries undergo many changes of both external and internal appearance, as well as of position, at no time in their growth or development can they be said to be exactly the same as at any other time. After the ova are shed, in those species which normally survive the spawning period, the ovaries undergo many retrogressive changes. Furthermore, the conditions are not always uniform in the same species. Somewhat different conclusions might be reached from observations upon examples representing one or two periods of development only than from a more complete series. Therefore it has required many individuals to permit of an exact determination of conditions. In fact it was only after careful dissection of more than a hundred American smelts that one which seemed to conform to the conditions in the European smelt, as described by Huxley (1883), was found. Probably the failure of the anatomists, to whom reference is made in this paper, to recognize the conditions which are herein described, is attributable to some such facts as the foregoing.

As this paper is primarily intended for fish-culturists and those unfamiliar with anatomy, definitions of the principal abdominal structures precede the discussion. Although desirable, it has been impossible to entirely eliminate scientific phraseology.

At the end of this paper is given an alphabetical list of the authors and works consulted. In the text of this discussion these works are referred to by author and date of publication.

ABDOMINAL VISCERA.

The abdominal viscera comprise the greater portion of the alimentary tract, secretory, excretory, and reproductive organs, together with certain nervous and vascular connections. The present discussion is principally concerned with the supporting and

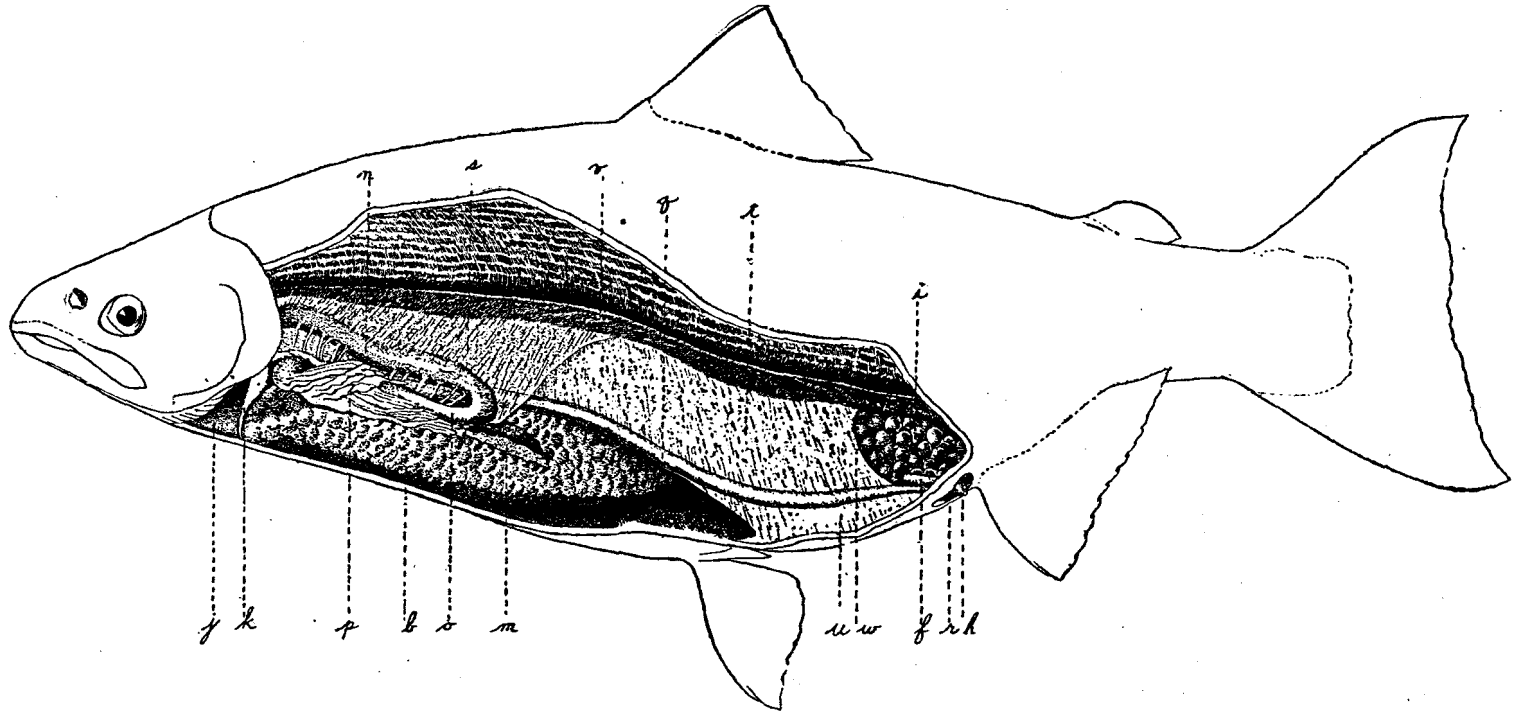


FIG. 1.—Drawing made by Mrs. Effie B. Decker, from a specimen of *Oncorhynchus nerka*, $2\frac{3}{4}$ inches long, collected by Ernest P. Walker, salmon inspector, Wrangel, Alaska, at the mouth of a small stream tributary to Stikine River, some ten miles from mouth of river, August 12, 1917; about one-third natural size; *b*, left or inner side of right ovary; *f*, left side of oviducal channel, anteriorly severed; *h*, genital papilla and pore; *i*, free eggs in oviducal channel; *j*, heart; *k*, anterior septum or diaphragm, separating the abdominal cavity from the anterior body cavity; *m*, spleen, the left ovary rests in the upper groove; *n*, cardiac end of the stomach; *o*, pyloric arm of stomach extending forward to the junction with the pyloric end of the intestine; *p*, pyloric caeca or appendage with attached adipose tissue arising from the pyloric ends of stomach and intestines and lying upon the pyloric arm of the stomach and resting against the ovaries; *q*, intestine; *r*, anus; *s*, gastric mesentery; *t*, intestinal dorsal mesentery; *u*, ventral mesentery; *v*, left longitudinal side of air bladder; *w*, posterior termination of the dorsal mesentery.

investing membranes (peritoneal membranes) associated with the digestive and reproductive systems.

ALIMENTARY TRACT.—In the Salmonidæ the alimentary tract forms a loop within the anterior half of the abdominal cavity or cœlome, so that three portions are recognized: The stomach (fig. 1 *n*), a thick-walled arm extending backward to the point where it makes a sharp bend and as the pyloric arm (fig. 1 *o*), more or less covered by the mass of pyloric appendages or cæca (fig. 1 *p*), extending forward to the posterior surface of the liver, where another sharp bend occurs and from which the intestine (fig. 1 *q*) extends back to the vent.

LIVER.—The liver (fig. 2 *l*) is relatively massive and fills nearly the whole anterior end of the abdominal cavity, on each side more or less overlying the other anterior viscera.

KIDNEYS.—The kidneys lie immediately below and in contact with the dorsal surface and extend from the anterior septum or diaphragm (fig. 1 *k*) to the region of the vent.

PANCREAS.—The pancreas is an elongated lobulated digestive gland, more or less embedded in fat, lying on the upper surface of the stomach and often more or less upon the upper surface of the intestine posteriorly to the stomach.

SPLEEN.—The spleen (fig. 1 *m*) is a dark-colored lymphoid or fluid gland of variable size, irregularly a three-surfaced pyramid, situated close behind the posterior curve of the stomach.

AIR BLADDER.—Immediately below the kidney mass, in contact and approximately coextensive with it, is the air bladder.

GONADS.—The reproductive glands of the Salmonidæ are paired, more or less symmetrical organs, one on each side of the abdominal cavity.

THE PERITONEUM AND SUPPORTING MEMBRANES OF THE VISCERA.

The peritoneum is a serous membrane lining the abdominal cavity and sending out various folds which support and more or less attach to each other the visceral organs. Anteriorly, in conjunction with other tissues, it forms a partition analogous to the diaphragm of higher vertebrates, separating the abdominal cavity from that part of the cœlome containing the heart, gill, esophagus, etc. (fig. 1 *k*). A fold extending to the digestive organs, infolding and forming suspensory membranes, or filamentous and ligamentous attachments, is called the mesentery (fig. 1 *s* and *t*).

HISTOLOGICAL STRUCTURE AND EMBRYONIC DEVELOPMENT.—According to Bridge (1904), the peritoneum histologically consists of a stratum of connective tissue, supporting on its free surface an epithelial stratum (cœlomic epithelium). Primarily, the investing peritoneum is continued both dorsally and ventrally into bilaminar suspensory folds, the dorsal and ventral mesenteries, which extend to the mid-dorsal or mid-ventral line of the abdominal cavity. The two layers then separate and become continuous with the parietal layer of peritoneum lining the whole of the inner surface of the body wall. Embryologically, the two mesenteries owe their formation to the fusion above and below of the mesenteron of the contiguous walls of two laterally and primarily distinct cœlomic cavities. The dorsal mesentery in the adult is occasionally complete, as in the myxinoid Cylostomata and in a few teleosts, but much more frequently is reduced by absorption to anterior and posterior rudiments, or to a series of isolated bands, or even,

as in the lamprey (*Petromyzon*), to a few filaments accompanying the intestinal blood vessels.

THE DORSAL MESENTERY OF SALMONIDÆ.—In adult Salmonidæ the supporting membrane of the alimentary tract diverges from near the longitudinal median line of the peritoneal covering of the air bladder and is attached to the upper surface of the canal as follows: From the diaphragm (fig. 1 *k*) and along the mesial line of the air bladder (fig. 1 *v*), a fold (fig. 1 *s*) is sent out to the upper surface of the stomach on which it ends near the posterior bend or sometimes extends to the spleen (fig. 1 *m*). The pyloric arm has no supporting membrane, but is connected to the cardiac arm of the stomach by filamentous bands, though sometimes anteriorly there may be a trace of membrane. Again, beginning near the diaphragm is another fold (fig. 1 *t*), which, attached to the backward prolongation of the intestine, extends nearly to the vent in the female and quite to the vent in the male.

THE VENTRAL MESENTERY.—Concerning fishes in general, Bridge writes that the ventral mesentery is rarely present and, if present, is never complete. In *Lepidosteus* a ventral mesentery is said to be present in connection with that part of the intestine which contains the spiral valve. In *Protopterus*, and also in *Neoceratodus*, there is a well-developed ventral mesentery in relation with the greater part of the length of the intestine, although in the former Dipnoid its continuity is interrupted by one or two vacuities, and in the latter the mesentery is incomplete posteriorly. A ventral mesentery is also present in the intestinal region of some of the Murænidæ among teleosts, but no mention is made of it in Salmonidæ.

I have examined four species of *Oncorhynchus* (*O. kisutch*, *O. gorbuscha*, *O. tshawytscha*, and *O. nerka*); several species of *Salmo* (*S. salar*, *S. sebago*, *S. trutta*, *S. gairdnerii*, and *S. shasta*); and several *Salvelinus* (*S. stagnalis*, *S. aureolus*, *S. oquassa*, *S. marstoni*, *S. malma*, *S. kundsha*, and *S. fontinalis*), all of which possess a certain extent of ventral mesentery (fig. 1 *u*). Its anterior ventral insertion is a little behind the base of the ventral fins, and the corresponding intestinal insertion somewhat in advance of the ventral insertion, thus presenting a vertical concave edge toward the front. This mesentery in its ventral and intestinal attachments extends to the posterior end of the abdominal cavity. According to Felix (1906) the embryo salmon has a complete ventral mesentery.

By these vertical dorsal and ventral mesenteries and the intestine to which both are attached, about one-third of the abdominal cavity is posteriorly divided into two lateral longitudinal chambers, with a posterior communicating aperture of varying length, but always short, in the dorsal mesentery above the intestine of the female.

STRUCTURE AND DEVELOPMENT OF GENITAL ORGANS OF FISHES IN GENERAL.

The suspensory portion of the ovarian membrane is known as the mesovarium, or mesoarium, and that of the spermary as the mesorchium. Morphologists state that the gonads of the majority of teleosts are completely enveloped by the peritoneal membrane and that the ova and sperm of oviparous forms are conveyed to the exterior of the body cavity by closed canals or tubes composed of the same enveloping membrane extending from the gonad to the genital pore (fig. 2 *h*). The previous state of knowledge regarding especially the ovarian membranes of Salmonidæ is well indicated by the following review of the opinions or statements of principal writers.

One authority (Wiedersheim, Parker, 1897) states that the male and female gonads of teleosts closely correspond with one another as regards position and the arrangement of their ducts. Dorsal and ventral folds of the peritoneum are developed in connection with the elongated ovary, and these in most cases meet along its outer side, so as to inclose a portion of the coelome, and thus convert the ovary into a hollow sac, blind anteriorly, on the inner folded walls of which the ova arise; this sac is continued backward to form the oviduct, which is generally short and fuses with its fellow to form a tube or "ovipositor"; or the ducts may communicate with the urogenital sinus.

The same authority describes the development of the ovary as originating in at first undifferentiated cells of coelomic or peritoneal epithelium on the dorsal side of the body cavity at either side of the mesentery in which the adjacent mesoblastic stroma penetrates. Into the stroma of an ovary thus formed, the cells of germinal epithelium grow in the form of clustered masses; some of which cells increase in size more than others, giving rise to ova, while the smaller cells form investment of follicle around each and serve as nutritive material.

From the foregoing it is understood that the ovaries of most teleosts are derived from folds of the peritoneum, usually one on each side of the body cavity, and, as a rule, are closed sacs consisting of an outer enveloping membrane and inner laminae of ovigerous stroma. Each egg is inclosed in a follicle from which, as it ripens, it breaks out into the inner or central cavity of the ovary and makes its exit from the fish by the way of a tube, or oviduct, of the same membrane and the genital pore.

Some exceptions to this arrangement have been noted. Something over 90 years ago, Rathke (1824) described the ovarian membranes of certain salmonoid fishes, and nearly 60 years later Huxley (1883) reviewed Rathke's work, from which he quotes as follows:

In certain fishes the oviducts have entirely disappeared; this is the case in the eel, the sturgeon, *Cobitis tania*, and in the lamprey. In others, however, such as the higher kinds of salmonoids, there extends back behind each ovary a narrow band which may be regarded as the remains of an oviduct. In all these fishes, therefore, the central abdominal cavity must take the place of an oviduct, as it receives the eggs when they are detached, and allows them to make their exit by a single opening at its posterior extremity.

Still quoting from Rathke, Huxley continued to the effect that, while a proper oviduct is absent from the Salmonidæ, there is an analogue of that structure, consisting of a flat, narrow band, commonly arising at the upper and posterior end of a platelike ovary, gradually diminishing in width backward, and finally becoming lost toward the end of the abdominal cavity. It was stated that in the salmon proper it disappears upon the air bladder opposite the commencement of the last fifth of the abdominal cavity; in the fresh-water trout on the sides of the intestine not far from the anus; in the whitefishes (*Coregoni*) on the intestine close to its end.

In describing the ovary of the European smelt *Osmerus eperlanus*, which was at that time regarded as a member of the salmon family, Huxley stated that in all essentials of the structure of the ovigerous portion or body it agreed with that of the other Salmonidæ. It was said to have the form of a half-oval plate, with the curved edge ventral and the straight edge dorsal. To the latter a narrow mesovarial fold of the peritoneum was said to extend "from that part of the dorsal wall of the abdominal cavity which corresponds with the ventral surface of the air bladder" and the line of attachment to be

parallel with that of the mesentery and a little distance from it. The ovary, described as a broad, thin plate, was stated to have its inner surface covered by the peritoneum, which is continued over the ventral edge, ending about a third or fourth of the height of the outer face by a well-defined margin and its outer face "to give rise to a great number of ovigerous lamellæ of broadly triangular form, which are disposed transversely to the length of the organ and perpendicularly to the body." Huxley went on to say that superficially the ovary appears to be laminated only above the reflected membrane, but that transverse section revealed that the ovigerous laminae pass under the band to the ventral wall and that their outer edges are attached to the band.

In the Salmonidæ, then, according to both Rathke and Huxley, ovigerous laminae without peritoneal covering occupy the outer surface of the pendent mesovarial fold, thus constituting the ovary, from which as they ripen and burst from their investing follicles, the ova fall into the abdominal cavity. As will be seen later, the foregoing observations pertain to only one stage, that of a collapsed and retracted ovary.

Prior to Huxley's description of the oviduct of the smelt, no salmonoid was supposed to have such a structure. In the smelt, according to Huxley, the mesovarial fold continues backward from the posterior end of the ovary to the oviducal apertures, while laterally it passes into the peritoneal lining of the lateral wall of the abdomen, ending in a free concave edge immediately behind and on the outer side of the posterior extremity of the ovary. It thus forms the ventral boundary of a passage which opens in front by a wide ostium into the abdominal cavity. As the posterior end of the right ovary lies very far behind that of the left ovary, it follows, Huxley says, that the right ostium is equally far behind the left. The mesentery, he continues, terminates by a free posteriorly concave edge just opposite the level of the posterior end of the right ovary; and, behind this free concave edge of the mesentery, the left and right passages unite in a short but wide common chamber which opens externally in the middle line behind the anus and in front of the urinary outlet.

It appears that it must be to this structure in the smelt that all subsequent writers refer when mentioning oviducts of Salmonidæ, many regarding the smelt as a member of this family.

This idea that the salmonoids have no oviducts and that the ova are deposited free in the abdominal cavity has been handed down to the present day in all literature pertaining to the subject. Owen (1866) said that the salmon is an example in which the ova are discharged by dehiscence into the abdominal cavity and escape by the peritoneal outlets, as in the eel and lamprey, and that the free surface of the stroma of the ova is exposed.

Gegenbaur (1878) said that in the Salmonidæ the eggs are passed into the abdominal cavity and are evacuated through the abdominal pore.

Günther (1880) wrote that in some families of fishes the ovaries are without closed covering and without oviduct, as in Salmonidæ, Galaxidæ, Notopteridæ, Murænidæ, and others. He stated that the surface of such an open ovary—as, for instance, that of the salmon—is transversely plaited, the ova being developed in capsules in the stroma of the laminae; after rupture of the capsules, the mature ova drop into the abdominal cavity and are expelled by the porus genitalis.

Day (1887) makes practically the same statement, saying that the ovaries are symmetrical organs and destitute of a closed covering, while their internal surface is lined

with stroma and transversely plaited. Here, he said, the development of the eggs takes place, each of which is invested by a fine membrane, by which they hang suspended to the ovary, the length of the pedicle decreasing as the egg augments in size. But as the ovaries are destitute of oviducts it necessarily occurs, he continues, that when the investing membrane bursts, the ovum falls into the abdominal cavity, from whence it is extruded through the abdominal pore.

Jordan and Gilbert (1882) and Jordan and Evermann (1896) make similar statements: "Ova falling into the cavity of the abdomen before exclusion."

In discussing the brown trout (*Salmo fario*) as an example of "subclass III Teleostomi" Parker and Haswell (1897) state that the ovaries extend the full length of the abdominal cavity and are covered with peritoneum on their inner or mesial faces only, and that, when ripe, the numerous ova are discharged from their outer faces into the abdominal cavity. They then go on to say that there are no oviducts, but that the anterior wall of the urogenital sinus is pierced by a pair of genital pores through which the ova make their way to the exterior.

A previously cited authority (Wiedersheim, Parker, 1897) wrote that the ovary of some teleosts is solid and that the ova are shed into the body cavity. The oviducts of the smelt (*Osmerus*) and capelin (*Mallotus*) were referred to as peritoneal funnels having open cœlomic apertures close to the ovaries, into which the ova pass. In the case of other Salmonidæ, the Murænidæ, and Cobitis, it was stated that these peritoneal funnels are shorter and even absent, the ova then being shed into the urogenital sinus through paired or single genital pores.

After describing the genital structures of the Salmonidæ, Bridge (1904) states that in all instances the eggs are set free from the ovaries into the cœlome, whence they escape through the peritoneal funnels or genital pores. The foregoing statements reveal the influence of Rathke and Huxley upon all subsequent interpretations of the structures.

The only teleosts besides Salmonidæ mentioned by Rathke as possessing no oviducts were two species of loach (*Cobitis barbatula* and *C. taenia*) and the eel. Regarding these Huxley says that in *Cobitis barbatula* the single ovary has an oviduct of the same character as other Cyprinoid fishes, but that he had not examined *C. taenia*, about which, in other parts of his memoir, Rathke's statements were full and precise.

Inasmuch as one of the species of the loach was found to have an oviduct, it is quite possible that the other has also. If such is the case, according to Rathke, the only supposedly oviductless species, besides the Salmonidæ, left without such a duct is the eel. However, a few other fishes have since been stated to be oviductless.

The salmonoids, according to the authorities mentioned, appear to occupy almost a unique place among teleosts; but in the discussion which follows I hope to show that their position is not as anomalous as from the foregoing it would seem to be.

OBSERVATIONS UPON OVARIES AND OVARIAN MEMBRANES OF SALMONIDÆ.

The two ovaries in each of the salmonoids which I have examined are never exactly symmetrical in form or of the same length. They have a general primary shape which is maintained, but in their growth and enlargement such modifications of shape and position as occur are largely determined by contiguous internal organs and the abdominal walls. Each ovary is suspended by a membrane (fig. 2 c) originating in the dorsal

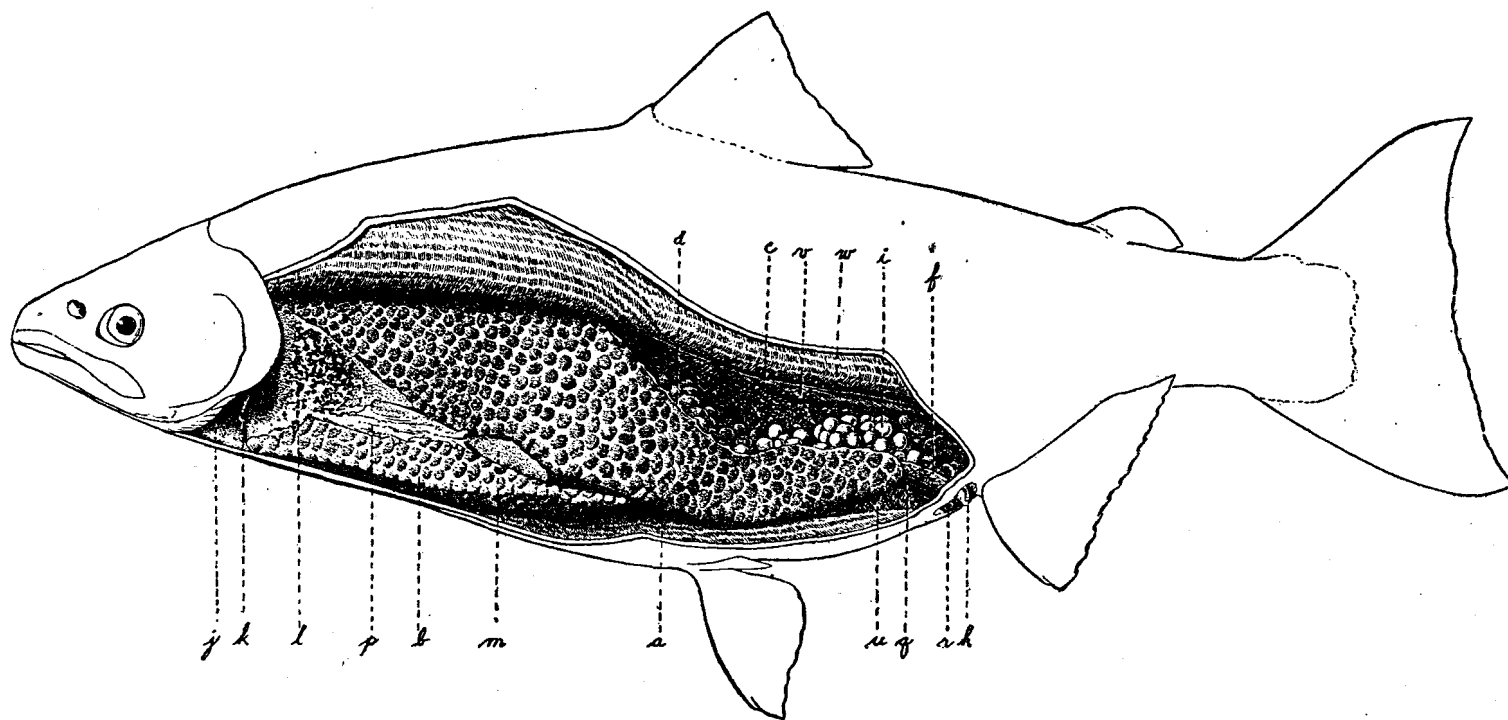


FIG. 2.—Drawing from the same specimen as shown in fig. 1. *a*, Left ovary and containing membrane (somewhat pulled down, revealing ova posteriorly); *b*, right ovary containing membrane showing below left ovary, fish somewhat oblique, opening toward observer; *c*, mesovarium, with air bladder showing through; *d*, outer edge of ovarian membrane; *f*, left side of oviducal channel; *h*, genital papilla and pore; *i*, free ova in oviducal channel; *j*, heart; *k*, diaphragm; *l*, liver; *m*, spleen; *p*, pyloric cæca; *q*, intestine; *r*, anus; *u*, ventral mesentery; *v*, posterior end of intestinal mesentery with confluent mesovarium; *w*, air bladder.

peritoneum at the side of the air bladder. This membrane covers the surface of the ovary which faces the longitudinal axis of the body cavity. From its posterior end a membranous band, which is a continuation of the mesovarium and ovarian covering extends toward the posterior end of the abdominal cavity. Up to this point the conditions are as stated by the anatomists previously cited.

An immature ovary shows that its membrane not only covers the mesial or inward surface as described, but envelops the entire organ. The edge of the membrane, which was stated to mark the termination of the covering at or near the lower margin of a

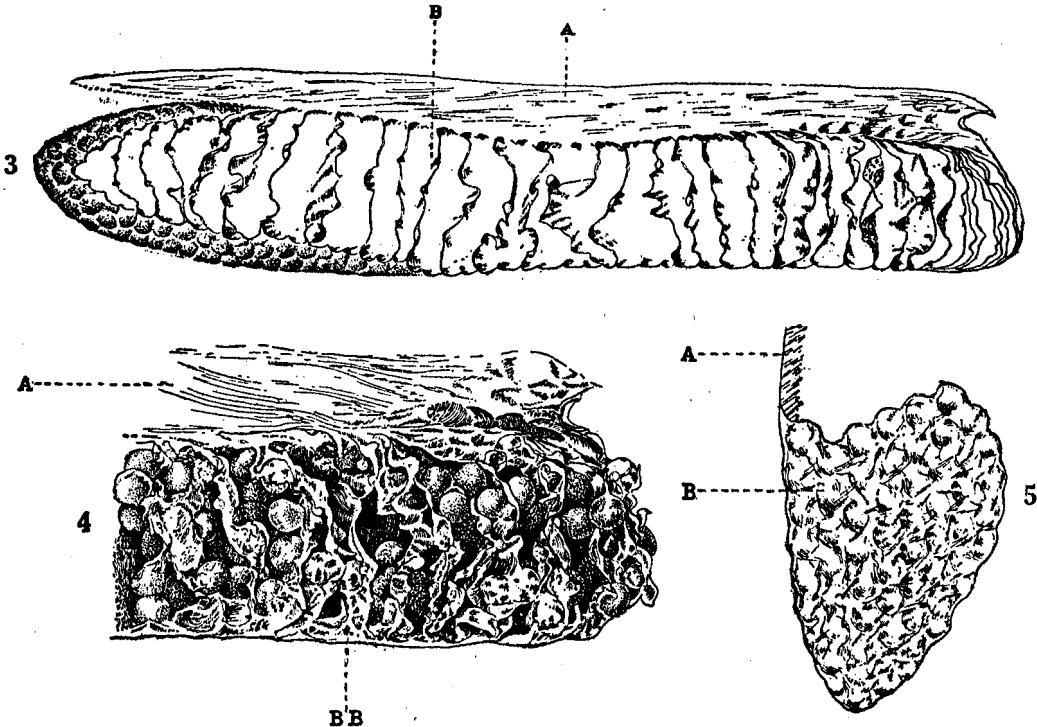


FIG. 3.—Upper view of left ovary, with most of ova removed, showing cross septa and membrane extending up over the forward end. A, mesovarium from which ovary is turned downward to show upper view.

FIG. 4.—Dorsal view of a section of same ovary as in fig. 3 from the region of B, BB representing the same cross septum as B in figs. 3 and 5. Some ova have been removed, others are shown still in the follicles. A, mesovarium.

FIG. 5.—Cross septum (B) in upright position. In natural position, mesovarium (A) would incline to right, and upper edge of septum (B) to left. Impressions of ova shown in septum.

Figs. 3 to 5 drawn by Mrs. Effie B. Decker.

platelike ovary, passes up over the outer surface and is in contact with the membrane of the inward surface. At this time the ovary has much the same general external appearance as that of the other isospondylous teleosts. At a later period, beginning at the posterior end of the ovary, the edge of the membrane of the outer surface to some extent parts from the membrane of the inward surface, leaving a narrow area of ova without attached membranous cover. The area thus uncovered gradually widens and extends forward as the ovary increases in size. Even at maturity the egg surface is to a certain extent infolded in membrane (fig. 2 a), due to the fact that the suspensory mesovarium does not hang vertically but, from its origin at the side of the air bladder slants inward toward the axis of the body cavity, and the egg surface is tipped over so that its

face is against the mesovarium. This position brings what has been termed the upper edge of the ovary downward, so that it is actually considerably lower than the supposed lower edge (fig. 2 *d*), so far as there is any edge. In other words, even the ovary is not platelike, but the supposed plate is folded in such a manner that it may be said in a general way to be boat-shaped with a decided list to starboard or port according to whether it is the left or right ovary. Posteriorly the exposed egg surface is usually proportionally wider and sometimes actually wider than at the anterior end. In fact, the anterior end is permanently covered to some extent by membrane, or to continue the boat simile, it is decked over forward (fig. 3). Furthermore, the ovigerous stroma, which has been stated to be arranged in vertical laminae, transversally and somewhat diagonally connects the two sides, dividing it into transverse compartments (figs. 3 *B*, 4 *BB* and 5 *B*).

OVIDUCTS OF SALMONIDÆ.

As relates to the vestigial or rudimentary¹ oviduct in the form of a narrow band to which the previously quoted anatomists have referred, it is necessary to say that it varies in extent according to the species and does not terminate as described by Rathke, but, without close examination, in an immature, or spent, fish it might be so interpreted.

In a silver salmon (*O. kisutch*), which was unripe, but approaching breeding condition, the lesser backward extent of the ovary resulted in a relatively longer band than was evident in ripe fish, by which the general arrangement is more clearly defined. This band (fig. 6 *e*) arises from the posterior end of the ovary whence backward it is an extension of the ovarian covering and the mesovarium. The line of attachment of the mesovarium (fig. 6 *c*) to the air bladder extends obliquely inward and backward toward the median line of the air bladder until it attains a point near the termination of the mesentery at the anterior end of the communicating aperture above the intestine previously mentioned (fig. 6 *w*). Here the mesovarium, as such, apparently ends. Fusing with the mesentery at a corresponding point on the upper surface of the intestine, the mesovarian membrane joins the membrane of the opposite side, forming a single band, which is attached to and extends along the intestine backward. The outer edge of this band, at the posterior end of the ovary, in unripe or immature fish at least, appears to fold over onto the band forming a sort of hem to the edge (fig. 6 *f*), later becoming the outer edge of the trough, which is supported by the lateral walls of the narrow posterior portion of the abdominal cavity. This outer edge pursues a similar direction to the air-bladder attachment of the mesovarium to the point where the mesentery and mesovarium terminate, whence it takes a course parallel with the middle or line of attachment of the band to the intestine. Its outer edge remains free, and the fold, though becoming narrower, is continued to within a short distance from the genital pore, where it seems to vanish. The membranous band is deflected to either side and becomes attached to the lateral abdominal wall (fig. 6 *g*). Thus from each ovary a troughlike oviduct passage is formed as far as the termination of the mesentery of the intestine, the two passages then merging into one which, not far from the outlet, spreads out and joins the lateral wall on each side. This terminal structure would appear to be a reduced homologue of the so-called funnel described by Huxley in the case of the smelt.

¹ Wiedersheim (Parker), 1897, p. 360, referring to these structures, says: "It is uncertain whether the latter is the primitive arrangement among teleosts, or whether the peritoneal funnels represent reduced oviducts."

As the ova approach maturity,¹ the left ovary is nearly or quite always the longer, and it extends, tapering, to the posterior end of the abdominal cavity (fig. 7 a). About at the point where the mesovarium as a suspensory membrane ends and forms the

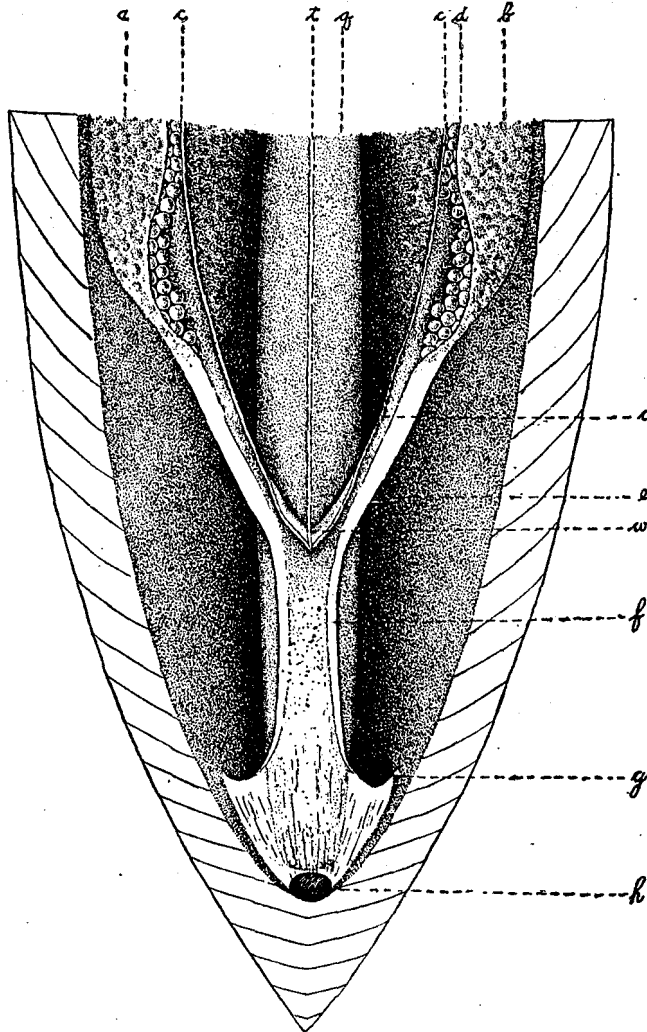


FIG. 6.—Drawing by Mrs. Effie B. Decker from a specimen of *Oncorhynchus kisutch*, 26 inches long, from Ankon Slough, Alaska, July 10, 1917, collected by Ernest P. Walker, salmon inspector. Dorsal view of the posterior end of the abdominal cavity, the abdominal wall somewhat spread out. In natural position this portion of the abdominal cavity is very narrow, and the walls closely approximate. The intestine is laterally flattened and compressed so that it does not show beyond the edges of the superimposed membrane, and the edges of the membrane are turned upward, forming a trough. *a*, Left ovary; *b*, right ovary; *c*, upper severed edge of mesovarium; *d*, outer edge of ovarian membranous covering; *e*, fold or free border of the posterior extension of ovarian membrane, which joins with the other on median line of intestine forming an oviducal channel or trough; *f*, oviducal channel, combination of *e* from both sides; *g*, lateral deflection and junction of oviducal membrane with abdominal wall; *h*, genital pore; *g*, intestine; *t*, severed dorsal intestinal mesentery; *w*, posterior end of severed mesentery.

beginning of the trough mentioned (fig. 7 *w*), the posterior extension of the ovary has no membranous attachment to the trough, but has a free fold or flap of mesovarial, or ovarian membrane along its upper inner side which narrows posteriorly to the end

¹ As observed in one specimen each of Atlantic and humpback salmon.

of the ovary where it again completely infolds the organ (fig. 7 *c*). This flap and the inner side of the ovary probably lie in the trough on the top of the intestine, and the greatly narrowed or pointed end of the ovary rests on the bilateral expansion formed by the deflection of the edge of the trough to the abdominal wall (fig. 7 *g*).

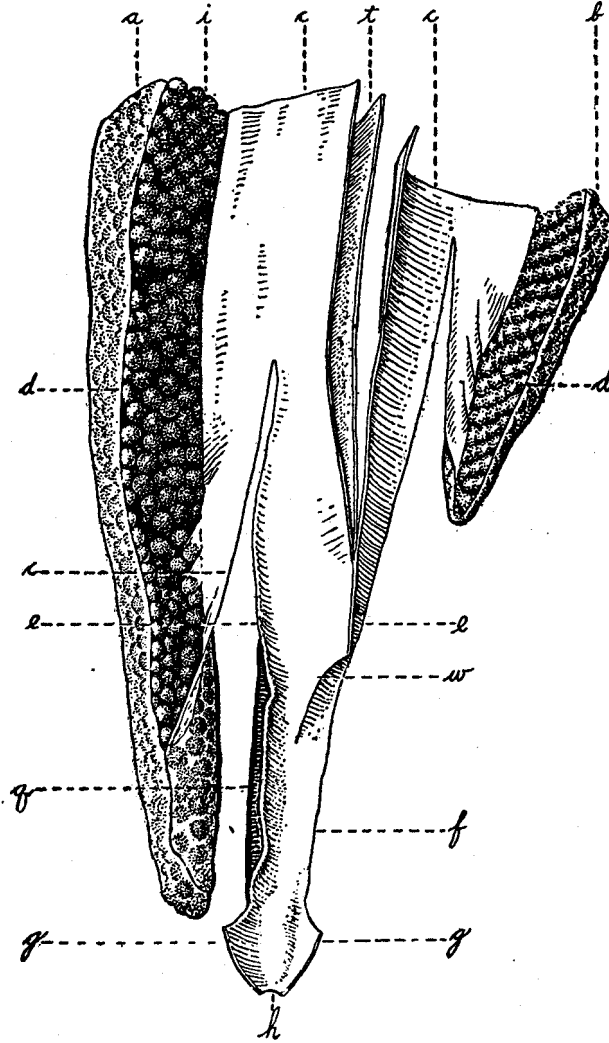


FIG. 7.—Drawing by F. E. Prior, from dissection of a specimen $2\frac{3}{4}$ inches long, from the Penobscot River, Me. Dorsal view of a spread-out section of posterior portion of abdominal viscera and membranes of nearly ripe Atlantic salmon (*Salmo salar*). *a*, Left ovary. *b*, right ovary, turned away from mesovarium showing eggs not covered by ovarian membrane; *c*, mesovaria laid back from normal position on surface of otherwise uncovered eggs; *d*, outer edge of ovarian membrane; *e*, fold or free borders of mesovaria which unite posteriorly to form the oviducal channel; *f*, oviducal channel continuation of *e*; *g*, posterior lateral expansion of oviducal channel, each side of which unites with peritoneum of the lateral walls of the abdominal cavity; *h*, genital pore; *i*, eggs not covered by ovarian membrane; *q*, intestine; *t*, dorsal intestinal mesentery; *w*, posterior end of intestinal mesentery with confluent mesovaria.

The right ovary (fig. 7 *b*), always somewhat shorter, seldom extends in this manner much behind the common opening above the intestine, and accordingly it may or may not have some extent of membranous flap as just described. The ova apparently run along the fold on the inner side of the ovary, and hence into and along the trough mentioned.

These backward extensions of the ovaries are formed by the maturing and enlarging ova filling the previously crowded interlamina spaces at the posterior end of the ovary (fig. 3), thus stretching it longitudinally.

PERITONEAL MEMBRANES, OVARIES, AND OVIDUCTS OF COREGONIDÆ.

A number of specimens of each of the genera *Coregonus* and *Leucichthys* were examined.

The arrangement of the visceral organs was similar to that of the Salmonidæ, but no ventral mesentery was observed. The ovaries and oviducts were much as in Salmonidæ.

OVARIES, OVARIAN MEMBRANES, AND OVIDUCTS OF SMELTS.

As has been seen, according to Huxley, the smelts were supposed to have free ovaries and oviducal funnels, while the salmonids were stated to have free ovaries and only narrow bands, or vestigial homologues of oviducts. My examination of many smelts reveals that, while Huxley was correct concerning the oviducal structures, his interpretation of the ovary was not in accord with all of the facts. He probably accurately described what he saw under certain limited conditions. I previously remarked that at no time in their development can the ovaries be said to be exactly the same as at any other time. This is particularly true as concerns the ovaries of the smelt (*Osmerus mordax*). If the ovary of a spent fish, or one from which the eggs have been removed or washed out, as Huxley stated of his example, is examined, the condition is likely to be as represented by Huxley. The ovary then is in a collapsed, flabby condition, or more or less shrunken state. When the ovaries are full-grown, just before spawning time, but before any ova have been discharged into the oviducts, they exhibit an entirely different appearance. As described of Salmonidæ, the air bladder is attached to each side of the dorsal portion of the abdominal cavity and is covered by the closely adhering peritoneal membrane, in which the mesovarium of each ovary originates.

Posteriorly the intestine is dorsally situated, and the mesentery is there so narrow that the intestine appears to be almost adherent to the peritoneum of the air bladder.

Huxley correctly described the anterior origin of the oviducal membrane at the posterior end of each ovary and the relative situation of each ovary, the right or smaller ovary being posterior to the left or larger ovary.

The oviducal membranes, as in the case of the salmonids, finally unite in a common channel above the intestine. Both of these oviducal membranes, when not containing ova, posteriorly, lie against the membrane of the air bladder which forms the roof of the so-called funnel.

The gravid ovaries practically fill all the space in the abdominal cavity not occupied by other viscera. Upon opening the fish from throat to vent along the median line of the belly and laying the lateral walls aside, at first glance there appears to be one single mass of eggs in front of which is the liver; posteriorly a small portion of the intestine may be visible. The greater portion of the egg mass is the anteriorly situated left ovary which extends from the liver to some distance beyond the base of the ventral fins (fig. 8 a). Closely juxtaposed to the posterior end of the left ovary is the right ovary (fig. 9 b) which extends nearly to the vent. The dividing line, which is often difficult to discern, beginning perhaps a little in advance of the ventral fins, extends obliquely from the right side (left as observed) backward to the left side (right as

observed). Both ovaries are ventrally convex from side to side, and concave above, thus forming a broad, more or less triangular, continuous groove in which anteriorly the stomach lies. The intestine, at first above the stomach, finally lies in the grooves of the left and right ovaries. These grooves are formed by the left ovary curving over so that its so-called lower edge is in contact, or nearly so, with the dorsal surface of the abdominal cavity on the right side, and the left ovary curving in like manner in the reverse direction.

Except in shape and relative position the ovaries are much like those of the salmonids previously described. They are nearly covered by a very delicate membrane which is so thin that it is easily broken or rubbed off, so that one may be easily deceived into believing that there is no membrane and that the eggs are free in the abdominal cavity.

The mesovarium (fig. 9 *c*) arises near the lateral edge of the air bladder, and, in the case of the anterior ovary, its line of attachment gradually passes obliquely inward to its attachment to the intestine. The mesovarium of the posterior ovary has a proportionally longer intestinal attachment.

As in the Salmonidæ, the dorsal mesentery (fig. 10 *t*) ends some distance from the posterior end of the intestine (fig. 10 *w*), and the mesovarial membranes unite to form the floor of the common opening above the intestine. The outer edges continue attached to the lateral walls of the abdominal cavity (figs. 9 *g* and 10 *g*). Thus the mesovarian membranes, originating on the outer side of each ovary and deflecting to the abdominal walls, form the floors of the respective oviducts, while the peritoneum of the air bladder, the abdominal walls, and the mesentery form the other boundaries.

As in the case of the Salmonidæ, the portion of each ovary uninvested with adherent membrane consists of a narrow dorsal area which is tipped in against the mesovarium. In these passages, formed by the investing membranes, the ova pass backward into the oviducts. If they are set free into the abdominal cavity, there appears to be no conceivable way by which they can be extruded. The smelt appears to have no ventral mesentery, unless a close adhesion to the ventral or abdominal surface near the vent is such.

As previously stated, the gravid ovaries are situated one behind the other and almost entirely fill the abdominal cavity, save the comparatively small space occupied by other viscera. Before the ova of the left ovary have entered the oviduct, the gravid right ovary presses the left oviducal membrane (fig. 9 *g*) against the air bladder and left abdominal wall.

The ova of the right ovary ripen, enter the oviduct, and are deposited first. As the right ovary is emptied and its oviduct (fig. 10 *g*) is filled, the ova of the left ovary enter its oviduct and the empty and collapsed right ovary is compressed between the distended left oviduct and the right abdominal wall. The left ovary and its distended oviduct, together with the distended right oviduct, then have the appearance of a single mass of eggs, but, by careful manipulation, a longitudinal line of separation may be detected. As the right oviduct is emptied the left becomes entirely filled and with the remaining ova in the left ovary has the appearance of a single continuous ovary. Probably this was the condition which deceived Bloch, causing him to think that the smelt had but one ovary. When both ovaries are emptied and collapsed, the left is considerably anterior to the right and may have the appearance as described by Huxley; that is, a semioval plate, laminated on the outside and having a marginal membrane of about one-third its width.

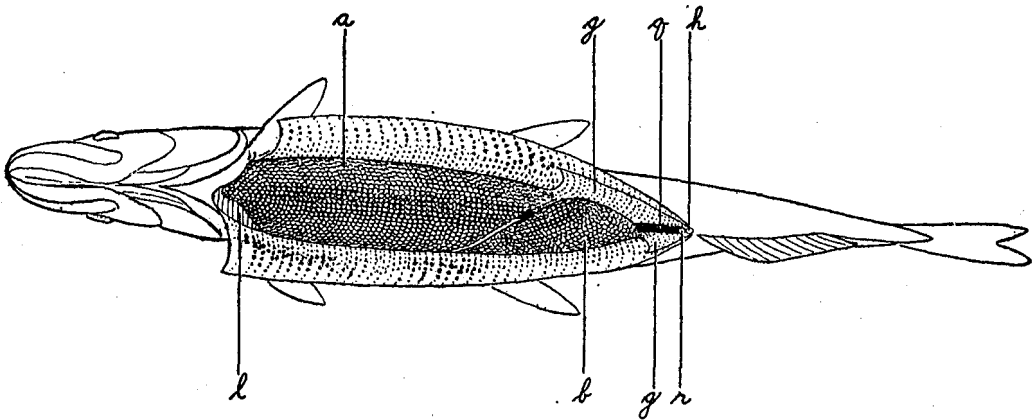


FIG. 8.—Semidiagrammatic drawing made by Walter H. Rich, from dissection by William C. Kendall. Specimen from Sebago Lake, Me. Ventral view of ovaries and oviducts of smelt (*Osmerus mordax*). *a*, Left or anterior ovary; *b*, right or posterior ovary; *g*, lateral expansions of mesovaria and ovarian membranes joining peritoneum of abdominal walls to form oviducts; *h*, genital pore; *l*, liver; *q*, intestine; *r*, anus.

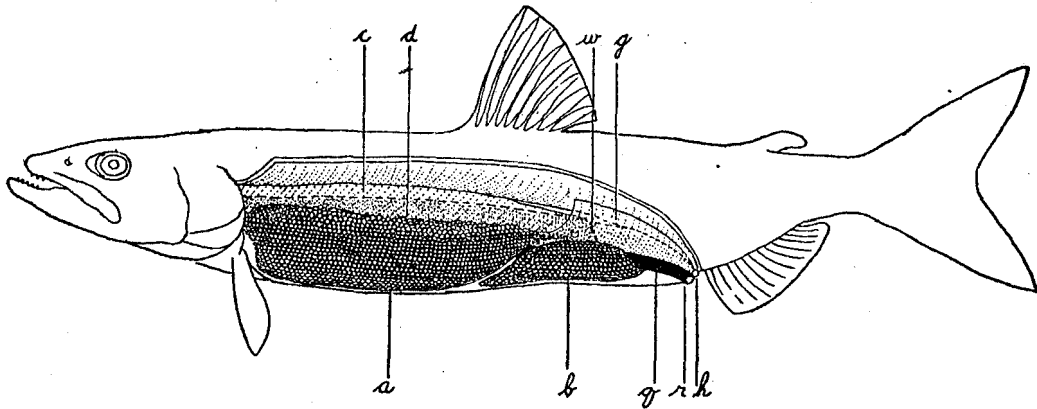


FIG. 9.—Left view of ovaries and membranes of same as fig. 8. *a*, Left ovary; *b*, left side of right ovary bending up on left side so that its lower portion is dorsally situated; *c*, left mesovarium; *d*, outer edge of ovarian membrane; *g*, posterior lateral expansion of mesovarium and ovarian membrane forming left oviduct; *h*, genital pore; *q*, intestine; *r*, anus; *w*, posterior end of intestinal mesentery with confluent mesovaria.

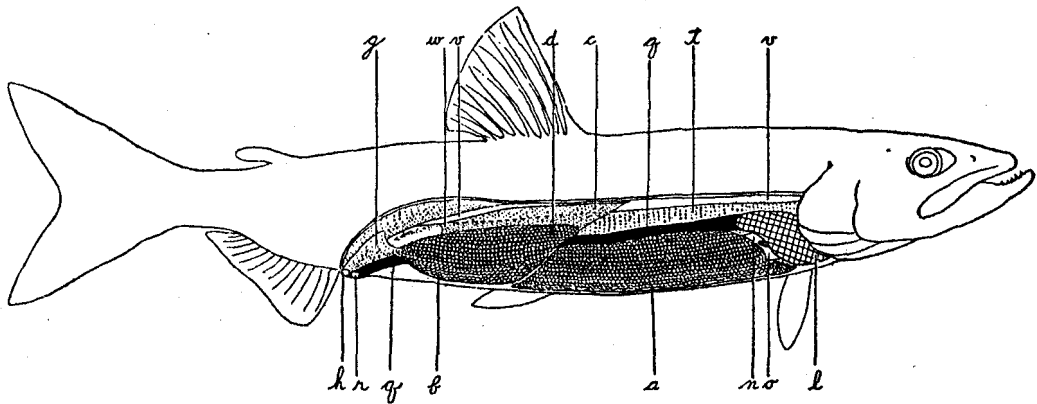


FIG. 10.—Right view of same as fig. 9. *a*, Left ovary bending up under stomach and intestine forming a groove in which the viscera extend; *b*, right ovary; *c*, mesovarium of right ovary; *d*, outer edge of ovarian membrane, between which and the mesovarium the egg surface not covered by membrane other than the mesovarium is situated; *g*, right posterior expansion of the mesovarium and ovarian membranes forming the short right oviducts or practically the right side of the common oviduct posterior to *w*; *h*, genital pore; *l*, liver; *n*, upper or cardiac arm of stomach; *o*, lower or pyloric arm of stomach; *q*, intestine; *r*, anus; *t*, intestinal mesentery; *v*, air bladder; *w*, posterior end of intestinal mesentery with confluent mesovaria.

SUMMARY.

The Salmonidæ have a ventral mesentery extending from near the ventral fin region to the posterior end of the abdominal cavity. The Coregonidæ and Osmeridæ appear to have no ventral mesentery.

The ovaries of the three families mentioned (Salmonidæ, Coregonidæ, and Osmeridæ), are structurally similar, consisting of a membranous covering continuous with the mesovarium and almost completely enveloping the ovigerous stroma.

A practically complete envelopment is formed by the position of the ovary and the mesovarium. The ovary is usually so inclined that the otherwise uncovered portion is protected by the mesovarium.¹ The prolongation backward of the mesovariums and ovarian investments form the oviducts, which in the Salmonidæ and Coregonidæ are trough-like, open above, the inner wall consisting of the mesovarium and the free outer wall (fig. 7 f) supported by the abdominal wall. Near the outlet, the two troughs unite into one above the intestine at the point of termination of the dorsal mesentery. At a short distance from the genital orifice each outer wall of the common channel is deflected and is attached to the respective wall of the abdomen.

The smelt differs from the other forms mentioned only in the position of the ovaries and in the extent of the laterally deflected portion of the oviducts.

RELATIONSHIP OF SALMONOID FISHES, GANOIDS, AND ELASMOBRANCHS AS
INDICATED BY THE OVIDUCTS.

A discussion of the origin and development of the oviduct in its relation to the nephridial system, concerning which morphologists still entertain different views, is not pertinent to this paper, but a brief consideration of the oviducts of other fishes may have some bearing upon the question of how widely the salmonoids differ from the other forms respecting these structures. Huxley wrote that, whatever their morphological nature, the arrangement of the membranes in the smelt in a physiological sense was, obviously, comparable to that of Fallopian tubes, and that everyone who was familiar with the anatomy of the female reproductive organs of the ganoids would at once perceive that these passages are the homologues of the oviducts of *Acipenser*, *Polyodon*, *Polypterus*, and *Amia*.

Huxley observed no difference in structure or essential anatomical relation of the oviducts of the smelt and the ganoids mentioned. In the structure and relations of its oviduct, he regarded *Osmerus* as forming the third term of a series of modifications,

¹ In two humpback salmon there appeared to be more or less free egg surface on the upper outer side of the left ovary, as though the ovary had been unduly stretched by the growing ova, and the surface usually inclined inward had been crowded so as to seem somewhat outward. The most marked instance was as follows:

The left ovary is about 250 mm. long, and about 45 mm. in vertical height near the posterior end of the lobe of the liver, extending to the outlet. The mesovarium is attached to the upper edge—the ovarian membrane comes up on the outside a little over one-third the width of ovary, making the exposed egg area comparatively wide.

About at the point of anterior attachment of the ventral mesentery, the ovary passes up to the top of the intestine. Then its vertical height is 25 mm. The end of the ovary within its almost completely infolding membrane lies in the trough with the free egg surface nearly dorsal.

The dorsal mesentery ends about 60 mm. from the posterior end of ovary. A little anterior to this, the mesovarium leaves the dorsal attachment and extends free on the inner side of the top of the ovary, lying in the trough (due to the prolongation of the ovary backward).

The right ovary is nearly 190 mm. long and 42 mm. wide, at about the anterior end of spleen. At this place is the only free egg space to be seen without tipping the ovary. This space is semioval in shape. These membranes are 14 mm. in narrowest place. The outer edge of membrane at posterior end runs diagonally across to mesentery and extends downward to form the side of the dorso-intestinal trough.

tending toward the separation of the ureteric from the oviducal ducts, two terms of which were presented by the ganoids, and the arrangement of the parts which obtain in the ordinary Salmonidæ a fourth term. Huxley stated as follows:

The abortion of the oviducts, commenced in *Osmerus*, is completed in *Salmo*, and all that remains of the primitive arrangement is the fold described by Rathke and the so-called abdominal pore, which, it will be observed, is the homologue of half of the urogenital opening of the ganoids and has nothing to do with the abdominal pores of these fish and of the selachians.

He also says that, as is well known, *Lepidosteus* presents an example of a ganoid with oviducts like those of the higher Teleostei; in *Osmerus*, on the other hand, we have a teleostean with oviducts like those of the ordinary Ganoidei. It is tolerably obvious, he continues, that, therefore, the characters of the female reproductive organs can lend no support to any attempt to draw a sharp line of demarcation between the ganoids and the teleosteans.

Bridge (1904) distinguishes two types of genital ducts in fishes: (1) Those which are obviously derived from some part of the kidney system; and (2) those which are special ducts and appear to have no connection with kidney ducts. The elasmobranchs offer a typical example of the first, and the Teleostei afford an equally typical example of the other. Representatives of certain other orders, among which are Acipenser, Polyodon, and *Amia* (*Amiatus*), are regarded as more or less transitional.

Whatever may have been their embryological origin, it is quite clear that in the adult teleost the ovaries and oviducts have no relation to organs other than that of peritoneal attachment. These fishes, according to previously cited authorities, present two types of ovaries, free and closed, and three oviducal adaptations, closed peritoneal tubes, peritoneal funnels, and no oviducts at all except the ovipore.

The closed ovary is said to develop in two ways from the genital ridge: (1) By the upturning and attachment above of the lower edge of the genital ridge, thus infolding the genital cells; and (2) by the formation of a groove on the surface of the ridge, the genital cells becoming infolded by the conjunction of the two edges of the groove.

The so-called free ovary, accordingly, was supposed to be formed by the genital cells developing on the outer side of the ridge and the lower edge folding up only slightly or not at all.

In each instance of closed ovary the closed oviduct is formed by a backward extension of the ovarian peritoneal membrane, the process of its formation being somewhat different, according to whether the ovary is of the upturning or groove development. In either case an extension backward of the mesovarium is involved. In the case of the free ovary, the oviduct, if any, is developed wholly from the backward extension of the mesovarium. In the case of the closed ovary, according to Goodrich (1909), the oviduct begins as a parovarial or endovarial channel blind in front. In the case of the free ovary, if there is any oviduct, it is said to begin as the wide mouth of a funnel near the posterior end of the ovary or at some distance behind it.

In the case of the ganoids previously mentioned, there is obviously a veritable funnel formed by the folding of the peritoneal membrane on itself, which is well exemplified by that of *Amia* (*Amiatus*), as shown by Huxley.

According to the same authority, the smelt differs from the ganoids in having the outer edge of the peritoneal fold attached to the abdominal wall, yet it is still called a "funnel" and considered homologous with the oviducal funnels of ganoids.

There is this difference between the oviducal membrane of the smelt and the funnel of the ganoids mentioned, that in the smelt the membrane turns outward to become attached to the abdominal wall (fig. 8 *g*), while in the other form it folds inward and is attached to the mesovarial membrane (fig. 11). In the latter a funnel is formed; in the former, only a half-funnel, which is not a homologue of the ganoidean funnels, but is homologous with the oviducts of other Isospondyli, even (some at least) of those with closed oviducts. Any phylogenetic significance of the smelt oviduct then would appear to pertain only to teleosts and to have no relation to the ganoids.

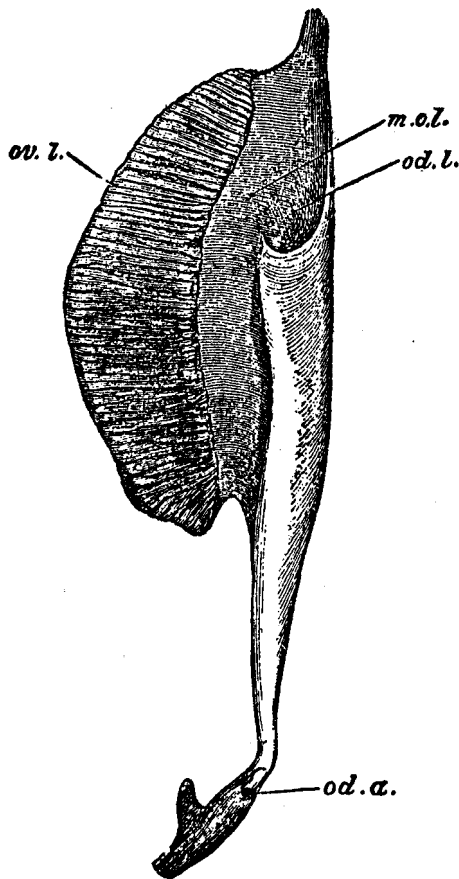


FIG. 11.—Left ovary and oviduct of bowfin (*Amiatus calurus*), after Huxley. $\times 643$. *ov. l.*, left ovary; *m. o. l.*, left mesovarium; *od. l.*, left oviduct; *od. a.*, opening of oviduct into the bladder.

The Isospondyli comprise forms which are stated to have closed ovaries and true oviducts as well as those which have free ovaries with funnel-like oviducts or only vestigial oviducts.

Besides the previously mentioned species, specimens of *Pomolobus pseudoharengus*, *P. mediocris*, *Dorosoma cepedianum*, and *Hyodon tergisus* have been carefully examined. The following two examples will serve to show that the Isospondyli, other than Salmonidæ, as represented by the specimens examined, are not radically different in their general structure from the Salmonidæ, but considerably different from other orders having closed ovaries.

The clupeoids are supposed to have closed ovaries and oviducts. In the alewife (*Pomolobus pseudoharengus*), the ovary of a large adult, taken July 4, therefore some time after the breeding season, is long and narrow, extending well back in the abdominal cavity. The mesovarium is narrow, the ovary lying close to the air bladder. Anteriorly the line of attachment of the outer edge of the enveloping membrane is close to the junction of the inner attachment of the mesovarium to the ovary, along the outer side of the air bladder, and there is a projection forward of the ovary, which is com-

pletely inclosed in membrane with no air-bladder attachment of the mesovarium. Posteriorly the lines of attachment diverge slightly, so that the inner line continues along the air bladder, but the outer one becomes attached nearer to the lateral abdominal wall at the side of the air bladder. The mesovarium is so narrow that it is scarcely perceptible except as a fold lying in the outside of the ovary, but the membranous attachment is wider and free from ovigerous laminæ, leaving a noticeable space of free eggs; that is, without other covering than the peritoneum of the air bladder. This free-ova portion constitutes the beginning of the oviduct within and on one side of the ovary. The remainder of the oviduct consists of the extension of the mesovarium and

outer attached edge of the ovarium membrane forming a channel with a very narrow roof of dorsal peritoneum. The two oviducts unite near the outlet. This alewife has a ventral mesentery of about the same relative extent as in the salmonids.

The hyodons are stated (Jordan and Evermann, 1896, p. 412) to have no oviducts, the eggs falling into the abdominal cavity before extrusion. An example of *Hyodon tergisus* in breeding condition showed that the ovaries are completely inclosed in membrane which, continuing from the mesovarium junction with the ovary, passes down its inner surfaces and up over the outer surface and upper edge, then downward again on the inner surface to the mesovarial attachment. The fusion of the outer edge of the ovarian covering with the mesovarium at its junction with the ovary appears to be complete as far back as the common opening in the dorsal mesentery. In this specimen the remainder of its backward extent seems to be still attached by fascialike, adhesive membrane similar to the adhesions of the viscera in general to the abdominal wall and to each other. At the termination of the mesentery posteriorly in the common opening an interovarian channel is formed by the continuation of the ovarian membranes. The membranes of the inner surface of each ovary fuse along the median longitudinal line of the upper surface of the intestine, forming the floor of a common oviducal channel, the outer sides of which are formed by the ovarian membranes of each ovary, beginning on the inner surface as a projecting fold. At this point the intestine and canal somewhat abruptly turn downward to the outlet. Another mesovariumlike membrane on each side begins forward, originating close to the mesovarium, and is attached to the upper surface of the ovary. It appears to continue backward beyond where the dorsal attachment of the true mesovarium ends and, by adhesion to the outer edge of the oviducal canal on each side, respectively, forms a closed oviduct. Excepting in this secondary membrane, this oviducal structure is very similar to that which has been described in connection with the Salmonidæ.

Since the intestine, with the superimposed oviducal canal, for the most of its extent is dorsally situated, it is quite evident that any ova falling into the abdominal cavity can not be extruded.

RELATION OF THE ANATOMICAL FACTS TO FISH-CULTURAL PRACTICES.

Boulenger (1904, p. 568) says of the Salmonidæ:

The large size of the eggs, their lack of adhesiveness, and the fact that the ova fall into the abdominal cavity, out of which they may be easily squeezed, renders artificial impregnation particularly easy and the species of *Salmo* have always occupied the first place in the annals of fish culture.

The error of this statement has been shown in the foregoing pages. It has been seen that the mature ovary is inclosed in a delicate membrane, which is a continuation of the peritoneal fold called the mesovarium. From the posterior end of each ovary an open membranous trough extends inward and backward to the median line of the upper surface of the intestine at the posterior termination of the dorsal mesentery, whence, by a fusion with each other mesially, a single oviducal trough, open above, which conveys the ova to the genital pore, is formed on the upper surface of the intestine.

Inasmuch as the ova do not naturally fall into the abdominal cavity and can not be extruded if they are displaced into it, it follows that their adventitious presence there can not be of advantage to the fish. Fish-cultural methods afford several means of

displacing eggs into the abdominal cavity. There is abundant evidence that present fish-cultural methods cause such displacements. They may be occasioned by dipping the fish head first into a scoop net, which causes considerable flopping by the fish; or by grasping the fish by the tail and holding her head downward until her struggles cease. If the fish is ripe, or partly ripe, the mass of eggs sags visibly toward the head, and it would seem inevitable that any free eggs would settle into the forward end of the abdominal cavity outside of the ova-containing membrane. It is, however, after the stripping process has begun that the danger of displacement is greatest, and particularly after some eggs have been expressed and the tense condition of the supporting abdominal wall is relaxed. It is largely due to displacement that the repeated stripping process fails to secure all of the ripe eggs, and even should the fish subsequently emit retained eggs, it is manifestly impossible for her to rid herself of displaced eggs.

Another disadvantage from which the fish may suffer is rupture of the membranes and injury to the ovaries by forcible pressure, so that the eggs falling into the abdominal cavity are not secured. The ovary thus injured may not recover its natural function and may thereby become sterile.

I have dissected various salmonids which have had deformed or distorted ovaries and others with postnuptial reduced ovaries containing hardened eggs of the previous or some preceding season, and have observed several instances of rainbow trout which had been stripped some months previously, containing masses of collapsed eggs adhering to each other, the viscera and abdominal walls, and others more recently stripped, in which the ovaries still contained eggs, in follicles, more or less crushed, and in one instance of which the posterior end of the ovary still containing eggs had been broken off and was loose in the abdominal cavity. Several samples of ruptured ovaries have been observed. In one example of landlocked salmon, several eggs had been pressed into the under side of the lobe of the liver so that they showed through on the outside. These facts can be ascribed to nothing except forcible attempts to strip the fish.

Some of these fish were artificially reared trout from a hatchery whence had come a complaint that the trout were yielding fewer eggs than the normal yield, and concerning which the suggestion was offered that the deterioration was due to inbreeding.

It is a common practice to begin the stripping pressure well forward and to repeat the movement until all eggs possible have been squeezed out, the last frequently being accompanied by fecal matter, mucus, and blood. This process is not only liable to injure the ovaries and membranes, but to express unripe eggs, impossible of fertilization. In fact, all of the eggs are never secured and some are retained and apparently are not subsequently naturally extruded.

In *A Manual of Fish-Culture*, Charles G. Atkins (1900, p. 35) thus describes the process of taking eggs from the Atlantic salmon:

The spawntaker clad in waterproof clothing and wearing woolen mittens, sits on a stool or box, and on a box in front of him is a clean tin pan holding about 10 quarts, which has been rinsed and emptied, but not wiped out. A female salmon is dipped up from one of the floating pens and brought to the operator, who seizes her by the tail with the right hand and holds her up, head downward. If unripe, the fish is returned to the pens; if ripe, the spawn will be loose and soft and will run down toward the head, leaving the region of the vent loose and flabby, and the operator, retaining his hold of the tail with his right hand, places the head of the fish under his left arm with the back uppermost, the head highest, and the vent immediately over the pan. At first the fish generally struggles violently and no spawn will flow; but as soon as she yields, the eggs flow in a continuous stream rattling sometimes

with great force against the bottom of the pan. Shortly the flow slackens and must be encouraged and forced by pressing and stroking the abdomen with the left hand. It is better to use the face of the palm or the edge of the hand rather than pinch between the thumb and fingers; the latter action, especially when working down near the vent, is apt to rupture some of the minor blood vessels, with the result of internal bleeding, and it is better to leave some of the eggs behind to be taken another day than to run the risk of such rupture.

In the same publication, George A. Seagle (1900, p. 66) describes a somewhat more careful method of taking eggs from the rainbow trout as follows:

In taking spawn the manipulation of the fish without injury is a very delicate and exacting task, full knowledge of which can only be acquired by experience, as it is difficult to squeeze the spawn from the fish without injuring or even killing it. In taking hold of the fish in the spawning tub the operator catches it by the head with the right hand, the back of the hand being up, and at the same time slips the left hand under the fish and grasps it near the tail, between the anal and caudal fins. If the fish struggles it must be held firmly, but gently, until it becomes quiet, and when held in the right position it will struggle only for a moment. A large fish may be held with its head under the right arm.

When the struggle is over the right hand is passed down the abdomen of the fish until a point midway between the pectoral and ventral fins is reached; then, with the thumb and index finger, the abdomen is pressed gently, and at the same time the hand is slipped toward the vent. If the eggs are ready to be taken they will come freely and easily, and if they do not the fish is put back in the pond until ready to spawn. If the eggs come freely from the first pressure the operation is repeated, beginning at or near the ventral fin.

After the first pressure has been given, by holding the head of the fish higher than the tail, all of the eggs that have fallen from the ovaries and are ready to be expressed will fall into the abdomen, near the vent, so that it will not be necessary to press the fish again over its vital parts, the eggs having left that portion of the body. All of the eggs that have fallen into the abdomen below the ventral fin can be easily ejected without danger of injury to the fish, caused by unnecessary pressure over its important organs after the eggs have left that part of the body. If these directions are judiciously and carefully followed, but little, if any, damage will result; and, as an illustration, it may be mentioned that fish have been kept for 14 years and their full quota of eggs extracted each season during the egg-producing term, which is normally from 10 to 12 years. The male fish is to be treated very much in the same manner as the female, except the milt must not be forced out, only that which comes freely being taken.

At the thirteenth annual meeting of the American Fish Cultural Society, Charles G. Atkins presented some notes on the landlocked salmon, regarding which, among other things, he said:

Among the migratory salmon of the Penobscot, ovarian disease is rare; but with the landlocked salmon of the Schoodic Lakes it is very common. In 1883, by careful observation, we learned that 18 per cent of the female fish were affected with some disease of the ovaries, resulting in defects of the eggs which were apparent to the eye, in some instances involving the entire litter, but generally a very small number of eggs. The phenomenon was observed before artificial breeding began at Grand Lake Stream, and does not appear to be influenced thereby.

Atkins does not state under what circumstances or conditions the phenomenon was previously observed, but it is, perhaps, significant that following the adoption of the gradual stripping process at Grand Lake Stream there were no further reports of "ovarian trouble" or defective eggs among the salmon.

These facts indicate that in the case of those salmonoids which normally survive the season of reproduction, all care possible should be exercised in the process of manipulation for the purposes of artificial propagation.

The fish should be gently handled and at no time should be permitted to hang and struggle head downward. Inasmuch as the fish does not naturally emit the eggs at one

time, in stripping a fish this fact should be borne in mind, and no forcible attempt should be made to express more than those eggs which easily flow under gentle pressure. It may take several operations to secure all of the eggs, and as the eggs begin to ripen in the posterior part of the ovary, to obtain them it is not necessary to squeeze the whole length of the abdomen. In fact, it is liable to injure the eggs or rupture the ovarian membrane to do so. Experiments indicated that by the usual method of stripping a large percentage of the eggs are obtained in the first operation. The question, therefore, arises whether the number of good eggs obtained would be reduced by a gentler operation and whether a second operation is necessary. In any event it would seem to be a more rational procedure to follow nature and first remove the eggs in the posterior end of the fish, using no more force than gentle pressure near the vent, with a movement toward it. If eggs do not flow at first, repeated, short, gentle strokes may cause them to, if they are ready to be deposited. Some egg takers hold the fish belly up at an angle which will permit the eggs to fall into the pan for receiving the eggs. It would seem to be more in accordance with nature if the fish were held belly down thus permitting the eggs to flow or roll along the oviduct toward the vent, as others are emitted. The flow may be aided by gentle stripping motions repeated each time a little further forward, not going further than the region of the middle of the ventral fins. When the eggs cease to flow under gentle stripping pressure the operation should cease. Possibly not as many eggs would be obtained by this method as by the usual forceful method, but by operating only once or twice with due care, the danger of both external and internal injuries is lessened, and the breeder is saved, providing retained eggs are not harmful. This latter point remains to be ascertained.

LIST OF WORKS CONSULTED.

Atkins, Charles G.

1900. The Atlantic and landlocked salmons. *In* A manual of fish-culture, revised edition, pp. 17-60. Washington.

Balfour, Francis M.

1878. On the structure and development of the vertebrate ovary. *Quarterly Journal of Microscopical Science*, new series, vol. 18, pp. 383-438, Pls. XVII-XIX. London.
1881. A treatise on comparative embryology. Vol. II, 677 pp., illus. London.

Beard, J.

1890. The inter-relationships of the Ichthyopsida: A contribution to the morphology of vertebrates. *Anatomischer Anzeiger*, Bd. 5, pp. 146-159 and 179-188. Bardeleben: Jena.

Boulenger, G. A.

1904. Teleostei (systematic part). *In* The Cambridge natural history, vol. 7, pp. 539-727. MacMillan & Co. New York, London.

Bridge, T. W.

1904. Fishes, exclusive of the systematic account of Teleostei. *In* The Cambridge natural history, vol. 7, pp. 139-537. MacMillan & Co. New York, London.

Day, Francis.

1887. British and Irish Salmonidæ. 298 pp., illus., 12 pls. London.

Felix, W.

1895. Über die Entwicklung des Excretionssystems der Forelle (Vorniere, Urnieren, Nachnieren). *Verhandlungen der anatomischen Gesellschaft*, 9 vers, pp. 147-152. Basel.
1897. Beiträge zur Entwicklungsgeschichte der Salmoniden. *Anatomische Hefte*, Abth. 1, Bd. 8, pp. 249-466, 8 pls., and 39 figs. Wiesbaden.

- Felix, W., and Bühler, A.
1906. Die Entwicklung der Keimdrüsen und ihrer Ausführungsgänge. *In* Handbuch der Entwicklungslehre der Wirbeltiere, Bd. 3, Teil 1, pp. 619-690, 742-750, and 815-821, figs. Hertwig: Jena.
- Gegenbaur, Carl.
1878. Elements of comparative anatomy. Translated by E. Jeffrey Bell. The translation revised and a preface written by E. Ray Lankester. 645 pp., illus. London.
- Goodrich, E. S.
1909. A treatise on zoology. Edited by Sir Ray Lankester. Part IX, Vertebrata Craniata (First fascicle: Cyclostomes and fishes). 518 pp., illus. London.
- Günther, Albert C. L. G.
1880. An introduction to the study of fishes. 720 pp., 320 figs. Edinburgh.
- Haller, B.
1905. Über den Ovarialsack der Knochenfische. *Anatomischer Anzeiger*, vol. 27, pp. 225-238, 9 figs. Jena.
- Hertwig, Richard.
1902. A manual of zoology. Translated and edited from the fifth German edition by J. S. Kingsley. xi+704 pp. Henry Holt & Co. New York.
- Howes, G. B.
1891. On the arrangement of the living fishes, as based upon the study of their reproductive system. Report, 61 Meeting, British Association for the Advancement of Science, pp. 694-695, fig. 1
- Huxley, Thomas H.
1883. Contributions to morphology. Ichthyopsida, No. 2. On the oviducts of Osmerus; with remarks on the relations of the Teleostean with the Ganoid fishes. *Proceedings, Zoological Society of London*, pp. 132-139, illus. London.
- Hyrtl, J.
1850. Beiträge zur Morphologie der Urogenital-organe der Fische. *Denkschriften der Kaiserlichen Akademie der Wissenschaften zu Wien*, Bd. 1, pp. 391-411, 2 pls. Wien.
- Jordan, David Starr.
1905. A guide to the study of fishes. 2 vols., 1223 pp., 427 illus. Henry Holt & Co. New York.
- Jordan, David Starr, and Evermann, Barton Warren.
1896. The fishes of North and Middle America: A descriptive catalogue of the species of fishlike vertebrates found in the waters of North America, north of the Isthmus of Panama. *Bulletin, U. S. National Museum* No. 47, Part 1, lx+1240 pp. Washington.
- Jordan, David Starr, and Gilbert, Charles H.
1882 (1883). Synopsis of the fishes of North America. *Bulletin, U. S. National Museum* No. 16, lvi+1018 pp. Washington.
- Jungersen, H. F. E.
1889. Beiträge zur Kenntniss der Entwicklung der Geschlechtsorgane bei den Knochenfischen. *Arbeiten aus dem zoologisch-zootomischen Institute in Würzburg*, Bd. 9, pp. 89-219, 2 pls. Würzburg.
- Kendall, William Converse.
1915. Taxonomic and fish-cultural notes on the chars or trouts of New England. *Transactions, American Fisheries Society*, Vol. XLIV, No. 2 (March), pp. 97-108. New York.
- MacLeod, J.
1881. Recherches sur la structure et le développement de l'appareil reproducteur de la femelle des Téléostéens. *Archives de Biologie*, Bd. 2, pp. 497-530, 2 pls. Gand.
- Owen, Richard.
1866. On the anatomy of vertebrates, Vol. I. Fishes and reptiles. London.
- Parker, T. Jeffrey, and Haswell, William A.
1897. A text book of zoology, Vol. II, xx+683 pp., illus. New York.

Rathke, Heinrich.

1820. Über die weiblichen Geschlechtsteile der Lachse und des Sandaales. Deutsches Archiv für die Physiologie, Bd. 6, pp. 589-600. Meckel: Halle.
1824. I. Über den Darmkanal und die Zeugungsorgane der Fische. Beiträge zur Geschichte der Thierwelt. II. Über die Geschlechtsteile der Fische. Neuste Schrift der Naturforschenden Gesellschaft in Danzig, Bd. 1, Heft 3, 116 pp. Halle.

Richardson, John.

1836. Fauna Boreali-Americana. Part third. The fish. 327 pp., 24 pls. London.

Seagle, George A.

1900. The rainbow trout. In A manual of fish-culture, revised edition, pp. 61-79. Washington.

Weber, M.

1887. Die Abdominalporen der Salmoniden nebst Bemerkungen über die Geschlechtsorgane der Fische. Morphologisches Jahrbuch, Bd. XII. Gegenbauer: Leipzig.

Wiedersheim, Robert.

1897. Elements of the comparative anatomy of vertebrates. Adapted from the German by W. N. Parker. Second edition (founded on third German edition), 488 pp., illus. New York.