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THE EFFECT OF WATER CONSERVATION ON THE STRUCTURE OF MARINE FISH EMBRYOS AND LARVAE

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(Plate I and Text-figs. 1–2)

Fish eggs can be divided into three main groups: marine pelagic eggs which float of their own accord, marine demersal, and freshwater demersal eggs. The embryological development of freshwater teleosts follows an accepted pattern, demonstrated by morphologists during the nineteenth century. Marine embryos, both pelagic and demersal, do not conform in all respects to this pattern, and misunderstandings have frequently arisen by lack of attention to known structural differences between the three groups. McIntosh & Prince (1890), in their comprehensive review of fish development, emphasized some outstanding anomalies in pelagic structure, but gave no adequate explanation of their occurrence.

The present purpose is to draw attention to a striking divergence in the morphology of these three groups; to relate it to the difference in habit; and to demonstrate how it affects the transport of yolk derivatives during the embryonic and larval phases. Here the term 'larva' refers to the yolk-sac stage after hatching. The post-larval phase begins with the final disappearance of the yolk.

The Subdermal Space of Pelagic Embryos and Larvae

Pl. I, fig. 1, is a transverse section through the trunk of a 4-day-old demersal trout (*Salmo trutta*) larva, showing the nerve cord, notochord, urinary vessels, gut and axial blood vessels, all surrounded by the heavy myotome musculature. The integument is closely apposed to the underlying mesoderm, and is extended dorsally and ventrally as the marginal or embryonal fin.

This orthodox picture should be compared with that shown in Pl. I, fig. 2, which is a transverse section through the trunk of a 2-day-old pelagic plaice (*Pleuronectes platessa*) larva. The myotomes are relatively weak, and the integument is well separated from the underlying mesoderm to give a voluminous subdermal space. This space has already been recorded by earlier workers. A day before his cod hatched, Meek (1924) observed: 'During the preceding day or two, a space has been gradually forming on each side of the body,

separating the ectoderm from the underlying parts. This space is now a prominent feature of the body and tail. It is the preparation for a subdermal space which forms an important larval feature; it is lined with mesenchyme and is apparently a lymph sinus.' McIntosh & Prince (1890) also described the same space as a late embryonic structure, filled with a jelly-like lymph and extraordinarily enlarged above the cephalic region.

In the cod (*Gadus callarias*) larva (Pl. I, fig. 3), the separation of integument from mesoderm is complete in the gut and pectoral region. There is no separation in front of the eyes and over the mandible, nor posteriorly in the caudal region, where the integument is closely knitted to the lateral mesoderm of the main axis, but separation dorsally and ventrally produces the lumen of the big marginal fin, which must be supported, in view of the lack of fin-rays, by turgor within the space.

When larval fin-rays are absent, or just developing, it is reasonable to suppose that the size of the marginal fin, in relation to the more compact axial structures, will vary according to the extent of the subdermal space. The transverse sections in Pl. I show a marked difference in relative fin size between a pelagic marine larva with a big subdermal space, and a demersal freshwater larva with little integumental separation.

I scoured the literature for drawings of newly hatched fish larvae from the three egg types, to see if there were consistent differences in marginal fin size. Ten representative drawings per group are displayed in Text-fig. 1. The drawings are simplified reproductions from various publications; the outlines are exact. My tentative conclusions from this visual comparison are that larvae from pelagic marine eggs, with consistently big fins, have extensive subdermal spaces, and that these spaces are not well defined in demersal

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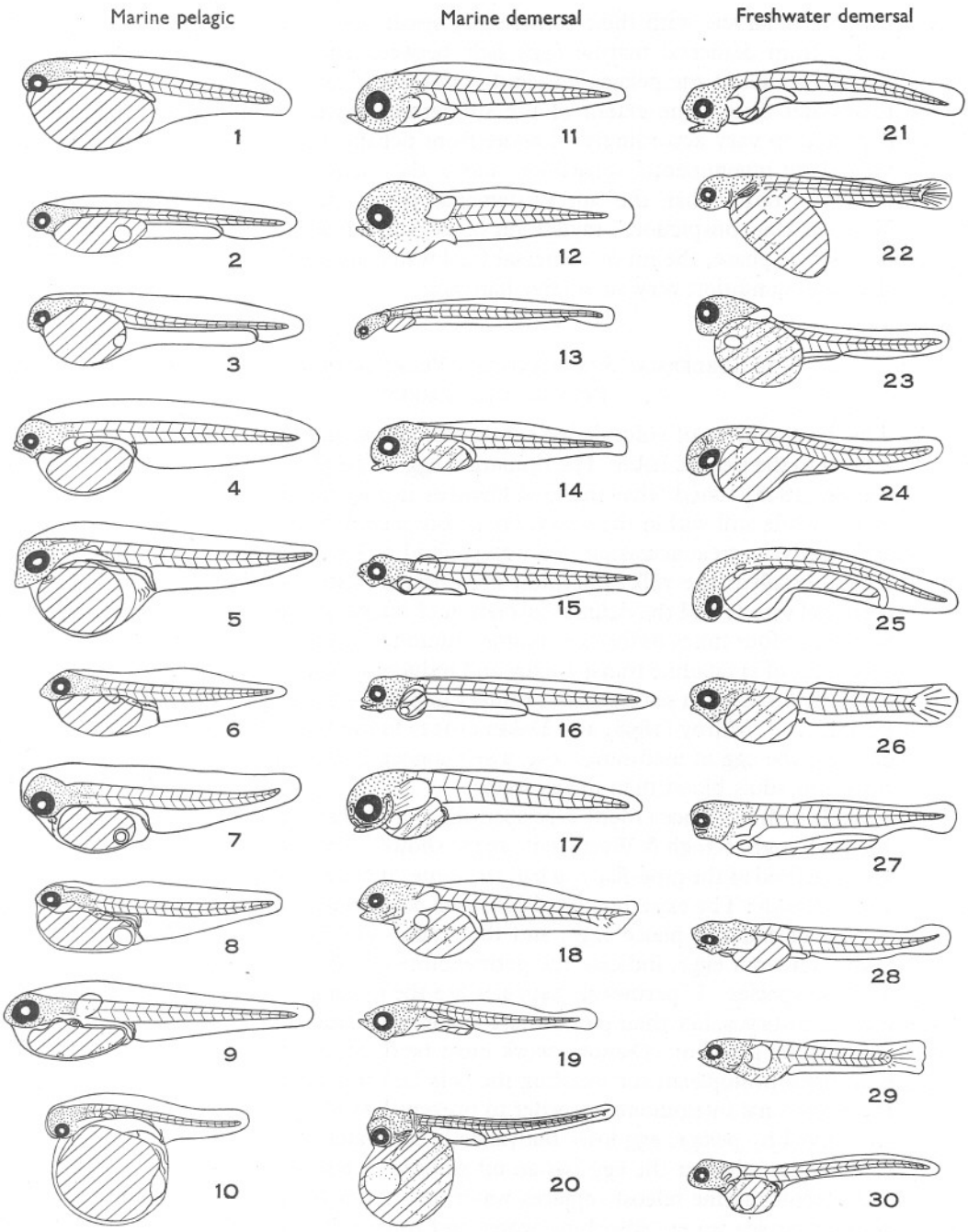
Legend to Text-fig. 1.

Text-fig. 1. A comparison of marginal fin size in early larvae from different types of teleost eggs, i.e. marine pelagic (left), marine demersal (centre), and freshwater demersal (right). 1, *Gadus luscus*, 3·0 mm; 2, *Argentina sphyraena*, 6·9 mm; 3, *Clupea pilchardus*, 3·5 mm; 4, *Pleuronectes platessa*, 8·0 mm; 5, *Solea vulgaris*, 3·2 mm; 6, *Callionymus lyra*, 2·2 mm; 7, *Rhombus laevis*, 4·0 mm; 8, *Scomber scombrus*, 3·5 mm; 9, *Trachinus vipera*, 3·3 mm; 10, *Lophius piscatorius*; 11, *Hypleurochilus geminatus*, 2·1 mm; 12, *Chasmodes bosquianus*, 3·6 mm; 13, *Clupea harengus*, 7·0 mm; 14, *Myoxocephalus scorpius*, 8·2 mm; 15, *Chirolophis galerita*, 12·0 mm; 16, *Pholis gunnellus*, 9·4 mm; 17, *Cyclogaster montagui*, 3·8 mm; 18, *Cottus gobio*, 8·0 mm; 19, *Gobius niger*, 3·0 mm; 20, *Anarrhichas lupus*, 12·0 mm.; 21, *Lota maculosa*, 3·5 mm; 22, *Salmo trutta*; 23, *Gasterosteus aculeatus*, 4·7 mm; 24, *Richardsonius balteatus*, 5·3 mm; 25, *Labeo gonius*, 3·6 mm; 26, *Crenichthys baileyi*, 4·3 mm; 27, *Notropis girardi*, 5·5 mm; 28, *Percopsis omiscomaycus*, 6·0 mm; 29, *Plancterus kansae*, 6·6 mm; 30, *Boleosoma n. nigrum*, 5·0 mm. Nos. 1, 4–10, 13 and 15–20 after Ehrenbaum, 1904, 1905–9; nos. 11 and 12 after Hildebrand & Cable, 1938; nos. 2 and 3 after D'Ancona & Sanzo, 1931; no. 14 after Bigelow & Welsh, 1925; nos. 21, 28 and 30 after Fish, 1931; no. 22 after Stuart, 1953; no. 23 after Ved Vrat, 1949; no. 24 after Weisel & Newman, 1951; no. 25 after Nazir Ahmad, 1944; no. 26 after Kopec, 1949; no. 27 after Moore, 1944; no. 29 after Koster, 1948.


Marine pelagic
Marine demersal
Freshwater demersal
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Text-fig. 1.

freshwater larvae, with their consistently small fins. The relative fin size of larvae from demersal marine eggs falls between these two extremes, with *Hypleurochilus* at the pelagic end and *Anarrhichas* approaching the demersal freshwater state. The extent of the subdermal space in this group can be expected to vary accordingly. Larvae from pelagic eggs are usually characterized by integumental separation above the medulla. This feature is the exception rather than the rule in demersal larvae from both environments. Whereas the conspicuous, rayless fin of pelagic larvae persists well into the post-larval phase, the fin of demersal freshwater larvae may begin to assume the adult condition very soon after hatching.

The Subdermal Space and the Problem of Buoyancy in Pelagic Fish Embryos

The development of voluminous subdermal spaces in fish embryos is clearly related to the pelagic habit. The immature egg of the plaice sinks in sea water. Fulton (1898) stated 'that the final changes in the maturation of the pelagic ovum, while still within the ovary, are accompanied by a comparatively rapid and relatively great accession of a watery fluid of low density from the ovary, which dissolves the yolk spherules, is associated with the dissolution of the germinal vesicle and the definite formation of the periblast, distends the ovum to three or four times its former volume, thinning the capsule correspondingly, renders it of crystalline transparency and reduces its specific gravity, so that it is enabled to float in sea water of ordinary density—in other words, to become pelagic. . . .' Milroy (1898) and Dakin (1912) found that the vitelline diluent entering the egg at maturation had a salt concentration with a greater resemblance to adult blood than to sea water.

McIntosh & Prince (1890) described the porous nature of certain fish egg-shells. Krogh, Krogh & Wernstedt (1938) showed that the 'amniotic' or perivitelline fluid of the pipe-fish egg had the same chloride concentration as the sea water outside. The experiments of Jacobsen & Johansen (1908) on the specific gravity of cod and plaice eggs, and the studies of Svetlow (1929) and Gray (1932) on trout eggs, indicate the permeability of the shell to salts and water in these species. If permeable capsules are the general rule among fish, then marine embryos, like their parents, are in constant danger of desiccation under the osmotic gradient. Osmotic work must be done, in the first place, by the peripheral protoplasm surrounding the yolk before gastrulation, and later, by the embryonal integument, in order to prevent loss of water and gain of salts. An unhealthy pelagic egg loses buoyancy in sea water; a dead egg sinks. This rule applies whether the egg has an oil globule or not.

An adult marine teleost replaces water lost under the osmotic gradient by swallowing sea water, absorbing water and some salts through the gut wall, and secreting the excess blood chloride to the outside, through special cells

in the gills (Keys, 1931; Keys & Willmer, 1932). This osmo-regulatory mechanism requires an open gut, a well-developed blood circulation and an advanced gill system, for efficient functioning.

The gut of a pelagic plaice embryo opens at a very late stage in incubation (Fullarton, 1891). The blood circulation is ill-developed, as will be shown in the next section, and the gill-bars lack filaments at hatching. The adult osmo-regulatory mechanism cannot apply, in its entirety, to the embryo. A method of direct water acceptance through the integument, to the exclusion of salts, is difficult to conceive in the prevailing osmotic conditions; we must assume, lacking concrete evidence to the contrary, that the permeability of the embryonal integument is normally maintained at a low level, by the expenditure of energy in the form of osmotic work. There is direct evidence to support this assumption in freshwater fish eggs. Krogh & Ussing (1937), using heavy water, confirmed the conclusions of Gray (1932) on the high degree of water impermeability of the trout egg membrane during early development. The evidence for marine eggs is not so substantial. Experiments by Loeb & Wasteneys (1915) led them to believe that the protoplasmic membrane of the fertilized *Fundulus heteroclitus* egg was impermeable to salts and almost impermeable to water. Conversely, Krogh *et al.* (1938) found that unfertilized eggs of *Pleuronectes flesus* and *Crenilabrus exoletus* exchanged water and ions with the surrounding solution. The act of fertilization, however, may have an important bearing on the subsequent permeability of the peripheral protoplasm.

The efficiency of the embryonal integument as a water barrier will depend largely on the health of the embryo and the favourability of its environment. Any osmotic water 'leak' must be followed by adjustment of the internal salt balance. The salt-regulatory mechanism of marine fish embryos and larvae is not yet known, although Krogh *et al.* (1938) showed that such a mechanism must exist in the egg of the pipe-fish *Nerophis ophidium*.

Apart from the question of salt balance, the embryo cannot afford to lose too much water if the egg is to remain buoyant. The limit of water loss, in this context, will be determined by the initial reserve buoyancy at liberation and the loss of weight due to the excretion of respiratory metabolites. A healthy plaice egg remains buoyant until hatching, even though its degree of reserve buoyancy at liberation is not great. If the embryonal weight decreases but little during incubation, then it follows from the simple relationship, mass/volume = density, that little change can take place in the volume enclosed by the embryonal integument. During development, there is a withdrawal of soluble nutrients from the dilute fluid yolk. They are used in the synthesis of the compact embryonic axis, and in respiration. But the low-density yolk diluent remains. It accumulates beneath the integument, forms and fills the voluminous subdermal spaces, and thus maintains an overall embryonal volume in keeping with the buoyancy requirements of the egg.

The problem of water conservation does not arise in a demersal freshwater embryo. One can, therefore, readily understand the lack of a subdermal space in this group, and hence, the ill-developed marginal fin.

A floating marine egg accepts sufficient yolk diluent at maturation to meet both osmotic and buoyancy requirements during early development. A non-buoyant marine egg, on the other hand, requires enough yolk diluent to provide against the osmotic hazard only. Accordingly, one might expect the subdermal spaces of this group to be less capacious than in pelagic eggs; to be more developed than in freshwater eggs; and to vary with specific differences in the reserve of yolk diluent below that necessary to float off the egg. The picture of relative fin size from Text-fig. 1 supports this view.

The Evolution of the Pelagic Egg

The palaeontological record suggests that modern marine teleosts are derived from freshwater ancestors (Romer & Grove, 1935; Moy-Thomas, 1939). The comparative anatomy of adult osmo-regulation is in accord with this view (Baldwin, 1937). There is no reason to suppose that the process of marine colonization by freshwater fish has now ended, nor that reversion back to freshwater is impossible (Hoar, Black & Black, 1951).

Complete physiological adaptation to one or other of these habitats implies the development of a mechanism capable of maintaining the internal environment against the external change, in the egg as well as the adult. The spawning migrations of the salmon, shad and eel can be interpreted as evidence that the embryo is unable to develop in the physico-chemical conditions of adult life.

Assuming teleost embryos to have only a limited tolerance to internal salt change, then what are the essential requirements for the adaptation of a freshwater type of egg to a truly marine existence? First of all, a vitelline membrane highly impermeable to salts and water. The evidence for early impermeability in modern teleost eggs had already been given. Secondly, a means of balancing the internal salt concentration should an osmotic water 'leak' occur in less than optimum conditions. A freshwater embryo, without a functional renal system, must then secrete salts from the outside in. The reverse applies in a sea embryo, and although mechanisms of embryonal salt control are not yet known, it is significant that the chloride secretory cells in the adult *Fundulus heteroclitus* can reverse their polarity when the fish is transferred into fresh water (Copeland, 1948). The ability of the cell membrane to work against a chloride gradient is the essential property of the chloride secretory cell (Hoar *et al.*, 1951). Do such cells occur in fish embryos?

When the external osmotic pressure exceeds that inside the embryo, sufficient water must be present, throughout early incubation at least, to supply the needs of the embryo in the event of osmotic loss. This third requirement is specific to a change from fresh water to marine conditions for egg

development. An egg is supplied with water, in the form of yolk diluent, at maturation within the ovary. The specific gravity of teleost body fluids is less than that of sea water. The degree of yolk dilution at liberation may be enough to supply embryonal water needs (in co-operation with a salt-regulatory mechanism) and yet not sufficiently advanced to float off the egg. This is the demersal marine condition. An extension of the process of yolk dilution must inevitably produce a buoyant form of egg, when the upthrust exerted on the distended egg by displaced sea water exceeds the gravitational pull.

Thus, by considering the embryonal adaptations necessary for colonization of the sea, it is possible to arrive at an intrinsically buoyant type of egg. The vast majority of pelagic eggs are, in fact, marine. Buoyancy in the freshwater environment involves a completely different mechanism. This attempt to trace the evolution of buoyancy in fish eggs is intended to be provocative rather than informative, particularly as the mechanism of embryonal salt-regulation is not yet understood and measurements of yolk dilution over a whole range of fish species are not yet available.

Some marine fish families are more advanced in the direction of pelagic egg production than others. The pleuronectids produce floating eggs only; the gadoids have a demersal representative in *Lota maculosa*. Among salmonids, the trout has a freshwater habit throughout its life-history; the salmon is not yet embryologically adapted to a marine existence; whilst the related *Argentina sphyraena* is completely marine, and has a pelagic egg. There are both demersal and pelagic egg producers among the clupeoids. Early larval representatives of all these families are displayed in Text-fig. 1. Those issuing from pelagic eggs have large, inflated embryonal fins, a feature clearly related to the pelagic habit rather than to family affinities.

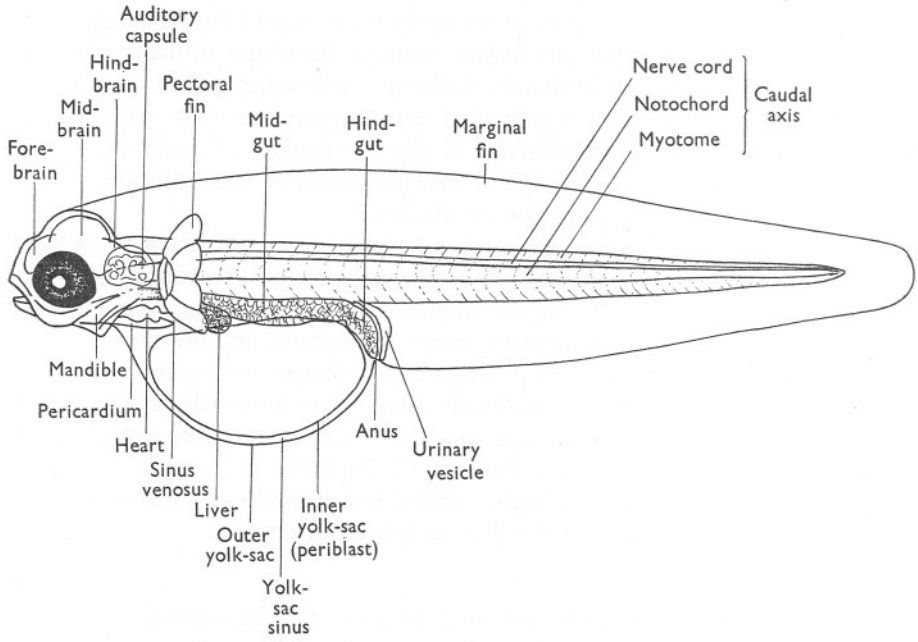
The Role of the Subdermal Space in the Transport of Yolk Derivatives

From the time when segmentation starts after the fertilization of a fish egg, to a stage preceding the formation of a pulsating heart and a primitive blood circulation, it is clear that the embryo appropriates yolk by a direct process of incorporation, without the aid of a blood-vascular system. With the subsequent thickening and lengthening of the main embryonic trunk, an increasing volume of tissue is moving out of contact with the yolk in its inner sac, thereby creating problems of food transport.

At this point, the yolk-sacs of most demersal freshwater eggs diverge structurally from those of pelagic marine forms. The former develop a complex system of circulatory vessels around the yolk; in pelagic eggs, this system is always absent, and its function is taken over by the yolk-sac sinus, into which the heart opens directly (Text-fig. 2). The yolk-sac sinus is, in reality, a subdermal space, formed when the extra-embryonal mesoderm

around the yolk breaks down into isolated mesenchyme cells during gastrulation (Meek, 1913).

At some stage in embryonal development the ventral yolk-sac sinus is put in lateral communication with the lumen of the rapidly growing marginal fin, on the dorsal side. Pl. I, fig. 3, is a slightly oblique transverse section of a cod larva through the pectoral fin region, showing the gross separation of the integument from the main larval axis, to give a lateral channel connecting the yolk-sac sinus ventrally, to the fin space dorsally.



Text-fig. 2 Diagram of a newly hatched plaice larva.

It would seem, therefore, that nutrient derivatives from the yolk of pelagic eggs have easy access to embryonic and larval tissues via the subdermal spaces. To test this supposition I immersed newly hatched plaice larvae in fast fixatives containing corrosive sublimate. A dense brown coagulation quickly appeared in the yolk, the yolk-sac sinus, beneath the integument around the base of the pectoral fins, and in the lumen of the marginal fin. In some normal early larvae, coagulation extended throughout the lumina of both dorsal and ventral portions of the fin (Pl. I, figs. 4, 5). The coagulated moiety of the plasma was frequently washed out of transverse sections during staining. If remaining, it appeared as a decolorized reticulation in the subdermal spaces of the marginal fin, in the cardial and pericardial cavities, and around the base of the pectoral fin.

In case yolk derivatives in the fin were a fixation artifact caused by a strongly contracting yolk-sac, I narcotized five normal larvae in menthol, and measured the length, depth and width of the inner sac. The larvae were then transferred to a mild fixative, Baker's calcium formaldehyde, for 5 min, and the measurements repeated. Later immersion in Heidenhain's Susa intensified the initial coagulation. Table I shows that the inner yolk-sacs of three of the five specimens contracted a little after fixation, but not enough to account for the volume of coagulated derivatives seen in the fin. There was no noticeable movement of plasma from the yolk-sac sinus to the fin during the experiment. The progress of coagulation in larval spaces was watched under a high-power dissecting microscope, and seen to be always from the outside inwards for the dorsal fin, compatible with the view that soluble proteins were already there, before the addition of preservative.

TABLE I. INNER YOLK-SAC MEASUREMENTS IN MICROMETER UNITS

Larva no.	Narcotized			Fixed			Coagulation in Susa
	Length	Depth	Width	Length	Depth	Width	
1	29	31	32	28	31	32+	Heavy
2	10	24	25	10	24	25	Heavy
3	12	25	26	12	25+	26	Heavy
4	46	27	29	43	27+	29	Heavy
5	11	26	32	10	26	31	Heavy

We think of the heart and developing vascular system as becoming vital to the transport of yolk nutrients at an early stage in fish egg development. This may be substantially true for the demersal freshwater egg, with its yolk capillaries and closed vascular system. But in pelagic marine embryos there is an unusual extension of the primary method of direct yolk appropriation, independent of a blood vascular system, well into the larval phase. This is undoubtedly a consequence of the formation of subdermal spaces, dictated by the requirements of water conservation in the marine environment, and of buoyancy.

In the third group of fish eggs, demersal marine, yolk-sac vascularization is as variable as marginal fin development, and probably for the same reason. McIntosh & Prince (1890) related the presence of a vitelline circulation to the demersal habit, irrespective of environment. This is an over-generalization. The herring egg has a yolk-sac sinus and lacks capillaries; *Anarrhichas*, on the other hand, has a conspicuous yolk circulation.

If there is an early separation of the embryonal integument from the inner yolk-sac endoderm, causing the breakdown of the extra-embryonal mesoderm noticed by Meek (1913), then capillary formation becomes impossible. The degree of separation in this region will depend on the volume of yolk diluent left between the two membranes, on the completion of gastrulation. This, in turn, will depend upon the extent of yolk dilution. I have already suggested

that variable fin size in demersal marine eggs may be related to variable conditions of water reserve, or yolk dilution. The similar inconsistency in yolk-sac vascularization is in direct line with this view.

In conclusion, it is necessary to reformulate the ideas put forward in this paper, and state that some major differences in the structure and habit of fish embryos and larvae appear to be closely related to a very simple factor, namely, the concentration of soluble nutrients per unit volume of yolk, at the time of egg liberation.

Summary

Fish eggs can be divided into three groups according to habit: pelagic marine, demersal marine, and demersal freshwater. Embryos emerging from these eggs show group differences in the extent of the subdermal space, as inferred from the relative size of their embryonal or marginal fins. Pelagic marine embryos have large, inflated marginal fins, in contrast with the ill-developed fin of the demersal freshwater embryo. The fins of demersal marine embryos lie between these two extremes.

There is a parallel variation in the degree of vascularization of the yolk-sac: pelagic marine embryos have no vitelline circulation, demersal freshwater forms have good vascularization, whilst that of demersal marine embryos is variable.

These differences in both structure and habit can be related to group differences in the degree of dilution of the yolk by ovarian fluid at maturation, and the subsequent need for marine embryos to conserve water under the osmotic gradient. It is possible to construct an argument to explain the evolution of the pelagic marine egg, by considering the embryonic osmoregulatory adaptations necessary for the complete colonization of the sea by ancestral freshwater fish.

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EXPLANATION OF PLATE I

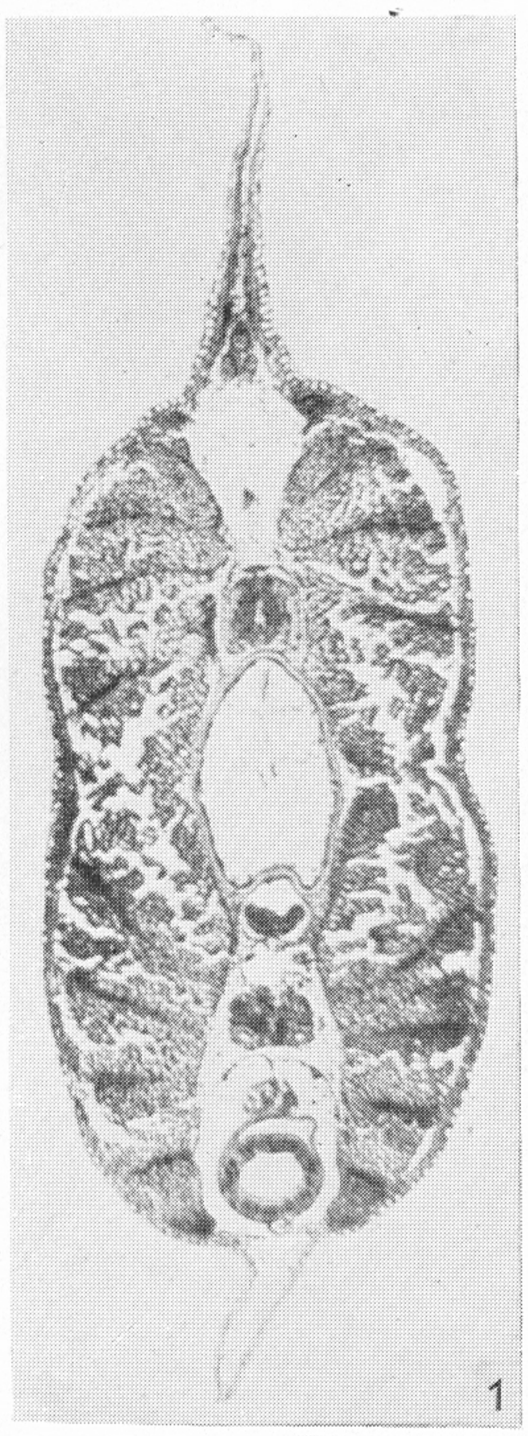
Fig. 1. Transverse section through the trunk of a 4-day-old demersal trout larva, showing the close connexion between the integument and underlying mesoderm. × 50.

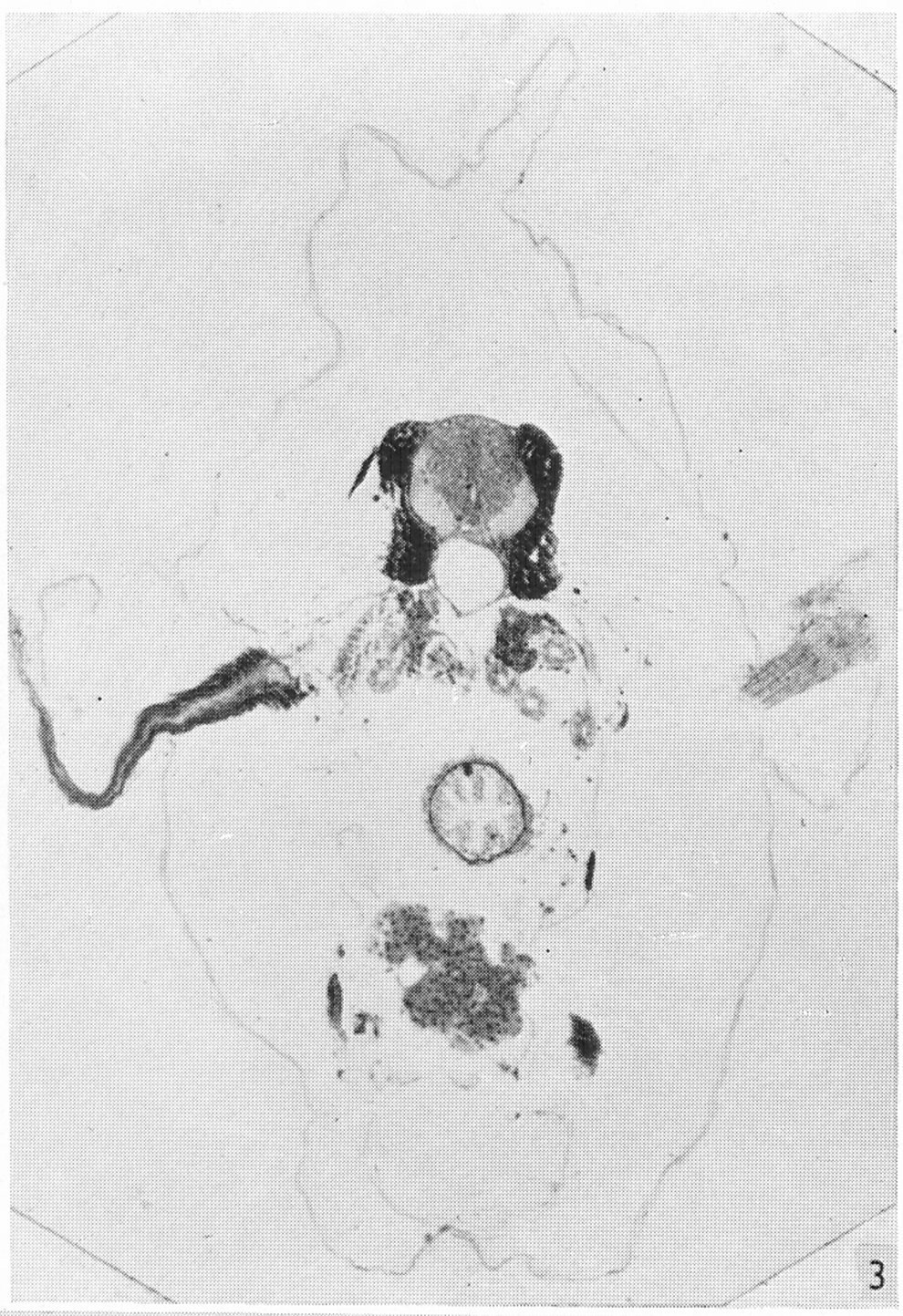
Fig. 2. Transverse section through the trunk of a 2-day-old pelagic plaice larva, showing the separation of the integument from the underlying mesoderm to give the superficial subdermal space. × 100.

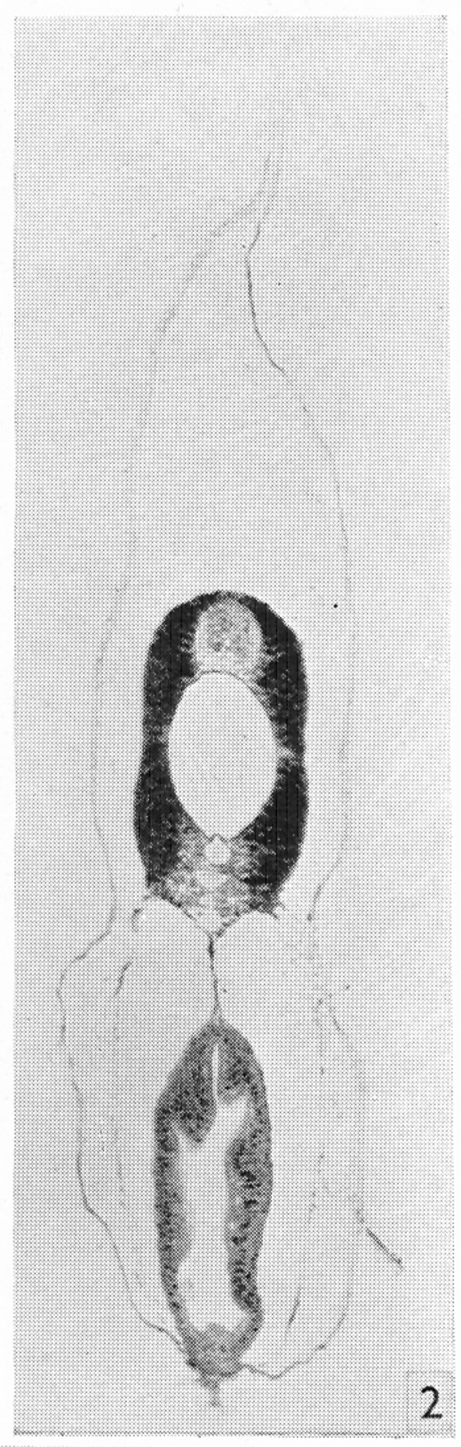
Fig. 3. A slightly oblique transverse section through the pectoral region of an early cod larva, showing gross integumental separation, and the continuity of the yolk-sac sinus ventrally, with the lumen of the dorsal marginal fin. × 100.

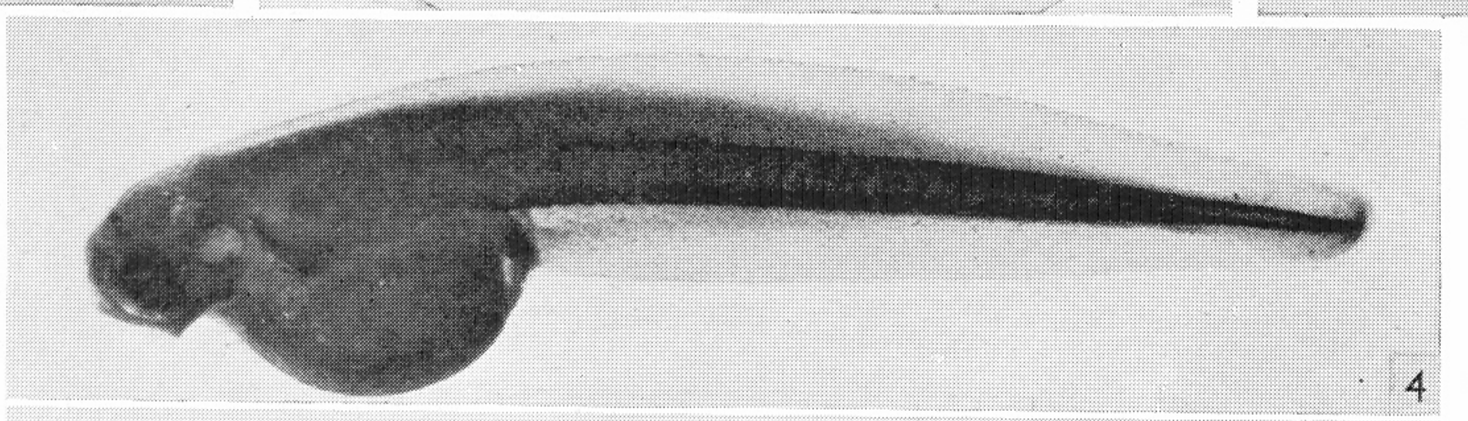
Figs. 4, 5. Newly hatched plaice larvae with extensive coagulation of plasma in dorsal and ventral portions of the marginal fin, after fixation in Heidenhain's Susa. × 12.

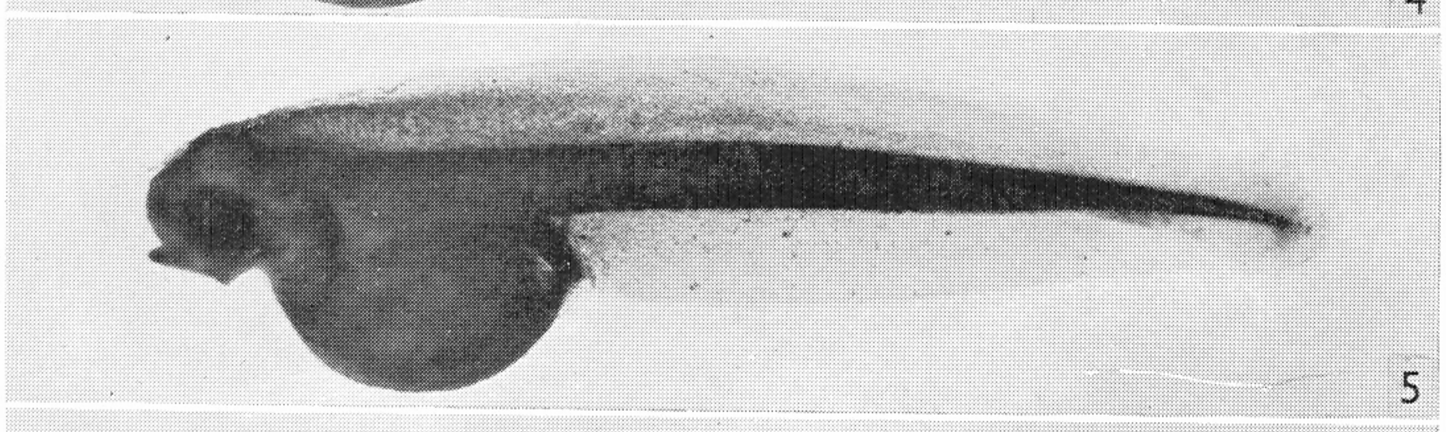
Figs. 6, 7. Day-old plaice larvae with heavy plasma coagulation in the anterior part of the dorsal marginal fin, above the head and gut. Fixed in Heidenhain's Susa. × 12.

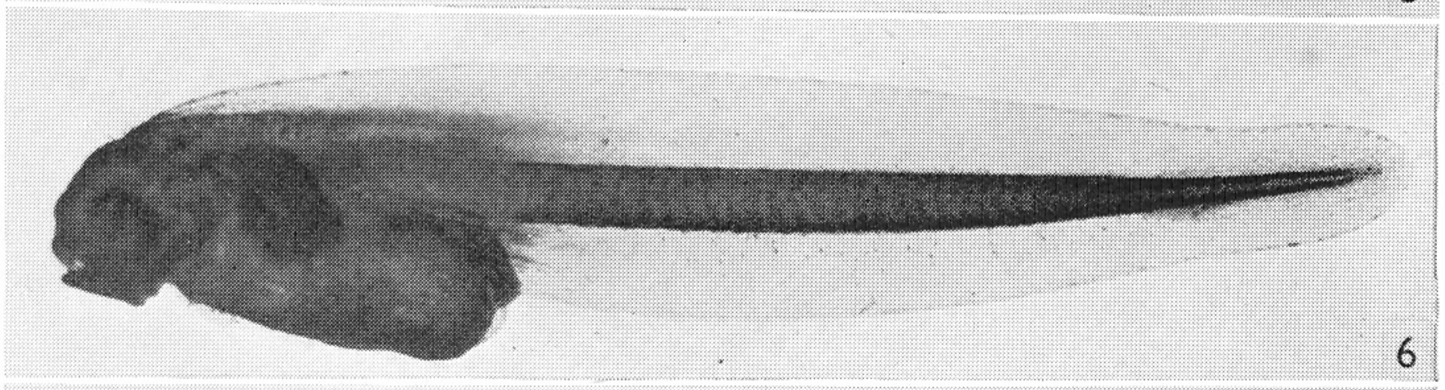


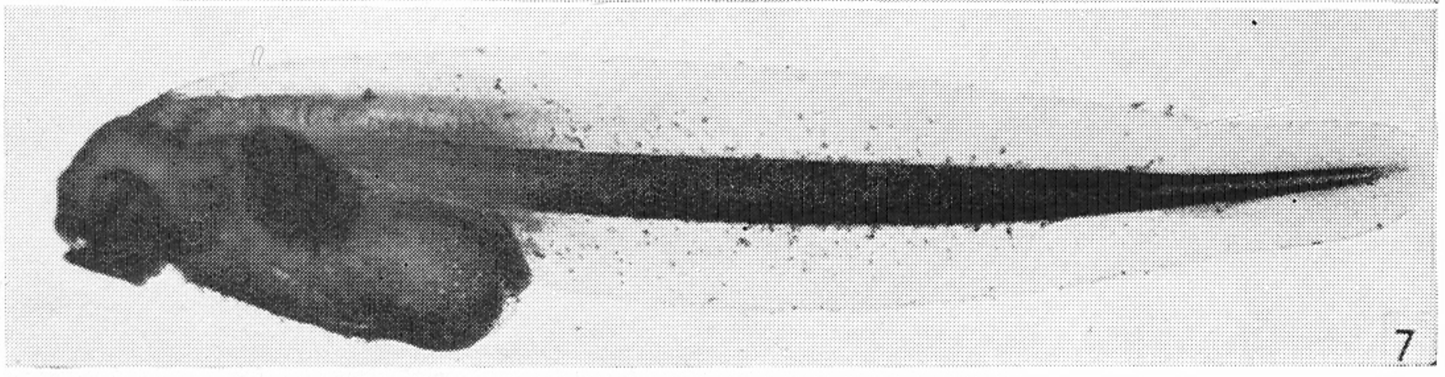












Figs. 1–7.

(*Facing p.* 286)