

The Digestive Tract of the Cod *Eleutheroembryo* (“Yolk-sac Larva”) and Larva*

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Abstract

Adult gadidae have the most differentiated digestive tract in the Teleostei, with glands in the stomach and many pyloric caeca, but the digestive tract of fish *eleutheroembryos* and larvae is relatively simple. It is initially narrow and straight, and there are no glands in the stomach, so it resembles the digestive tract of stomachless teleosts.

The *eleutheroembryo* is a free-living (*eleutheros*=free) embryo, which still depends mainly on its yolk-sac for food. This phase lasts from hatching, when the embryo is about 3–5 mm long, to the start of exogenous feeding at about 5 or 6 days.

No mouth is present at hatching, but the oropharyngeal membrane is perforated after 1 day, and it was found (Mangor-Jensen and Adoff, 1987) that *eleutheroembryos* drink to maintain their osmotic state. The mouth is fully open at 2 days, and movements of the lower jaw, which contains well developed cartilages, have been reported (Yin and Blaxter, 1987). There is active feeding at 5 days. The digestive tract shows differentiation along its length even at this early stage. There is a wide pharynx containing the gill arches, followed by a narrow oesophagus or foregut, which is surrounded by a layer of striated muscle. Initially the apices of the epithelial cells lining the lumen of the oesophagus are in contact with each other, so that the lumen is partly occluded. At the posterior end of the oesophagus there are ciliated cells in the 1-day old larva, which presumably help to circulate the contents of the intestine, since the anus is still closed. The swimbladder is still attached to the intestine just after hatching, and forms a forwardly directed pouch. Its lumen is small, and its lining, like that of the intestine, consists of columnar cells.

Posterior to the swimbladder the digestive tract widens to form the mid-gut. Initially, it forms a straight tube dorsal to the yolk-sac, but as the *eleutheroembryo* develops and starts to feed the tract becomes longer and convoluted. The epithelial cells lining the gut have microvilli at their apical surfaces and contain well-developed organelles, as well as some dark inclusions. There is a little pinocytotic activity, and no mucous cells.

The posterior part of the digestive tract is the rectum or hindgut, which becomes separated from the midgut by an externally evident constriction and valve at 3 days. The rectum contains apical vesicles and lysosomes, and there is active pinocytosis at the epithelial surface. Other workers have shown evidence for pinocytotic absorption of protein macromolecules from the gut lumen into the hindgut, followed by intracellular digestion. This is thought to be a larval specialization, since there are no glands in the stomach to produce proteolytic enzymes to start the extracellular digestion of proteins.

The posterior part of the hindgut loses microvilli at the lumen, and just after hatching the lumen is occluded. The anus becomes functional at 2–3 days, and the valve separating the midgut from the rectum may help to keep enzymes in the midgut, so that they are not lost in the faeces. The anus and urinary duct open on a papilla to the left of the base of the fin-fold.

The yolk-sac is surrounded by a periblast of flattened cells. There is not a well-developed blood supply surrounding the yolk-sac, as in some larvae, and yolk products apparently can pass directly from the surface of the periblast into a subdermal sinus which extends around the gut and myotomes, and into the finfold. Yolk products can also go directly to the liver to be metabolised, since this is very closely associated with the periblast. The liver is a circular mass in the anterior part of the body cavity. It is separated from the pancreas, which contains only one islet, by the gallbladder.

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Once exogenous feeding starts, the developing cod enters the larval phase, which lasts from 5 or 6 days or about 5 mm, to the completion of metamorphosis, at about 75 days or 20 mm. At 9 days, or 5.5–6.0 mm, the digestive tract is wide and sinuous, and the yolk-sac much reduced, so that larvae are dependent on the availability of planktonic food. It has been proposed that this is a "critical period" which determines the strength of the year-class (Browman, 1989). The lower jaw is well articulated with the lower, posterior part of the otic capsule; and membranous bone, the maxilla, is starting to form the anterior part of the upper jaw.

The oesophagus is usually lined by two layers of epithelial cells, and there are still no mucous cells. Posterior to this the digestive tract widens to form an expanded region, which differs from the adult stomach in not having glands. It contains food in feeding larvae, and may be important for storing food since the supply of plankton is patchy. Unlike the eleutheroembryo, the cuboidal to columnar cells lining the stomach contain vesicles with dense material, some apparently lipid, and there are more abundant organelles. Posterior to the stomach the intestine becomes narrower and convoluted, and there are fewer dense vesicles. Entero-endocrine cells are common. These are chemoreceptors, which often have processes at the luminal surface. These processes interact with the luminal contents, which may cause exocytosis of dense-cored secretory granules containing peptides at the bases of the cells. This secretion controls many functions, such as peristalsis of the gut wall. The rectum has more vesicles in the apical cytoplasm than the eleutheroembryo, indicating more activity. The swimbladder is no longer connected to the digestive tract, and contains presumed gas-forming bodies and vesicles as in the adult.

The liver is still closely associated with the remains of the yolk-sac, the gallbladder has a larger lumen than in the eleutheroembryo, and the pancreas extends posteriorly dorsal and lateral to the digestive tract.

At 5.6–5.9 mm or 17–20 days, the maxilla is more elongate, the intestine forms a ventral loop anteriorly, and the rest is convoluted. There are still remains of the yolk-sac. By 6.5 mm or 32 days, there is a dorsal pharyngeal tooth. It has been reported in other larvae that the pharyngeal teeth appear dorsally before they appear ventrally, and before teeth on the jaws. The oesophagus now has a few mucous cells in its mucosa, and there are still a few vesicles containing yolk beneath the liver and gut.

At 6.6–7.3 mm or 35 days, the liver is larger, and it has lost its rounded shape as it fills the space available in the body cavity. The outer end of the maxilla is also larger, and two more dermal bones, the premaxilla in the upper jaw, and the dentary in the lower, are being laid down. At 12.0 mm or 52 days, and 9.3–11.0 mm or 54 days, there are several teeth on the dorsal and ventral pharyngeal tooth plates, and teeth have begun forming in projections on the dorsal surfaces of the gill arches. There are many goblet cells in the oesophagus. The stomach mucosa is becoming more folded; and posterior to these pouches, the beginning of the pyloric caeca have begun forming in the mucosa of the gut. There are still small vesicles of yolk-sac remaining.

Teeth are present on the premaxilla and dentary, as well as on the pharyngeal tooth plates and the gill arches at 15.0 mm or 62 days. The mucosa lining the stomach is very folded, giving a glandular appearance. By 19.0 mm or 70 days small glands are present in the mucosa of the stomach, there are pyloric caeca posterior to the stomach, and some mucous cells are present in the mucosa of the rectum.

Cod of about 20 mm or longer are juveniles which have completed metamorphosis, so are essentially like the adult in structure.

Key words: Cod, *Gadus morhua*, digestive tract, eleutheroembryo, histology, larva

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