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DEVELOPMENT OF THE DIGESTIVE TRACT OF IDE *LEUCISCUS IDUS* (L.) DURING THE LARVAL STAGE

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ABSTRACT. The morphogenesis of the digestive tract and swim bladder of ide *Leuciscus idus* (L.) was analyzed using histopathological methods. At the moment of hatching, ide larvae are more advanced in their development than the larvae of other teleost fish species. Endo-exogenous nutrition began on day 2 post hatch. At this stage of development, the intestine was lined with a single-layered cylindrical epithelium, and both liver and pancreas began to function. Signs of digestion and enterocyte protein and lipid absorption were observed on day 6 of development. The mucus cells in the mouth, esophagus and gullet produced neutral and acidic mucins. Intestinal cuboid cells appeared on the fourth day and only began secreting acidic carboxyl and sulfate mucins. The differentiation of the air duct and the posterior chamber of the swim bladder was observed on the day of hatching, and the bladder inflated after 24 hours. The anterior chamber began to form on day 9, and it inflated with gas between days 23 and 25 of larval development.

KEY WORDS: IDE (*LEUCISCUS IDUS*), LARVAL PERIOD, DIGESTIVE TRACT

INTRODUCTION

Ide *Leuciscus idus* (L.) is a cyprinid from the order of Cypriniformes whose range of occurrence is the northern and central areas of the Eurasian continent. This rheophilous fish inhabits the upper and central parts of clean, cold rivers and winters in lakes. Rheophilous cyprinids increase the "production potential" of rivers by occupying niches which other species are not able to take (Błachuta 1998). Ide is a good example. This species is omnivorous, and when the availability of fauna food items are limited, it increases the percentage flora food in its diet (Brabrand 1985). Witkowski (1992) includes ide among species which are endangered by extinction due to overfishing, river regulation and pollution. Based on an ichthyofauna inventory, Błachuta and Witkowski (1997) reported that fish resources in Polish rivers are unstable and qualitatively poor. Eliminating adverse anthropogenic factors and employing artificial reproduction and cultivation to produce stocking material can play an important role in increasing the population numbers of endangered fish species. In Poland, and in many

other European countries, this is the impetus behind current interest in issues related to artificial reproduction and the production of stocking material for open waters. Studies on intensive ide hatch production under controlled conditions using industrial feed were carried out by Wolnicki (1996), Wolnicki and Górny (1992) and Kujawa et al. (1998). Applying the correct type of food at particular larval developmental stages is the key problem in intensive fish culture (Yúfera et al. 1996, Fontagnè et al. 1998, Navarro and Sarasquete 1998, Kujawa et al. 1998, Kolkovski 2001).

Therefore, morphological studies of the ontogenesis of the digestive tract during feeding studies using artificial feed increase knowledge of larval feeding requirements. During the period between hatching and the end of yolk sac resorption, the teleost fish larvae must develop the organs which allow them to effectively find, consume, absorb and digest food. As is the case with other fish species (Blaxter 1988), ide larvae have limited endogenic energy and food resources during the endotrophic stage (Mani-Ponset et al. 1996). The main morphological and functional changes in the digestive tract must occur before the yolk sac reserves are exhausted if the larvae are to survive this period, one of the most critical in their lives.

The aim of this work was to analyze the development of the digestive tract of ide *Leuciscus idus* (L.), including the associated glands and swim bladder, during the period from hatching and day 25 post hatch.

MATERIAL AND METHODS

The study was conducted at the Ichthyology and Fisheries Laboratory of the Warsaw Agricultural University. The study material consisted of newly hatched ide larvae from the Warsaw Agricultural University Fisheries Research Station in Łąki Jaktorowskie. The study was conducted in three 20 dm^3 aquariums. The initial density of the freshly hatched ide larvae was 50 specimens per dm^3. The larvae developed in water at a temperature of 20°C until day 25 post hatch. Beginning on the second day post hatch, the larvae were fed *ad libitum* with *Artemia salina* nauplii, (about 100 nauplii per individual per day). From day 6 post hatch the larvae were fed with Belgian granulated feed LANSY A2 manufactured by INVE Aquaculture, Belgium (protein 50%, fat 15.5%).

The water in the aquaria was aerated throughout the study, and the aquaria were cleaned every 24 h. The oxygen saturation of the water was 80-90%, the pH = 7.4-8.0, and the ammonia content was below 0.005 mg $N\text{-}NH_4$ dm^{-3}.

Every 24 h during the study from hatch until day 25 post hatch, ten specimens were collected and preserved for further histological studies and histochemical assays. The collected larvae were anesthetized (MS 222), fixed (10% buffed formalin and Bouin's solution) and subjected of standard histological procedure. They were dehydrated in an ethanol series and then embedded in paraffin. Serial paraffin slices 5 μm thick were cut with a MicroTec CUT 4050 microtome.

The larval morphology was evaluated using slices dyed with hematoxylin-VOF (light green, orange G, acidic fuchsin) according to Gutiérrez (1967). Mucins (glycogen-related compounds) and proteins were identified using histochemical methods. The staining techniques applied were those proposed by Martoj and Martoj-Pierson (1970) and Pearse (1985). Cells and tissues were measured under a Nikon-Alphaphot-2YS2 microscope coupled with a Mintron camera and MicroScan for Windows (v. 1.5). The total larval length on particular days of development was measured to the nearest 0.01 mm under a light microscope. The average total length (Lt) of larvae after 25 days of culture was 18.44 mm (n=100), and the average survival rate in the three aquaria was 89.2%

RESULTS

LARVAL DEVELOPMENT DURING THE RESORPTION OF THE YOLK SAC

At hatch, the ide larvae had an average total length of 6.91 mm. The pear-shaped yolk sac was surrounded by a periblast layer (perivitelline syncytium). The syncytial layer showed a strong affinity for acidic fuchsin (H-VOF) (Photo 1).

The yolk sac contained fat drops, which were dispersed in the yolk mass. Blood circulated in the vessels surrounding the yolk sac. The yolk contained glycogen (diastase PAS negative staining) and proteins rich in amino acids - such as lysine (Ninhydrin Schiff -positive staining), arginine (8-hydroxyqinoline - sodium hypochlorite - positive staining), cysteine (ferrous ferricyanide (Fe III positive staining) and cystine performic acid – Schiff positive staining).

The digestive tract in the freshly hatched larva was not yet morphologically differentiated and it rested on the yolk sac. The mouth, esophagus and gullet showed a single-layered hexagonal epithelium of irregular cells. Among the undifferentiated epithelial cells in the gullet were singular mucus cells which produced acidic mucins (alcian blue pH 2.5 - positive staining). The primordial intestine was very narrow and

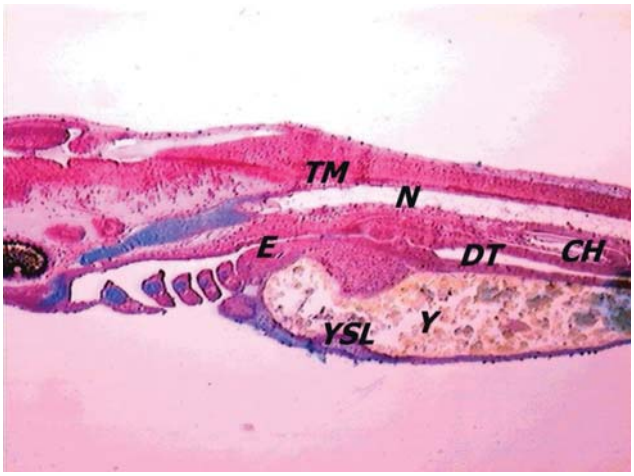

Photo 1. Longitudinal section through an ide larvae on the day of hatch. Esophagus (E), truncal muscle (TM), dorsal cord (N), yolk sac (Y), primordial intestine (DT), primordium of the anterior chamber of the swim bladder (CH), perivitelline syncytium (YSL). x 100.

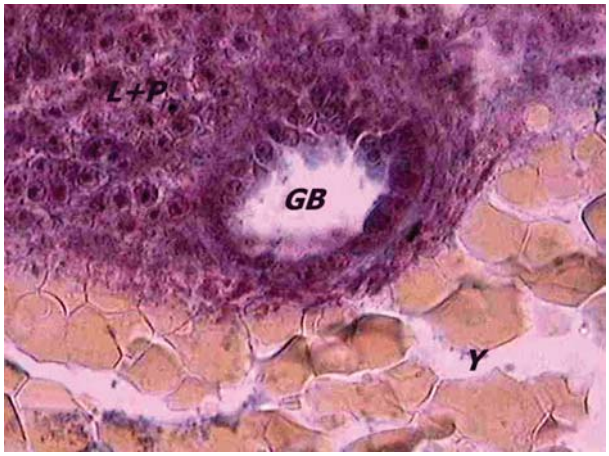

Photo 2. Gall bladder (GB) on the day of hatch surrounded by differentiating liver and pancreas cells (L+P). Yolk sac (Y). x 1000.

still blind in some places and showed a single-layered cylindrical epithelium of irregular, differentiating cells, which were from 18 to 20 μm in height. The end of the intestine (anus) was not open.

The liver and pancreas primordium appeared as a dense clump of cells located between the digestive tract and the yolk sac (Photo 1). The undifferentiated cells of the liver and pancreas surrounded the forming yolk sac (Photo 2), and they were basophilic (H-VOF).

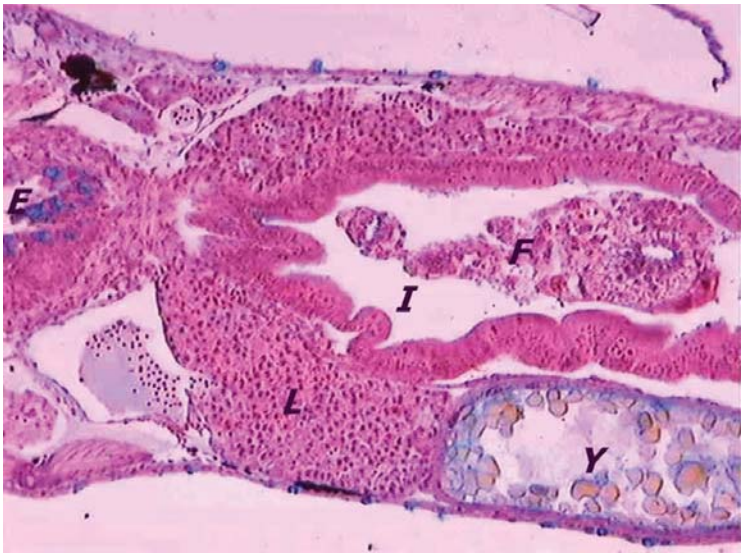

Photo 3. Longitudinal section of an ide larva on day 2 post hatch. Liver (L) surrounds the anterior section of the intestine (I). Yolk sac (Y), esophagus (E), food (F). x 250.

On the day of hatching, the respiratory tract was seen to be developing in the upper portion of the gullet, as were the differentiating cells of the swim bladder which was located between the dorsal cord and the digestive tract (Photo1).

The resorption of the yolk sac reserves and the differentiation of the digestive tract were both very fast during ide larva development.

On day 2 post hatch, the intestine showed a folded, single-layered cylindrical epithelium. The lumen of the anterior intestine section increased significantly. At this developmental stage, the liver grew due to the proliferation of hepatocytes, and was translocated by morphogenetic movements to a ventral position, enclosing the widened part of the intestine (Photo 3). It was during this stage that larvae began to utilize natural food, i.e., *Artemia* nauplii.

Sinusoidal blood vessels appeared among the hepatocytes. The pancreas was a separate organ, and the main part of it, with the centrally-placed Langerhans isle, was located dorsally above the anterior segment of the intestine (Photo 4).

The eosynophilic pancreatic cells stained positively with bromophenol blue and showed close affinity with orange G (H-VOF). They formed vesicles, and in the centers of them the first proenzyme granules were observed. These granules contained proteins rich in arginine, tryptophan, tyrosine and cystine.

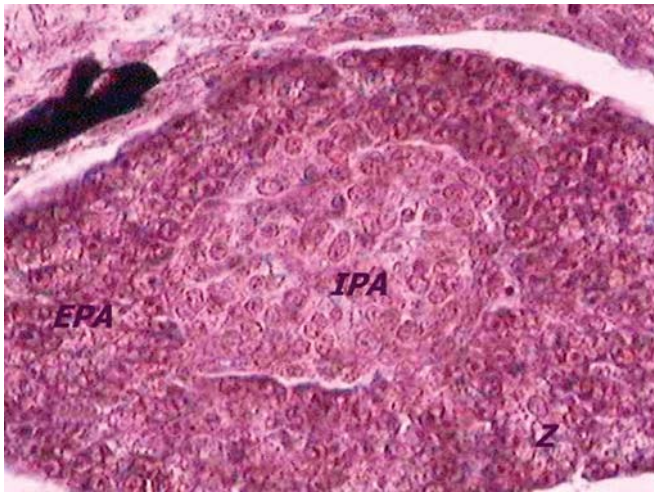

Photo 4. Section through the exocrine pancreas (EPA) and islet of Langerhans (IPA), day 2 post hatch. Proenzyme granules (Z). x 1000.

The inside diameters of the gall bladder and the bile duct were covered by a single-layered hexagonal epithelium. The bile duct opened in the anterior part of the intestine.

Between days 2 and 3 post hatch, the epithelium of the mouth and esophagus changed into multi-layered, smooth epithelium. Differentiating throat teeth and quern were observed in the esophagus. The inner lining of the gullet became folded. Cuboid cells that produced neutral mucins (positive PAS staining), sialomucins (alcian blue, pH 2.5) and sulfate mucins (alcian blue, pH 0.5) were observed among the epithelial cells of the mouth cavity. The largest aggregation of mucus cells which produce acidic mucins (carboxyl and sulfate) was observed in the posterior segment of the gullet (Photo 5).

During this period the height of the folds of the intestinal mucus membranes was an average of 29 μm. Enterocytes were covered by a low (about 2 μm) brush border.

The posterior chamber of the swim bladder was filled on the second day of larval development.

LARVAE DEVELOPMENT FOLLOWING THE RESORPTION OF THE YOLK SAC

On day 4 post hatch, the yolk sac was fully resorbed (Lt 9.18 mm), and the larvae began the exclusively exotrophic stage. The intestine increased in length, as did the number of mucus membrane folds and their height (57 μm). The accumulation of gly-

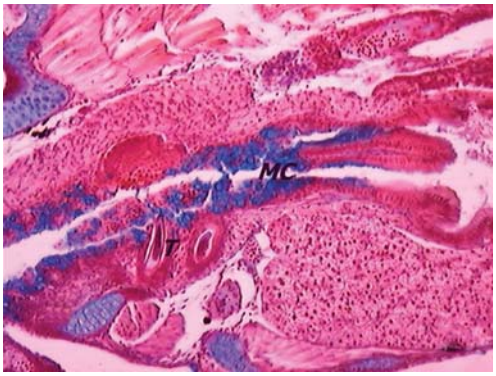

Photo 5. Differentiating throat teeth (T) and quern, day 3 post hatch. Accumulation of mucus cells (MC) in the posterior section of the esophagus.

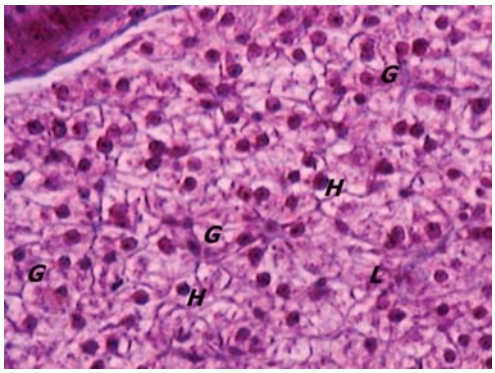

Photo 6. Section through the liver (L), day 4 post hatch. Accumulation of glycogen (G) in the hepatocytes (H). x 1000.

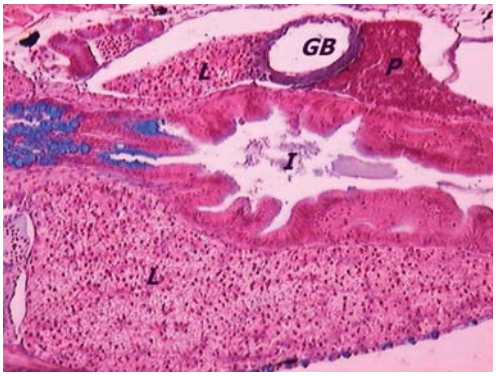

Photo 7. Gall bladder (GB), liver (L), pancreas (P), day 4 post hatch. x 250.

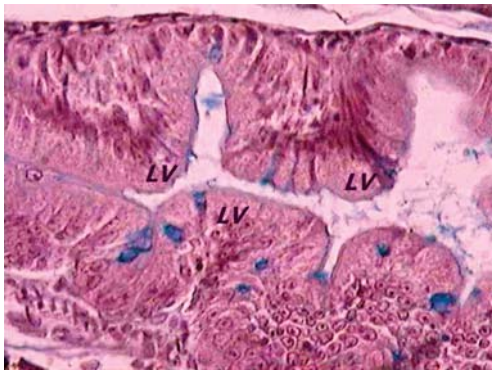

Photo 8. Transverse section through the mid section of the intestine (I), day 6 post hatch. Lipids (LV) in the supranuclear region of the cytoplasm of enterocytes. x 1000.

cogen in the hepatocytes was observed (positive PAS staining) and blood cells appeared in the sinusoids (Photo 6). The gall bladder, filled with bile, was located between the liver and the pancreas (Photo 7).

The pancreas was growing and was located between the swim bladder and the middle section of the intestine, but the main part remained above the anterior section of the intestine (Photo 7). At this developmental stage, mucus cells appeared among the enterocytes of the intestine. Single mucus cells were observed in the widened anterior section of the intestine, and the number of them increased towards the anus. The cuboid cells produced carboxyl and sulfate mucins.

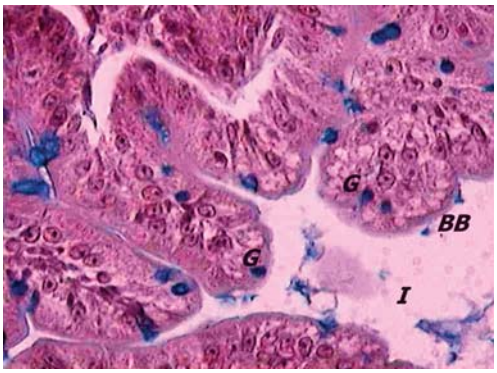

Photo 9. Longitudinal section of the posterior section of the intestine (I), day 6 post hatch. Acidophilic granules (G) in the supranuclear region of the cytoplasm of enterocytes. Brush border (BB). x 1000.

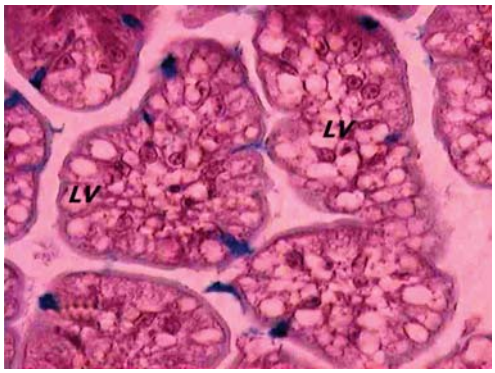

Photo 10. Longitudinal section through the mid section of the intestine, day 12 post hatch. Large lipid vacuoles (LV) in the supranuclear region of the cytoplasm of enterocytes. x 1000.

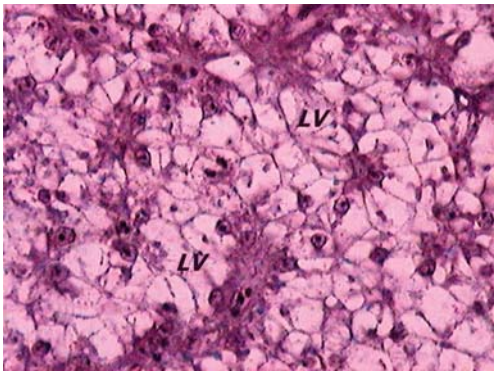

Photo 11. Accumulation of lipids (LV) in the hepatocytes, day 12 post hatch. x 1000.

On day 6 post hatch (Lt 10.32 mm) fat droplets were observed in the supranuclear region of the cytoplasm of enterocytes in the intestinal middle section (Photo 8). Simultaneously, acidophilic granules, which stained orange G and light green (H-VOF), were observed in the posterior section. The supranuclear granules contained protein (positive PAS reaction) (Photo 9).

In the following days of development the intestine length, the height of folds (average height - 108 μm) and the number of mucus cells all increased. The progressively increasing number of droplets in the enterocytes indicated that lipids were being accumulated. On day 12 post hatch (Lt 13.73 mm) large lipid vacuoles were observed in the supranuclear region of the enterocytes in the middle section of the intestine (Photo 10).

The level of protein accumulation in the enterocytes of the posterior section of the intestine did not change, while lipid accumulation increased in the hepatocytes (Photo 11).

The height of the brush border of the enterocytes did not change, and there were PAS-positive areas in the posterior segment of the intestine. From day 16 post hatch, lipid accumulation decreased significantly in the supranuclear region of the cytoplasm of the enterocytes, and lipid droplets again were observed. The first intestinal loop in the studied larvae was observed on days 23-24 post hatch. The liver exhibited the appropriate build until the termination of the study. Hepatocytes accumulated glycogen and fat. The anterior swim bladder chamber was formed when the posterior chamber protruded - it began to differentiate on day 9 post hatch. The anterior chamber gradually increased in size and in the final period of the study it was inflated with gas. The air duct was opened between the anterior and posterior bladder chambers.

DISCUSSION

When ide larvae hatch, their organs are more developed in comparison with those of other fish species (Rombout et al. 1978, Stroband et al. 1979, Gisbert et al. 1999, Ostaszewska and Węgiel 2002). The newly hatched ide larvae had passable mouths and gullets, and the gall bladder and swim bladder were formed. The majority of teleost larvae still have impassible mouths, gullets and anuses directly after hatching (Bisbal and Bengtson 1995, Sarasquete et al. 1995, Calzada et al. 1998, Hamlin et al. 2000, García Hernández et al. 2001). The gall bladder in larval *Paralichthys dentatus* (L.) was fully formed on day 3 post hatch, i.e., in the middle of the endotrophic stage, while in larval *Sparus aurata* (L.) - not until the end of this period (Bisbal and Bengtson 1995, Guyot et al. 1995). Only Hamlin et al. (2000) observed the gall bladder on the day of hatching, as was observed for ide larvae. In many teleost species, the swim bladder inflates with gas in the final period of resorption (Makino et al. 1995, Dinis et al. 1997) or when it is complete (Grizzle and Curd 1978). The swim bladders of the ide larvae from the current study filled with gas on day 2 post hatch when there were still significant stores in the yolk sac. In larval vimba bream *Vimba vimba* (L.) the primordium of the swim bladder was observed on day 3 post hatch, and it started to inflate with gas on days 4-5 post hatch (Ostaszewska et al. 1997). The swim bladder of larval *Morone saxatilis* Wal. inflates with gas between days 5-7 post hatch (Doroshev and Cornacchia 1979), and that of larval *Solea solea* (L.) following day 14 post hatch (Boulhic and Gabaudan 1992). The early filling of the swim bladder meant that ide larvae were able to move freely in the water column in search of food.

When the ide larvae began to consume exogenous food (*Artemia* nauplii), the yolk sac still contained reserves of nutritive substances and the digestive tract was not yet fully differentiated. Similar observations were recorded for the larvae of *Solea solea* and *Sparus aurata* (Boulhic and Gabaudan 1992, Sarasquete et al. 1995). In other fish species the digestive tract is fully formed prior to the onset of the larval exotrophic stage (Segner et al. 1994, Ribeiro et al. 1999).

In the larvae of some fish species yolk sac reserves were seen to accumulate in the enterocytes during the endotrophic stage (Deplano et al. 1991, Calzada et al. 1998, García Hernández et al. 2001). The first signs of absorption activity in the supranuclear region of the cytoplasm of enterocytes in ide larvae were observed during the exotrophic stage (6 days post hatch). Lipids accumulated in small droplets in the enterocytes of the middle section of the intestine, while protein was accumulated as acidophilic granules in the enterocytes in the posterior section of the intestine. The supranuclear vacuoles with acidophilic granules in the cytoplasm of enterocytes in the posterior segment of the intestine which were observed in ide larvae, were also reported in the larvae of other fish species, such as *Leiostomus xanthurus* Lacépède, *Engraulis mordax* Girard, *Solea solea*, *Sparus aurata*, *Hippoglossus hippoglossus* (L.) and *Dicentrarchus labrax* (L.) (Govoni 1980, O'Connell 1981, Boulhic and Gabaudan 1992, Sarasquete et al. 1995, Luizi et al. 1999, García Hernández et al. 2001). The results obtained indicate that the acidophilic granules result from the pinocytotic absorption of protein macromolecules from the intestine lumen. This was confirmed using peroxidase (Georgopoulou et al. 1986, Govoni et al. 1986) and by studies of the ultrastructure of intestine enterocytes (Segner et al. 1994, Calzada et al. 1998). It is suggested that pinocytosis, caused by the low concentration of digestive enzymes, is an alternative means of protein absorption by larvae.

The presence of lipid droplets in the supranuclear region of the cytoplasm of enterocytes in the middle section of the intestine in the studied ide larvae is confirmed by the studies of the larvae of other fish species (Stroband et al. 1979, Cousin and Baudin-Laurencin 1985, Kjørsvik et al. 1991, Boulhic and Gabaudan 1992). The lipid digestion process in fish larvae was described by Eckmann (1987), Kjørsvik et al. (1991) and Sarasquete et al. (1995). Lipids are hydrolyzed into fatty acids and monoglycerides in the inner lining of the intestine and then absorbed. Lipid resynthesis occurs in the smooth endoplasmatic reticulum, and they are deposited as lipid droplets in the enterocytes of the intestinal mucous membrane (Loewe and Eckmann 1988, De Silva and Anderson 1995). In the first days of ide larvae feeding, lipids were

observed in the enterocytes as small droplets. During larval growth and development, the amount of lipid absorbed from the inner lining of the intestine in the cytoplasm of enterocytes increased and then decreased. This process is explained by the excessive absorption of fatty acids (from artificial feed), the amount of which exceeded the excretion ability of the enterocytes. Enterocytes absorb lipids from feed, but since their ability to synthesize lipoproteins is insufficient, they are stored as lipid droplets and vacuoles. The development of enterocytes during organogenesis and more effective lipoprotein synthesis was probably accompanied by a decrease in large lipid vacuoles in the enterocytes. Deplano et al. (1991) observed the disappearance of lipid vacuoles from the cytoplasm of enterocytes in larvae of *Dicentrarchus labrax* and Hamlin et al. (2000) in the larvae *Melanogrammus aeglefinnus* (L.).

Mucus cells were already present in the gullet of ide larvae at hatching, and the excretion of acidic mucins was observed from the start. The quantity of them increased as the larvae grew and cells which produced neutral mucins appeared. The intestinal mucus cells produced acidic carboxyl and sulfate mucins; these were observed on the fourth day of larval development. The number of mucus cells in the intestine epithelium increased towards the anus.

A similar, mixed mucin excretion (neutral and acidic) was observed in the larvae of *Sparus aurata*, *Acipenser baeri* Brandt and *Melanogrammus aeglefinus* (Domeneghini et al. 1998, Gisbert et al. 1999, Hamlin et al. 2000). Inter- and intraspecial differences in the content of intestinal mucus cell excretions (Ferraris et al. 1987, Grau et al. 1992, Gisbert et al. 1999) may be caused by varied larval nutrition (Reifel and Travill 1979). The mucus excretion produced by cuboid cells has the same role as in mammals (Scocco et al. 1998), i.e., to protect of the mucus membrane of the digestive tract.

In summary, the application of mixed feeding during the culture of ide larvae had a positive impact on their development. The digestive tract had not fully formed when the first food was consumed. The ability of ide larvae to digest and absorb this food was probably due to enzymes from *Artemia* (Dabrowski 1984, Lauff and Hofer 1984, Kolkovski et al. 1993). The morphology of the digestive tract of ide larvae which begin to consume dry feed was at such a developmental stage that the enterocytes were able to absorb and the liver and pancreas were functioning. According to Kalkovski et al. (1997), providing larvae with natural food, such as *Artemia*, just before dry food is provided may heighten digestion thus improving the ability of the larvae to absorb dry food. The results of the current study confirmed those obtained by Wolnicki and Górny (1992), who, during controlled rearing of ide larvae (between

days 2 and 17 of life), obtained a higher survival rate, a faster growth rate and greater growth increments in larvae fed with a mixed diet (carp starter and *Artemia*) than for larvae fed only with carp starters.

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STRESZCZENIE

ROZWÓJ PRZEWODU POKARMOWEGO JAZIA *LEUCISCUS IDUS* (L.) W OKRESIE LARWALNYM

Celem pracy było prześledzenie zmian morfologicznych w przewodzie pokarmowym i pęcherzu pławnym podczas rozwoju larwalnego jazia *Leuciscus idus* (L.). Badania przeprowadzono przy użyciu metod histologicznych. W dniu wyklucia przewód pokarmowy jazia był niezróżnicowany morfologicznie (fot. 1). Larwy rozpoczęły samodzielne pobieranie pokarmu w 2 dobie, a całkowita resorpcja pęcherzyka żółtkowego nastąpiła w 4 dobie od momentu wyklucia. Obserwacje histologiczne wątroby i trzustki wskazywały na zaangażowanie tych gruczołów w procesy trawienne (fot. 4). W końcowym okresie endo-egzogennego odżywiania się larw stwierdzono w gardzieli obecność zębów gardłowych oraz żarna, służących do rozdrabniania pokarmu (fot. 5). Komórki śluzowe jelita rozpoczęły sekrecję kwaśnych mucyn w 4 dobie. Oznaki trawienia i wchłaniania białek i lipidów przez enterocyty obserwowano w 6 dobie rozwoju larwalnego (fot. 8 i 9).

Zastosowane żywienie mieszane (pasza sztuczna + pokarm naturalny) podczas podchowu larw jazia miało korzystny wpływ na rozwój larwalny. Stadium rozwoju przewodu pokarmowego, w którym larwy jazia zaczęły pobierać paszę komercyjną wskazywało na funkcjonowanie wątroby i trzustki oraz zdolność absorpcyjną enterocytów. Początek wypełniania dwukomorowego pęcherza pławnego obserwowano w 2 dniu (tylna komora), a przednia komora napełniała się gazem między 23-25 dniem wyklucia.

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