

Scanning electron microscopic observations of the chemo- and mechanoreceptors of carp larvae (*Cyprinus carpio*) and their relationship to early behaviour

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Abstract

Scanning electron microscopic observation of embryos and larvae of the carp (*Cyprinus carpio*) in the course of development was undertaken to further understanding of the relationship between larval behaviour and their chemo- and mechanoreceptors. Free neuromasts and olfactory pits equipped with mechano- and sensory-cilia were found on carp embryos. During larval development, the number of neuromasts and the olfactory mechano- and sensory cilia steadily increases and they become more morphologically differentiated. The olfactory features, presented in early larval stages, indicate that although the olfactory organ at this early life history has not yet attained its final configuration, it can perceive odour stimulation. The neuromasts found on the forehead of the newly hatched larvae seem to assist in the early behavioural selection, approach and attachment to a substratum, before the stage of filling of the gas bladder. The increasing number of neuromasts during development reflects the larvae's capability of capturing food items in the absence of visual stimulation. The rapid maturation of free neuromasts, the lateral-line system and the olfactory organ, is evidence of their post-metamorphosis position in the search for, location and successful capture of food.

Keywords: Carp larvae, *Cyprinus carpio*, neuromasts, olfaction, taste buds, feeding behaviour.

Observations en microscopie électronique à balayage des chimio- et mécano-récepteurs des larves de la carpe (Cyprinus carpio) en relation avec leur comportement.

Résumé

L'observation en microscopie électronique à balayage des embryons et des larves de la carpe (*Cyprinus carpio*), au cours du développement, a été entreprise pour une meilleure compréhension de la relation entre le comportement des larves et les chimio- et mécano-récepteurs. Les neuromastes isolés et les fosses nasales équipés de cils sensoriels ont été trouvés chez les embryons de carpe. Durant le développement larvaire, le nombre de neuromastes et de cils sensoriels olfactifs augmentent et se différencient morphologiquement. Les particularités du système olfactif présent dès les premiers stades larvaires indiquent qu'une stimulation olfactive peut être perçue bien que l'organe olfactif n'ait pas atteint sa conformation finale. Les neuromastes trouvés sur le front des larves nouvellement écloses, avant le stade de remplissage de la vessie natatoire, semblent participer aux premières approches comportementales et notamment à la détection du substrat. L'augmentation du nombre de neuromastes durant le développement reflète la capacité des larves à capturer des particules alimentaires en l'absence de stimuli visuels. La maturation rapide des neuromastes isolés, du système de la ligne latérale et de l'organe olfactif est le signe évident de leur position caractéristique, après la métamorphose dans la recherche, la localisation et la capture effective de l'aliment.

Mots-clés : Larves de carpe, *Cyprinus carpio*, neuromastes, olfaction, comportement alimentaire.

INTRODUCTION

Numerous publications are available on the biology, nutrition and growth of the carp larvae (*Cyprinus carpio*) (Depêche and Billard, 1994; for overview, see Kamler, 1992). In the late 1960s and early 1970s, studies searched for a nutritionally adequate, inert diet as a substitute for the natural live food of carp larvae. During the late 1970s and early 1980s, diets for carp larvae were manufactured. Nevertheless, the degree of success in the exclusive use of such diets varies considerably between users. A major contribution in establishing proper diets and their effective use, is the understanding of larval behaviour, particularly their feeding behaviour, stimulated by their sense organs. Any diet remains unsatisfactory if not sufficiently ingested, which necessitates a proper interaction between larvae and food.

In this contribution, our findings and others from the literature are related to the behaviour, particularly the feeding behaviour, of early carp stages throughout and beyond metamorphosis. Similar studies have already been made on the *Solea solea* (Appelbaum *et al.*, 1983) and on turbot and sole (Knutzen, 1992), but not previously on carp.

MATERIALS AND METHODS

Embryos and larvae

Embryos and larvae were obtained through induced spawning of brood stock using the hypophysation technique. Female carp were injected twice with carp pituitary extract, ("Dag-Shan", Israel), with an interval of 7 hours; males received one injection at the time of the females' second injection. Stripping of gametes took place twelve hours after the second injection. The gametes were gently mixed, stickiness was removed (Woynarovich and Woynarovich, 1980), and fertilized eggs were incubated in "zuger jars" at a water temperature of 24°C. Larvae were kept at 24°C and fed dry feed to beyond metamorphosis.

Behaviour

Swimming and behaviour of the newly hatched larvae were observed in outdoor earthen nursery ponds and indoor experimental tanks. Initial exogenous feeding and feeding behaviour of larvae hatched indoors has been observed in experimental tanks using live food and compound diets. Observation of larval feeding and behaviour in earthen ponds has been made several times previously (Appelbaum 1976, 1977, Appelbaum and Dor, 1978, Appelbaum and Uland, 1979).

In the following study, "embryos" refers to the stage before hatching, and "larvae" to the stages after hatching until completion of metamorphosis. Metamorphosis refers to the stage at which typical

larval characteristics (yolk-sac, fin-fold, etc.) have vanished and other characteristics, resembling those of an adult, appear. For the observation, the embryos were released by carefully cutting and removing the egg envelope.

For the scanning electron microscopy, the embryos and larvae were fixed with 2.5% glutaraldehyde in cacodylate buffer at pH 7.3 for 24 hours. After several washings in the same buffer, dehydration was carried out in a graded acetone series. The specimens were dried in a Balzers critical point dryer, mounted on brass supports with hot glue, and then coated with a 25 µm thick layer of gold in an Emscope SC 500 sputter coater. The specimens were examined with a Leitz AMR 1000 scanning electron microscope.

RESULTS

Morphology

Embryos – 50 hour post-insemination (ca. 4 mm T.L.)

The embryo has a relatively large yolk-sac and a large, toothless mouth. The beginning of keratinization is visible on the lower jaw (Fig. 1). Two shallow indentations in front of the eyes indicate the position of the immature olfactory organ (Fig. 1). At this stage the longer mechanocilia and the shorter sensorycilia, are already present. The mechanocilia are mainly concentrated on or close to the peripheral edge of the depression, but very few in the depression itself. The star-like sensorycilia are situated in the inner part of the depression (Fig. 2). The few neuromasts present are mainly on the head and forehead (Fig. 3). No cupulae is observed on neuromasts at this stage. The epidermis of the embryo shows the typical features of a fish epidermis – a pattern of microridges. There are large numbers of protrusions of the squamous epidermal cells present on the surface of the yolk-sac (Fig. 4).

Larvae – 66 hours post-insemination (ca. 4.5 mm T.L.)

The yolk-sac and fin-fold are well developed. Numerous keratinizing cells are visible on both jaws, but mainly on the lower jaw (Fig. 5). The olfactory indentations have become larger and more pronounced. Mechanocilia density has increased (Fig. 6). More neuromasts are presented and there is evidence of cupulae (Figs. 7, 8).

Larvae – 71 hours post-insemination and two to three hours after hatching (ca. 5.5 mm T.L.)

The artery is visible on the surface of the yolk-sac (Fig. 9). The mouth has enlarged, olfactory indentations have deepened and the number of cilia continues to increase. Mechanocilia form clusters in the area of the depression and the number of neuromasts remains relatively small. Four neuromasts

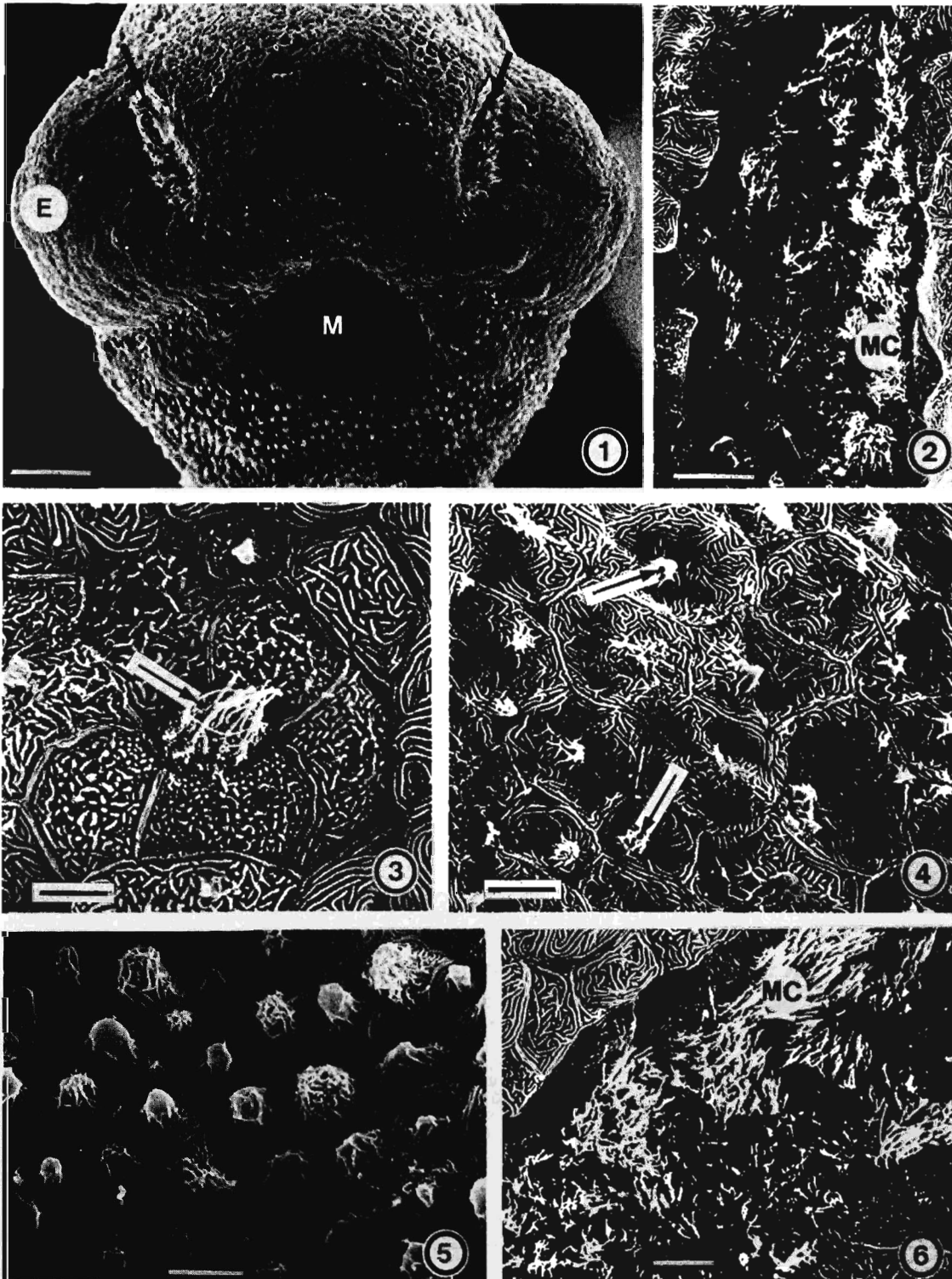


Plate 1. – Figures 1-4: Stage 1 (embryo, 50 hours post-insemination; ca. 4 mm T.L.); Figures 5-6: Stage 2 (embryo, 66 hours post-insemination; ca. 4.5 mm T.L.).

1 – Head of an embryo. E = eye, M = mouth, arrow = olfactory organ, arrowhead = taste bud. bar = 50 μ m. **2** – Developing olfactory organ of an embryo. Most of the mechanocilia (MV) are concentrated on or close to the peripheral edge of the depression. White arrow = star-like sensory cilia. bar = 10 μ m. **3** – Neuromast (arrow) on the head of an embryo. A cupula is still lacking. bar = 5 μ m. **4** – Surface of the yolk-sac with a large number of protusions of the squamous epidermal cells (arrows). bar = 10 μ m. **5** – Numerous keratinizing cells from the lower lips. bar = 10 μ m. **6** – Olfactory organ with an increased number of mechanocilia (MC). bar = 5 μ m.

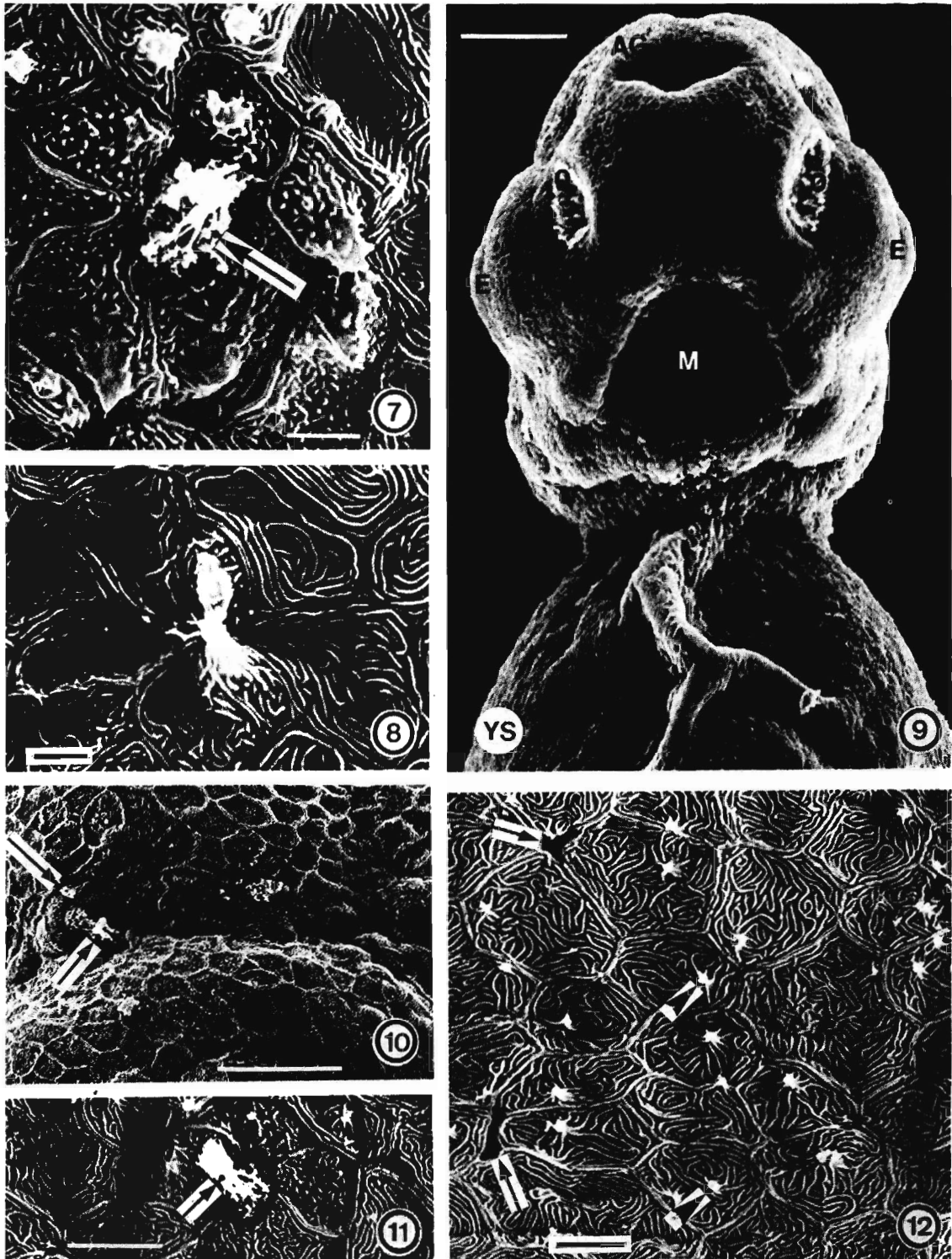


Plate 2. – Figures 7-8: Stage 2 (embryo, 66 hours post-insemination; ca. 4.5 mm T.L.); Figures 9-12: Stage 3 (larva, 71 hours post-insemination; ca. 5.5 mm T.L.).

7 – Neuromast without cupula (arrow). bar = 5 μ m. 8 – Neuromast with developing cupula. bar = 5 μ m. 9 – Ventral view of a larva. AG = adhesive gland, E = eye, M = mouth, o = olfactory organ, YS = yolk-sac, arrow = artery of the yolk-sac. bar = 100 μ m. 10 – Three of four neuromasts (arrows) on the forehead which are arranged symmetrically. bar = 50 μ m. 11 – Neuromast with cupula. bar = 10 μ m. 12 – Surface of the body with numerous protrusions of the squamous epidermal cells (arrowheads) and a few openings of goblet cells (arrows). bar = 10 μ m.

appear symmetrically arranged on the forehead, between the mouth and the olfactory region (Fig. 10). These four neuromasts remain distinct even at later stages. A few large neuromasts appear above each eye in the region of the supraorbital. Apart from those on the head, several neuromasts are now present on other parts of the body. At this stage, cupulae can be detected on neuromasts (Fig. 11). Figure 9 shows the location of the large adhesion gland on the forehead. This location does not remain visible at later stages (about 48 hours post-hatching). Numerous protrusions of the squamous epidermal cells are present and a few openings of goblet cells may be observed on various parts of the body (Fig. 12).

Larvae – 88 hours post-insemination, shortly after detaching themselves from substratum and before swimming freely (ca. 6.5 and 7.0 mm T.L.)

A proportion of the yolk-sac has already been absorbed. The fin-fold is extant and the mouth continues to enlarge. The olfactory indentation has become larger and deeper (Fig. 13) and the number of mechanocilia has increased. More neuromasts are evident, particularly on the head and around the eyes in the supraorbital and the hyomandibular region, and also on the body. The four symmetrically arranged neuromasts on the forehead possess long stereocilia and prominent cupulae (Fig. 14). The adhesion area has become less conspicuous (Fig. 13).

Larvae – 101 hours post-insemination, free-swimming, (ca. 7 mm T.L.)

The yolk-sac is significantly reduced and the fin-fold is beginning to disappear. The olfactory indentations are more pronounced (Fig. 15). The number of mechanocilia continues to increase at the edge of the depression, almost completely covering it. In the depression itself, groups of mechanocilia are interspersed among the stereocilia. Neuromasts with distinct cilia and cupulae have further increased in number and become more morphologically differentiated (Fig. 16). Particularly distinct are the neuromasts around the eyes and the olfactory pits. The adhesion area is no longer defined.

Larvae – 111 hours post-insemination (ca. 7.5 mm T.L.)

At this stage, exogenous feeding has started and the fin-fold is hardly recognizable. The mouth has reached a remarkably large size. The olfactory indentation has widened, deepened and has a thick covering of cilia, the longer mechanocilia being more visible and partially hiding the shorter sensory cilia. The edges of the olfactory indentations show a greater concentration of mechanocilia along the lateral and caudal region than in the remaining area; these cilia extend over the edge onto the surrounding epidermis. The number of neuromasts has greatly increased (Fig. 17). They are mainly distributed on the head, the dorsal part of the trunk and the tail (Fig. 17). Here,

too, distinct neuromasts are concentrated around the eyes; particularly noticeable are the four neuromasts, symmetrically arranged between the olfactory pits (Fig. 18).

Larvae – 210 hours post-insemination (ca. 11 mm T.L.)

Though metamorphosis is not completed, most of the larval characteristics are now barely visible. The mouth is large and there is active feeding (Fig. 19). Differentiated taste-buds can be seen on the lips (Fig. 20). The olfactory pits have deepened and become more caudally elongated, resembling a pear. The edges of the pit remain covered with a thick layer of mechanocilia. Part of the base of the pit, free of cilia, has risen, showing the typical pattern of the epidermis (Fig. 21); the remainder of the pit-base is covered with a carpet of both types of cilia. The number of neuromasts seems to have significantly increased compared to the former stages: they have become more distinct, well arranged around the eyes, the cheeks and the trunk, forming a typical, symmetrical pattern on the head. The arrangement of the neuromasts on the head, starting with the four symmetrical ones mentioned previously, indicates the beginning of the frontal part of the lateral line system (Fig. 22).

Juvenile carp (13 mm T.L.)

All larval features have disappeared and the external appearance is that of an adult. Scales are visible on the dorsal-lateral and ventral-lateral regions of the body (Fig. 24). The four symmetrically arranged neuromasts on the forehead are still easily recognizable. The lateral line system of the head is well developed and numerous neuromasts are arranged in a characteristic pattern of rows, radiating from the eye down to the edge of the suborbital, as well as on the operculum (Fig. 23). The typical line of neuromasts is also visible on the body (Fig. 24). The lips of the lower jaw show the keratinized squamous epidermal cells before reaching their final form (Fig. 25). The epidermal bridge, which separates the olfactory pit into inlet and outlet nares, is almost completely formed (Fig. 26).

Juvenile carp (25 mm T.L.)

The olfactory organ has almost reached its final external shape. The two nares of the olfactory organ are, externally, completely separate (Figs. 27, 30). Many more neuromasts are scattered on the head (Fig. 30), some of which have sunk down and become hidden (Figs. 28, 29). This can now be regarded as a fish beyond metamorphosis.

Behaviour

For about one day after hatching, carp larvae stay attached to a substratum in the midwater. They then detach themselves and swim energetically to the surface to gulp for air to fill their gas-bladder. They reach the water surface via a winding-like

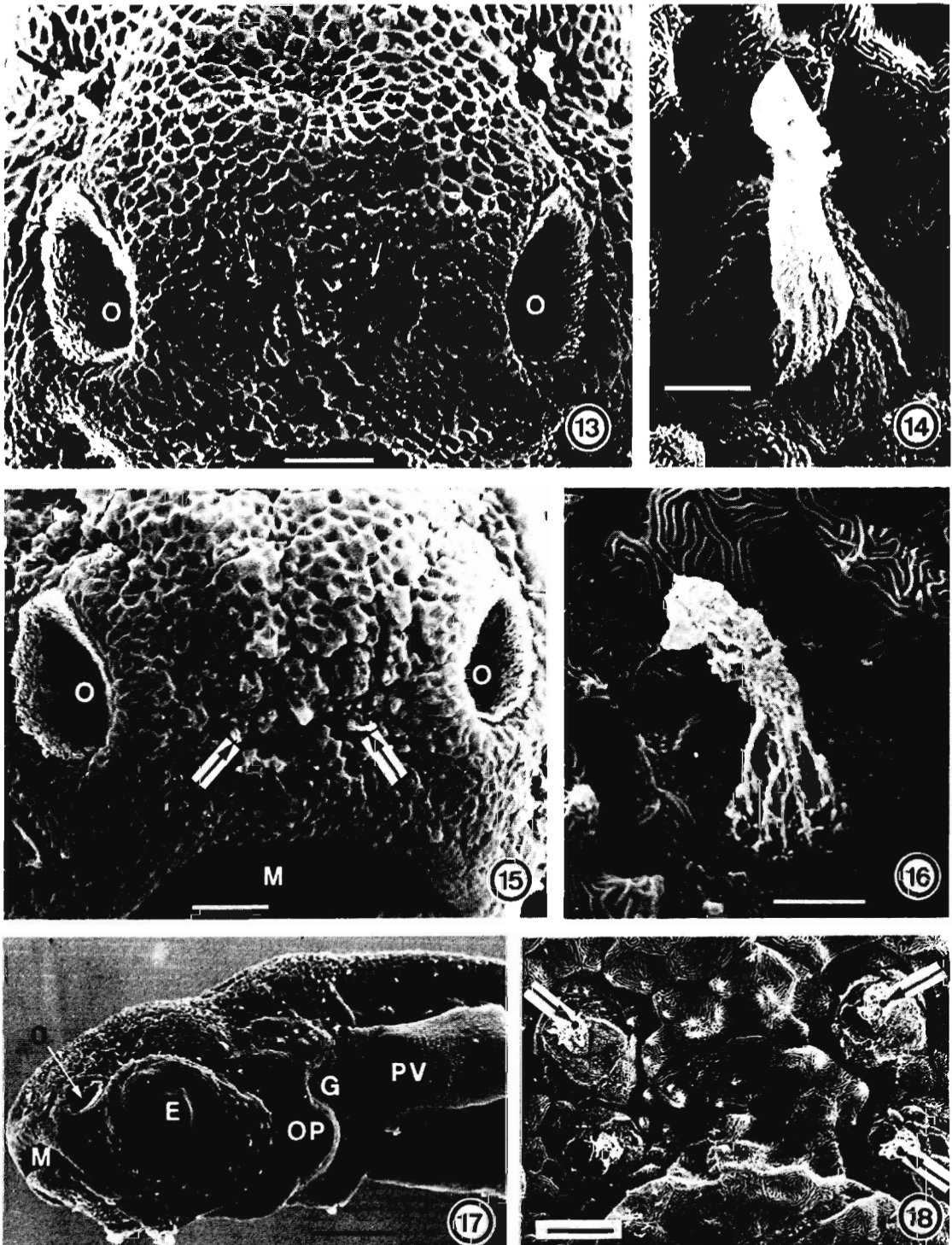


Plate 3. – Figures 13-14: Stage 4 (larva, 88 hours post-insemination; 6.5 mm T.L.); Figures 15-16: Stage 5 (larva, 101 hours post-insemination; ca. 7 mm T.L.); Figures 17-18: Stage 6 (larva, 111 h post-insemination; ca. 7.5 mm T.L.).

13 – Forehead of a larva. The olfactory indentation (O) became larger and deeper. There are well-developed neuromasts (black arrows) in the supraorbital region. White arrows indicate two of the four symmetrically arranged neuromasts between the olfactory pits. bar = 50 μ m. **14** – Higher magnification from one of these neuromasts. There is a prominent cupula. bar = 10 μ m. **15** – Forehead of a free-swimming larva. M = mouth, O = olfactory organ, arrows = neuromasts between the olfactory pits. bar = 50 μ m. **16** – Higher magnification of a neuromast with distinct cilia and cupula. bar = 10 μ m. **17** – Lateral view of a larva with numerous neuromasts distributed on head and body. E = eye, M = mouth, O = olfactory organ, OP = operculum, PV = pectoral fin. bar = 200 μ m. **18** – Symmetrically arranged neuromasts (arrows) between the olfactory pits. bar = 20 μ m.

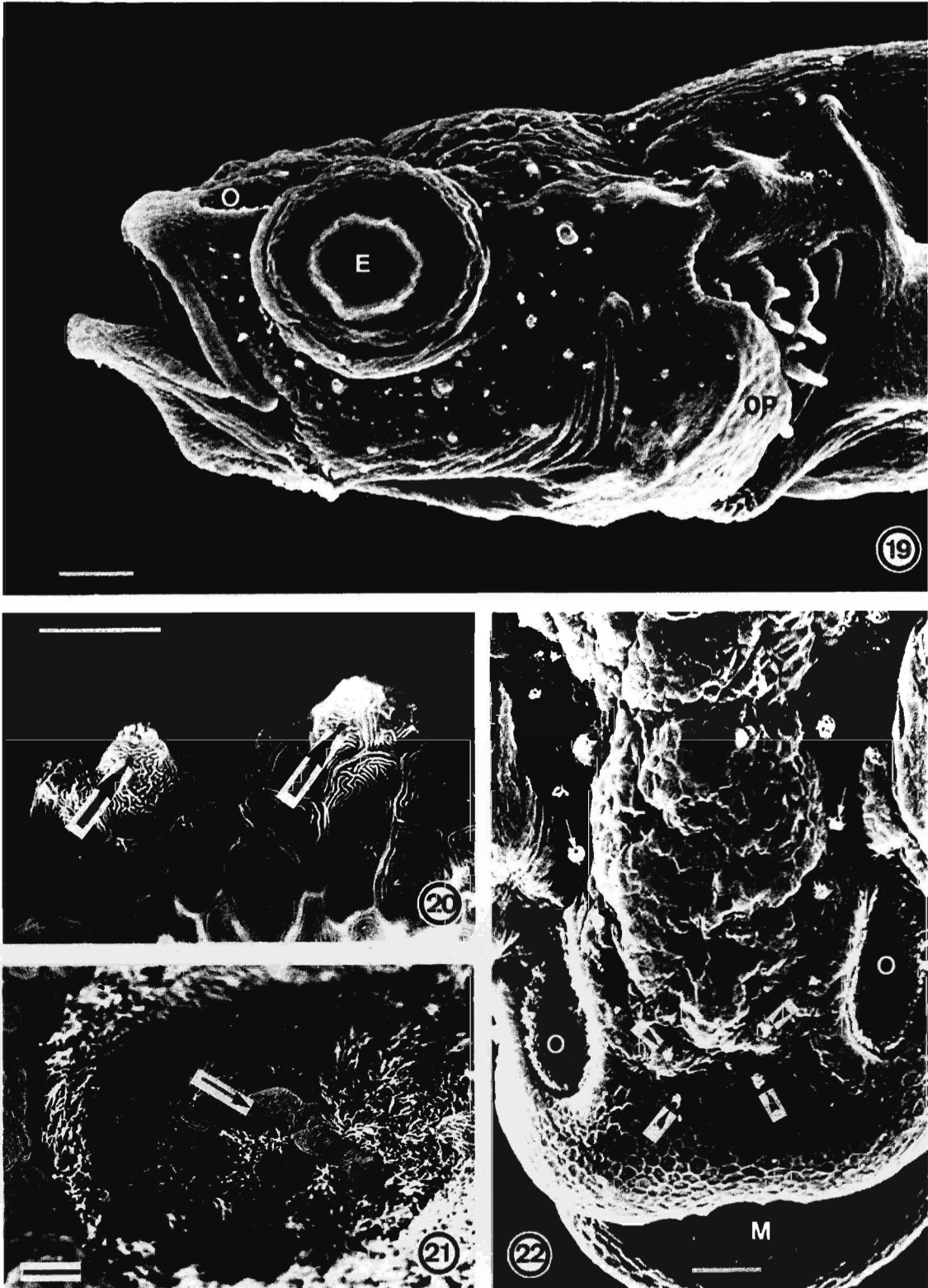


Plate 4. – Figures 19-22: Stage 7 (larva, 210 hours post insemination; ca. 11 mm T.L.).

19 – Lateral view of a feeding larva. Note the numerous neuromasts (arrowheads) on head and body. E = eye, G = gill, O = olfactory organ, OP = operculum. bar = 100 μm . **20** – Two taste-buds (arrows) from the lower lip. bar = 10 μm . **21** – Olfactory organ; note the part of the pit free of cilia (arrow). bar = 10 μm . **22** – Neuromasts arranged in symmetrical patterns (white arrows, black arrowheads). M = mouth, O = olfactory organ. bar = 50 μm .

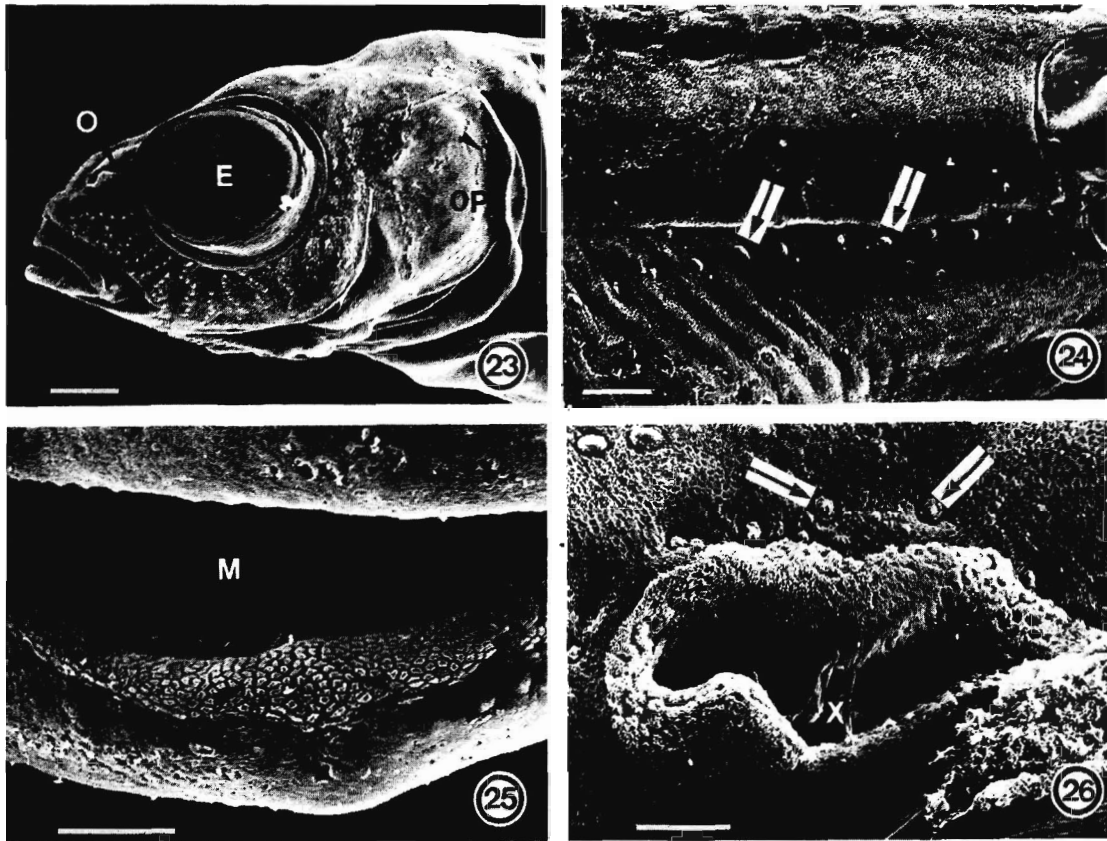


Plate 5. – Figures 23-26: Stage 8 (carp, 13 mm T.L.).

23 – Lateral view of the head. The arrowheads point to the pattern of neuromasts. E = eye, o = olfactory organ, OP = operculum. bar = 500 μ m. **24** – Lateral line on the body with neuromasts (arrows). bar = 250 μ m. **25** – Mouth (M) with lips. Note the keratinized squamous epidermal cells in their final state (arrowheads) on the lower lip. bar = 100 μ m. **26** – Olfactory organ. The nares are nearly separated by connective tissue (x). The arrows point to neuromasts. bar = 100 μ m.

swimming motion, activated by the caudal part of their body. Several repeated attempts, each accompanied by renewed attachment to substratum, may be necessary before the water surface is reached. When the larvae reach their proper buoyancy and swim freely, they start to search for food. Through their well-developed sense of vision, larvae are attracted to mobile feed items in the water. Feed particles are captured less successfully in the first few days, but as they gain experience, the larvae improve their swimming and capture technique.

While the sense of vision is used, food items can be seen from a greater distance: mechanoreceptors, however, allow detection from a shorter distance only (Appelbaum, 1979).

DISCUSSION

On hatching, carp larvae are moderately pigmented, heavier than water, inefficient swimmers, and therefore vulnerable. As their development proceeds, a protective mechanism forces them, for shelter, to seek attachment to a midwater substrata via an adhesion substance secreted from a large gland in

the forehead. Among other things, this mechanism prevents the larvae from becoming easy prey and from suffering oxygen depletion at their natural spawning habitat when sinking to the bottom. Maitland and Campbell (1992) and Steffens (1980) mention that carp larvae on hatching, while sinking, are able to attached themselves by the mouth to leaves of aquatic plants. This contradicts our observations.

After detachment from a substrata, the larvae swim to the surface by negative geotaxis (Bühringer, 1967) and eventually positive phototaxis, to gulp air to fill their gas-bladder. They can now swim freely, faster, avoid predators and actively search for food (Eaton and Nissanov, 1985; Blaxter, 1986; Eaton and DiDomenico, 1986).

Chemoreception

Carp larvae can complete metamorphosis within a few days. Similarly, their olfactory organ advances quickly. The two, small, shallow indentations in front of the eyes, indicating the location of olfactory placods, are visible on the embryo. At this stage, the placods already show the longer mechanocilia

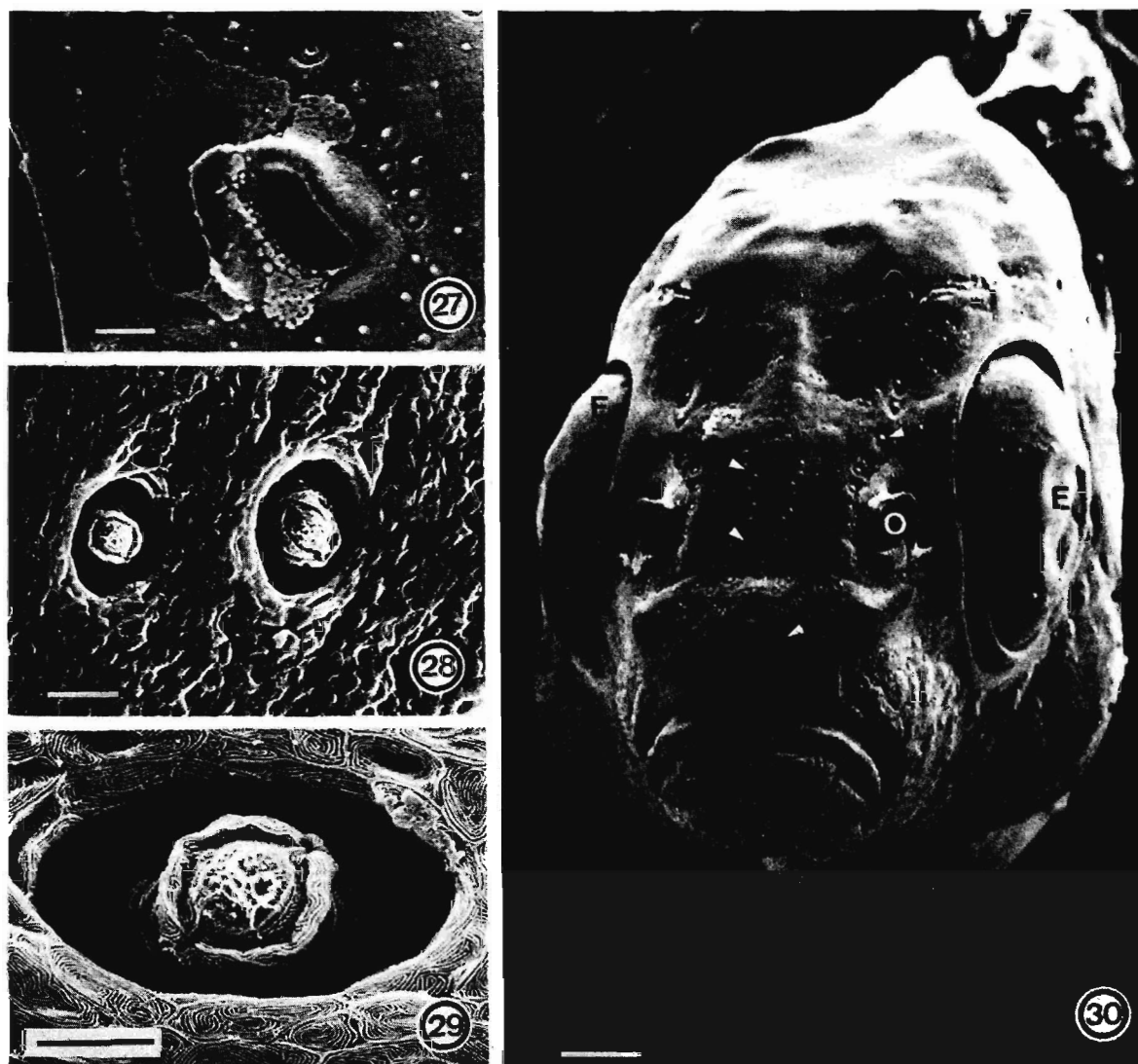


Plate 6. - Figures 27-30: Stage 9 (carp, 25 mm T.L.).

27 - The nares are completely separated in this stage. arrowheads = neuromasts. bar = 100 μm . 28 - Two sunken neuromasts. bar = 50 μm . 29 - Higher magnification of a neuromast. bar = 10 μm . 30 - Front view of the head showing a symmetric neuromast pattern (arrowheads). E = eye, O = olfactory organ. bar = 500 μm .

responsible for active motion in the olfactory pit, and the shorter sensory cilia for perceiving odour stimulation (Iwai, 1980). These cilia were also found in other fish upon hatching (Harder, 1975; Galman and Avtalion, 1989; O'Connell, 1981; Werner and Lannoo, 1994). The indentations undergo a rapid deepening and widening, simultaneously becoming covered with the above-mentioned cilia. Each indentation develops further into a tunnel-like chamber which gradually approaches its external "figure-of-eight" shape, forming, after metamorphosis, the inlet and outlet nostrils. During the carp larval stage, the nervous olfactory is already present (Appelbaum, 1981). The presence of such olfactory features indicates that although the olfactory organ, at this stage, has not attained its final configuration, it can perceive

odour stimulation. O'Connell (1981) demonstrated that olfactory receptor cells in anchovy larvae (*Engraulis mordax*) are connected to the brain and suggested the larvae can probably recognize odour stimuli.

No taste-buds were found in the oro-pharyngeal cavity of one-day-old cyprinid *Tribolodon hakonensis* (Komada, 1994). Iwai (1980) reported that in several marine teleosts, taste-buds had not been differentiated within the first ten days of hatching.

No chemotaxis was found in newly hatched carp larvae, but at a later stage, when they swim freely, they react chemotactically (Bühninger, 1967). This initially weak reaction becomes stronger and more obvious in the course of their development. Carp larvae respond to taste substances by touch with the front of their mouth (Appelbaum, 1980). Caprio (1988) and Kiyohara *et al.*

(1985) reported that taste-buds respond to chemicals and tactile stimuli, allowing them to combine touch and taste.

Insufficient investigation leaves room for speculation regarding the use by carp larvae of their chemoreceptors for the search for, detection, location and ingestion of food items. Although research has shown clearly that carp larvae, at some point, respond chemotactically, studies have not yet revealed sufficient evidence that they utilize their chemoreceptors for feeding. Nevertheless, the fact that carp larvae, in the absence of light, do, to some extent, ingest non-motile food items (Appelbaum, 1976), indicates that chemoreception is, in fact, used. It is unclear whether olfaction or taste, or both, lead to ingestion in the absence of vision. Iwai (1980) found increased activity in red sea bream larvae when contacted with juice of clams. Tanaka *et al.* (1991) suggested that newly hatched red sea bream are capable of detecting food by olfaction. Knutsen (1992) found chemosensory reaction at an early larval stage in Dover sole (*Solea solea*) and turbot (*Scophthalmus maximus*), and concluded that the chemical stimuli have an effect on the behaviour of turbot and sole larvae at the start of exogenous feeding. While in larger fish olfactory deprivation via disconnection of the nervous olfactorious or blockage of the olfaction pits has been undertaken and the resultant behaviour observed, (Goz, 1941; Bardach, 1967; Atema, 1971; Essler and Kotrschal, 1994; Dempsey, 1978) this is technically not yet practicable in larval fish.

Mechanoreception

Before hatching, small numbers of cupula-free neuromasts were detected on the head of the carp embryo. The lack of cupula at this stage may be a result of the preliminaries for the SEM observation. However, in later stages cupula were observed on specimens prepared in the same way. Moreover, a specific technique has been developed for removal of cupula (Mukai and Kobayashi, 1995). All this suggests that the neuromasts may not be functioning at the embryo stage. Iwai (1980) reported that, in general, cupula develop quickly on naked neuromasts of newly hatched larvae of freshwater fish. The number of neuromasts in carp increases rapidly throughout the larval stage towards metamorphosis, their coverage gradually spreading from the head to the trunk. During larval development, the neuromasts attain their mature, functional form, with a prominent cupula. The question may arise as to whether or not there is a need for functional neuromasts immediately after hatching when larvae are attached to substratum and therefore in limited motion. The attachment to substratum is achieved by positive thigmotaxis, requiring a sensory apparatus allowing the larvae to approach, touch and attach themselves to a substratum. Possibly, the few neuromasts found on the forehead of the hatching larvae act as an apparatus by which they choose,

approach, and then touch a substratum. Once the contact has been established, adhesion is activated. This is clear as larvae do not react phototactically during the first day after hatching (Bühninger, 1967).

We assume that the precursors of the lateral line at the earliest larval stage are the four symmetrically arranged neuromasts on the forehead, seen repeatedly in subsequent stages. The initial formation of the lateral-line canals which eventually hide the neuromasts is already detectable in the latter larval stages. In most teleosts, the lateral-line canals and organs typically develop a few days after hatching, the exact timing being species-dependent. It appears, therefore, that in teleosts, the mechanoreceptors of the lateral system are functional at hatching or shortly thereafter (Cahn *et al.*, 1968; Blaxter, 1986).

The basic unit of the mechanosensitive lateral-line, the neuromast, consists of pear-shaped sensory hair cells, supporting cells and mantle cells which are sited above the basement membrane in the epidermis. Single neuromasts are distributed in a definite arrangement on the head and trunk of teleost fishes. These "free organs" or "superficial neuromasts", are often found at the bottom of a shallow pit or groove in the skin of many bony fishes (Bleckmann, 1993; Noakes and Godin, 1988).

The larva's use of neuromasts when searching for food can be strongly supported by a study using infrared light (Appelbaum, 1976), which showed that in the absence of light, carp larvae react to motile food items and also to nearby, artificially created, water motion. Mukai and Kobayashi (1995) reported that seven-day-old *Gnathopogon elongatus* larvae would feed on *Artemia* in complete darkness. Appelbaum *et al.* (1995) have shown that Lingcod larvae feed and grow on *Artemia* in permanent darkness. Free neuromasts play an important role in the sensory awareness of teleost larvae. If a probe approaches a larva, it will respond by evasive swimming. Experiments show that the observed responses are partially mediated by the lateral-line, rather than by inner ear or touch receptors (Blaxter and Fuiman, 1989; Bleckmann, 1993).

Feeding pattern

A combination of taste and olfaction, with or without vision, helps the carp larvae not only in food detection but is the primary sense in the process of either ingestion or rejection. Other criteria, such as size and texture of the item, affect this process. When the sense of vision is utilized for food detection, the larvae, as typically planktonic feeders, swim mainly in the mid-water searching for appropriate food items. In the absence of vision (loss of sight, darkness), the larvae tend to remain in contact with substratum, possibly to locate food more efficiently. This is achieved by swimming along the surface in a grazing motion, at a sharp angle, with the forehead pointing towards the substratum. This facilitates the

detection and ingestion of motile as well as non-motile particles. Motile particles can stimulate the mechanoreceptors from a relatively short distance, ca. 2-3 mm, (Appelbaum, 1976). Non-motile particles are therefore sensed through the chemoreceptors.

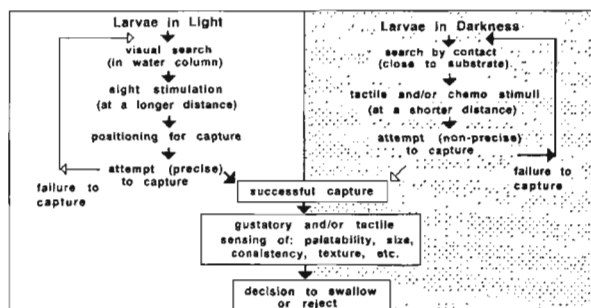
As development proceeds, the larvae rapidly gain "experience" – they have greater success in catching food items and feeding becomes more efficient. With practice, feeding preferences and specializations develop (Dill, 1983; Ringler, 1983). Under optimal water conditions and with sufficient appropriate food, carp larvae develop rapidly and can gain about 1.0 mm in length daily. In such an environment, metamorphosis can be completed within a few days from the time of first feeding. After metamorphosis, the young carp fish gradually alter their feeding behaviour; they slowly change from a typical planktonic carnivorous feeder to a more benthic-omnivorous feeder.

At this stage, the mechanoreceptors are well spread over the body, the lateral-line system has developed and taste-buds have become more numerous. The olfactory organ has undergone a rapid change during which the olfactory pits have elongated, and the central sections of the two longest edges have gradually joined, creating an epidermal bridge, forming the inlet and outlet nostrils on each side.

The altered feeding pattern of carp after metamorphosis is also reflected in the development sequence of the sense organs involved in feeding behaviour. Vision is dominant in the search and capture of food at the carp larval stage. Light stimulates and enhances feeding and carp larvae feed effectively in light. Under reduced light or in darkness, feeding is much less efficient (Appelbaum, 1979) and the

chemo- and mechanoreceptors remain supplementary and complimentary. After metamorphosis, the fish gradually becomes a more benthic feeder, and feeding occurs at the bottom, where visibility is limited. The chemo- and mechanoreceptors now take the primary position, necessitating a well-developed apparatus, and vision becomes secondary. The increase in number of free neuromasts, the rapid development of the lateral-line system and of the olfactory organ, indicate the ability of these organs to take a dominant position in searching for and location of food. Observations indicate that without vision, carp larvae will possibly feed only when they are in close contact with a high density of food items, otherwise they will starve to death, but metamorphosed carp are able to feed successfully and develop without vision (Appelbaum, 1979). Based on our observations, we suggest a pattern of feeding behaviour in carp larvae under light and in darkness (Table 1).

Table 1. – The pattern of feeding behaviour in carp larvae (*Cyprinus carpio*) in light and darkness (frequent →; less frequent ⇨).



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