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Development of Organ Systems in the Northern Anchovy, *Engraulis mordax*, and Other Teleosts[1]

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SYNOPSIS. Certain aspects of development that are indicative of changing functional and ecological capabilities are reviewed for six different organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. The six organ systems are the integument, the lateral line system, the eye, the digestive tract, the gas bladder, and the trunk musculature. The integument develops gradually but also has transient specialized cells during the larval period. The lateral line system is functional at hatching and then elaborates by recruitment proportional to growth during the larval period. The eyes are capable of photopic binocular vision when feeding starts, and later gradually develop a scotopic system. The digestive tract develops a capacity for protein digestion and filtering during the mid and late larval period. The gas bladder gradually develops an expansion capability by muscle differentiation after initial inflation. The trunk musculature differentiates and recruits two fiber types that gradually supercede the embryonic musculature during the larval period. Thus much of the development of organs in the anchovy after hatching or after feeding starts can be characterized as initial differentiation and then continued recruitment of specialized cell arrays. Behavior patterns appear to develop in conjunction with such recruitments. This may apply to fishes generally, but pattern and tempo of development must differ among species. Brief comparison of the anchovy and the Pacific mackerel, which has a more rapid and direct development, suggests that some of the differences in the two types of larvae relate to the marked difference in feeding modes of the adult stages.

INTRODUCTION

In teleost fishes that hatch from pelagic eggs in the sea most organ systems originate in the late embryonic period or the larval yolk sac stage, and become functional by the end of this stage. The yolk sac stage lasts for a few days to a week, depending on temperature, and when yolk is gone the larvae must start feeding. As they grow during the ensuing larval period, nutritional demand increases continually, and feeding habits, locomotor patterns and other ecological characteristics change. The maturation of organ systems that occurs over the larval period must involve capacity and function changes that support the changing ecology of the larva.

Most comprehensive studies of teleost development today are concerned with external aspects—morphometrics, meristics, pigmentation—for purposes of stage and species identification. Such information, though usually compiled for individual species (Watanabe, 1970; Louw and O'Toole, 1977; Doyle, 1977), also appears in massive regional surveys, such as the six volume "Development of fishes of the mid-Atlantic Bight" (Jones *et al.*, 1978). These data are crucial in fisheries, oceanographic, and environmental investigations, but usually contain only limited information on development of viscera and sensory organs. Other comprehensive studies of larvae are undertaken to compile baseline information for experimental work (Ballard, 1973), to extend knowledge of exotic life histories (Hulet, 1978) or to characterize development for taxonomic assemblages (Moser and Ahlstrom, 1970), and these often contain more information on internal aspects of development. However, there are also many studies undertaken to describe the development of particular organ systems in teleosts, usually to delineate the processes of differentiation involved, or to estimate functional and ecological parameters. In this paper I will review certain aspects of development in each of six organ systems, and their ecological implications, primarily as they occur in the northern anchovy, *Engraulis mordax*. Most

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of the information on the anchovy was derived from study of serial sections of specimens reared at 16–17°C in the laboratory of the Southwest Fisheries Center, La Jolla, California.

TEMPERATURE AND GROWTH

Temperature can effect growth rate and hence the age-length relationship markedly in fish. The growth rate for northern anchovy reared at 22°C was about 1.75 times that of larvae reared at 17°C (Kramer and Zweifel, 1970), producing an average length of 13.3 mm at 17 days as compared to 9.5 mm at the lower temperature. Doyle (1977), in constructing a morphological staging system for *Clupea harengus*, estimated that time to metamorphosis was 153 days at sea temperatures (7–12°C) and 121 days at laboratory temperatures that were 1 to 3°C higher. Hayes *et al.* (1953) suggested that temperature or other factors could differentially effect the rate of development of different organs in *Salmo salar*, but Ballard (1973) found that such irregularities were generally minor.

In teleosts the variation in length for larvae of the same age usually increases with age. In anchovy larvae the coefficient of variation (SD/x·100) was about 5% shortly after hatching, and increased to 15–20% by age 20 days (Kramer and Zweifel, 1970; Hunter, 1976). Whenever I examined such samples histologically, the extent of organ development varied with length rather than age.

Events in organ development of the anchovy are expressed in this paper in terms of standard length. The larvae I studied were reared at 16–17°C. At 16°C anchovy larvae hatch at 2.9 mm, reach 4 mm at three and a half days, 10 mm at 16.4 days, and 20 mm at 33 days (Hunter, 1976).

THE YOLK SAC PERIOD

At hatching the anchovy has a large yolk mass and pulsating heart, functional trunk musculature, lateral line neuromasts that are probably functional, and olfactory organs that may be functional. Most other organs are present as rudiments or appear and differentiate to a functional state by the time yolk is gone and feeding begins (4 mm). All systems increase greatly in complexity during the remainder of the relatively long larval period. Metamorphosis of the anchovy is considered to be complete by 35 mm SL when much of the body is scaled and digestive tract torsion is complete (Hunter, 1976). I will comment here on vitelline circulation, olfactory organs and Mauthner neurons before going on to descriptions of the integument, the lateral line system, the eye, the digestive tract, the gas bladder, and the trunk musculature.

According to Soin (1968) the vitelline or yolk sac circulation is developed poorly or not at all in Clupeiformes and many other pelagophilic teleost larvae because they do not need it as a specialized mechanism of respiration in oxygen rich waters. He implied that yolk absorption is accomplished by a different route. However, the entire yolk surface is a syncytial periblast which undoubtedly processes and delivers yolk to the circulatory fluid (Bachop and Schwartz, 1974). Al-Adhami and Kunz (1977) observed that while the only vessels on the yolk in *Brachydanio rerio* are the ducts of Cuvier, these fan out over the whole anterior part of the yolk sac so that blood cells are moving close to the yolk syncytium as well as the yolk sac ectoderm. In the anchovy the ducts of Cuvier are obvious over the front of the yolk mass and a subintestinal vitelline vein does attenuate rostrad on the posterior ventral surface of the yolk. My impression is that there is a diffuse movement of plasma over the yolk syncytium into the ducts of Cuvier. Capillaries are probably absent because the blood does not contain cells that need to be channeled. Though occasionally noticed in small numbers by day 7 or 8, erythrocytes were not consistently present until about day 14 or 15 when the larvae were approaching 10 mm SL.

The two olfactory primordia are small antero-ventral-facing ectodermal plaques between the eyes and the forebrain when the anchovy hatches. Each has a 20 μm depression on the free surface where the cells have a sensory epithelial organization (distal portions slenderized and nuclei located basally). Moreover, there are indications of cilia on the pit surface and a

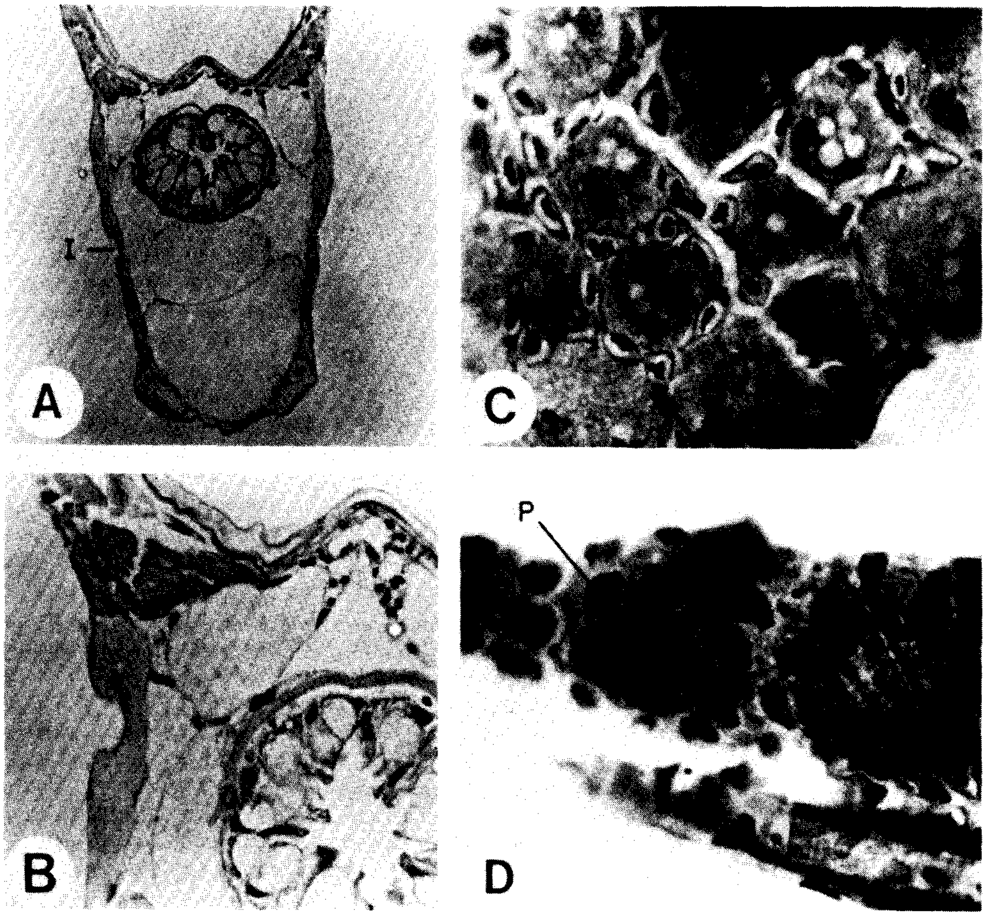

FIG. 1. Transient features of the epidermis of the anchovy larva. A. Cross-section of a 7 mm larva at the level of the esophagus. The lateral walls of the coelom are composed of large "chloride cells." One cell shows a central pit (I) indicating secretion to the exterior. ×100. B. Closer view of another cell with an excretory pit. ×630. C. Tangential section of the body cavity wall of a 14 mm larva. The chloride cells contain large vesicles, and the Malpighian cells surrounding the chloride cells are starting to proliferate. ×630. D. Sagittal view of the body surface of an 8 mm larva showing integumentary plate cells (P) that overlie the trunk musculature. ×400.

neuropil bridge extends from the olfactory capsule to the forebrain. In the cutthroat trout (*Salmo clarki*), which hatches at 35 days post fertilization, some axons extend from the olfactory epithelium to the brain at 20 days and recognizable cilia occur at 27 days, but cilia are not abundant until 40 days post-fertilization, or 5 days after hatching (Jahn, 1972). Jahn (1972) concluded that the cutthroat trout was probably capable of recognizing olfactory stimuli shortly after hatching. Though the anchovy has a much shorter incubation and yolk sac period, the probable existence of some cilia and the connection to the brain suggest that the olfactory system may function shortly after hatching. By 4 mm SL, when feeding begins, the olfactory plaques have shifted to a more dorsal position and enlarged slightly with some rostrad elongation.

I first found Mauthner neurons in anchovy larvae about 1 day after hatching. Kimmel (1972) observed that Mauthner

TABLE 1. *Summary of the development of the integument of the northern anchovy.**

Standard length (mm)	Observation
3.5	Epithelial plate cells differentiate Epithelial chloride cells differentiate
9.0	Epidermis starts thickening
10	Chloride cells start separating Dermis developing on head
17	Epithelial plate cells sloughed Goblet cells appearing
21	Chloride cells widely scattered
28	Scale development starts

* See text for details.

neurons (which mediate the startle response) are sometimes visible after 1 day of development in fish larvae. He concluded that the system is probably not functional until the fourth day of development because there is no well defined startle response over the next few days while the axons are extending towards the caudal region. Kimmel *et al.* (1978) showed that in the zebra fish the Mauthner cell "birthday," probably the earliest neuron birthday in the hindbrain, occurred during the late gastrula stage. Gideiri (1966) found Mauthner fibers extending to the tail at 56% of embryonic (pre-hatching) life in several species with long incubation periods.

INTEGUMENT

The development of the integument in the northern anchovy (Table 1) conforms in general with that of the plaice, *Pleuronectes platessa* L. (Roberts *et al.*, 1973) and with that of teleosts as a group (Bullock and Roberts, 1975). In newly hatched larvae the epithelial epidermis is two cells thick and subtended by gel-filled dermal spaces (including finfold spaces) over much of the trunk region. In the plaice there are some large "chloride cells" and a few mucous cells at this stage.

In the anchovy chloride cells are not found at hatching but are present by 3.5 mm SL. As yolk recedes, chloride cells differentiate over much of the wall of the pericardio-coelomic cavity (Fig. 1A). Occasional cells show a central pit, indicative of secretion to the exterior (Fig. 1B). Though the chloride cells are broad and contiguous, small Malpighian cells are present in the interstices among them from an early period. Beyond 10 mm SL the Malpighian cells start to proliferate (Fig. 1C) and the chloride cells gradually separate. By 20 mm SL the chloride cells are widely scattered and perhaps degenerating. The epidermis is thickening over the entire body at this time. The dermis starts to thicken in the head region at 11 or 12 mm SL, but remains thin on the trunk.

In many specimens the chloride cells contained a central cluster of clear vesicles (Fig. 1C). These may bear some relation to the surface pits observed in other specimens. Chloride cells in the skin of the larval puffer (*Fugus niphobles*) were often found to contain vacuoles filled with an amorphous substance that was released at the free apical surface of the cells (Iwai, 1969*a*).

Though chloride cells were not found in the herring (*Clupea harengus*) (Jones *et al.*, 1966), they were found in the Pacific sardine (*Sardinops caerulea*) (Lasker and Threadgold, 1968), where ultrastructural changes under osmotic stress and other factors indicated that these cells mediated osmoregulation in the developmental period preceding gill differentiation. Roberts *et al.* (1973) cautioned that it was not yet clear if integumentary cells of this kind found in the plaice and the sardine performed the same task as chloride cells found in the gills of mature stages of many fish. However, Bullock and Roberts (1975), in a review of the development of teleost skin, noted that for both species salinity stress did change the chloride cell volume without affecting the ordinary Malpighian cells.

Another transient feature of the epidermis of the anchovy larva is the presence of dense hyaline plates in the bases of the outer layer of cells. Such structures were reported in the Pacific sardine (Lasker and Threadgold, 1968) and the herring (Jones *et al.*, 1966). In the herring they were found in regions of the head, the buccal cavity, the yolk sac and the tail, and were believed to be either support structures or barriers to diffusion. In the anchovy all outer layer cells of the epithelium contain these plates over the trunk musculature (Fig. 1D). The plates are eosinophilic, and are detectable though not prominent one day after hatching. They grow rapidly and soon occupy most of the basal area of the cell. The plate cells extend onto part of the head and on the trunk they extend down to the junction with the wall of the pericardio-coelomic cavity. They overlap the upper margin of the chloride cell tissue only slightly. They extend onto the bases of the median finfold, but are entirely lacking over most of the finfold, where the nucleus is the only prominent structure within the epithelial cells. The plates on the bases of the finfolds soon move down against the musculature, as the muscle mass enlarges and the finfold narrows. These plate cells remain unchanged in appearance, except for enlargement, until the larva is 16 or 17 mm SL. By this time the epithelium has increased to five or six squamous layers and has shed the outermost cell layer containing the plates. The structural evidence in the anchovy—presence over the musculature, absence over the chloride cell tissue, and eventual disappearance when development of functional gills and a thickened integument are well along—indicates that the plates constitute a diffusion and an osmotic barrier.

THE LATERAL LINE SYSTEM

Most teleosts hatch with a series of latero-sensory neuromasts on the head and trunk that are functional or very close to being functional. The goby (*Tridentiger trigonocephalus*) has three pairs on the head and five on the trunk, all with gelatinous cupolae, when it hatches at 2.6 mm on day 7 (Iwai, 1963). The Japanese medaka (*Oryzias latipes*) has 8 pairs of neuromasts with cupolae just starting to bud at hatching, but the cupolae are well developed 20 hr later (Iwai, 1964). The newly hatched pilchard (*Sardina pilchardus*) has neuromasts with prominent cupolae at least on the trunk (Blaxter, 1969). Meyer-Rochow (1972) did not find cupolae on neuromasts of larvae of *Cataetyx memorabilis* but concluded that this was an artifact of fixation and that the organs probably were functional because they were innervated. Cahn *et al.* (1968), using silver staining techniques, concluded that neuromasts of *Menidia* were not innervated until the larvae, which hatch at 4 mm, were 7 mm in length and tentative schooling activity was starting.

At hatching the anchovy has one row of neuromasts along each side of the trunk and three or four pairs on the head, and all have cupolae (Fig. 2). Each row of trunk neuromasts is closely subtended by a lateralis nerve that extends back between the musculature and the epidermis from the posterior tip of the post-otic vagus ganglion (Fig. 3). A slender nerve root from the anterior tip of the ganglion penetrates the floor of the hindbrain. There is also a pre-otic ganglion on each side, and presumably these provide innervation for the head neuromasts.

After hatching, the neuromasts on the head increase in number and in diameter more or less in proportion to standard length. At 33 mm SL there are almost 50 pairs of organs on the head, and they are about 150 μm in diameter, as compared to 25 μm at hatching. Canal formation starts with development of a lateral recess in the temporal region at 18–20 mm SL, as in the herring (Allen *et al.*, 1976). The various branches gradually extend over the head from the recess, enclosing the developing neuromasts. During and following the last stages of canal formation, a new set of neuromasts, small surface pit organs, differentiates on the head. At 33 mm SL there are more than 80 pit organs on each side; they are not much larger than the original neuromasts were on the newly hatched larva.

The neuromasts on the trunk also increase in number as the anchovy larva grows. By 20 mm SL there is a dorsal and a ventral line of organs in addition to the midline. As growth continues these become patches of perhaps as many as four pit organs at each location. In juveniles the pit organs are always located over exposed portions of scales.

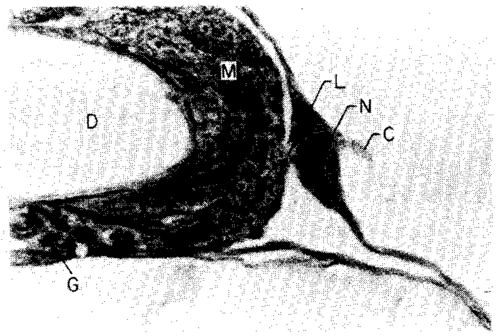

FIG. 2. Cross-section of a newly hatched anchovy larva showing a trunk neuromast (N) with a gelatinous cupola (C) and underlying lateralis nerve (L). The trunk musculature (M), notochord (D) and rudimentary foregut (G) are also visible. ×630.

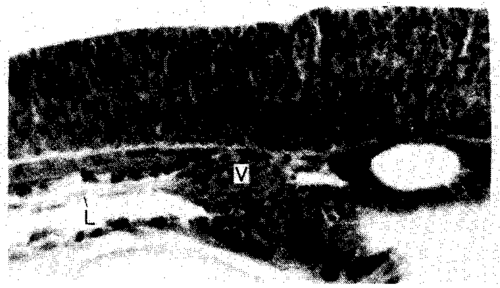

FIG. 3. Sagittal view of the vagus ganglion (V) and lateralis nerve (L) of a newly hatched anchovy larva. The ganglion is behind the otic capsule and below the hindbrain. ×400.

In the Cyprinidae and some other teleosts the neuromasts appearing in the larval and juvenile stages are known to arise differently than the primary neuromasts present at hatching. Disler (1960) observed that the primary neuromasts in the Cyprinidae develop in the embryo from subcutaneous primordia related to the preauditory and postauditory ganglion plaques, whereas the later appearing neuromasts arise *in situ* from the basal layer of the epidermis under the influence of nerve endings. In regard to function, he postulated that the organs enclosed in canals were thus shielded from small local disturbances, which would then only be registered by the surface neuromasts.

THE EYE

Differentiation of the retina will be described elsewhere in this symposium, so I will make just a few observations about the anchovy eye, which are summarized in Table 2.

TABLE 2. *Summary of the development of the eye of the northern anchovy.*

Standard length (mm)	Observation
3.5	Oculomotor muscles differentiated
4.0	Photopic visual system functional
5.0	Area temporalis present
7.0	Lens retractor muscle appears
10.0	Earliest incidence of rod differentiation

The retina of the anchovy is undoubtedly functional when feeding starts at about 4 mm SL. The visual cells are more slender and abundant towards the temporal part of the eye. By 5 mm SL there is a point of maximum visual cell density not far from the ventro-posterior margin of the retina and perhaps 20° below the horizontal meridian, constituting an *area temporalis*. The center point of the *area* is identifiable from the lateral view (Fig. 4) because nuclei of the outer nuclear layer tend to be laterally displaced and slanted towards this point, probably to accommodate the close packing of the slender visual elements. The surface of the eyeball is also slightly peaked at this point, probably to accommodate increased length of the visual elements.

The lens retractor muscle does not appear until 7 mm SL, after which it increases steadily in size. The six oculomotor muscles, on the other hand, are well differentiated with typical teleost insertions around the periphery of the eye by 3.5 mm SL, when feeding activity should be starting. Considering these features, it is reasonable to assume that the early feeding anchovy larva has a well defined axis of maximum visual acuity, and good eye mobility, and therefore can probably exercise an effective binocular vision in aligning itself to close objects. There is probably some depth of focus at the start, and the ability to accommodate to greater distances must increase as the retractor muscle

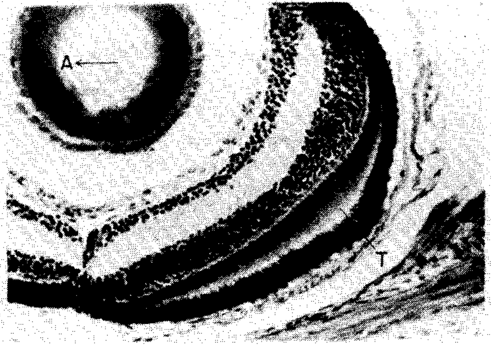

FIG. 4. Sagittal view of the *area temporalis* (T) of the left eye of an 11.6 mm anchovy larva. (A) indicates the anterior direction. ×250.

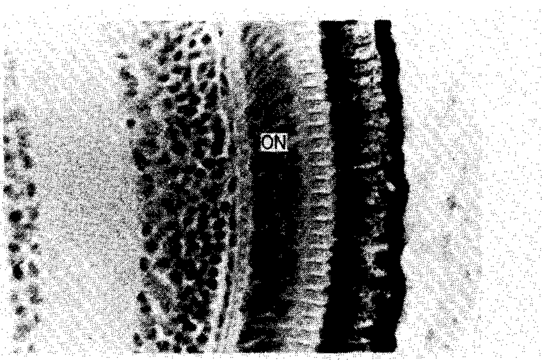

FIG. 5. Cross-section of the retina of a 16 mm anchovy larva with two mitotic figures in the outer nuclear layer (ON). ×630.

grows after 7 mm; this would increase the perceptive field for feeding.

Although the adult anchovy has a well developed duplex retina with abundant rods as well as cones (O'Connell, 1963), the early larva appears to have a simplex retina in which the one class of visual cell is presumed to be cones. The outer nuclear layer does become 2-tiered as the visual elements are first budding, and this could signify early appearance of rods along with cones, but since the broadly overlapping nuclei of the two tiers have the same elongate appearance, it is more likely that they indicate the differentiation or formation of twin cones. Grün (1975) described a double layer of nuclei in the outer nuclear layer of the early stage retina of *Tilapia leucosticta* and identified both rods and cones in electron micrographs of initial visual cell differentiation. In this case, however, the nuclei of each of the two layers were different in character. Functioning rods were not found in the retina of *Nannocara anomala*, another cichlid, until day 16, although free swimming (and vision) starts on day 5 (Wagner, 1974). Rods were first found at 20 mm in the retina of the herring, *Clupea harengus* (Blaxter and Jones, 1967). In the anchovy the outer nuclear layer remains 2-tiered until 10 or 12 mm SL, after which mitotic figures are occasionally found and the layer increases to three and soon to four and more tiers of nuclei, undoubtedly indicating rod recruitment, which is well underway when the larvae are 16 mm in length (Fig. 5).

Thus, while variations in timing exist, rods probably appear sometime later than cones in many teleosts. In the anchovy a continual recruitment of rods occurs for a long period, and there is probably a commensurate increase in visual sensitivity. Such a developmental sequence appears to be adaptive to the changing feeding and behavioral patterns described by Hunter (1972) for the anchovy. When rods start to appear after 10 mm SL, vertical migration is also starting (Hunter and Sanchez, 1976), and larvae are moving into and becoming more active in dimmer light.

THE DIGESTIVE TRACT

As is the case with many marine teleosts, the northern anchovy hatches with a large yolk mass, no mouth, and a rudimentary gut. The gut differentiates to a functional digestive tract by the time yolk is exhausted in a few days, but there is extensive development beyond this point, as outlined in Table 3. While there is no mouth at hatching, there is a spiracle-like opening extending laterally under each otic capsule from the rudimentary pharynx (Fig. 6). This is the hyobranchial cleft, separating the presumptive mandibular and hyoid arches from the presumptive branchial arches. By the time yolk is exhausted the mouth and a simple hyoid suspension have differentiated. The lower jaw has grown to

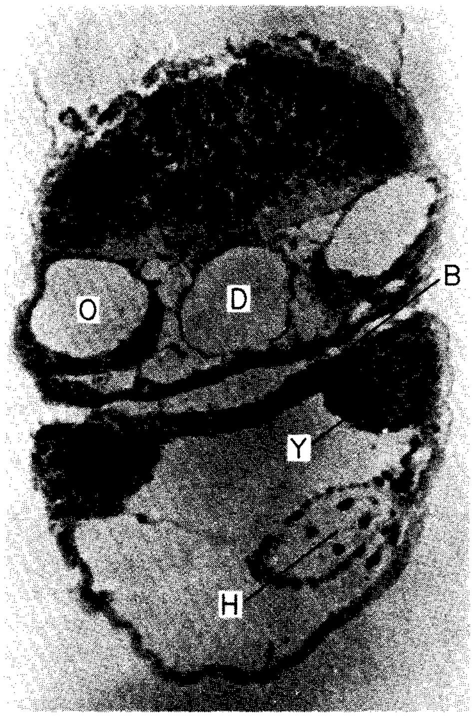

FIG. 6. Cross-section of a recently hatched anchovy larva at the level of the otic vesicles (O) and heart (H) to show the spiracle-like hyobranchial clefts (B) that extend lateral from the rudimentary pharynx at time of hatching. (Y) is an element of the developing hyoid arch and (D) is the notochord. ×250.

almost the length of the snout and there is a jaw joint (mouth corner) where the mandibular cartilage articulates with the hyomandibular above. The hyoid cartilage, still a bar behind the mandible, articulates with a small caudad extension of the hyomandibular. Flüchter (1962) described the junction of the mandible with the hyomandibular in first feeding herring as a narrow, flexible continuation rather than an articulation. The branchial apparatus is also well formed in the anchovy when yolk is exhausted, with three gill clefts open. There are also two upper and two lower tooth capsules at the back of the pharynx, which become functional recurved teeth as feeding starts and undoubtedly guard against reverse movement of material from the esophagus into the buccal cavity. They increase in number during larval growth.

TABLE 3. *Summary of the development of the digestive tract of the northern anchovy.*

Standard length (mm)	Observation
3.0	No mouth; gut rudimentary
3.5	Liver, pancreas differentiated
4.0	Mouth and digestive tract functional
4.5	Four pharyngeal teeth present
15	Upper limbs of branchial arches start differentiating
19	Eight pharyngeal teeth present
20	Upper limbs of branchial arches becoming free
21	Gastric glands, pyloric caecae start differentiating
22	Jaws lengthening
24	Stomach blindsac buds

When feeding starts, the digestive tract proper is composed of a foregut, midgut and hindgut. In the anchovy the foregut is relatively long with the liver and compact pancreas beneath the rear portion. The digestive tract remains straight during the larval period, except for a vertical flexure and constriction denoting the pyloric valve. The midgut is larger in diameter than the foregut. The gas bladder diverticulum appears at top left of the flexed region perhaps two days after hatching. In the larvae of many fishes, such as the Pacific mackerel (*Scomber japonicus*), the anus is much further forward on the body and the foregut is short, but a strong lateral flexure and expansion occurs in the pyloric region as feeding begins.

The midgut mucosa in the anchovy is composed of absorptive cells that are cuboidal or low columnar at best. Ridges are incipient and they develop during the larval period by mitosis of the mucosa cells, which in the anchovy seems to occur late at night when the digestive tract is empty. Mitosis of mucosa cells has been found to occur in certain spatial patterns in the sea lamprey (Youson and Connelly, 1978), and also in *Xenopus* (Marshall and Dixon, 1978). In the anchovy the midgut ridges are transverse, and give the midgut a vertical striated appearance in later larvae. Louw and O'Toole (1977), in the course of describing larval development of *Sardinops ocellata,* comment that this feature is probably responsible for some earlier workers regarding the posterior gut as convoluted.

The hindgut is not easily distinguished from the midgut until feeding starts, at which time each mucosa cell in the hindgut develops a large supra-nuclear eosinophilic inclusion body that appears to have an intimate relation with the nucleus (Fig. 7). Such bodies occur also in the Pacific mackerel and have been reported for other fish larvae, but there is still uncertainty about their role in the digestive process. Iwai (1968, 1969*b*) and Iwai and Tanaka (1968) found such structures in the hindguts of certain freshwater teleosts and suggested that they were indicative of intracellular digestion of proteinaceous food particles engulfed by pinocytosis. It is not known whether pinocytosis occurs in the anchovy, or whether the bodies are proteinaceous. Govoni (1980) found similar bodies in the hindguts of larval *Leiostomus xanthurus,* but questioned their presumed role as a pregastric protein digestive mechanism because they continued to be present after complete stomach differentiation. Gauthier and Landis (1972) considered the role of such structures found in adult *Carassius auratus* to be intracellular (protein) digestion.

In the anchovy major changes in the digestive tract (considered part of metamorphosis) start at about 20 mm SL. Gastric pits appear behind the pneumatic duct origin, the pyloric flexure strengthens and shows a few pyloric caecal buds. Within a few days, as the fish approaches perhaps 24 mm, the stomach blindsac buds from the dorsal wall of the pylorus, and the pylorus begins to bulge forward below to form the cardiac portion of the stomach. Late differentiation of the stomach is common in teleosts, and implies a shift towards ingestion of larger quantities of food in short periods (Reifel and Travill, 1978), and perhaps a shift to a diet heavier in protein. In the plaice, the stomach starts to differentiate at 20 days and peptidic activity increases sharply at about 30 days (Yasunaga, 1972). In *Plecoglossus,* gastric glands start to develop at about 25 mm and pepsin-like activity rises from virtually none to a much higher level by 40 mm than amylase or trypsin activity (Tanaka *et al.,* 1972). Bream (*Acanthopagrus*) has a pattern of digestive enzyme development similar to that of *Plecoglossus,* while the carp (*Cyprinus*) develops trypsin and amylase activity gradually from hatching but shows only insignificant pepsin activity (Kawai and Ikeda, 1973). Bream shifts from smaller zooplankton to larger zooplankton and fish at metamorphosis, while the carp is stomachless as an adult.

FIG. 7. Sagittal view of the hindgut of a 5.6 mm anchovy larva. The large eosinophilic inclusion bodies are in close contact with the basal nuclei. ×630.

In anchovy larvae of about 15 mm changes start in the jaws and branchial apparatus that indicate a change in feeding mode. As Flüchter (1962) noted for the herring larva, the gill arches are almost straight and extend obliquely up and back in the early feeding anchovy. Arches I through IV are composed of small basibranchials and hypobranchials, and long ceratobranchials, which terminate in dense connective tissue below the otic vesicle (Fig. 8). This arrangement means that mouth opening is essentially a lower jaw movement. At about 15 mm SL the upper limbs of the branchial arches begin to condense in the tissue of the palate and they begin to break free by 20 mm. The upper limbs remain relatively short until about 23 mm, when they are clearly differentiated into epibranchials and pharyngiobranchials with some development of rakers and gill septa (both of which had started much earlier on the lower limbs). At this time the

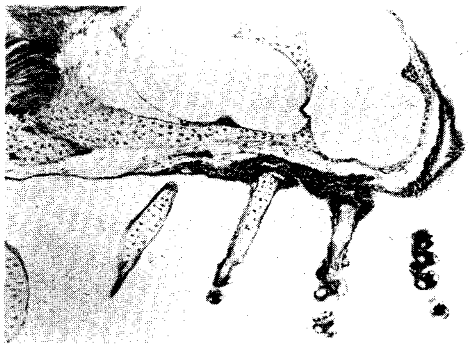

FIG. 8. Sagittal view of branchial arches II and III on left side of an 11.6 mm anchovy. The upper ends of the ceratobranchials join dense connective tissue of the palate below the developing ear. Upper limbs of the arches have not yet differentiated. Some parts of gill filaments with lamellae are visible. ×100.

branchial arches start to lengthen, as do elements of the snout and the upper and lower jaws. This sequence of events (and some changes in the suspensorium) results in a mouth of large and expandable gape involving mobility of upper and lower jaws and branchial elements. It is probably becoming functional as a filter feeding apparatus before the larva reaches 30 mm SL.

THE GAS BLADDER

The gas bladder, an organ unique to teleosts, is one of the few systems that is not present when the anchovy larva starts to feed. It is represented at this time by a bulge in the dorsal wall of the pyloric flexure; it splits the ridge of primordial germ cells as it rises. Within a few days it is a small thick-walled rudiment with a patent lumen and a short pneumatic duct originating from the upper left surface of the pyloric flexure. The clupeoids are the only large group of ocean fishes that have pneumatic ducts as adults (Marshall, 1966), and they are also the only group with a rostral extension of the gas bladder that is in intimate contact with the inner ear. In the anchovy this extension first appears at about 5 mm SL as a slender tubule with a slightly bulbous tip that grows forward from the anterior tip of the rudimentary bladder. It bifurcates when beyond the pectoral girdle and reaches the prootic cartilage at 9 or 10 mm SL. The development of the gas bladder in the northern anchovy is outlined in Table 4.

TABLE 4. *Summary of the development of the gas bladder of the northern anchovy.*

Standard length (mm)	Observation
5	Bladder anlage appears
9	Anterior duct of bladder reaches ear
10	Bladder inflates Musculature of bladder wall starts differentiating
15	Bladder thin walled; highly contractile
28	Anterior bladder chamber differentiates

As the rostral extension approaches the prootic cartilage, the bladder itself has enlarged but is still less than half a millimeter long and smaller in diameter than the digestive tract. The lumen is a narrow horizontal slit and the wall is relatively thick, composed of a pavement epithelium of large cuboidal cells (continuous with the digestive tract mucosa) and a thick, dense layer of transversely aligned mesenchyme or myoblast cells (Fig. 9). This layer is continuous with a thin layer of splanchnic mesenchyme cells that invest the pneumatic duct and pyloric valve region. Both of these layers are part of what will be the tunica interna of the bladder. Schwarz (1971) described a similar layer of mesenchyme cells continuous with the mesenchyme layer of the gut in the bladder wall of the haddock embryo. In anchovy larvae of 10–12 mm the lumen often shows a degree of distension, but the wall does not expand or change in thickness. Beyond this size range the wall changes rapidly in character. The pavement epithelium is thinning and myoblasts become longer and more slender smooth muscle fibers. Bladder walls characterized by myoblasts are on the order of 20–25 μm thick. By 15 or 16 mm SL the musculature is well developed and the walls can be less than 10 μm thick when the bladder is expanded. As the anchovy is approaching 25 mm SL the bladder is about 5 mm long and some-what larger in diameter than the digestive tract when fully inflated.

The growth in length of the bladder is exponential. That is, at 6 mm SL the bladder is 2% of standard length, at 16 mm it is 6%, and at 30 mm about 15%. At about 28 mm SL an anterior chamber develops from the posterior part of the slender rostral extension. This anterior chamber connects to the much larger posterior chamber through a thin sphincter, which must increase in complexity as well as size to achieve the configuration described for the adult (O'Connell, 1955). The cartilaginous sheath of the rostral extension differentiates as the anterior chamber differentiates.

One area of preoccupation with gas bladder development has been the mode and timing of initial inflation, which can have implications for energy conservation and survival *vis á vis* the ability to adjust buoyancy. The salmon and the brook trout probably inflate by gulping air at the surface, and initial inflation can be delayed several days by the presence of strong water currents that would sweep alevins off station (Saunders, 1964). Cichlids, which do not have pneumatic ducts even in the early stages, apparently inflate by internal gas secretion (McEwen, 1940; Doroshev and Cornacchia, 1979). The cichlid, *Tilapia mossambica*, and the striped bass, *Morone saxatilis*, which has a pneumatic duct and possibly inflates by surface gulping, both showed critical periods of time during development, after which normal inflation, if delayed, was impossible (Doroshev and Cornacchia, 1979). The larvae of several clupeoids, including *Engraulis mordax*, have been shown to undergo a daily cycle of bladder inflation and contraction in conjunction with vertical migration (Uotani, 1973; Hunter and Sanchez, 1976). The northern anchovy, *Engraulis mordax*, which starts this pattern at 10 mm SL, evidently cannot accomplish daily inflation without access to the surface, and it appears that inflation may be a mechanism to conserve energy during nighttime non-feeding hours (Hunter and Sanchez, 1976). The differentiation of the bladder musculature, described above, appears to take place in the anchovy during the first days that the bladder inflation-contraction cycle is operating.

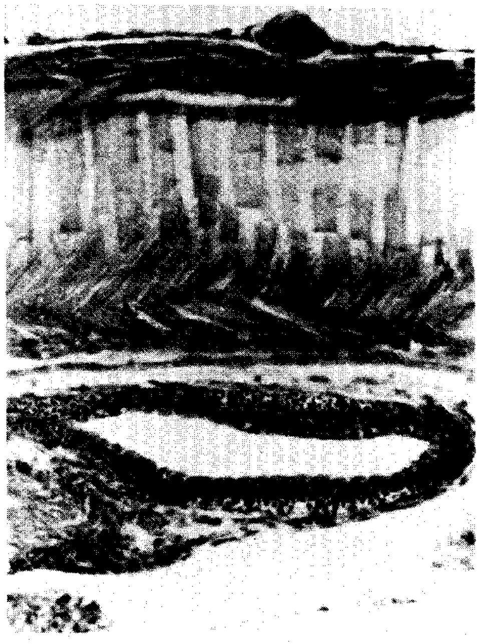

FIG. 9. Sagittal view of the gas bladder of an 8 mm anchovy larva. The bladder wall is still myoblastic but the lumen shows some expansion. The vertical structures above are developing collaginous bands of the notochordal sheath. One lateral line neuromast is visible. ×250.

Uncertainty about the function of the gas vesicles associated with the inner ear in clupeoids continues to generate investigation of this mechanism. While the question of function is usually addressed to the system as it exists in adults, Blaxter and his co-workers (Allen *et al.*, 1976; Blaxter and Denton, 1976; Denton and Blaxter, 1976) considered the function of the system in early as well as mature stages. They found that the prootic bulla (adjacent to the ear) first appeared at 18 mm SL in the herring, started filling with gas at 25 mm, and was always full by 30 mm. They considered that in the adult the gas bladder proper served as a reservoir to maintain gas at a constant volume in the prootic vesicle under changing ambient pressure. This

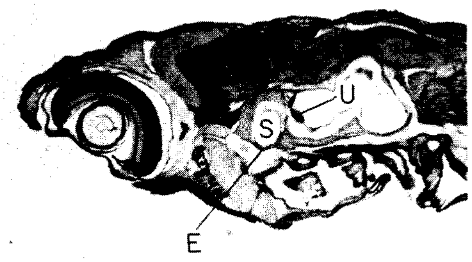

FIG. 10. Sagittal view of a 16 mm anchovy larva showing the gas vesicle (S) in the prootic bulla, which still includes areas of fibroelastic membrane (E). The branches of the macula utriculus (U) are distinguishable but not yet well separated. ×25.

would preclude distortion of an associated resonating membrane that presumably responds to and enhances transient vibrations that are transmitted to a portion of the inner ear. In larvae, before the bulla enclosing the vesicle was rigid, the membrane sustained appreciable distortion under ambient pressure changes, and could be part of a pressure sensing system (in the range 30–40 mm SL).

The system in the anchovy develops essentially as described for the herring. It should be noted, however, that the prootic vesicles tend to inflate at about 12 mm SL when the bladder itself first inflates, but great variation occurs. Some of this variation appears to be associated with the inflation-contraction status of the bladder up to about 25 mm SL. Up to this size the bulla enclosing the vesicle is composed of surfaces of the prootic and certain other cranial cartilages and fibroelastic membranes bridging gaps between them (Fig. 10). At this size intramembranous bone starts to develop in these membranes and also in the area where the edges of the fenestra will project toward the utriculus wall. By 30 mm SL all of these areas are solid bone, more distinctly so than any other elements in the head. Beyond this size, or probably beyond 25 mm SL, the vesicles appear to remain inflated all the time. The bladder may then function primarily as a reservoir to maintain the vesicles in the face of external pressure change as suggested by Allen *et al.* (1976), whereas it appears to function primarily as a buoyancy device in smaller larvae (Hunter and Sanchez, 1976).

One of the most recent observations on the function of the ear-gas bladder connection (Popper and Platt, 1979) indicates that the orientation pattern of hair cell bundles on the divided sensory macula of the utricle is unique among vertebrates and not incompatible with the argument that the (herring) utricle may respond to acoustic stimuli. An important feature of this mechanism is the division of the utricular maculus into three lateral branches or "fingers," with the fenestra of the prootic bulla facing the space between the anterior and medial branches. In regard to development, I have observed in the anchovy that the separation of the utricular maculus into three branches starts at about 12–14 mm SL and is not well defined until 18 or 20 mm SL. The size range over which the macular branches differentiate coincides generally with the range in which inflation of the prootic vesicle is highly variable.

TRUNK MUSCULATURE

The myotomes of fish contain two main types of muscle fibers: "fast" white fibers presumed to be important in burst activity, and "slow" red fibers presumed to be important in slower cruising activity. According to Bone (1978) there is considerable uncertainty about how these two types differentiate and how the two populations change in proportion during growth. In general, it appears that differentiation proceeds from the inner myotome face outward, with deep myoblasts differentiating into white fibers and surface myoblasts later differentiating into superficial red fibers (Waterman, 1969; Nag and Nursall, 1972). Red fibers are generally smaller than white fibers as well as superficial, but small fibers have been found among the white fibers in later developmental phases of several species; in clupeids and gadoids the small fibers appear to be growth stages of the white fibers, but for salmonids it is not yet clear whether they are "slow" fibers or simply growth stages of "fast" white fibers (Bone, 1978).

Development of the musculature of the northern anchovy, which is outlined in Table 5, exhibits some of the variable features mentioned above, but in addition it shows a specialized organization at hatching. There are two layers of fibers aligned obliquely in opposite directions, and interdigitating to form a kind of basketweave configuration (Fig. 11A). These fibers each have a number of axial nuclei and a thin peripheral layer of myofibrils. Presumably they had arisen by fusion of mononucleate myoblasts prior to hatching. This musculature, which is myotomal but thin relative to the large notochord, is probably characteristic of at least the clupeoids. It is obvious, for instance, in newly hatched *Sardina pilchardus* (Blaxter, 1969). By contrast, *Scomber japonicus* has relatively thick musculature at hatching and fibers have a near-horizontal alignment. In the anchovy the oblique fibers, which enlarge as the larva grows, are prominent to about 20 mm SL. They could not be identified in larvae approaching 30 mm, but might still be present against the notochord.

TABLE 5. *Summary of the development of the trunk musculature of the northern anchovy.*

Standard length (mm)	Observation
3	Embryonic oblique muscle fibers only
4	Myotube generation of white fibers starts
6	White fiber mass thickening dorsally and ventrally. Red fibers appear, single superficial layer
10	White fiber mass covers midline of body
12	White fiber mass well above spinal cord
16	Red fibers 2–3 layers thick at midline
20	Red fibers 3–4 layers thick at midline
21	Myosatellite cell proliferation of white fibers starts
23	Myotube generation of white fibers declines
26	Red fibers 7–8 layers deep

The addition of new muscle fibers over the surface of the oblique musculature starts at 3.5–4.0 mm SL. The fascia on the outer surface of the myotomes produces a compact matrix of very small myotubes that contain just a few slender myofibrils. Proliferation starts dorsally and ventrally, filling in against the spinal cord and dermatome as it also extends toward the midline. The fibers enlarge steadily as they are overlaid by new surface additions (Fig. 11B). The myofibrils within them are laminar and radially disposed, and undoubtedly increase in size and number by branching, splitting, and addition of myofilaments centrifugally, as described by Patterson and Goldspink (1976). This myotube musculature finally covers the oblique musculature at the midline at about 12 mm SL. By 20 mm it is moderately thick at the midline and has risen well above the spinal cord dorsally as already indicated; these fibers have a near-horizontal alignment. Surface addition by myotube proliferation declines appreciably beyond 20 mm SL, remaining highest, perhaps, near the lower margin of the muscle mass, which is in the process of extending ventrally in the wall of the body cavity.

As surface addition declines, small muscle fibers appear among the larger ones, noticeable first in the deeper portion of the myotomes. Eventually they are abundant and widespread, and of various diameters (Fig. 11C). They must arise from the large fibers by myosatellite cell differentiation, as has been suggested by others (Greene and Greene, 1913; Bone, 1978; Greer-Walker and Emerson, 1978). All of the above constitute the white muscle mass of the trunk.

The red musculature first arises in the anchovy not long after the myotube addition of white muscle fibers has started. It appears at 6 or 7 mm as a single layer of fibers on the outer face of the myotube-producing membrane. The fibers are aligned horizontally and have the more or less rectangular cross section characteristic of the type in the anchovy (Fig. 11B). They also characteristically have a high myoplasm content with one or two serpentine arrays of well spaced myofibrils. Loose packing of myofibrils and high myoplasm content was noted for red or superficial fibers of the zebra fish (Waterman, 1969) and the cod (Greer-Walker, 1970). The same arrangement occurs in the sound

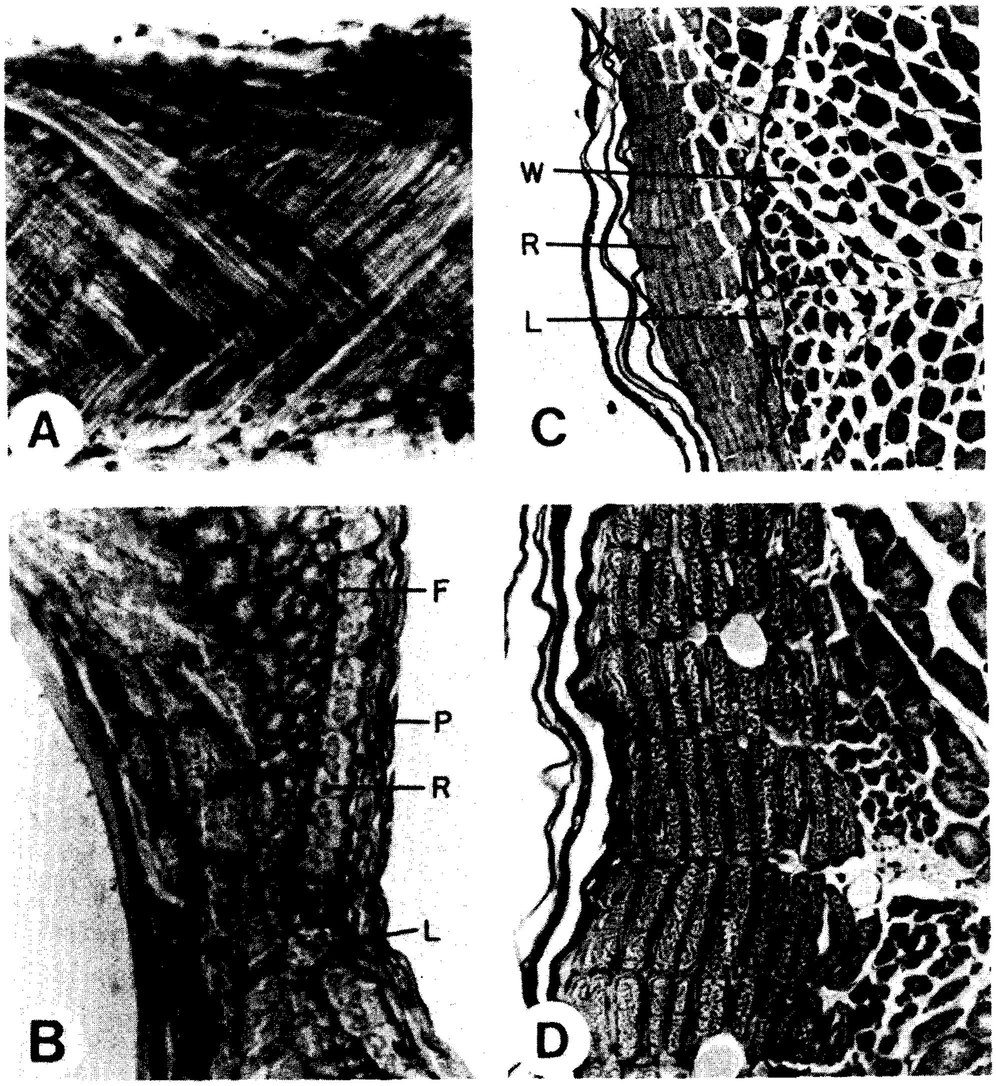

FIG. 11. The trunk musculature of the anchovy larva. A. Sagittal, tangential section of a 7 mm larva showing the oblique muscle layers that are dominant in the early weeks. ×100. B. Cross-section of the trunk musculature of a 14 mm anchovy above the midline. The large fibers close to the notochord are the original oblique fibers. White fibers are added by myotube differentiation at the fascia (F) and increase in diameter as more new fibers are added at the surface. The light band outside the fascia is a single layer of red fibers (R) above and below the lateralis nerve (L). The epidermis has about four layers of squamous cells, the outer layer containing hyaline plates (P). ×400. C. Cross-section of a 33 mm larva, showing many smaller white fibers (W) that arise by satellite cell differentiation from the larger fibers. The zone of red fibers (R) laterad of the lateralis nerve (L) is multilayered. ×25. D. Cross-section of the red muscle zone of a 31 mm larva. Close pairing of some fibers indicates that red fibers proliferate by equal division. ×250.

muscle of the cod, where it is presumed to promote a high rate of metabolism and fast twitch activity (Odense *et al.*, 1978).

The red muscle tissue remains a single layer of growing fibers interrupted only by the lateralis nerve at the midline until the anchovy reaches a length of about 14 mm, when a second layer may appear, and when a small zone of small nondescript fibers becomes evident around the lateralis nerve. This is the intermediate zone as described by many workers, and it is the only group that cannot readily be classified as either the white or the red type. When a third layer of red fibers appears at 18–21 mm SL, one or two of the red fiber layers usually cover the lateralis nerve. By 30 mm there are 8–10 layers outside the lateralis nerve, and the typical triangular cross section of the midline band of red muscle is evident.

The manner of red fiber proliferation is not clear. The first layer quickly covers the surface of the myotome when it appears and possibly is produced by myotube generation from the outer face of the fascia covering the myotome. Additional layers may arise in this way, but the "intermediate" fibers around the lateralis nerve may also be involved. However, frequent close pairing among the red fibers indicates that they may proliferate by equal vertical division (Fig. 11D).

The different phases of muscle development are distinct and occur in sequence, although with broad overlap. Presumably each phase has some adaptive role in the growth and changing behavior of the fish. The oblique musculature that is dominant for the first few weeks possibly confers some advantage relating to the elongate body form and the sustained S-shaped posture that precedes food strikes (Hunter, 1972). The second phase of muscle development, myotube generation at the surface, probably serves in the anchovy to gradually superimpose the fusiform body shape of the juvenile on the elongate body shape of the larva. The myosatellite phase, on the other hand, probably serves to further enlarge the muscle mass without appreciably altering body or myomere form. The superficial red musculature, though it originates early, does not show any appreciable thickening until the myotube addition of white musculature has almost run its course at 20 mm SL. Schooling behavior is in a formative stage at 20 mm, and continues to develop as the fish grows beyond this (van Olst and Hunter, 1970).

CONCLUDING REMARKS: ANCHOVY AND MACKEREL

The features of development described here demonstrate that in the anchovy most organ systems are functional after only a brief, early rudimentary period, and then increase in complexity and size throughout the larval period, expanding functional capabilities and ecological interaction together. This sometimes includes appearance and disappearance of transient structures, but more often relates to the differentiation and gradual recruitment of new elements in a system. Behavior patterns, in fact, tend to change gradually in close conjunction with these recruitment processes. Such a relationship may apply widely to teleosts, but at the same time the pattern and tempo of development among species may differ considerably from that of the anchovy, even where the larvae similarly hatch from pelagic eggs after a short incubation period. One of the more obvious contrasts is that of mackerel and anchovy.

Hunter (1981) states that while adults of different marine species may feed in various specialized ways, the larvae are all diurnal particulate planktivores with feeding behavior that is most similar at first feeding, but diverges as development proceeds towards metamorphosis. He frequently contrasts the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*, as representatives of the "sinuous" clupeoid type and the more rigid, more agile scombroid type. Larvae of the anchovy strike only once at food items from a carefully adjusted S-shaped posture. Larvae of the mackerel feed "in a manner more typical of the biting attack of many adult fishes" and frequently repeat if the strike misses. Body depth and head size, and also mouth size and thus

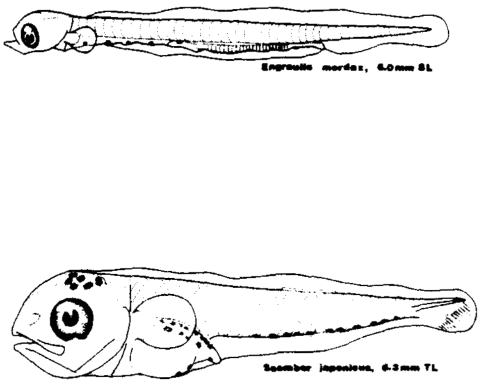

FIG. 12. The northern anchovy and the Pacific mackerel (after Watanabe, 1970) at about the same length. Both species would be expected to reach these lengths about 9 or 10 days after hatching at 16–17°C.

prey size increase more rapidly in the mackerel than in the anchovy. The mackerel becomes piscivorous at 10 mm SL.

The anchovy and the mackerel hatch at about the same length but with different body configurations, and within a few days they differ strikingly in body form (Fig. 12). The anchovy has an almost anguillid form with a long digestive tract, and thus it has a long trunk and a short (post-anal) tail. The mackerel has a short visceral mass in which organs tend to be spheroid and flexures appear early. According to Watanabe (1970) torsion of the gut occurs during the yolk sac stage and the stomach is formed at 10 mm. Consequently the trunk is short and the post-anal tail is long. In contrast to the thin oblique musculature of the anchovy, the first-feeding mackerel has relatively thick musculature with fibers in a near-horizontal alignment that foreshadows the definitive adult arrangement (though without red muscle development). Fibers grade from small to larger diameter mesially, which suggests that new additions occur over the entire surface of the myomere essentially from hatching. This would permit uninhibited increase in body depth, and along with it head depth.

The mackerel, of course, is a particulate, piscivorous feeder as an adult, and this is quite close to the feeding mode that is obligate for all larvae in the plankton. The anchovy, on the other hand, is primarily a filter feeder as an adult, and this is quite different than the obligate larval mode. The difference in the early and later feeding modes of this species is probably responsible for the notable metamorphosis it undergoes, which includes marked changes in the locomotor apparatus, the digestive tract and the jaw-branchial apparatus. In the mackerel, since feeding mode does not change in kind, development can progress towards the definitive adult configuration from an early stage. For example, the mackerel shows branchial arches with free, albeit short, upper limbs by 10 mm SL. The mouth and branchial apparatus can enlarge without restriction during early growth, whereas in the anchovy changes in jaws, branchial arches and suspensorium towards the wide gape capability of the filter feeding mode would probably be unwieldy in the particulate feeding larval period. The mouth of the anchovy larva is relatively small, possibly because of these developmental limitations, and this in turn may account in part for the precise nature of the feeding attack.

Between them, the northern anchovy and the Pacific mackerel probably represent the developmental patterns of a large portion of larvae that occur in the marine plankton. There are several dozen genera of Clupeoidei, most of which are filter feeding planktivores, and there are over a dozen genera of Scombridae (and probably several genera of Carangidae), all of which are pelagic marine carnivores. However, the plankton supports larvae of many other teleosts, the adults of which may be adapted to different ecological niches than either of the above. Thus, clupeoids and scombroids aside, there are probably many other patterns of development, resulting from accommodation to different adaptations of the adult along with the universal necessities of the larval period in the plankton.

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