The development of the digestive tract and eye in larval walleye pollock, *Theragra chalcogramma**

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First feeding (FF) is a time at which a fish larva must initiate feeding or face starvation that will weaken it and eventually lead to its death. In most oviparous fish with pelagic eggs, organ systems develop that allow larvae to switch from an internal nutrient source (yolk) to an external source (prey) during the time between hatching and FF. Starvation may be a major cause of the high mortalities that occur during the larval period and thus may affect recruitment (Hjort, 1914; O'Connell, 1980; Theilacker, 1986). Indeed, some studies suggest that recruitment is determined in this period (Houde, 1987; Freeberg et al., 1990).

Laboratory experiments show that at FF, the growth rate of walleye pollock, *Theragra chalcogramma,* larvae decreases (Yamashita and Bailey, 1989), or even ceases for a period (Theilacker and Shen, 1993). Furthermore, delaying the introduction of food at FF causes a reduction of the growth rate and size-at-age (Theilacker and Shen, 1993). These studies indicate that FF walleye pollock lack energy reserves, and thus the availability of nutritious prey at this time is critical. Theilacker and Porter (1995) found that the largest proportion of starving walleye pollock larvae in Shelikof Strait, Gulf of Alaska, are in the size class that includes FF larvae. Thus, the FF period appears to be the time when walleye pollock larvae are most vulnerable to starvation. Studies involving larvae of other marine fish have found similar results (Atlantic mackerel, *Scomber scombrus,* Ware and Lambert, 1985; jack mackerel, *Trachurus symmetricus*, Theilacker, 1986).

Larval walleye pollock survival is dependent upon timely development of organs required for feeding. Of the many developmental changes occurring during the early larval period, two of the most important for walleye pollock may be vision and the digestive tract. Eyesight is probably the most important sense walleye pollock larvae use in finding prey because they are visual predators (Paul, 1983) and do not use chemosensory cues (Davis and Olla, 1995). Digestive tract development is important for efficient assimilation of nutrients needed for growth. In this study, histological sections were used to describe the development of the mouth, digestive tract, and eyes in laboratory-reared walleye pollock, from hatching to 31 days after hatching (DAH), to examine how organs necessary for feeding develop. This is essential to an understanding of why walleye pollock larvae are most vulnerable to starvation during the first week of feeding.

Materials and methods

In 1991 and 1992, adult walleye pollock were collected from Shelikof Strait, Gulf of Alaska, and spawned aboard ship. Fertilized eggs were maintained aboard ship at 3ºC for a few days, then transported to the laboratory. In 1991, walleye pollock larvae were reared at Friday Harbor Laboratories, University of Washington, San Juan Island, Washington, and in 1992, at the Alaska Fisheries Science Center, Seattle, Washington. Between 500 and 1000 larvae were reared in a black, circular, 120-L fiberglass tank (62 cm diameter, 43 cm deep) filled with 90 L filtered seawater (salinity=28.0 ±0.5 ppt) and maintained at 6° ±0.5°C, the typical seawater temperature in Shelikof Strait when walleye pollock larvae initiate feeding (Kendall et al., 1987). Larval rearing procedures followed Porter and Theilacker 1996.[1]

Fluorescent fixtures were used with a 16-hour light cycle; the amount of light at the surface of the water in the rearing tank was 17 µ mol photon/m^2/s. Prey consisted of the rotifer *Brachionus plicatilis*, raised on an algal diet of *Isochrysis galbana* and *Pavlova lutheri* high in unsaturated fatty acids (Nichols et al., 1989), as well as of *Acartia* sp. copepod nauplii and copepodites collected from a local lagoon. At 3 DAH, four to five days before FF, rotifers were added at 10/mL and *Acartia* were added at 3/mL to the rearing tank and maintained at this level throughout the rearing

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[1] Porter, S. M., and G. H. Theilacker. 1996. Larval walleye pollock, *Theragra chalcogramma*, rearing techniques used at the Alaska Fisheries Science Center, Seattle Washington. AFSC processed report 96-06, 26 p. U.S. Dep. Commerce, NOAA, NMFS, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA., 98115.

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period. Eight to 10 larvae were sampled every day or every other day after hatching to 23 DAH in 1991 and to 31 DAH in 1992. Larvae were placed into either Bouin's fixative which was replaced with 70% ethanol 24 to 48 h later, or Z-fix[2] (a solution of 10% formalin with zinc and buffers added). Larvae were dehydrated in a graded series of butyl alcohols, embedded in paraffin wax, sectioned sagittally into 6-µm serial sections, and stained with hematoxylin and eosin (H and E). Standard lengths (SL, tip of upper jaw to end of notocord) of preserved larvae were measured to the nearest 0.08 mm and adjusted to live SL (Theilacker and Porter, 1995). To describe development of the mouth, digestive tract, and eyes, histological sections of 5–10 larvae were examined from each sampling day.

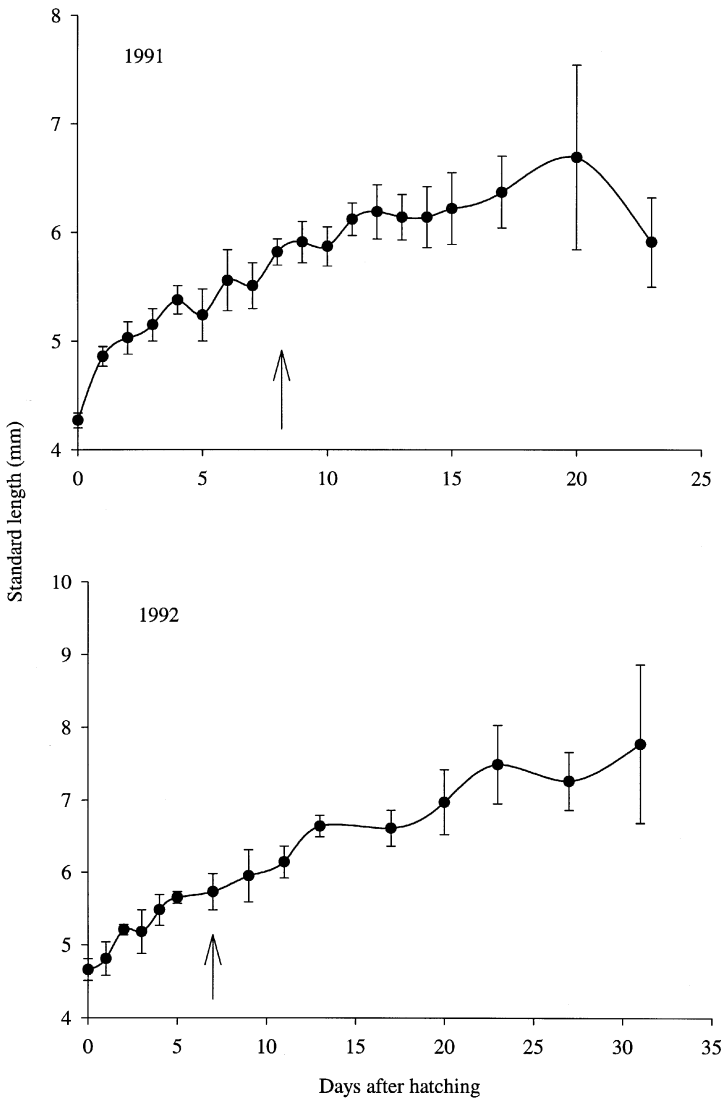

Figure 1

Growth of walleye pollock, *Theragra chalcogramma*, reared at 6°C in the laboratory from hatching to 23 days after hatching in 1991, and to 31 days after hatching in 1992. Mean standard length (preserved length adjusted to live length, see text) and standard deviation are shown; 5 to 10 larvae were measured at each age. The small size for 1991 at 23 days after hatching may be due to sampling slow growing larvae in poor condition (see text). Arrow indicates day of first feeding.

Results

Larval growth

In 1991, the mean SL at hatching was 4.27 ±0.07mm, whereas in 1992 hatching size averaged 4.66 ±0.15mm (Fig. 1). The decrease in average size of larvae sampled on day 23 in 1991 (Fig. 1) was probably due to the sampling of slow growing larvae in poor condition. A bowl was used to sample larvae from the tank, and we suspect that for this sample only slow growing larvae were captured. The overall mean growth rate from hatching to 20 DAH was 0.12 mm/d in both 1991 and 1992. In 1992, experiments continued until 31 DAH and average growth from hatching was 0.10 mm/d. The onset of FF occurred over a period of three days; day of first feeding was defined as the time when 50% of the larvae began feeding. In 1991, day of first feeding occurred at 8 DAH, and the mean SL was 5.82 ±0.12 mm. In 1992, larvae began feeding at 7 DAH, and the mean SL was 5.73 ±0.25 mm (Fig. 1).

Mouth and digestive tract development

At hatching a membrane covered the mouth, and jaw cartilage had not yet formed. At 2 DAH the membrane began to degenerate leaving an orifice that was 22 to 55 µm wide. Mouth and jaw cartilage also began forming at this time, and the cartilage in the roof of the mouth, the trabeculum cranii, became most distinct. All jaw cartilage elements were present and almost completely formed at 5 DAH (approximately 2 days before FF); the mouth was considered functional 5 to 6 DAH (Table 1).

At hatching the gut was a straight tube with a narrow lumen. The foregut could be distinguished

[2] Anatech, Ltd., Battle Creek, MI.

Table 1

Mean standard length (tip of upper jaw to end of notocord) and age at the development of various elements of the mouth, digestive tract, and eye for walleye pollock, *Theragra chalcogramma*, reared at 6°C in the laboratory in 1991 and 1992. '+', vacuoles were not observed at 23 DAH in 1991, the last sampling day. Preserved standard length adjusted to live standard length (Theilacker and Porter, 1995). SD = standard deviation. *n* = number of larvae measured. Age = days after hatching.

	Mean standard length mm (SD)				
	1991	*n*	1992	*n*	Age (year)
Mouth and digestive tract					
Foregut, midgut, and hindgut separated by valves	5.15 (0.15)	5	5.18 (0.30)	5	3 (1991,92)
Jaw developed and mouth functional	5.56 (0.28)	5	5.65 (0.08)	5	5 (1992) 6 (1991)
Folding of midgut epithelium	6.19 (0.25)	5	6.14 (0.22)	10	11 (1992) 12 (1991)
Midgut coiling, eosinic vesicles in the hindgut	6.14 (0.28)	5	6.64 (0.15)	8	13 (1992) 14 (1991)
Lipid vacuoles in midgut	+		7.49 (0.54)	10	23 (1992)
Eye					
Ocular motor muscles apparent	5.15 (0.15)	5	5.18 (0.30)	5	3 (1991,92)
Eye fully pigmented	5.38 (0.13)	5	5.48 (0.21)	5	4 (1991,92)
Lens retractor muscle developed	6.22 (0.33)	5	no samples taken		15 (1991)

by its cuboidal epithelium, but no distinction could be made between the midgut and hindgut which were lined with similar columnar epithelium. At 1 DAH, the gut lumen widened and began to separate into a long midgut and short hindgut that were demarcated by a constriction at the future site of the ileocaecal valve. At 3 DAH, the pyloric valve separated the foregut and midgut, and the ileocaecal valve separated the midgut and hindgut (Table 1; Fig. 2). At 11 to 12 DAH (4 days after FF) the gut began to develop large folds, and began to coil 13 to 14 DAH (6 days after FF) (Table 1). Also, at 13 to 14 DAH, eosinic vesicles (also referred to as eosinophilic granules or inclusions), ranging in size from 1 to 3 μm, began appearing in the apical cytoplasm of the hindgut epithelial cells (Table 1). Vacuoles in midgut epithelial cells were first observed at 23 DAH in 1992 larvae (Table 1). The vacuoles were not distinct and observed only in one larva out of ten. Walleye pollock larvae showed no other changes in gut structure (i.e. no stomach, or pyloric caeca) up to 31 DAH.

Eye development

At hatching, a lens was present, and small scattered patches of pigment were located throughout the retina (Fig. 3). The pigment patches increased in size and joined to form the pigment layer; by 4 DAH the eye was fully pigmented (Table 1). Ocular motor muscles were not developed at hatching, but at 3 DAH these muscles became apparent (Table 1). At 9 DAH, the lens retractor muscle was identified as a thin structure that connected the lens to the retina. From 9 to 15 DAH the muscle increased in width as it grew. The size and shape of this muscle changed very little beyond 15 DAH; therefore it was considered functional beginning at this time (Fig. 4, Table 1).

Discussion

Larval growth

Growth of walleye pollock larvae in this study was similar between years (0.12 mm/d from hatching to 20 DAH for both 1991 and 1992) and to rates found by others for walleye pollock larvae reared at 6°C in the laboratory; 0.14 mm/d from hatching to 19 DAH (Theilacker and Shen, 1993), 0.11 mm/d from hatching to 21 DAH (Yamashita and Bailey, 1989) and 0.065 mm/d from hatching to 15 DAH (Nishimura and Yamada, 1984). Growth was slightly lower than the 0.14 to 0.23 mm/d calculated for field-collected walleye pollock larvae (Bailey et al., 1996).

Mouth and digestive tract

From observations on live larvae, Bailey and Stehr (1986) found that walleye pollock have no mouth at hatching; the mouth begins to develop 2 days later

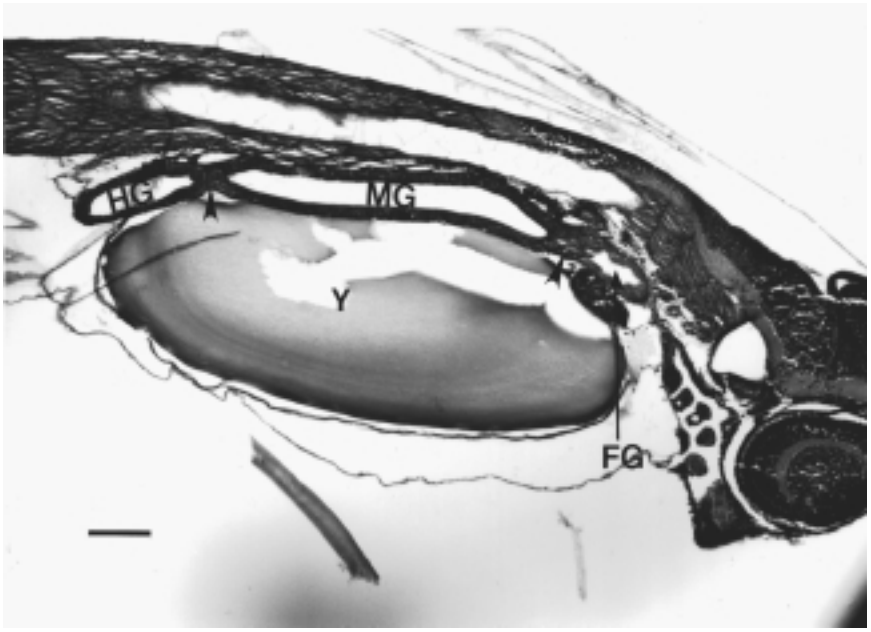

Figure 2

Walleye pollock, *Theragra chalcogramma*, larva 3 days after hatching. The foregut (FG) and midgut (MG), and midgut and hindgut (HG) are separated by the pyloric and ileocaecal valves respectively (arrowheads). (Bouin's fixative, H and E; standard length=5.24 mm; scale bar=100 µm). Y = yolk.

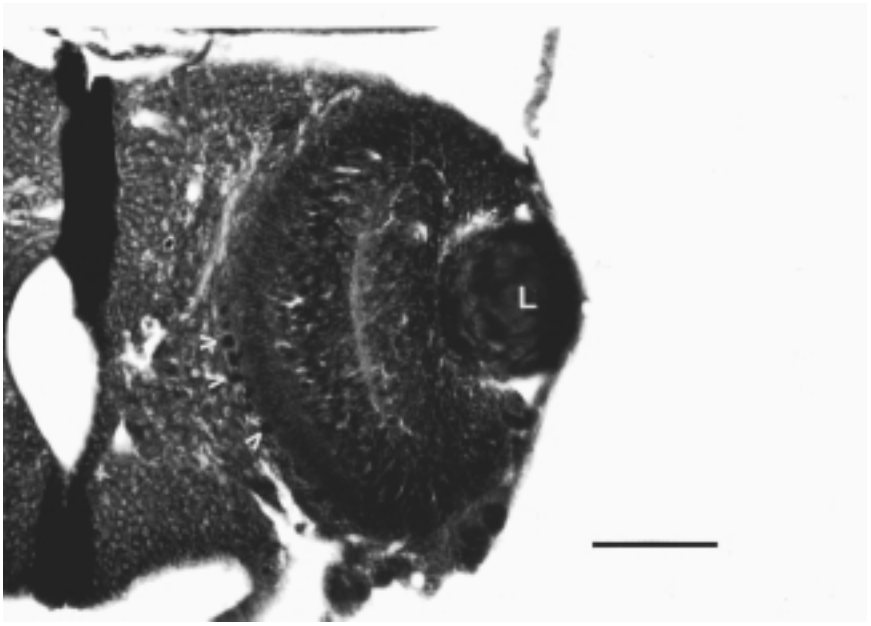

Figure 3

Walleye pollock, *Theragra chalcogramma*, eye at hatching. The eye is not fully pigmented. Arrowheads identify patches of pigment. (Bouin's fixative, H and E; standard length=4.34 mm; scale bar=50 µm). L = lens.

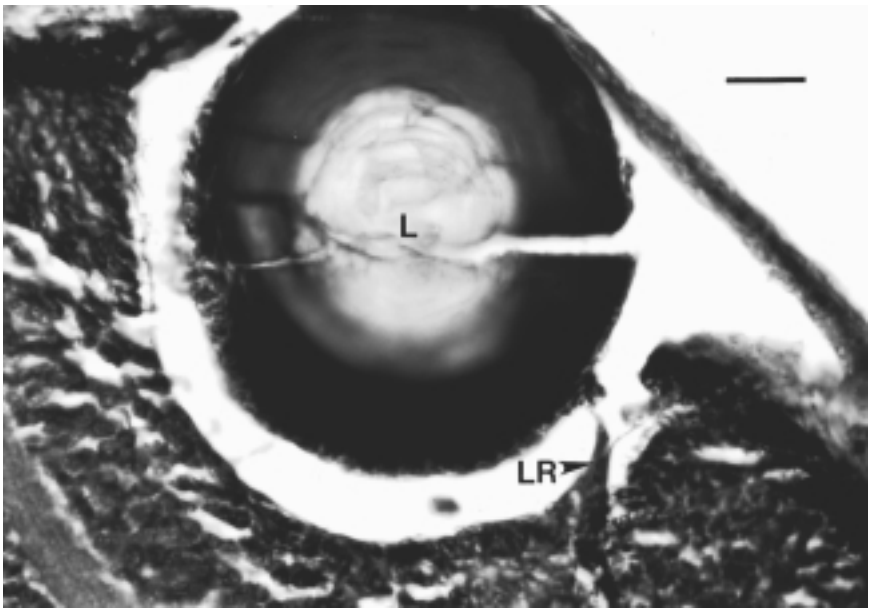

Figure 4

The lens retractor muscle (LR) in the eye of a 15-day posthatching walleye pollock, *Theragra chalcogramma*, larva. (Bouin's fixative, H and E; standard length=6.65 mm; scale bar=20 µm). L = lens.

and is functional by 4 to 5 DAH. Histological analysis in this study showed that mouth and jaw development proceeded at a similar rate; the jaw was fully formed and the mouth was functional 5 to 6 DAH. As in Atlantic cod, *Gadus morhua*, larvae (Kjørsvik et al., 1991), the first feature of the walleye pollock mouth to form was the trabeculum cranii ("roof of the mouth").

At hatching, walleye pollock larvae had a straight-tube gut. This simple gut arrangement has been noted for larvae of other species of fish as well (northern anchovy, *Engraulis mordax*, O'Connell, 1981; Atlantic cod, *G. morhua*, Kjørsvik et al., 1991; turbot, *Scophthalmus maximus*, Segner et al., 1994). At 3 DAH, three distinct portions of the gut could be identified: the foregut, midgut, and hindgut. This gut arrangement is typical of larval fish (Govoni et al., 1986) and walleye pollock larvae showed no major changes in gut structure (i.e. no stomach, or pyloric caeca) up to 31 DAH. For larval fish, major changes in gut structure happen rapidly at metamorphosis rather than gradually during the larval period (Govoni et al., 1986). However, at 11 to 12 DAH (4 days after FF) the larval walleye pollock midgut epithelium began to develop large folds, and the gut began to coil 13 to 14 DAH (6 days after FF). For walleye pollock larvae reared at 6ºC, Oozeki and Bailey (1995) noted that gut coiling began on 16 DAH and was complete by day 23. Midgut coiling increases the length of the gut, and the residence time of prey in it (Yamashita and Bailey, 1989). At one week after FF, both epithelial folds and gut coiling enable walleye pollock larvae to assimilate nutrients more efficiently through increased absorptive surface area and longer residence times.

Histological evidence suggests the larval walleye pollock gut functions in the same manner as in other fish larvae. The midgut of fish larvae digests and absorbs lipids (Govoni et al., 1986) and this appears to be the function of the larval walleye pollock midgut as well. For larval whitefish, *Coregonus fera*, lipid vacuoles appear as circular "voids" in the apical portion of the midgut epithelial cells one day after feeding (Loewe and Eckmann, 1988). In other species of fish, similar vacuoles are also reported to contain lipid (goldfish, *Carassius auratus*, Iwai, 1968; turbot, *S. maximus*, Segner et al., 1994). In our study, vacuoles (circular voids) were observed in midgut epithelial cells of one walleye pollock larva at 23 DAH. This is later in development than they have been observed in other fish larvae but lipase is present in walleye pollock larvae at hatching; therefore lipid digestion could occur at FF. Lipase activity increases with age (Oozeki and Bailey, 1995) so that as larvae grow, more lipid can be digested and this could produce larger, more visible (by H and E stain-

ing) vacuoles with age. There was probably lipid in the midgut cells earlier than 23 DAH but in such small amounts so that it could not be identified without special staining. The larval walleye pollock hindgut appears to function in protein digestion like the hindgut of other species of fish larvae (Govoni et al., 1986). Watanabe (1984) demonstrated that protein is pinocytotically moved into hindgut epithelial cells for intracellular digestion. Iwai and Tanaka (1968) stated that the intracellular protein appears as eosinophilic granules (also referred to as eosinophilic vesicles or inclusions) within the apical portion of the hindgut cells. At 13 to 14 DAH (5 to 7 days after FF), eosinic vesicles appear in the apical cytoplasm of the hindgut epithelial cells of walleye pollock larvae. For Atlantic cod, *G. morhua*, larvae (Kjørsvik et al., 1991), a close relative of walleye pollock, inclusions were not observed until 2 to 5 days after FF. In other studies eosinophilic inclusions have been observed soon after FF (northern anchovy, *E. mordax*, O'Connell, 1981; whitefish, *C. fera*, Loewe and Eckmann, 1988; turbot, *S. maximus*, Segner et al., 1994). Trypsin is present in walleye pollock larvae at hatching, its activity increases with age, and it is not supplemented by prey in the gut (Oozeki and Bailey, 1995). Eosinophilic vesicles appeared at the time the gut began to coil, and both coiling and increased trypsin would allow increased digestion of prey making more protein available to the hindgut, possibly explaining why vesicles were not apparent until some time after FF. The appearance of lipid vacuoles and eosinophilic vesicles after the first week of feeding provides evidence for improved digestive capability.

Eye

Sight is probably the most important sense walleye pollock larvae use for feeding. Walleye pollock rely on vision to search for prey (Paul, 1983) and do not respond to chemosensory cues (Davis and Olla, 1995). Laboratory experiments show that a group of walleye pollock larvae, age 21 DAH, remains aggregated when rotifers are introduced into the group, but when only the scent of rotifers is introduced, the group disperses (Davis and Olla, 1995). Because they are visual predators and because light below 0.006 μ mol photon/m^2/s limits their ability to capture prey (Paul, 1983), walleye pollock larvae probably have a pure-cone retina like many other species of fish larvae. Blaxter and Staines (1970) examined the retina of 12 species of fish larvae including haddock, *Melanogrammus aeglefinus* (which belongs to the same family as walleye pollock, Gadidae), they showed that haddock and seven other species have a pure cone retina. Olla and Davis (1990) stated that the retina of walleye pollock larvae most likely does not contain rods. It is unknown when rods begin to appear in walleye pollock, but for herring, *Clupea harengus* (Blaxter and Jones, 1967), plaice, *Pleuronectes platessa* (Blaxter, 1968), and sole, *Solea solea* (Sandy and Blaxter, 1980), rods begin to appear at metamorphosis.

The lack of eye pigmentation at hatching has been found for many teleosts (Blaxter, 1986), including walleye pollock (Bailey and Stehr, 1986; our study), and eyes are probably nonfunctional at this time (Blaxter, 1986). Ocular motor muscles developed just as walleye pollock eyes became fully pigmented (3 DAH). The development of eye pigmentation and ocular motor muscles should provide a FF larva with sight and the ability to move its eyes. The lens retractor muscle did not develop until after FF; it was considered functional beginning at 15 DAH. The lens retractor muscle develops after FF in other species of fish as well (northern anchovy, *E. mordax*, O'Connell, 1981; white seabass, *Atractoscion nobilis*, Margulies, 1989). This muscle allows a larva to focus on objects at different distances, thereby increasing the field of vison (Munz, 1971). Because this muscle was not functional until 15 DAH, for about a week after FF a larval walleye pollock's field of view is restricted because it is unable to change the focus of its eyes. Thereafter, visual acuity improves, allowing walleye pollock larvae to detect both prey and predators more easily.

In Shelikof Strait, Gulf of Alaska, the proportion of starving walleye pollock larvae decreases dramatically after the first week of feeding (Theilacker and Porter, 1995; Theilacker et al., 1996) and the physiological condition of walleye pollock larvae improves as they grow; that is, fewer larvae are found in poor condition (Theilacker et al., 1996). Improvements to vision (the lens retractor muscle) and a combination of morphological changes to the gut (folding and coiling) as well as an increase in digestive enzymes (Oozeki and Bailey, 1995) contribute to walleye pollock larvae becoming less vulnerable to starvation after the first week of feeding. Additional contributing factors may include developmental changes occurring to other organ systems (e.g. development of trunk musculature and lateral line system as has been shown for other species of fish larvae; Blaxter, 1986; O'Connell, 1981), and larvae becoming better predators as they grow. For northern anchovy, *E. mordax*, larvae, feeding success rapidly improves during the first week of feeding (Hunter, 1972). At hatching walleye pollock larvae lack functional eyes and mouth, and have a straight-tube gut; the development of these between hatching and FF allows larvae to begin feeding, and their continued development after FF improves the larvae's chance of survival.

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