

## Chapter 7

# Intensive Culture of Walleye Fry

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### Introduction

Walleye may be raised from newly hatched fry to phase I fingerlings (1.25–3.0 in; 32–76 mm) in extensive (i.e., ponds) or in intensive culture, that is in tanks and raceways. Currently, the predominant method for raising phase I fingerlings is in drainable (Summerfelt et al. 1996) or undrainable ponds (Kinnunen 1996). Nickum and Stickney (1993) stated that “Since successful rearing of first-feeding fry under intensive culture conditions has not been economically accomplished, walleye culture has been based on pond rearing until the fish reach at least 2.5 in. Thereafter, the fish may be offered formulated feeds.” The latter refers to the procedure of habituated pond-raised fingerlings to formulated feed in intensive culture systems (Malison and Held 1996). However, walleye fingerlings may be raised from first-feeding fry in intensive culture systems, hereafter called “intensive culture of fry.” This can be done because major constraints to intensive culture of fry (noninflation of the gas bladder, nonfeeding, and maladaptive clinging behavior) have been resolved, and production-scale systems for intensive culture have been developed. The case studies by Colesante (1996), Moodie and Mathias (1996), and Moore (1996) provide technologies for production to advanced fingerlings in intensive systems. Intensive culture is the only technology that can make use of fry produced by out-of-season spawning (i.e., fry hatched in February).

The purpose of this chapter is to provide historical perspective, describe critical developmental events, and to summarize personal experience and related literature on methods for intensive culture of walleye to fingerlings.

### Advantages of intensive culture

Not many years ago, the prospects for intensive culture of walleye fry seemed remote because of seemingly insurmountable biological and technical difficulties. Nickurn (1978) said that “It is extremely speculative to suggest a culture method for walleye fry at this time ...” However, this chapter and the case studies that follow will demonstrate that critical problems have been solved, and many aspects of the culture process have been fine-tuned. It can now be stated that intensive fry culture is a viable production technology to produce walleye fingerlings. Pond culture is economically effective for the production of large numbers of phase I fingerlings, but it is far less so for the production of large, phase II fingerlings ( $\geq 6$  in;  $\geq 152$  mm), or for the commercial grow out from fry to food fish. Pond culture of phase II fingerlings requires relatively low initial pond stocking densities, or partial harvest and restocking, followed by provision of substantial quantities of minnows (Jorgensen 1996; Raisanen 1996). Because of the high cost and problems with the availability of minnows, tandem pond-tank (i.e., extensive-intensive) culture methods have gained popularity as a method to raise fingerlings 22.5-in (264 mm) (Cheshire and Steele 1972; Beyerle 1975; Nagel 1974, 1976; Nickum 1978; Colesante et al. 1986).

The extensive-intensive method involves the transfer of pond-raised phase I fingerlings to intensive culture systems where the fish are habituated to formulated feed—details are described in the chapter by Malison and Held (1996). In extensive-intensive culture, substantial mortality typically occurs at two intervals—first in the pond (McIntyre et al. 1987), and secondly in the intensive culture system during the first 21-days when fish are habituated to formulated feed (Kuipers

and Summerfelt 1994). Pond culture techniques must be contrived to manipulate complex ecosystems within the constraints of variable weather: fertilizers are added with the expectation that food webs will provide the right kind and size of zooplankton for first feeding walleye, but without over fertilizing, causing an oxygen depletion, or growing aquatic weeds. When zooplankton populations are lacking, cannibalism may occur in the pond (McIntyre et al. 1987). Also, insect predation may contribute to fry mortality.

Intensive culture may be a better alternative for hatcheries that lack the pond facilities or sites for cage culture. In intensive culture of walleye, a single interval of high mortality occurs during the critical period when fish switch from yolk-sac nutrition (endogenous feeding) to active feeding (exogenous feeding), which coincides with the interval of gas bladder inflation. The critical interval occurs before the fish reach 21-d posthatch; thereafter, with suitable feeds and appropriate husbandry, fingerlings may be raised to whatever target size is needed, or to the limits of the cultural system, whichever occurs first.

Techniques for intensive culture of fry on formulated feed have developed sufficiently to make the intensive culture of fry to fingerling a practical alternative to the extensive-intensive system. Will intensive culture of fry replace pond culture of fingerlings? Intensive culture has many factors in its favor: It is not subjected to variable environmental conditions, so cultural conditions are fairly stable, temperature can be controlled to lengthen the growing season, nuisance aquatic organisms are eliminated, and the quality and quantity of the feed is controlled. Technological advances are more likely applicable in an intensive culture system than in pond culture. In spite of high stocking density, cannibalism may be less of a problem in intensive culture than pond culture because in intensive culture cannibalism is easier to monitor, and the environment (temperature, light, turbidity) or feeding rates can be adjusted to reduce the intensity of the problem. In intensive culture, growth rates can be stepped up or slowed by temperature manipulation to meet production schedules for fish of different size.

Intensive culture is the only technology that can be used to raise fry produced by out-of-season spawning. The advantage of out-of-season culture is that it increases the growing season. Ambient water temperature during

the natural culture season is usually too short to raise a phase II fingerling to a target size of 6 to 8 in (152-203 mm) by fall in either ponds or cages. In 1995 and 1996, Moore (Alan Moore, Iowa Department of Natural Resources, personal communication) spawned walleye in late January at the Rathbun Fish Hatchery. A sample of eggs from those spawns hatched in mid February. Fry produced by out-of-season can be raised in intensive culture, but they could not be stocked in ponds anywhere in the Midwest. In Iowa, pond stocking is not feasible until mid-April in the southeastern corner of the state, and the first week in May in the northwest corner (Jorgensen 1996). Pond stocking begins in mid-to late April in Ohio, mid-April in western Nebraska (Summerfelt et al. 1993), late April-early May in lower Michigan (Gustafson 1996), early May-early June in North Dakota (Summerfelt et al. 1993), the third week of May in northern Michigan (Wright 1996), and late May-early June in May in Ontario (Flowers 1996).

Would intensive fry culture with heated water be economical for commercial producers? As a rule, heating water for production aquaculture is uneconomical, but several small and a few large commercial aquaculture facilities in the Midwest, including sites in Minnesota and North Dakota, raise tilapia indoors; they heat and recycle water at temperatures 84-88°F (28.9-31.1°C). The larger operators typically have a source of steam or warm water from coal-fueled electric generating plants or facilities that distill alcohol. Recycle systems have been used for intensive culture of walleye fry at sites as far north as near Gunton, Manitoba (Loadman et al. 1989; Moodie et al. 1992). Walleye can be raised from hatch to a subadult in one calendar year in an intensive system with optimum water temperature.

Fingerlings started from out-of-season spawning and raised in intensive culture may find a special niche for commercial production of feed-trained fingerlings for cage culture and other intensive culture systems. Fingerlings from early spawned fish can be available in advance of young-of-the-year fingerlings produced from ponds or from extensive-intensive culture. Because of the difficulty in habituating pond-raised fingerlings to formulated feed, a commercial source of feed-trained fingerlings is critical for the successful cage culture of walleye to a fall (advanced) fingerling. Disease and cannibalism are less and survival is greater in cages stocked with feed-trained walleye fingerlings than in cages where pond-raised fingerlings are

habituated to feed (Blazek 1996; Bushman 1996; Harder and Summerfelt 1996).

### Historical perspective

Public hatcheries have spawned, incubated, and hatched walleye for more than 100 years. The Manual of Fish-Culture published by the U.S. Commission of Fish and Fisheries in 1900 has a chapter on “The Pike Perch or Wall-Eyed Pike” (USCF 1900). That chapter describes spawning and spawn-taking, use of “swamp muck” to prevent adhesion of eggs, egg-incubation, transportation of eggs, description of cannibalism (including some excellent photographs of cannibalism), and prey selectivity by first feeding fry when lake water containing zooplankton was used for the water supply. There was no mention, however, of pond culture of fingerlings or any attempts at intensive culture of walleye.

Since 1900, techniques for spawning, incubation and hatching of fry improved and substantially expanded. A survey conducted by Tunison et al. (1949) in 1948, with data for hatcheries of 44 States and the U.S. Fish and Wildlife Service, listed the distribution of 596.4 million “wall-eyed” pike, and 79.6 million yellow pike-perch fry, and 485.4 million “unclassified” pike-perch. If we presume that all of these categories are walleye, the total was 1.16 billion fry. That level of production seems to have persisted for forty years. A survey in 1983-84, indicated a similar number of fry were stocked annually by state, federal and provincial agencies in the U.S. and Canada (Conover 1986).

The first mention of pond culture of fingerlings dates from the early 1920's (Cobb 1923). Thereafter, accounts of distribution of walleye fingerlings were reported. In 1948, using the same categories noted above, fingerling distribution was more than 4 million (Tunison et al. 1949). By 1983/84, more than 9 million pond cultured fingerlings were stocked (Conover 1986).

The beginnings of intensive culture is somewhat obscure. But because many public hatcheries had tanks and raceways available at the time walleye fry were hatching, and plenty of fry available for experimentation, the commencement of intensive culture was inevitable. Hatchery biologists carried out many trial-and-error experiments to culture walleye fry. Olson

(1974) reported stocking 20,000 walleye fry in a 750 gallon (2839 L) tank (7 fry/L) and providing them with zooplankton from the water supply taken from a nearby lakes. The fry refused to eat the zooplankton, and cannibalism was severe; less than 100 fry survived to 12 days.

Some early studies were reported at the annual meetings of the Coolwater (Fish) Culture Workshop. Begun as a small group of hatchery biologists that gathered to discuss cultural problems of muskellunge and tiger muskie, in recent years, more presentations have been made on walleye than any other species. Certainly, the development of the cultural technology for walleye owes much to exchange of information that occurs at the annual workshop meetings. Unfortunately, due to the informality of the meetings, proceedings or minutes of the meetings have been limited to the registrants, and no repository for the minutes exists.

Cheshire and Steele (1972) stated that no literature could be found on the culture of walleye fry using artificial food. But they were among the earliest investigators to train 2-in (50-mm), pond-cultured fingerlings to accept formulated feed. Beyerle (1975) cited four unpublished reports by personnel at state and federal hatcheries on intensive culture of walleye fry using formulated feed, but those attempts were “uniformly unsuccessful”, no fry survived beyond 17 days after yolk sac absorption (i.e., about 22-25 days posthatch), and no dry diet was accepted by walleye fry. In 1974, the inadequacy of hatchery technology for the culture of larval walleye on artificial diets was noted by the National Task Force for Public Fish Hatchery Policy (FWS 1974) as “the most critical bottleneck in the national fish-culture program.”

The earliest success with intensive fry culture was obtained by feeding live food. Beyerle (1975) raised walleye fry in fiberglass troughs to 32 days with 3.9% survival by feeding them a combination of brine shrimp and daphnians. Thus, aside from what may have been done by others but not published, or that which was described in the so-called “gray literature” (unpublished reports and workshop proceedings that are difficult to obtain), Beyerle's (1975) report may be marked as the start for intensive culture of walleye fry using live feed. In summarizing the state of the art on feeding formulated feed, Nickum (1978) stated that although fry often ingested formulated feed, survival to 21 days posthatch

was less than 1%. Also, few fry survived weaning to formulated diets when they were started feeding on brine shrimp and zooplankton (Nickum 1978).

Krise and Meade (1986) reviewed unpublished and published reports on intensive culture of walleye fry through 1983. The early 1980's was a period of intense activity; the topics included: developmental biology of the fry; the visual system of walleye, especially how color contrasts of food and tank affect feeding success; phototaxis of larvae (photopositive until they reach 31 mm); and effects of light intensity, water flow, temperature, stocking density, feeds and feeding techniques. "Ineffective feeding" was considered the major problem, but cannibalism during the first two weeks was also considered to be a significant problem. For the most part, formulated diets were not successful as starter feed. Fish that ate the feed died within a few weeks for unknown reasons.

Howey et al. (1980) obtained a remarkable 43.5% survival through three weeks "post-swimup" by starting walleye fry on live food (brine shrimp, followed by daphnia), then weaning them to a formulated feed. They stocked fry at 14 fry/L, and fed them brine shrimp nauplii at 30-min intervals over an 18-h photoperiod at a water temperature at 64.4-68°F (18-20°C). They fed daphnia for an additional 3-4 weeks, then gradually converted the fish to the U.S. Fish and Wildlife Service W-7 diet formulation. They reported about 20% of the surviving fish had failed to inflate their gas bladder, which seem to be the first report on the problem of non-inflation of the gas bladder (NGB). Howey et al. (1980) stated that NGB "may be embryological or related to low level (100-103%) nitrogen gas supersaturation in the water supply." Although their conjecture was wrong, their discovery of the NGB problem was subsequently regarded by many as the major problem in the intensive culture of walleye fry (Colesante et al. 1986; Barrows et al. 1988; Kindschi and MacConnell 1989; Loadman et al. 1989). Kindschi and MacConnell (1989) reported gas bladder inflation from 0 to 50%, and mostly less than 30% in 20 trials using five formulated feeds and combinations of formulated feeds with brine shrimp. Some efforts to develop commercial scale fry culture systems are still plagued by problems with NGB (Moodie et al. 1992).

Hokensen and Lien (1986) obtained 71% survival of walleye fry to 21 days in 20 L aquaria feeding zoop-

lankton captured from a pond, but fry survival in experiments with formulated feed was usually <10% (Colesante et al. 1986; Barrows et al. 1988; Kindschi and MacConnell 1989). However, the availability of a commercial fry feed, the Fry Feed Kyowa (FFK) (Eiokyowa Inc., Chesterfield, Missouri) E-series feed was an important advancement. The B-series, designed as a replacement for artemia, became the standard starter feed used by most investigators (Loadman et al. 1989; Moore et al. 1994a, 1994b; Bristow and Summerfelt 1994; Bristow et al. 1995; Moodie and Mathias 1996; Moore 1996). The B-series is available in nominal sizes categories: E-400 (400 µm), E-700 (700 µm), etc. Most investigators start fry on the FFK B-400, then upgrade to the E-700, and so forth, as the fish grow. Because of a large price difference between the B and C series, most culturists now start fry on the E-400, then switch to the C-700. Barrows (1996) describes a less expensive, open formula starter diet for walleye (WS-9501) developed at the U.S. Fish and Wildlife Service Fish Technology Center, Bozeman, Montana.

The experiments with the FFK formulated feed gave promising survival rates, but NGB continued to be a problem. For example, Loadman et al. (1989) reported survival of 27.7% to 30 d for walleye raised at 66.9°F (19.4°C) and fed exclusively with formulated feed, but gas bladder inflation was about 16%. Viability, the product of survival and gas bladder inflation is a measure of potential for longterm survival. In the study by Loadman et al. (1989), viability was only 4.4% ( $[0.277 \times 0.161 \times 100]$ ). Loadman et al. (1989) reported that of the survivors to 132 d posthatch, 40% had inflated gas bladders. Because fish cannot inflate their gas bladder much later than 12-d posthatch (Marty et al. 1995), my calculations suggested that 52% of the fish with the NGB problem died between 30 and 132 days.

The development of intensive culture technology has been accomplished through a succession of successful problem solving of critical bottlenecks. For example, a water spray has been used to overcome the NGB problem (Barrows et al. 1993b; Moore et al. 1994a). A portion of the inflow is passed through a 90" perimeter nozzle directed perpendicular to the water surface. The impact of the spray seems to clean the surface of oil and other debris from the tank surface, but whatever the physical mechanism, it works. Since tanks have been equipped with a surface spray gas bladder inflation rates of 90 to 100% have been common (Barrows et al.

1993b; Moore et al. 1994b; Bristow and Summerfelt 1994; Bristow et al. 1996). Gas bladder inflation is discussed in the section on Noninflation of the Gas Bladder.

Another critical bottleneck is the tendency for fry to cling to the culture tank. Some investigators suggested that the clinging behavior was the result of stress syndrome behavior, or from NGB. Fish with the stress syndrome behavior (Beyerle 1975) swim in a circular motion or move to the sides of the tank and face the tank wall (Krise and Meade 1986). Clinging behavior may be an attraction of the fry to reflected light. Walleye fry are strongly attracted to strong overhead light, but they also cling to the tank walls, standpipe or any other shiny surface that reflects light. Two techniques have been used to disperse the fry and prevent clinging: Bristow and Summerfelt (1994; Bristow et al. 1996) use turbid water and Colesante (1996) uses high intensity light. Further discussion of the problem of clinging behavior is given in the section on Clinging Behavior.

### Developmental biology of walleye

**T**o this point, what has been referred to as a fry is really a vernacular name used by fish culturists to encompass several discrete developmental stages from hatching to juvenile, that is from fry to fingerlings. Development does not proceed by gradual changes, but by major steps, a process called saltatorial development (Balon 1975). The technical terminology used to describe the developmental stages of larval fishes is diverse, only those few that concern walleye will be referenced here. Hubbs (1943) used prolarva for the stage with the yolk sac, postlarva for the stage after disappearance of the yolk. Balon (1975) called the yolk sac stage an embryo and the larva stage as the interval from first feeding to the juvenile. Nelson (1968) used similar terminology to that of Hubbs but defined the change from prolarva to postlarva by disappearance of the oil globule, an event that takes about 5 days additional days after disappearance of the yolk. Li and Mathias (1982) used prolarva for fish with a yolk sac, and divided the postlarva into a postlarva I and II. Krise and Meade (1986) used stages and temperature units (TUs, cumulative daily temperature in °C): Stage I, surface suspension (7-29 TU); Stage II, initiation of gill respiration (70 TU); Stage III, initiation of feeding

(120+ TU); and Stage IV, initiation of cannibalism and gas bladder inflation (100-214 TU).

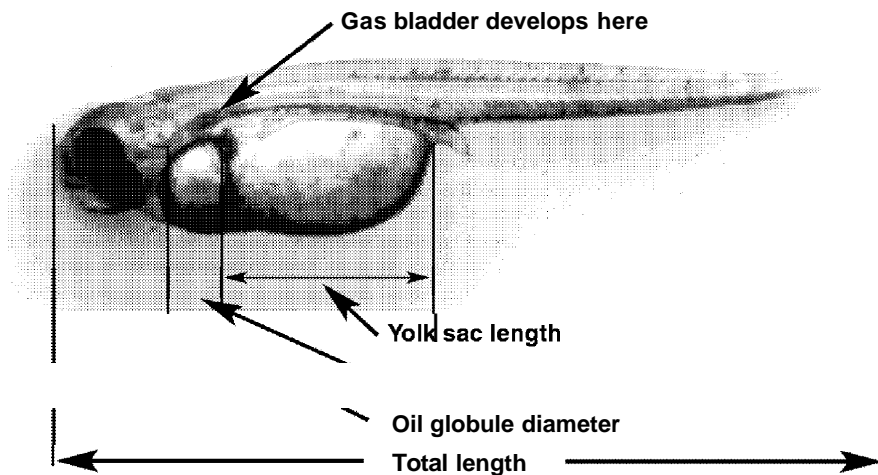
The terminology of Li and Mathias (1982) is that most commonly used by most US and Canadian researchers. Their report suggests that at 64.4 to 68°F (18-20°C), the prolarva lasts 5-6 days, postlarva I and postlarva II about 5 days each for a total of 15-16 days from hatch to juvenile. In my laboratory, where culture temperatures do not reach 20°C until about 30 days posthatch, the postlarval II stage does not end until 16- to 19-d posthatch.

### *Prolarval stage*

The prolarval stage is also called a free embryo or eleutheroembryo (Balon 1984), or finfold stage. Fish culturists call them sac fry because it is the first period of life post-hatch when the yolk sac is present (Figure 1). No paired fins are present and the median fin (fin fold) is transparent, and continuous from the head around the tail to the anus. Yolk sac length measured by Bristow and Summerfelt (in preparation) was  $1.34 \pm 0.16$  mm (coefficient of variability, CV, was 11.9%), or 18.1% of total length; the oil globule diameter was  $0.86 \pm 0.14$  mm (CV was 16.3%) at hatching, or 11.9% of total length at hatch. Li and Mathias (1982) reported that oil globule diameter was 0.4-0.6 mm for prolarva, but this seems more appropriate for larvae at the end of the prolarval phase. Olson (1974) reported an oil globule diameter of 0.9 mm at hatch for 1 day old, 7.1 mm, long fry.

At a mean temperature of 16.4°C, the yolk sac disappears in the 5th day posthatch, about 68 TU (Bristow and Summerfelt, in preparation), but it may persist up to about 13 days at a temperature of 13.2°C (calculated from data given by Hurley 1972). Olson (1974) reported that the yolk sac disappeared in 10-11 days (temperature not given). Larval nourishment at this time is said to be endogenous because it precedes (exogenous) feeding, in fact, the mouth is closed until 3- to 4-d posthatch.

The prolarvae are weak swimmers, so water currents in culture tanks should be low, because larvae are quickly exhausted. Their weak swimming ability also causes problems in shipping larvae in plastic bags. Prolarvae often are shipped in plastic bags at 100,000-150,000 per 15 L of water, and transported for up to 18 hours, but unless the bag is moved to and fro by the motion of the



**Figure 1. Photograph of the finfold, or prolarval stage of walleye taken 10-minutes after hatch. Dimensions used for measurement of yolk sac and oil globule are shown.**

vehicle, the larvae pile up and suffocate (Colesante and Schiavone 1980).

Length at hatching ranges from 4.8 to 9.0 mm (Table 1), but fry lengths of 9 mm probably represents measurements sometime after hatching. Li and Mathias (1982) report that the length of fry at the end of the prolarval

stage is 8-9 mm. In the spring of 1992, measurements were made of the total length of 150 fry from each of six stocks of walleye from the Midwest that were collected one-hour after hatch: the mean ( $\pm$ SD) total length for 900 newly hatched fry was  $7.4 \pm 0.55$  mm (CV was 7.4%), individual stock means varied from 6.9 to 8.2 mm (Hey et al. 1996). Oseid and Smith (1971) found that mean length of walleye at hatch varied in relation to lot (“five separate lots from three stripping stations”), which implies differences between stocks, parents, or both. It is not clear whether stock

differences in length at hatching are heritable or a function of variation in nutritional condition of the female before spawning. Oseid and Smith (1971) also found that oxygen concentration during incubation and length of the incubation interval affected length at hatching: the longer the incubation interval and the

**Table 1. Dimensions of newly hatched walleye fry<sup>a</sup>.**

Length		Weight		Volume	
mm	Reference	No./g	Reference	No./mL	Reference
4.8	USCFF (1900)	207-276	Summetfelt et al. (unpublished)	111-143	Summetfelt et al. (unpublished)
6-9	Scott and Crossman (1973)	357	Howey et al. (1980)	167	Loadman et al. (1989)
6-8.6	Craig (1987)	161.3 <sup>c</sup>	Kindschi and Barrows 1991a	160-210	Colesante (1996)
7.42 <sup>b</sup>	Bristow (1993)			220	Call (1996)
7.1	Olson (1974)				
5.7-7.8	Oseid and Smith (1971)				

<sup>a</sup>Newly hatched fry are called embryos by Balon (1975), or prolarvae by Li and Mathias (1982).

<sup>b</sup>Mean of 900 measurements taken within 30-minutes of hatch, 150 larvae were measured of each of six geographic stocks (OH, KS, IA, WI, MN, and ND) that hatched April 7 to May 29, 1992. Stock means ranged from 6.7-8.2 mm; there was a significant difference among all but two stocks.

<sup>c</sup>3-day old fry.

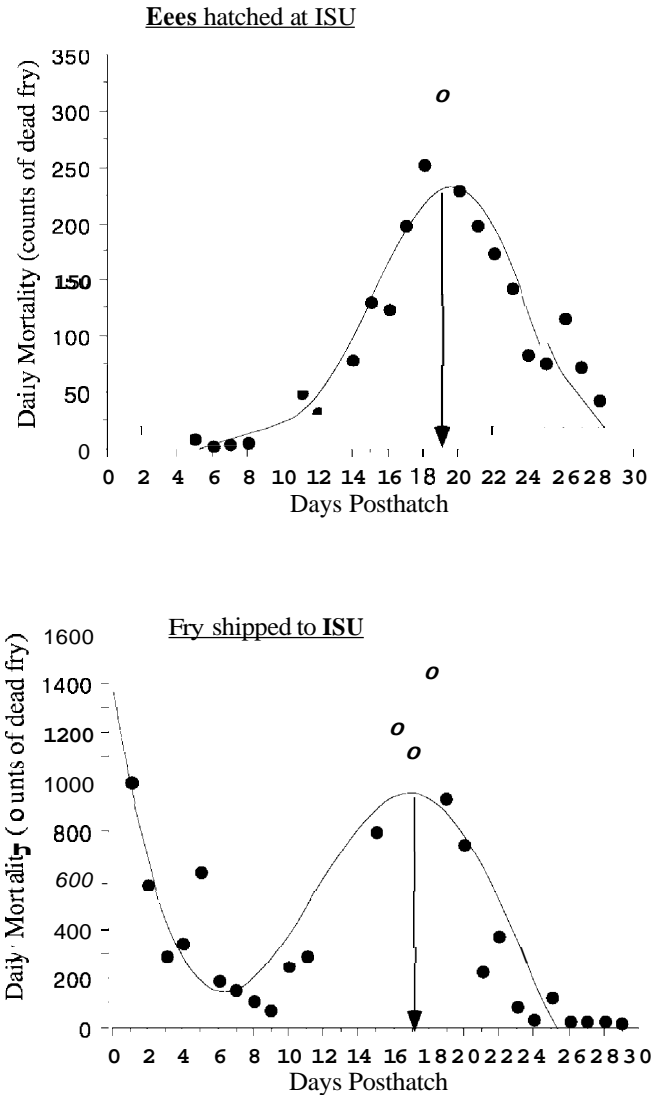
higher the oxygen concentration, the longer the fish at hatching. In my laboratory, the mean lengths of two groups of walleye hatched from fish spawned out-of-season were smaller than newly hatched walleye from the same stock that are spawned in the normal season (unpublished data).

Hatchery personnel frequently measure the volume of a known number of 2- to 3-day-old fry as a basis for estimating number of fry for stocking. Information on number of fry/mL has not been published. In the course of our research, many volumetric measurements of fry for stocking experimental tanks have been made but the values are variable (Table 1). Variability may be related to the diversity of stocks that were used, the care or lack of it in removing excess water, but especially the age of the fish at the time of stocking. Although the fish have not begun to feed, the number/mL decreases with age from 1-4 days; measurements in our laboratory are usually made at the time of stocking, about 2-3 d posthatch.

**Postlarva I**

Postlarva I is the stage following absorption of the yolk sac but before disappearance of the oil globule. After disappearance of the yolk, or slightly before then, larvae begin feeding (exogenous feeding), and gas bladder inflation begins. Krise and Meade (1986) indicated that first feeding begins at 100-122 TU. Our measurements (Bristow and Summerfelt, in preparation) indicate that the TU to yolk sac disappearance (68 TU) is much earlier than first feeding (132 TU). Before feeding, the energy requirements of the larvae for swimming and searching for food must be provided by the oil globule. First feeding walleye (8.5-9.0 mm) have a mouth width of 0.7 mm and a gape of 1.5 mm (Li and Mathias 1982), which is sufficiently large to cannibalize similar-sized siblings or to consume the standard size (400 µm) of the starter feed.

Balon (1984) considered the transition of the embryo (prolarva) to exogenous feeding to be the decisive event in development, because failure to accomplish first feeding results in mortality. Because persistence of the oil globule aides buoyancy and it serves the basic energy needs of the larvae, the peak period for mortality does not occur until the 16 to 19 days posthatch or at the end of postlarval II (Figure 2).



**Figure 2.** Mortality curve for walleye fry hatched at the culture site (upper) compared with curve for walleye hatched elsewhere and transported to the culture site in plastic bag (lower). It is typical to observe high mortality in the first few days after stocking of fry that were transported to the culture site, but not for fry hatched on site.

**Postlarval**

Postlarva II begins about the time the oil globule disappears (Li and Mathias 1982), which is about 226 TU, in the 14th day posthatch at a mean temperature of 61.5°F (16.4°C) (Bristow and Summerfelt, in preparation). Li and Mathias (1982) stated that the postlarval stage lasted about 8 days, that is from 5- to 6-d posthatch to about 13- 14 d posthatch at 20°C. They reported that fish were 16-19 mm long at the end of this stage. Nelson (1968) marked completion of the postlarval

stage when the adult complement of pyloric caecae (3) were developed.

After the yolk sac and oil globule disappear, nutrient reserves are exhausted and exogenous feeding must be effective or the larvae quickly starve. Starving fish exhibit a stress syndrome behavior (Beyerle 1975), or they revert to prolarval behavior, swimming to the surface and drifting back to the bottom (Krise and Meade 1986). These behavioral patterns may be related to noninflation of the gas bladder which is discussed in the section titled “Noninflation of the gas bladder.”

The end of the postlarval II stage marks the end of gas bladder inflation. Reports that show progressive increases in gas bladder inflation rates after this period are the result of mortality of fish that have not inflated the gas bladder, not because fish are continuing to inflate the gas bladder. After the first loop of the intestine develops the pyloric sphincter develops and separates the common bile duct in the intestine from the pneumatic duct in the dorsal wall of the stomach (Marty et al. 1995). This developmental event prevents walleye older than 12 days from inflating their gas bladder because air bubbles may enter the pneumatic duct only after the large ingested bubbles can be actively cleaved in the foregut. That process requires secretions with surfactant properties to decrease surface tension of the ingested bubble. The bile is a likely source of these secretions (Marty et al. 1995). The end of postlarval II stage and beginning of the juvenile (fingerling) stage is not marked by conspicuous and convenient developmental milestones. The swim bladder has inflated and feeding successful or the fish die. Other than mortality related to transportation stress, the period of greatest mortality is 16-19 days posthatch, that is the beginning of the juvenile stage (Figure 2).

### **Juvenile**

Juvenile stage begins about 15-18 days posthatch at a length of about 20 mm. At the end of the postlarval II stage, fin rays are limited to the lower lobe of the caudal fin, but as the juvenile stage progresses the fin rays develop in the rest of the caudal and other paired fins, and spinous rays develop. Further maturation of the gastrointestinal tract takes place, gill rakers differentiate, and pigmentation increases (Li and Mathias 1982). Scale development begins at 24 mm but it is not completed until they are 45 mm (Priegel 1964).

Bulkowski and Meade (1983) described a behavioral change in juvenile walleye from positive phototaxis to negative phototaxis behavior when they are 32 to 40 mm. In intensive culture, this change begins in juveniles as early as 25 mm. The changing response of juveniles to light is important in both extensive and intensive culture. In intensive culture, relatively high light intensity (680 lux) is used by (Colesante 1996) until gas bladder inflation is first detected (8-10 d posthatch) as a means to attract fry to the surface for gas bladder inflation. After gas bladder inflation began, he reduces light intensity to 140 lux for the duration of the culture interval to disperse the fry vertically in the water column. Before they change from positive to negative phototaxis, fish in ponds can be attracted to light for night harvest (Summerfelt 1996). The change in behavior is also important in habituating pond-raised fingerlings to formulated feed, because after 40 mm walleye fingerlings are cultured at low (<16 lx) light intensity (Kuipers and Summerfelt 1994) or intank lighting is used (Siegwarth and Summerfelt 1992) to reduce stress and enhance feeding and growth.

### **Critically important cultural problems**

The most critical problems affecting success of walleye culture are:

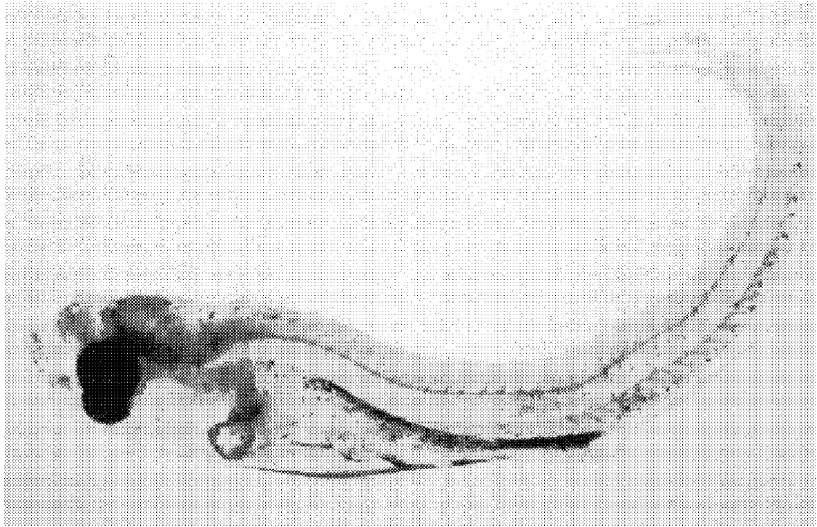
1. Noninflation of the Gas Bladder (NGB)
2. Clinging behavior
3. Nonfeeding
4. Cannibalism

These constraints had to be overcome before intensive culture became possible, but it seems from present perspective, that NGB and clinging behavior have had a greater impact on nonfeeding than the suitability of fry feeds, and both problems influence incidence of cannibalism.

### **Noninflation of the gas bladder (NGB)**

NGB is important because it contributes to mass mortality, larval deformities (lordosis) (Figure 3), susceptibility to stress-induced mortality, diseases and toxicant, it slows growth, and increases susceptibility to cannibalism or predation (Chatain 1986; Kitajima et al. 1994). Fry without an inflated gas bladder struggle to maintain position and they eventually starve because of the high energy cost of swimming and difficulty in capturing food. NGB makes fry vulnerable to cannibalism because fry without an inflated gas bladder have





**Figure 3. Lordotic deformity of postlarval I walleye associated with noninflation of the gas bladder.**

erratic behavior and poor swimming ability (McElman and Balon 1979). NGB in striped bass leads to decreased growth rates and increased susceptibility to stress (Lewis et al. 1981). Walleye fry lacking an inflated gas bladder are typically smaller than siblings which have inflated their gas bladders (Kindschi and McConnell 1989). NGB is not limited to walleye, it has been a major problem in the intensive culture of striped bass (Bulak and Heidinger 1980; Cornacchia 1981; Bennett et al. 1987; Chapman et al. 1988) and other species (Weppe and Bonami 1981; Chatain 1986; Chatain and Ounais-Guschemann 1990; Kitajima et al. 1994; ).

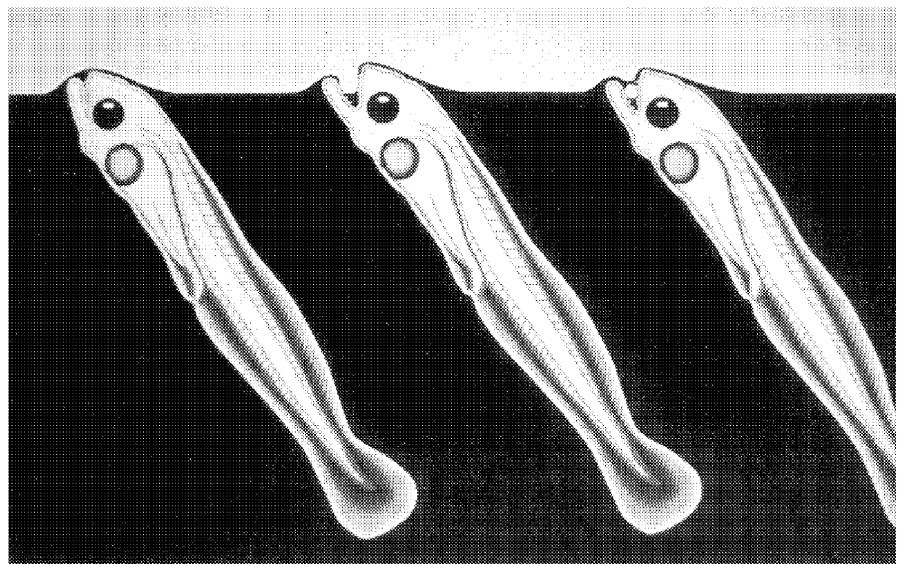
It was essential to develop effective strategies to overcome this imposing problem. When the problem was first recognized, many hypothesis were proposed as to its etiology, including nutrition, genetics and several environmental factors (Howey et al. 1980; Barrows et al. 1988; Kindschi and MacConnell 1989; Loadman et al. 1989; Bushman 1992).

In most fish, initial filling of the gas bladder is accomplished by gulping and swallowing air (Figure 4), then mechanically forcing air bubbles from the foregut through the lumen of the pneumatic duct to

the gas bladder (Vogt 1842, cited by McEwen 1940; von Ledeber 1928; Tait 1960; Marty et al. 1995; Rieger 1995). Salmonids, catfishes, minnows, and other soft-rayed (physostomous) fishes have a permanent connection (pneumatic duct) between the foregut and the gas bladder, and gas bladder inflation may occur over an extended interval. Salmonids may fill their gas bladder at least three months after hatching (Tait 1960). On the other hand, most spiny-rayed (physoclistous) freshwater and marine fishes have a functional pneumatic duct for only a brief interval; thus, their ability to fill the gas bladder is limited to a short interval after yolk sac absorption. A few species of physoclistous fish do not possess a

pneumatic duct in early larval stages—they seem to fill their gas bladder by secretion of gas ( $\text{CO}_2$  or  $\text{O}_2$ ) into the lumen of the gas bladder from the gas gland epithelium (McEwen 1940; Doroshov et al. 1981).

For walleye, the interval of gas bladder inflation after hatch is said to be 214 TU (that is 10.7-12.5 days at 20-17°C, respectively) (McElman and Balon 1979), 5-11 days (Barrows et al. 1988), 7-14 days (Kindschi and Barrows 1993), and 6 to 12 days (Marty et al. 1995). Although these dates differ slightly, it is certain that the window of opportunity for initial gas bladder inflation is relatively short. It is assumed that failure of the gas



**Figure 4. Larval walleye penetrating water surface to gulp air for first filling the gas bladder. Third fish on right is ingesting an air bubble.**

bladder to inflate during this specific period of development is irreversible. In many teleosts, gas bladder inflation typically takes place shortly after the transition of the prolarva from yolk sac respiration to gill respiration (McElman and Balon 1979), concurrent with yolk sac absorption (Tait 1960), and the initiation of exogenous feeding (Battaglione and Talbot 1990).

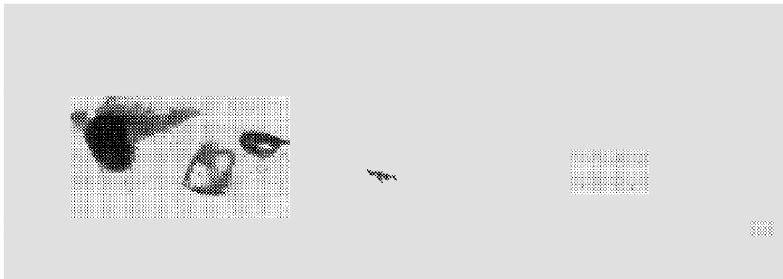
It has been conjectured to state that the interval for gas bladder inflation ended with atrophy of the pneumatic duct, in fact the pneumatic duct is still present when gas bladder inflation ceases (Marty et al. 1995). The inflation process is a two step procedure: The first step is to initiate inflation; the second is to fully extend the gas bladder. In the first step, air gulped at the water surface (Figure 4) is ingested, but bubbles must be small enough for passage through the 25- to 45- $\mu\text{m}$  diameter pneumatic duct. The relatively large bubbles ingested at the surface are fragmented by surfactant-like secretions in the foregut. Marty et al. (1995) suggest that the surfactant is derived from the bile, which is discharged into the same part of the undifferentiated foregut as the opening from the gut to the pneumatic duct. The bubbles are forced by mechanical pressure from flexing of the gut through the pneumatic duct into the gas bladder (Rieger 1995). At the end of the primary

inflation stage, the gas bladder has a spherical shape (Figure 5). Immediately following initiation of gas bladder inflation, the second stage begins when the vascular rete of the gas gland (located on the ventral surface of the gas bladder) functions to continue the inflation process, stepping up pressure within the gas bladder until the gas bladder assumes an elongated-shape (Figure 6).

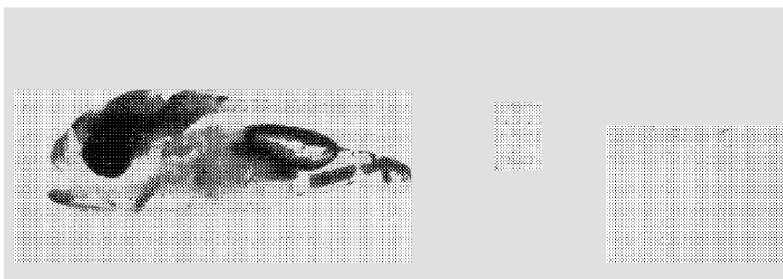
An oily layer on the water surface will prevent the larvae from breaking the water surface, and the primary stage of gas bladder inflation will not occur. Thus, NGB is most often the result of contamination of the water surface by oil. This may be from compressors or submersible pumps, feed or even the fry (Boggs and Summerfelt 1996). Interference with the second stage of inflation, which takes place 12 to 19 days posthatch, results from bacterial aerocystitis, an inflammation of the gas bladder epithelium. With or without oil, the surface tension is usually sufficient to support small particles of feed as well as bacteria and fungi. If the fry ingest surface film or partially decomposed feed that is heavily contaminated with microbes, feed and microbes may be aspirated into the gas bladder on the microfilm surrounding the air bubble (Figure 7). Although gas bladder inflation advances to the spherical stage,

inflammation of the epithelial lining of the gas bladder will lead to dysfunction of the gas gland, which prevents full extension and can cause deflation of the small, gas bladder. However, in an intensive culture environment, where formulated food is abundant, some fish without inflated gas bladders may survive. In our laboratory, some walleye have been raised without an inflated gas bladder to more than 200 mm.

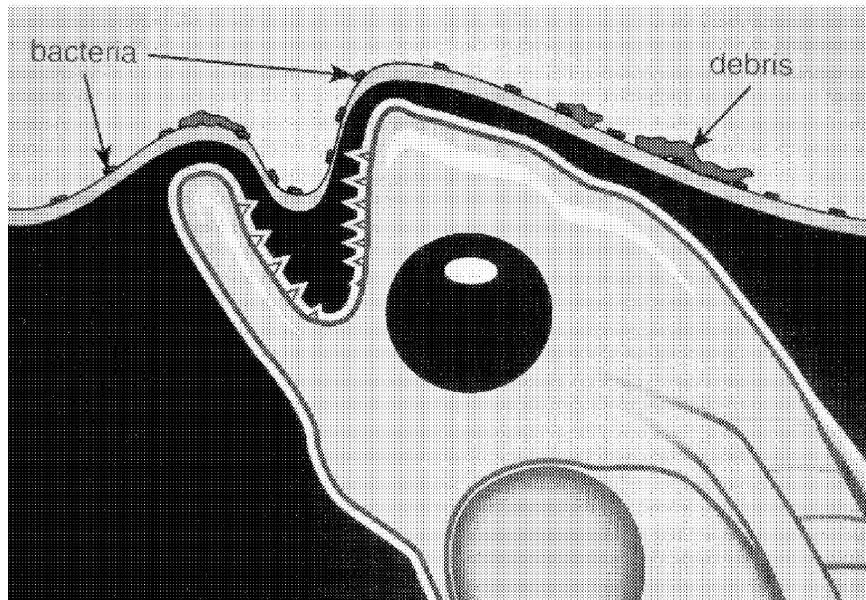
In the past, some investigators regarded NGB an artifact of intensive culture, but Kindschi and Barrows (1993) established the fact NGB occurs in pond-raised walleye as well. They found NGB in fish from 53.7% of 188 ponds sampled from 15 pond culture facilities in nine states. Although, only 3.5% of 4,229 fish examined did not have an inflated gas bladder, the incidence of NGB was 55% in one pond. In another study, Barrows et al. (1993a) noted finding an incidence of 74% of 13,000 pond-raised fingerlings; they did not state whether that



**Figure 5. Early gas bladder inflation (gas bladder is spherical) of 9-d-old, postlarval II stage walleye (16.8°C average, 151 TUs) with remnant oil globule.**



**Figure 6. A 14-d posthatch (17.2°C average, 240 TUs) walleye (no oil globule) with elongated gas bladder and food in gut.**



**Figure 7. Larval walleye gulping air at the water surface that is contaminated with microbes and feed particles may cause bacterial aerocystitis, an inflammation of the gas bladder epithelium that causes collapse of a partially inflated gas bladder.**

was from one or many ponds. The reports by Kindschi and Barrows (1993) and Barrows et al. (1993a) demonstrate that NGB is not unique to walleye reared in tanks.

Kindschi and Barrows (1993) also found that a small, but unrecorded percentage of walleyes with uninflated gas bladder had lordotic deformities, a condition I have seen in intensively raised walleye (Figure 3). Lordotic changes caused by vitamin C deficiency are most often located below the soft-rayed dorsal fin (Kindschi and Barrows 1993), whereas lordotic changes in the vertebral column from NGB are located below the spiny-rayed dorsal fin. Vitamin C deficiency produces other clinical signs of pathological changes, especially breaking of the isthmus, but we have not observed isthmus breakage or other signs of vitamin C deficiency in fish with NGB.

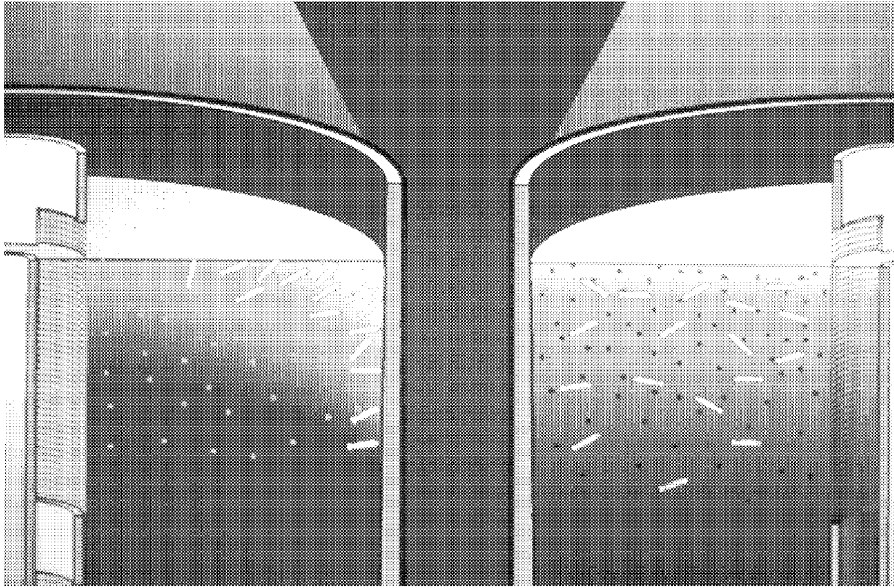
The effectiveness of the culture system to produce high percentage of fish with inflated gas bladders should be determined for a new system, but also routinely for quality control. Fish lacking an inflated gas bladder should not be stocked, and pond-raised fish that are habituated to formulated feed in the extensive-intensive culture procedure or stocked in cages should be checked for gas bladder inflation. In my research on intensive culture of walleye, gas bladder inflation is examined in fish samples from all culture tanks at

weekly intervals from 7 to 28 days. At least 30 days, and 1.1 in (28 mm), walleye are quite transparent and the gas bladder easy to observe (Figure 13). Fry are observed in a petri dish on a dissecting microscope, using transmitted light with 6-7 x magnification. Barrows et al. (1993a) compared four methods (light Table, anesthesia, saltwater floatation, and X-rays) for detecting the presence of an inflated gas bladder in fingerings 3.1-6.6 in (80-167 mm). They recommended the light Table method or the anesthesia method (used with a 3% salt solution) for routine screening.

#### ***Clinging behavior***

In intensive culture of walleye in relatively clear water (i.e., low turbidity), a large portion of fry cling to the walls of the tank. This seems to be an innate phototactic behavior. They swim toward light, not only direct light, but reflected light, even in tanks painted with a flat black paint. Fry up to 3 weeks of age showed a marked preference for extremely bright light (7,800 lux), by week 9, most juveniles preferred lower (2-4 lux) light intensities (Bulkowski and Meade 1983). Corazza and Nickum (1981) observed greater fry dispersal in tanks with gray walls than in tanks with white, yellow, or green walls. A diffuse light source may be beneficial.

Turbid water (Bristow and Summerfelt 1994) does an exceptional job of dispersing the fry (Figure 8). In tanks with turbid water, fry are concentrated near the surface, but dispersed horizontally, in clear water, fry have a greater vertical distribution, even going to the bottom of tanks with black lateral walls but gray-colored bottom. The horizontal dispersal of fry in turbid water seems to be the consequence of the light-scattering effect of turbidity which reduces the amount of light reflected from the tank walls, thereby eliminating fry attraction to the tank walls. Turbidity also reduces cannibalism, perhaps because cohort encounters are reduced inasmuch as the fry are more evenly distributed throughout the tank. Loadman et al. (1986) suggested that cannibalism may be reduced when fry are dispersed throughout the water column.



**Figure 8. Comparison of larval behavior in clear (left) and turbid (right) water culture. Fry in tanks with clear water are attracted to reflected light from the sides of the culture tank. In turbid water the light scattering effect of the suspended clay particles diffuses the light and fish are distributed across the tanks. (Used with permission, Journal of the World Aquaculture Society).**

**Nonfeeding**

Early reports of nonfeeding by larval walleye raised in intensive culture were commonplace: “Typically, many of the walleye fry never showed any interest in the food” (Beyerle 1975). Nonfeeding fish and cannibalism were considered the major problems for intensive culture of walleye (Howey et al. 1980). The problem was related to color or palatability of the feed, or inadequate particle density, but success with brine shrimp was sometimes poor also. Fry distribution within the rearing tank may also affect the opportunity of fry to encounter and consume feed particles. Bristow and Summerfelt (1994) reported a major difference in feed acceptance of fry on the 7th and 14th days in turbid water compared to clear water tanks (Table 2).

It seems that turbidity improved the ability of larval walleye to distinguish and

eat. Perhaps it improves contrast between the brownish-orange feed and the milky gray color of the turbid water, or because the light-scattering effect of the turbidity may have better illuminated each feed particle (i.e., some light would be reflected on all sides of the feed particle as opposed to only the top half in clear water), thus increasing the ability of the fry to see the feed. Visual stimuli are said to be important for successful feeding of walleye (Rottiers and Lemm 1985). Corraza and Nickum (1981) observed that the phototactic behavioral response of walleye larvae exceeded the response to all other stimuli short of direct physical contact. Nonfeeding would be expected of larvae that are clinging to the walls of the

culture container, or in walleye that had not inflated their gas bladder. Reasons given for nonfeeding in previous experiments is inexplicable, however, transparency of the water may have been a major factor

**Cannibalism**

Walleye are predaceous fish, consuming zooplankton, aquatic insects, and fish in that order as they grow from first-feeding to juveniles in ponds. Cohort cannibalism

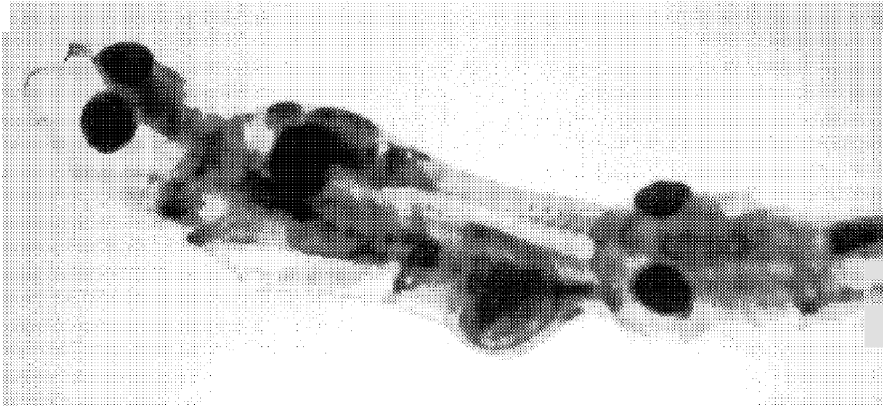
is the name given to sibling cannibalism, where fry of about equal size attack each other (Loadman et al.

1986). Most mortality from cohort cannibalism occurs from trunk attacks, not the result of successful consumption of the prey, which is from the tail first (Figure 9). Cannibalism begins as soon as the fry begin feeding (Howey et al. 1980) and it can be a major factor in total mortality when fish are not feeding (Olson 1974).

**Table 2. Age when walleye begin feeding for fish raised in clear (0.4 NTU) and turbid (23.8 NTU) water (Bristow and Summerfelt 1994)<sup>1</sup>**

Days posthatch	Fry (%) with food in gut	
	Clear	Turbid
4	0	6
7	13.3	94.7
14	90.7	98.7
21	98.7	100.0

<sup>1</sup> NTU is nephelometric turbidity unit.



**Figure 9. A chain of 10-day-old walleye fry feeding on similar-sized siblings (photo by B. T. Bristow).**

Cannibalism in intensive culture of walleye to 21-d posthatch differs among stocks: 3.4-5.4% for stocks from IA, KS, and OH, but 10.5 to 17.6% from ND, WI, and MN (Heys et al. 1996). Thus, certain wild stocks that exhibit an inherent tendency to cannibalize should be avoided also. It is important to avoid stocking fish that differ by more than 1-day of hatching. Fish hatched on separate days and fish from different stocks often have different initial lengths (Hey et al. 1996). It has long been known that fish-size differential in walleye populations increases cannibalism (Nickum 1978; Howey et al. 1980). Fish that differ by more than 1-day in age would have a size advantage over younger fish that may be sufficient to induce cannibalism.

Cannibalism can be avoided by feeding frequently with adequate amounts and appropriate sizes of a quality feed. Loadman et al. (1989) recommended a particle density of formulated feed close to 100/L. Cannibalism is reduced in turbid water culture (Bristow and Summerfelt 1994; Bristow et al. 1995), perhaps because fish accept formulated feed sooner than in clear water (Table 2).

### Basic methodology

Intensive culture of walleye from hatch to a small fingerling requires provisions for biological characteristics of the species and environmental factors:

- Culture tanks: size, shape, and color.
- Screens
- Surface sprays
- Aeration and pumping
- Light and temperature
- Turbid water culture

- Stocking
- Feeds, feeders and feeding
- Tank hygiene
- Water quantity and quality

### Culture tanks

Nearly all possible tank shapes have been investigated for fry culture. Bristow et al. (1988) described a double-tank made up with an inner 22 gal (83-L) plastic trash container submerged in a 55 gal (208-L) fiberglass barrel. The purpose of the design was to obtain an

upwelling distribution of water. An 11.8-in (30-cm) stainless steel screen was attached to the top of the 22 gal (83-L) inside container for an outlet screen. The double-tank was designed to obtain an upwelling current and circumferential ring of micropore tubing was used to keep fry from impinging on the screen. Another upwelling design was described by Kindschi and MacConnell (1989). Conical-bottom tanks were used to separate feed and fecal material from the rearing area, but fry were contained within a removable 12 mesh/cm (472  $\mu$ m) aluminum screen basket of 65-L volume.

Loadman et al. (1989) described a cuboidal tank with a flow pattern that was designed to keep the feed in suspension and maintain a high particle density. That design was not as effective as circular tanks, however (Barrows et al. 1993b; Moore et al. 1994a). The three case studies for this chapter provide a diversity of tank shapes and operations including rectangular fiberglass tanks (Colesante 1996), cylindrical (circular) fiberglass tanks (Moore 1996), and trough-shaped tanks with an upwelling current (Moodie and Mathias 1996).

Clinging of fry to the sidewalls of the tank will affect success of the culture system. The clinging behavior is a function of tank size, color of the tank walls, light intensity, and turbidity. Fry are strongly attracted to light, direct or reflected light. They will cling to the sidewalls, screens, and they are even attracted to the bottom of the tank in tanks with black sides but light colored, bottom. Their presence on the bottom results in some loss of fry when they are siphoned up in process of cleaning the tanks.

Tank size is another factor affecting clinging. A greater percentage of the stock cling to the sides of smaller than larger tanks because the lateral area (ft<sup>2</sup>, m<sup>2</sup>) per unit of tank volume (ft<sup>3</sup>, m<sup>3</sup>) of tanks walls of smaller tanks is larger than that of larger tanks. Also, in culture water with low turbidity (<10 NTU), the distance from tank side walls to locations in the tank away from the sides will increase beyond the reaction distance of the fish and a smaller percentage of the population will be attracted to the tank walls. The 179 gal (679-L) tank (123 cm across the top, and 109 cm across the bottom, and 76 cm deep), used by Moore et al. (1994b) and Moore (1996) is a desirable size. Moore et al. (1994b) obtained 74.9% survival to 21 days with 99.5% GBI when this tank was stocked at 20/L.

Colesante (1996) reports that darkened sides of the rearing tanks minimizes clinging behavior; and high-intensity lights help achieve uniform distribution of fry, and attracts the fry to the surface to aid in the process of gas bladder inflation. Corazza and Nickum (1981) observed improved larval dispersal in tanks with gray walls compared with tanks with white, yellow or green walls. A diffuse light source and a flat black or gray tank color is helpful to reduce reflection of the light from the tank walls. Survival in my laboratory was generally poor results until turbid water was used (Bristow and Summerfelt 1994). Artificial turbidity was developed by addition of a small volume of a clay slurry. With turbid water, clinging behavior is avoided and tank color does not matter. Some hatcheries have naturally turbid water ( $\geq 15$ -25 NTS) from colloidal clay (particle sizes  $\leq 2$  mm) that is not removed by rapid sand filtration.

### Screens

Whatever form of the standpipe or drain system, it must be equipped with a screen to retain the fry, but in feeding formulated feed, it is important to use the largest mesh size possible to keep the screens from clogging, even if feed is lost through the screen. The same problem occurs with feeding live food. The 400  $\mu\text{m}$  FFK (particle range 240-675  $\mu\text{m}$  [Loadman et al. 1989]) and brine shrimp nauplii, 200 to 250  $\mu\text{m}$  will pass through the smallest mesh needed to retain fry. Colesante et al. (1986) used screens with openings of 200  $\mu\text{m}$  to reduce loss of brine shrimp nauplii. Barrows et al. (1988) used a 600- $\mu\text{m}$ -mesh stainless steel screen. In 1988 I used stainless steel fabric with 0.380  $\mu\text{m}$  mesh and 30% or 36% open area, but that retained too

much waste feed and caused fouling; in 1989, a mesh size of 0.704 width of opening and 44.2% open area was used (Summerfelt 1990). Three- to 5-d posthatch fry were retained by screens not larger than 710  $\mu\text{m}$  (10.31 meshes/cm) between threads and no more than 53% open area (Kindschi and Barrows 1991a). Of course, fry grow in length between hatching and 3-days but depth of body decreases with yolk sac absorption, so the same 710  $\mu\text{m}$  screen seems to retain newly hatched as well as 3-day-old fry.

Since the 1990 culture season, the drain in our culture tanks has been surrounded by 6-in (152 mm) PVC pipe which has large areas of PVC cut away, the cut-away sections are covered with square-weave, monofilament nylon (Nitex™, Tetko, Inc., Briarcliff Manor, New York). After cleaning the PVC with PVC cleaner, the fabric is attached to the PVC pipe with PVC pipe glue. The fabric needs to be held in place for about a minute, but then it bonds tightly. In the first 21-d posthatch, 710  $\mu\text{m}$  mesh screens are used; after 21 days posthatch, a second set of screens with 1,000 $\mu\text{m}$  (1 mm) mesh with 58% open area to improve effluent flow. To prevent accidental use of the 1 mm mesh when fry are first stocked, the top rim of the pipe with 1000  $\mu\text{m}$  screens is painted red. Fry size at hatching varies with the stock, but the smallest size fry we have encountered are those produced by out-of-season spawning. A few of those fry were small enough to pass through the 710  $\mu\text{m}$  mesh.

### Surface spray

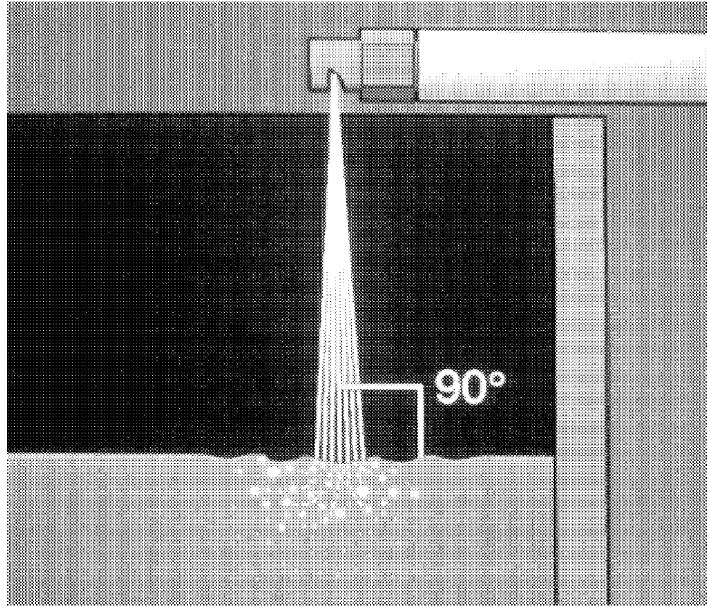
Moore et al. (1994a) reviewed GBI for seven studies on intensive culture of walleye fry, the most recent reference was 1991. Data given in that review for GBI for 23 trials ranged from 10 to 93.9%, with a mean of 42.1% (95% confidence interval of 30.3-53.9). Thus, GBI was typically poor until it was discovered that a spray of water to the surface would enhance gas bladder inflation (Barrows et al. 1993b; Moore et al. 1994a). Barrows et al. (1993b) reported 98.4% gas bladder inflation (GBI) in tanks with a spray and 51.7% GBI in tanks without a spray. Moore et al. (1994a) obtained 89% GBI in circular tanks with spray and 62% in tanks without a spray. In another study, using sprays on all tanks, Moore et al. (1994b) obtained 98.5 to 100.0% GBI in nine fry density trials with survival as high as 64.1%. Although Howey et al. (1980) found that 20% of walleye raised on brine shrimp and daphnia did not have an inflated gas bladder, seemingly, walleye fed brine shrimp during the interval of gas bladder inflation

inflate their gas bladders without a surface spray (Colesante 1996).

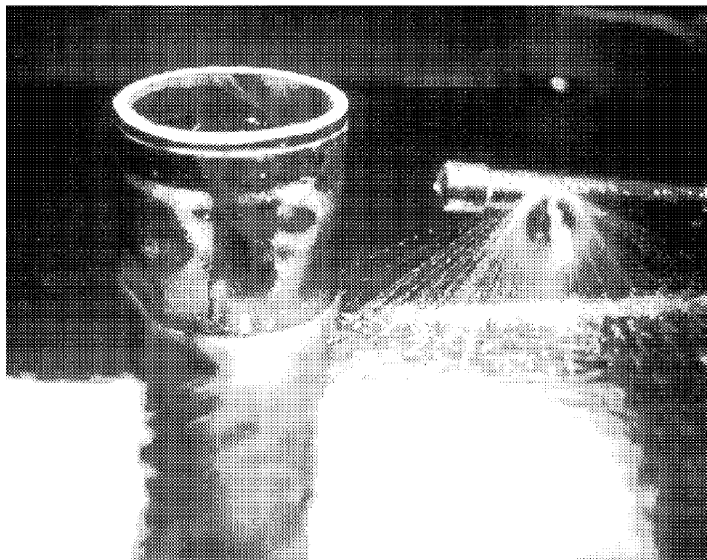
The spray removes the oil film and cleans the surface of feed and debris (Figure 10). In circular tanks with a circular flow pattern, the water passes under the spray head with each revolution of the water mass. The critical volume of flow needed for an effective spray has not been determined: Moore et al. (1994a) used a flow rate of 0.3 to 0.5 Wmin through the spray head and Bristow and Summerfelt (1994j) used 1 L/min. It seems important for the spray to impact the surface with enough pressure to produce a slight depression in the water under the spray (Figure 11). The sprayer is a 180" perimeter nozzle (A. H. Hummert Seed Co., Inc., St. Louis, Missouri) and it is directed at a 80-90" angle with the water surface from a distance of not more than 20 cm above the water surface. The number of spray-heads needed per 1,000 cm<sup>2</sup> of tank surface has not been critically evaluated, but Moore et al. (1994b) observed slightly higher GBI in tanks equipped with one spray per 5,941 cm<sup>2</sup> (GBI values were 99.5, 99.5, and 100%) compared with tanks with one spray per 4,778 cm<sup>2</sup> (GBI values were 88.7, 96.3 and 88.0%).

**Aeration and pumping**

Degassing and aeration of the water supply should be done before



**Figure 10. Sketch designed to explain how a surface spray works to clear oil from the water surface of a fry culture tank. The spray is a 180° perimeter nozzle (inset).**



**Figure 11. Small (150 L), experimental fry culture tank that shows the trough formed in the water surface by the impact of the surface spray operated at a flow rate of 1 L/min.**

the water is delivered to the culture tanks. Compressors should not be used to aerate water destined for use in intensive culture of fry because they often contaminate the air with oil in the compression cycle. Compressed air contaminated with oil that is bubbled through water will transfer the oil to the water. The oil will rise to the surface and interfere with gas bladder inflation. Submersible pumps should also be avoided. They often leak minute quantities of oil, but when a seal breaks, the pump releases a large volume of oil. To avoid contamination of fry culture tanks with even small quantities of oil, water should be pumped with centrifugal, axial flow or peristaltic pumps.

A column of rising air bubbles in a fry culture tanks may cause turbulence, and fast rising air bubbles will throw fry out of the water where they will stick to the side walls above the water line. Barrows et al. (1988) used a curtain of small air bubbles from micropore tubing to prevent fry impingement at the water outlet. In some hatcheries, an air line is placed around the center standpipe to keep fry from being impinged on the screen. A large surface area of the screen reduces current velocity. Also, if

screens are painted black, fry attraction to reflected light will be reduced.

**Light and temperature**

Research findings on light intensity are varied. It seems that fluorescent lights, flood lamps, and natural light at intensities of 100 to 700 lux are acceptable. Colesante (1996) uses high-intensity lights that produce 680 lx at the water surface; and Moore (1996) recommended 500 lux. Diffuse lighting is often recommended to distribute fry and to deter fry from clinging to the sides of the tank. However, light is a necessity. Fry do not feed in the dark.

The minimum water temperature should be 55°F (12.8°C) (Colesante 1996). Moore (1996) reported that feed acceptance and survival is greater at 65°F (18.4°C) than at 55°F (12.8°C), and an ideal temperature range is 60-65°F (15.6-18.4°C), with 65 (18.4°C) as optimum. Moodie and Mathias (1996) maintain a temperature of 68°F (20°C) throughout. Moore (1996) stimulates fry feeding by a sudden increase of 9°F (5°C) for 24-h when fry were 5 d posthatch. I also use a temperature rise to stimulate feeding, but a somewhat different regimen: the temperature is slowly increased from incubation temperature to about 59°F (15°C) by the 4th day, feeding is started and the temperature is increased about 5°F (2.8°C) to 63.5°F (17.5°C); it is not reduced in the 24-h, but incremented slowly over the next 25-d to about 20°C at 30-d post-hatch (Figure 12). Walleye typically grow about 0.67 mm/d in the first 30-d (7.5 mm at hatch to 27 mm in 30 days)

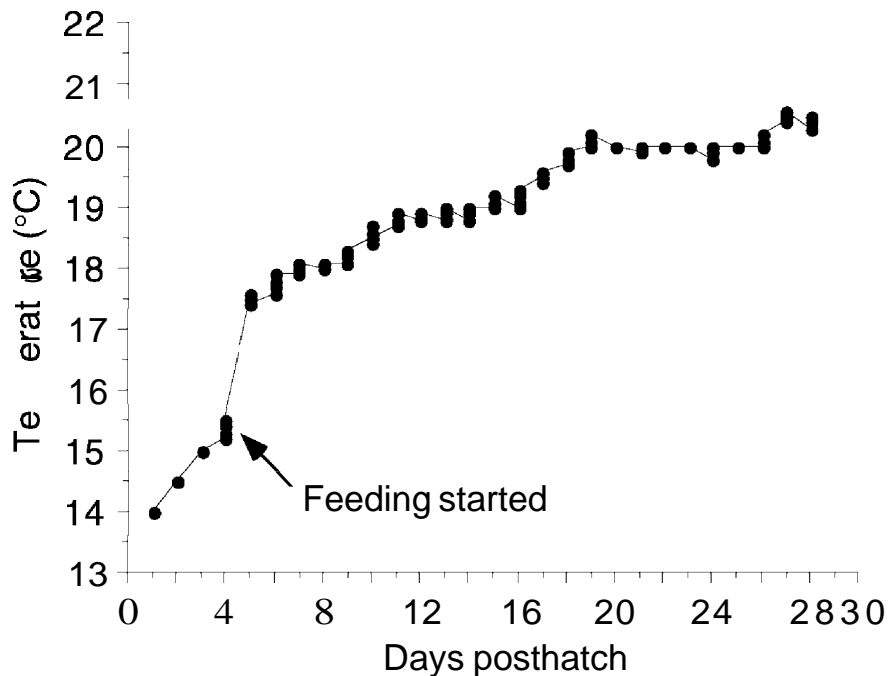
**Turbid water culture**

Survival, length, and weight of larvae raised in turbid water to 21-30 d were significantly greater than for larvae raised in clear water (Bristow and Summerfelt 1994). Larvae were more evenly distributed in the turbid water than in clear water (Figure 8). The turbid water was milky gray. In turbid water, larvae did not congregate on the tank walls as they did in clear water. The light-scattering effect of

turbidity seems to reduce the amount of light reflected from the tank walls. The clinging behavior of walleye to the sidewalls of the culture tanks was greatly reduced or eliminated in turbid water.

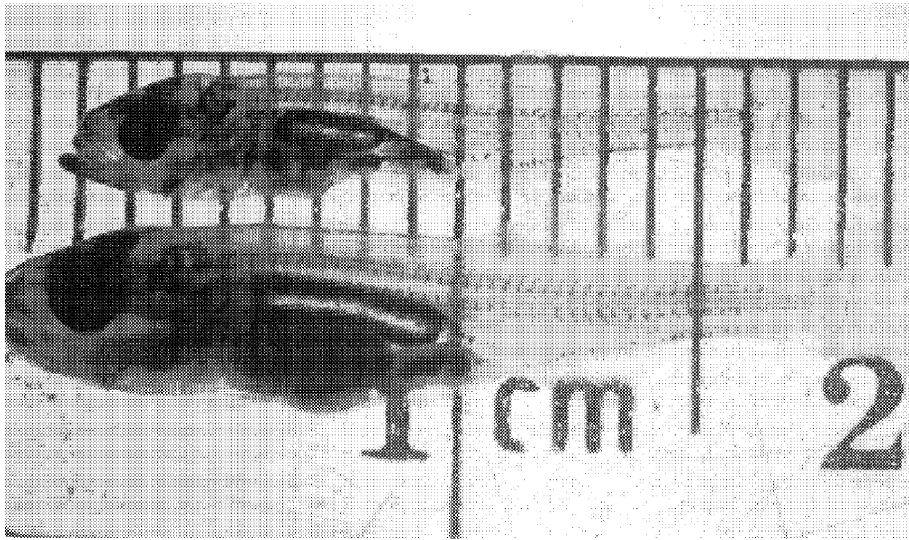
Survival is increased, the fish are on feed sooner; their weight at 21 to 30 d posthatch was 200 to 300% larger than weight of fry raised in clear tanks (Bristow and Summerfelt 1994). In all of the six comparisons of larval performance in clear and turbid culture since 1993, the fish in turbid grew substantial faster than fish in clear water (Figure 13).

Turbidity is defined as "an expression of the optical property that causes light to be scattered and absorbed rather than transmitted in straight lines through the sample" (APHA et al. 1989). In ponds, turbidity is caused by suspended inorganic matter (clay, silt, finely divided organic matter), soluble organic compounds, and phytoplankton. Suspended solids are defined as "the residue retained on a glass fiber filter dried to a constant weight at 103-105°C" (APHA et al. 1989). Typically, there is a strong relationship between the concentration of suspended solids and turbidity (Lloyd et al. 1987).



**Figure 12. Sample temperature (°C) profile of the temperature regimen used to raise walleye fry hatch to 30 d posthatch. The sharp increase on the 4th day coincides with initiation of feeding. The goal is to reach 20° C by the 28th day.**





**Figure 13. Comparison of 30-day-old juvenile walleye raised in clear (top) and turbid (bottom) water. The mean total length (weight) for fish raised in turbid water was 27.4 mm (0.16 g) compared with 15.0 mm (0.02 g) in clear water.**

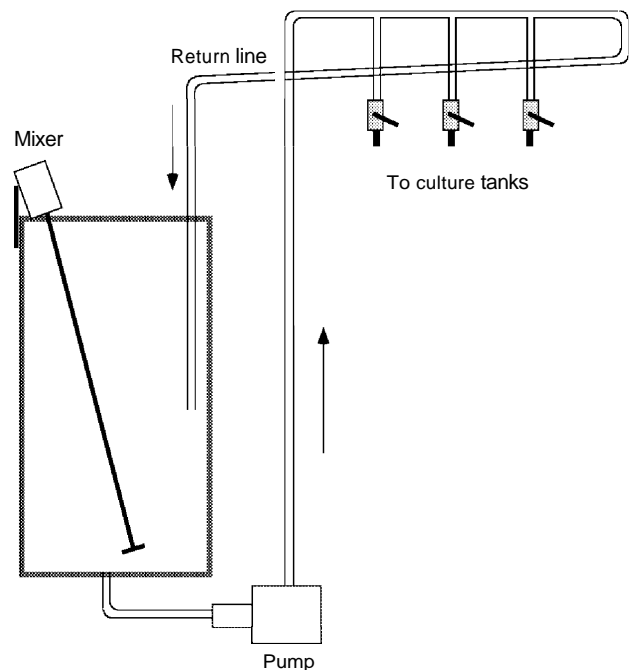
The system described by Bristow and Summerfelt (1994) to supply a clay-slurry for six, 40 gallon (150-L) tanks has been enlarged for use with six, production-scale (264 gal; 1,000L) tanks (Figure 14). The clay slurry (8 g of clay per L) is stirred with a commercial mixer with a ¼-hp motor that turns a shaft at 1,725 rpm. The clay slurry is distributed with a ½-hp pump that has a calibrated flow of 38 gpm with 10ft of head. To attain a turbidity level of 50 NTUs in a 1,000L tank would require addition of clay slurry every 20-minutes (Figure 15). To avoid running the clay-slurry tank *dry*, the setup is designed to not pump more than 144 of the 600 L capacity of the clay-slurry tank per day. The mixer runs continuously, and the pump distributes 2 L of stock every 20 minutes, 72 times each day. For a single 1,000L, it would require about 3.3 lb (1,500 g) of clay per day. To supply more culture tanks with the same system, the concentration of the clay slurry should increase proportionally, but the mixer and pump can handle at least six, 1,000L tanks.

**Stocking density**

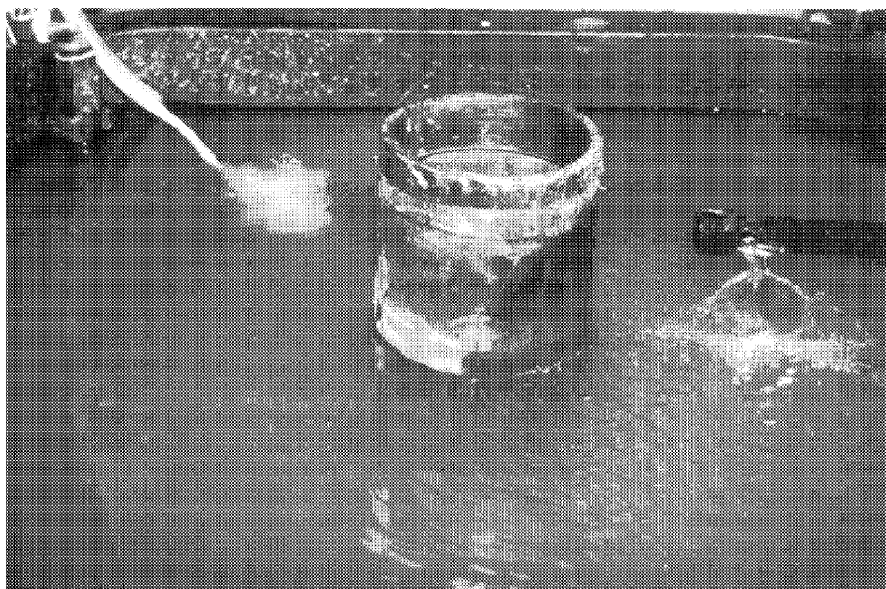
Populations of yolk sac fry (prolarvae) shipped in plastic bags to the culture site will often experience high mortality after stocking, which is a major contrast to stocking fry that are hatched on site, because substantial mortality in these populations rarely occurs until the critical period in the late postlarval II stage (Figure 2). Although shipment of eggs may result in some egg mortality, it is better that the mortality take

place in the hatching jar rather than the culture tanks because dead fry liberate oil from their oil globules (Boggs and Summerfelt 1996). Colesante and Schiavone (1980) attributed mortalities that occurred in the first 36-h after transporting walleye fry in plastic bags to suffocation of the fry in the bottom layers and corners of the bags, especially after the bags were tempered in holding troughs. The mortalities increased in relation to the length of time the bags are left stationary rather than to fry densities in the bag. We have observed substantial mortalities in the first few days after stocking fry that

were transported to our facility in plastic bags, but not in with fry that were hatched on site from eggs that were shipped (Figure 2). Mortality normally peaks at 17- to 19-d posthatch at 19–20°C when non-feeding fry starve.



**Figure 14. Design of a clay-slurry tank and distribution system for intensive culture of walleye fry in turbid water.**



**Figure 15. Experimental fry culture tank (150 L) showing injection (upper left corner) of a clay slurry that is used to maintain turbid water (50 NTU).**

Fry for stocking should be from those collected in the fry catch-tank that hatched within a short time interval, preferably within 12 hours, but not more than 24 hours. The fry are removed from the catch tank and placed in another holding tank for 2-3 days with low water flows before stocking the culture tanks.

Enumeration of fry for stocking can be done by hand counting, volumetrically, gravimetrically, or by an electronic counter (Kindschi and Barrows 1991b). The counter can count 500,000 fry per hour with an average error of 3%. They found that gravimetric methods were more accurate than volumetric estimates, which have been the standard hatchery procedure.

Recommendations for stocking density (number of fry/L) for large-scale production of walleye fry in intensive culture varies from 21 (Colesante 1996) for fry started on brine shrimp, to 40 (Moore 1996) and 56 (Moodie and Mathias 1996) for fry fed formulated feed. With improvements in survival, stocking densities of 80 to 100/L may result in excessive fry density before 30-days are reached, and problems may develop with poor water quality and disease (bacterial gill disease and columnaris disease) causing unnecessary mortality.

### **Feeds, feeders, and feeding**

The development of formulated feeds for fry (“starter” feeds) is reviewed by Barrows and Lellis (1996). Early

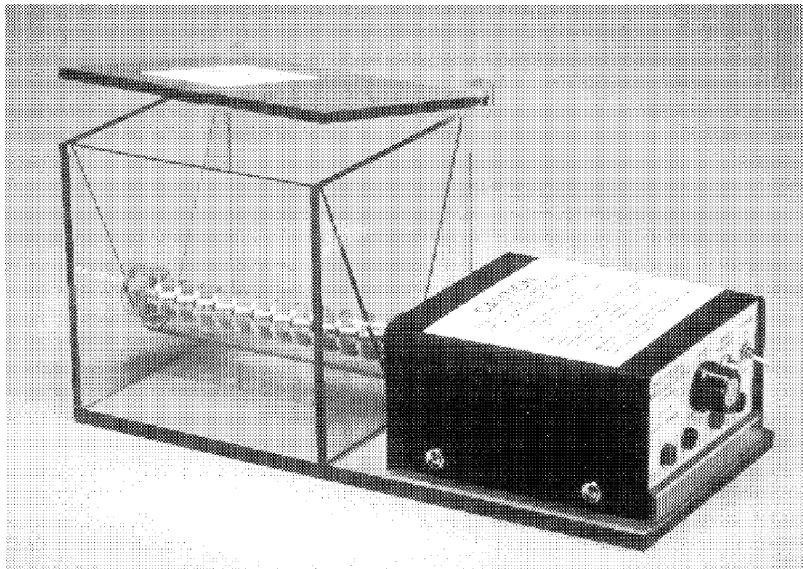
efforts in feeding formulated feeds quite naturally included trout and salmon feeds (Beyerle 1975), but all early efforts at feeding formulated feed were unsuccessful (Nickum 1978). The U.S. Fish and Wildlife Service W-series diets developed at the Spearfish facility were the most common. The W-16 formulation was the latest in that series. When added to the culture tank, rings of oil sheen were visible; perhaps the oily surface film that inhibited gas bladder inflation was the reason for poor performance on this diet rather than the composition and proximate analysis. Barrows et al (1988) used a feeding ring to confine the surface film from the feed to a portion of the water

surface. A feeding ring is not needed with use of a surface spray. Feed size, color, and texture have been considered the most important factors affecting acceptability. Failure of the fish to feed or digest the feed has been cited frequently as a major factor in the failure of walleye culture on formulated feeds.

The FFK B-series (B-400 and B-700) feeds (Biokyowa Inc., Chesterfield, Missouri) have been used by more investigators than any other for feeding fry formulated feeds (Kindschi and MacConnell 1989; Moodie and Mathias 1996; Moore 1996). In 1996, the FFK B-series cost \$40.86/lb (\$89.89/kg) plus delivery charge. However, it is not necessary to keep fry on the B-series for more than 7 d, a “phase” feeding strategy proposed by Barrows et al. (1993b) can be used. Fry can be started on the B-series then weaned to the FFK C-series or other feeds without loss of performance and with 76% less feed cost per fish produced than for fish kept on FFK-B for 30-d posthatch (Barrows et al. 1993b).

There is no consensus on the amount of formulated feed to feed walleye fry during the first 30 days. Typically, fry are started on FFK-B series (B-400), followed by either the E-700 (Moore 1996) or C-700 (Moodie and Mathias 1996). The kinds and amounts of FFK feed that we have found useful are given in Table 3.

Fish feeders found at most hatcheries are for dispensing much larger quantities of feed than used in fry culture system; they are not sufficiently precise for feeding small quantities of fry feed accurately and consistently to prevent food deprivation or excessive feeding and tank fouling. McCauley (1970) developed a scraper feeder using a clock mechanism. Many researchers have used vibrator feeders to dispense fry feed (Loadman et al. 1989; Summerfelt 1990), but the amount of feed the feeders dispense at each feeding could not be regulated with accuracy or consistency (Loadman et al. 1989). Moodie et al. (1992), and Moodie and Mathias (1996) used custom made, precision feeders that are not available commercially. The feeder used by Moore et al. (1994a, 1994b), Bristow (1994), Bristow et al. 1996), and Moore (1996) is a custom-made auger feeder (Northland Aquaculture, Inc., Ames, Iowa) that delivers small amounts of feed accurately and consistently (Figure 16). Timers must be capable of turning on every



**Figure 16.** An auger feeder used to dispense precise quantities of feed for feeding fry in small and production-scale tanks (Moore et al. 1994a and 1994b). Figure courtesy of Northland Aquaculture, Inc., Ames, Iowa.

**Table 3.** ISU guidelines for feeding fry.

Length (mm)	Quantity (g/1000 fry)	Ratio (B400/C700) <sup>a</sup>
<11	5.0	100:0
11-12.9	5.8	75:25
13-14.9	7.3	50:50
15-16.9	8.5	25:75
17-18.9	10.1	0:100
		C700:WG9206
19 -20.9	11.9	75:25
21 -22.9	13.6	50:50
223	15.0	100%

<sup>a</sup>B400 and C700 are FFK-series WG9206 is the walleye grower diet

5 minutes for intervals of less than 1 second.

Feeding rates and feeding frequency are important for successful fry culture.

Feeding should be at 3-5 min intervals at least 22-h/day. Feeding should be stopped only to clean the tanks. Survival has been poor when feeding was stopped for more than a 6-h interval per day.

**Tankhygiene**

In feeding formulated feed, tanks must be cleaned at

least once per day. During tank cleaning, the inflow is not turned off to avoid forgetting to return the flow. The bottom with food, debris and dead fish is siphoned out. A siphon hose is inserted between the screen and standpipe to lower the water halfway to allow wiping growth from the sidewalls of the tank; the wiping stroke is upward to facilitate removal of the scum from the walls and to avoid contaminating the culture water. When needed, the sidewalls are wiped to the bottom to remove accumulation of scum. Providing that water level is still sufficiently below the outflow level of the standpipe, the screen is removed and washed in warmwater with a spray and replaced. Other variations in tank cleaning procedures are given in the case studies.

**Waterflow**

Before walleye fry begin feeding (i.e., prolarvae), inflows are regulated to obtain 0.5 exchanges per hour. Once feeding begins, the exchange rate is increased to 0.75 exchanges per hour and eventually to 1.0 exchange by 21-days. Higher flow rates are recommended by others (Nickum 1978). Although high flow rates may be necessary to obtain desirable water quality, high exchange rates imply higher current velocities which may overtax the swimming ability of the fry and deplete their energy resources.

### Waterquality

Poor water quality causes stress and mortality, and reduces growth. The reduction in water quality which is sufficient to stress fish often increases the risk of bacterial gill diseases and catastrophic loss of fish, even if it does not have an immediate impact on production. The water quality parameters of primary concern are dissolved oxygen (O<sub>2</sub>), ammonia (NH<sub>3</sub>), nitrite (NO<sub>2</sub>), carbon dioxide (CO<sub>2</sub>), and gas supersaturation from either oxygen (O<sub>2</sub>) or nitrogen (N<sub>2</sub>). Dissolved oxygen should not be less than 5 ppm, preferable near saturation, but oxygen supersaturation should be avoided. Recent observations suggest that walleye fry are especially sensitive to supersaturation (Summerfelt 1990). In 1995 culture season, high mortality of walleye fry occurred in tanks supplied by surface water pumped from a pond that had supersaturated oxygen (Tom Harder, Max McGraw Wildlife Foundation, personal communication). When the problem reoccurred in the spring of 1996, it was resolved by passing the inflow through a degas column (pipe packed with plastic media, but open on both ends) into an extra tank; the water from that tank was pumped to the culture tanks. The problem seems similar to large diurnal swings in total gas pressure (AP) observed in ponds used to produce channel catfish and bluegill without artificial aeration (Boyd et al. 1994). Boyd et al. (1994) found that diurnal changes resulted primarily from DO supersaturation produced by phytoplankton; DO increased from a mean of 67.7% (AP -40 mm Hg) of saturation in the morning to a mean of 158.9% (AP, 111 mm HG) in the afternoon, with an exceptional value of 343.6% saturation. Thirty-four percent of afternoon values exceeded AP 115 mm Hg, pressure known to cause mortality during continuous exposure bioassay.

Upper limits for continuous exposure to the common metabolites (ammonia, carbon dioxide, nitrite), pH, and chlorine should not exceed general standards for fish culture as given by Piper et al. (1982) and Meade (1989):

unionized ammonia	< 0.0125 to 0.02 ppm
carbon dioxide	<10 ppm
nitrite	0.1 ppm in soft water, 0.2 ppm in hard water
pH	6.5-8.0

These values are guidelines, they should not be interpreted to mean that concentrations slightly above the

guidelines will be lethal. Toxicity will change with the age, temperature, pH, alkalinity, turbidity and other factors. Because walleye fry have been too difficult to raise in experimental systems, relatively little information is available on their sensitivity. However, Nickum (1978) stated that walleye fry “seemed to be unusually sensitive” to traditional chemical therapeutic agents.

High ( $\geq 9.8$ ) pH may be lethal to walleye in the absence of ammonia (Bergerhouse 1992), but pH as low as 8.3 (i.e., OH<sup>-</sup> ions) shifts the equilibrium of ammonia to the unionized form (NH<sub>3</sub>) that is more toxic to fish (Thurston et al. 1981):



Bergerhouse (1992) reported that in the absence of ammonia, mortality of 3-d-old walleye fry in a 6-h exposure was 37% at a pH of 10.3 and 100% at a pH of 10.5. However, mortality to 4-d-old fry was 100% after only 4-h exposure to pH 10 in the presence of 0.98 mg/L of unionized ammonia. Bergerhouse also found that 12-d-old fry were more sensitive than 3-d-old fry to pH. Bushman (1992) observed that pH values  $\geq 8.3$  reduced gas bladder inflation of larval walleye. Sudden changes in pH may occur when fry received in plastic bags are transferred to culture tanks. It is important to recognize that pH is a log scale, therefore, 1 unit decrease in pH (8 to 7) is a 10 fold increase in hydrogen ions. A pH change of 0.8-1.0 pH unit caused total mortality to striped bass larvae (Doroshev 1970). Water of very low alkalinity (< 10 ppm) is poorly buffered and may show undesirable pH fluctuations.

Tolerance of walleye for highly alkaline waters is not known. Obviously, the water supply should not be contaminated with pesticides, PCB's, heavy metals (mercury, lead, zinc, cadmium), chloramines, or free chlorine, or toxic residues from toxic paints or sealants.

### Case studies

The case studies by Colesante (1996), Moode and Mathias (1996), and Moore (1996) that accompany this chapter provide contrasting strategies for production-scale intensive culture of walleye fry. Colesante uses brine shrimp for 30 days, followed by 14 days of mixed feeding brine shrimp and formulated feed; Moode and Mathias and Moore use only formulated feed. Moode and Mathias use a unique trough and recycle system for

fry culture; Moore uses standard circular tanks with a central drain; Colesante uses rectangular tanks. Colesante does not report a problem with NGB but he describes some precautions undertaken to avoid the problem. Moore uses surface sprays to prevent NGB. Moodie and Mathias reported occurrence of the NGB problem with their system. To reduce the problem, they added much larger volumes of “new” water to the culture system when gas bladder inflation was taking place to remove surface oils during the period. However, they have had gas bladder inflation rates of only 16 to 23% in the production scale tanks. Stochng densities, fry/L, of 21 (Colesante), 40 (Moore) and 56 (Moodie and Mathias) are used.

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# Intensive Culture of Larval Walleye on Formulated Feed

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## Introduction

We developed a commercial scale culture system for raising walleye on formulated feed from the egg to fingerling stage, which makes efficient use of space and labor. The main obstacles to the commercial production of walleye larvae in the past have been the inability to successfully start large numbers of larvae (35,000–40,000) per rearing unit, failure of the fish to inflate their swimbladder during the first few days after hatching, and variable survival when using formulated feed. The critical requirements for a successful system are constant suspension of food particles, because walleye larvae will not feed from either the tank bottom or the water surface, conditions that allow the larvae to gulp air at the surface during the process of swimbladder inflation, and the use of high quality feeds.

## Methods

The culture system (Figure 1) we developed to meet these criteria consists of a 21 x 2.7 ft (6.4 x 0.82 m) trough with vertical, upwelling water currents; removable, oversized outlet screens; and a system of automatic, precision feeders. The unit is filled with 91.8 ft<sup>3</sup> (2.6 m<sup>3</sup>) of water. Water is supplied through a polyvinyl chloride (PVC) pipe perforated with a row of 0.06 in (1.5 mm) diameter holes. The pipe runs the length of the trough, along one side and near the

bottom. Water flowing through the holes produces an upwelling current. Water exits from the trough via five screened boxes, located along one side of the unit above the inlet pipe (Figure 1). Each screen has a surface area of about 8.1 ft<sup>2</sup> (0.75 m<sup>2</sup>). Mesh size of the screen is 500 μm. The purpose of the large screen surface is to reduce water velocity around the trough outlets. This results in minimal suction on larvae and food particles. Placement of the screens along one side of the trough reduces their influence on upwelling current patterns. The boxes are removable and can be opened to allow thorough cleaning. Precision feeders are designed to supply precisely controlled amounts of 400 μm diameter feed at specified time intervals.

Other components of the system include: a waste particle remover, biological filter, inline electric heater, and aeration tower. The relationship of all components are shown in Figure 1. These components (minus the

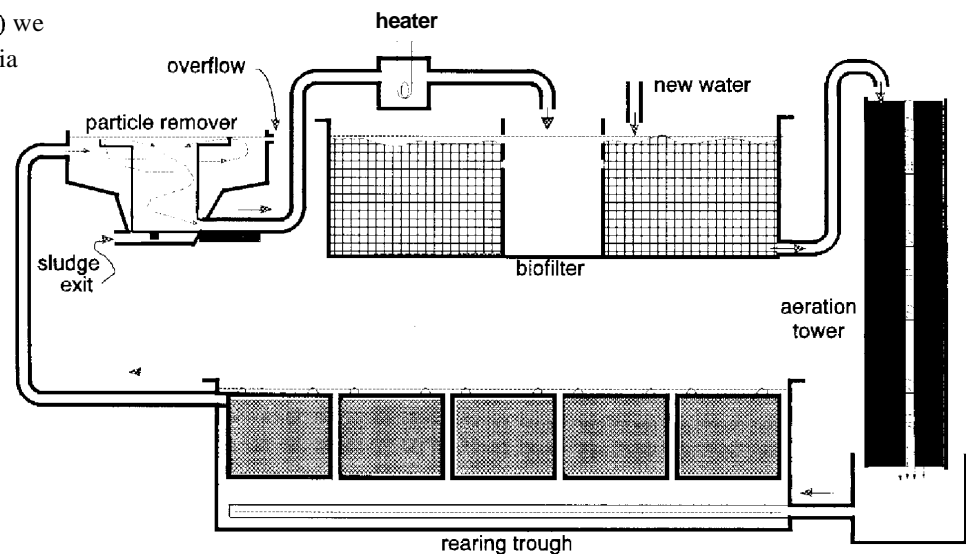


Figure 1. Larval rearing system components. Arrows indicate direction of water flow. Proportions not to scale.

screen boxes), together with additional tanks, are also used for juvenile grow-out after 30 d.

The rate of water flow to the trough is critical; although an upwelling flow is necessary to prolong the suspension of food, excessive water velocities are detrimental to the larvae. In our design, water exchange in the trough and water velocities within the trough can be varied independently within limits. Water exchange rate and velocities are kept relatively low before the larvae begin feeding. After feeding begins, we increase the exchange rate and water flow, to achieve a velocity of about 3.1 in/s (8 cm/s) at the surface.

Waste water from the trough flows by gravity to a particle separator. Water is then pumped to an inline water heater from which it flows by gravity through a 6.6 ft (2 m) oxygenation tower and a down-flow, submerged-medium biofilter. The tower contains a series of internal baffles designed to restore the oxygen content of water to about 94% saturation or about 8.4 ppm (8.4 mg/L) at 68°F (20°C), at a flow rate of 35 gpm (132 L/min). Water from the oxygen tower is collected in a small reservoir, from which it is pumped back to the trough. This pump is required to produce the pressure necessary to circulate water in the trough. The system is backed up by alarms that can be triggered by inappropriate water temperatures, low water levels, or a pump failure. Aeration with compressed oxygen is available in case of electrical or pump failure.

We believe that in any intensive culture system good hygiene is crucial to success. This is achieved through the use of water from deep ground wells and disinfection. At the start of each season, the entire system is treated with a 10% solution of Prepodyne (West Chemical Products Ltd.). During operation, the system is isolated from surface water, and workers involved with fish ponds are required to disinfect boots and equipment used in and around the system.

To maintain the disease-free certification of our hatchery according to Canadian Fish Disease Regulations, we prolong the walleye hatching period to 21 d using cold 50°F (10°C) water. This allows sufficient time to test parental fish for the presence of various diseases (infectious hematopoietic necrosis, infectious pancreatic necrosis, ceratomyxosis, furunculosis, bacterial kidney disease, enteric redmouth disease, whirling disease, viral hemorrhagic septicemia,

edwardsielliosis, pseudomonad septicemia, vibriosis, motile aeromonad septicemia, and myxobacterial infections). Prior to placement in the incubation jars and after the eggs are fully hardened, they are disinfected with a 10 min immersion in a 1% solution of Prepodyne. During incubation, additional prophylactic treatments are not required. Dead eggs are removed daily. Water recycling is high during egg incubation, minimizing water use.

We have also designed a system to exert control over the developmental age of larvae at the time of hatching. During the hatching period the larvae accumulate in a 158.5 gal (600 L) holding tank after leaving the incubation jars. The outlet of the holding tank is provided with a removable screen. During hatching water velocity through the incubation jars is increased to help move larvae out of the jars and to flush lipids and other wastes from the jars and tank. Larvae remain in the holding tank 3–4 d and are moved to the rearing trough about 1 d prior to disappearance of the yolk. During this period, we siphon out empty egg shells and dead larvae once or twice a day. The cleaning process is simplified by manipulating light levels, which in turn controls the behavior of the larvae. Newly hatched larvae avoid dimly lit areas and are strongly attracted to the beam of an ordinary flashlight or desk lamp.

Larvae are transferred from the holding tank by means of a small 0.005-in (125- $\mu$ ) mesh nylon net supported on two sides by wood dowels. In the absence of a fry counter, we estimate larval numbers volumetrically. Groups of 1,000–2,000 larvae are netted and most of the water drained from the net. The larvae are gently poured into a 50 ml graduated cylinder to which a 6 in (15 cm) diameter funnel is clamped. Prior to this, the number of larvae occupying 2–3 ml of a 10 ml graduated cylinder is determined by actual counts of several samples. Appropriate quantities of larvae are then placed in the trough, which was filled with water maintained at the same temperature as that of the holding tank. After the larvae are moved to the trough, the temperature in the trough is raised to 68°F (20°C) over the next 48 h.

The system requires a maximum flow rate of about 1,850 gal/d (7 m<sup>3</sup>/d). Water temperature is maintained at 68°F (20°C) during the 30-d culture period. We keep dissolved oxygen concentration close to the saturation level, or at least >65% of saturation. Unionized ammo-

nia concentrations are held at <0.1 ppm (<0.1 mg/L). Total ammonia concentrations do not exceed 0.7 ppm (0.7 mg/L). We find these levels can be maintained at the larval and feed densities we use. Declining oxygen levels can be corrected by more diligent cleaning, backwashing of the filter, and flushing of sludge in the particle remover trap.

During the period when the swimbladder is inflating we supply make-up (“fresh”) water at a rate of 1,664 gal/d (6.3 m<sup>3</sup>/d). This high level, which is equivalent to 2.5 exchanges/d, reduces the accumulation of surface oils and films which inhibit swimbladder inflation. During the remainder of the larval culture period this volume is reduced to 185 gal/d (0.7 m<sup>3</sup>/d) (equivalent to an exchange of the system every 2.5 d).

We have had good success by supplying feed shortly before the larvae will accept it. We now think that the percentage of fish with inflated swimbladders can be significantly improved by withholding food until the level of swimbladder inflation reaches 80%. Feeding attacks (attempted cannibalism) among larvae, the main cause of mortality at this stage, are minimized by uniform lighting to avoid dense concentrations of larvae in brightly lit localities and precision feeding to ensure an adequate density of food particles.

We feed the larvae Fry Feed Kyowa (FFK) B-400 (Biokyowa Inc., Chesterfield, MO) feed for the first 7 d and FFK C-700 feed thereafter up to 30 d. If necessary, larvae are fed B-400 feed longer to ensure that all individuals are ready for the larger C-700 feed. This feeding strategy gives smaller fish a chance to catch up in size to larger ones and may, to some extent, retard the growth of larger ones, so that variation in size will be minimized. The automatic feeders we use are custom built and are capable of reliably releasing about 0.002 oz (0.06 g) of B-400 food per delivery. We have been unable to obtain precise control of feed delivery using commercial vibratory feeders. We have used five of the custom built feeders per trough, but think ten would ensure a more even feed distribution. If ten feeders were used, each would need to deliver feed at about 2 min intervals to maintain the correct feed particle density in the water. The larvae are held under continuous illumination and fed on a 24 h cycle. We think that continuous light reduces the incidence of cannibalism which would result from food deprivation during hours of darkness if a light:dark rhythm was used.

Feed is supplied in quantities sufficient to maintain a density of at least 378 particles/gal (100 particles/L). We monitor feed particle density and adjust the output of the feeders to maintain the desired feed density. The same procedure is used after the diet is changed to C-700. Overall total quantity of B-400 used in a single rearing unit has averaged 12 lb (5.4 kg) over a 7 d period. The average total amount of C-700 has been 30.2 lb (13.7 kg) for the remaining 21 d. It is important to note that we do not base the feeding rate on the number of fish present, or the density of fish, but rather on maintaining in suspension about 378 particles/gal (100 particles/L).

A major objective of our research has been to reduce the labor requirements which constitute a substantial portion of aquaculture production costs. A system has been developed which minimizes labor costs. The system described above, requires 5 h of labor/d to produce the numbers of 30 d juveniles described below. At times the labor has to be dispersed over 24 h to monitor the larvae.

Much of the labor involves tank cleaning. The system relies on supplying an excess of food, which must later be siphoned from the trough once or twice daily. The outlet screens must be removed and cleaned once or twice daily, using a high-pressure water hose and long-handled brush. Every second day, after the fish are receiving C-700, the trough sides and bottom must be brushed or wiped as needed to remove the organic residue which accumulates on the trough surface (we use solid kitchen scrub pads). Sludge traps in the particle remover and elsewhere in the system need to be drained every 2–3 d.

Other tasks involve monitoring water quality parameters, swimbladder inflation, feed supply and particle density, level of feeding, growth rate, general well-being of the larvae, and level of cannibalism. The latter is determined if a fish is observed grasping another tail-first in its mouth. This kind of cannibalism is indicative of a much more prevalent form in which the victim is grabbed from the side, held for a few seconds and released after a struggle. Almost all fish held this way eventually die. These brief attacks outnumber the tail-first form by a factor of 9:1, hence evidence of even a few larvae being swallowed tail-first indicates that far more are being lulled by brief side attacks.

The system described has produced 23,000 30-d-old juveniles from a starting density of 72 larvae/gal (19 larvae/L). An initial density of 211 larvae/gal (56 larvae/L) produced 33,500 juveniles. Survival to 30 d was 47% and 23% respectively. Swimbladder inflation at 72 larvae/gal (19 larvae/L) was 16% and at 211 larvae/gal (56 larvae/L) was 23%. The primary goal of

our most recent research has been to restore successful swimbladder inflation to the level of over 80%, which occurred when the fish were raised in smaller 41 gal (154 L) tanks. Changes in culture procedure, by culturing identically-aged larvae and delaying feeding until swimbladder inflation is almost complete seems to result in 80% swimbladder inflation.

# Intensive Culture of Walleye Using Brine Shrimp and Formulated Diets

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## Introduction

Fisheries management programs in New York State annually require 300,000 advanced (4–6 in, 10.2–15.2 cm) fingerling walleyes. To fulfill management's request, a fish culture research project was established to develop methods to produce fingerlings efficiently. Over a 12 year period, this research evolved into an intensive culture protocol using brine shrimp and formulated diets. This case study describes the methods used by the New York State Department of Environmental Conservation (NYSDEC) to intensively culture advanced walleye fingerlings at the new Oneida Fish Cultural Station.

## Oneida Lake Fish Cultural Station

The new hatchery was completed in 1993. It is a single story building about 240 x 80 ft (73.2 x 24.4 m). Two thirds of this building is devoted to fish production with space for tanks, egg incubation, and brine shrimp production. The remaining portion of the building is devoted to water treatment including filtration, ultraviolet sterilization, oxygen injection, water heating, and fish culture research. The water used in the hatchery is from Scriba Creek, a soft-water (35 ppm calcium carbonate) tannin-colored stream. Water from Scriba Creek is impounded behind a concrete dam 0.3 mi (0.48 km) above the hatchery; water flows from the dam to the production facility by gravity. There is about 8 ft (2.4 m) of head in the production portion of the building; maximum flow of water is 1800 gpm (113 L/sec).

The Oneida Fish Cultural Station has 32 fiberglass rectangular tanks with charcoal-colored (gel-coated) sides and aqua blue bottoms. These tanks are 25 x 4 x 2.3 ft (7.6 x 1.2 x 0.7 m) (length x width x depth); water levels can be adjusted by changing the height of stand pipes, and volume will vary from 150 ft<sup>3</sup> (4.2 m<sup>3</sup>) when fry are stocked to 180 ft<sup>3</sup> (5.1 m<sup>3</sup>) when fingerlings are

trained to accept formulated diets. Twenty-three tanks are used to start walleye fry on brine shrimp. Each of these designated start tanks is equipped with a 15 gal (56.8 L) capacity liquid (brine shrimp) feeder supplied with air for aeration of the brine shrimp slurry, and a 0.625 in (1.6 cm) solenoid valve which is normally closed. A 22-ft long (6.7-m) fiberglass feeding tube with 0.125 in (0.3 cm) holes drilled at 6 in (15.2 cm) intervals is used to dispense nauplii along the length of the tank. This feeding tube has an independent water source, supplying up to 2 gpm (7.6 Lpm) to flush the tube and nauplii into the tank. The feeding tube is adjusted to about 6 in (15.2 cm) above the surface of the water. Two Loudon-type feeders are used for dispensing formulated diet. These feeders cover 18 ft (5.5 m) of the 23 ft (7.0 m) of usable space in each tank. A set of high-intensity lights can increase light intensity to 680 lux at the water's surface; ambient hatchery lighting produces 140 lux at the surface. The other nine tanks at the hatchery are equipped with Loudon-type feeders only and are used after fingerlings are trained to accept formulated diets.

A 50-mesh stainless steel screen is initially used to confine walleye fry and brine shrimp in each tank. A 38-mesh screen is sometimes used on or about day 15; however the 50-mesh screen is often left in place until 30 d. At this point, a slotted 3/64 in wide x 0.5 in long (0.1 x 1.3 cm) aluminum panel is used to facilitate increased flows. After fish are trained to accept a pelleted ration, a 0.125 x 0.75 in (0.3 x 1.9 cm) slotted panel is used until fall when fish are harvested for stocking.

## Brine shrimp production

The production of brine shrimp nauplii at the Oneida Fish Cultural Station is accomplished using 15, 70 gal (265 L) cylindrical, insulated tubs which are 24 in diameter x 43.5 in height (61 x 110.5 cm). Each unit is

equipped with an aeration ring made of 0.5 in (1.3 cm) PVC with 0.125 in (0.3 cm) holes, a 300 w submersible aquarium heater, a clear plexiglass cover, and a remote 25 w light source. Aeration is provided by two high-volume, low-pressure air pumps. Heated and unheated cultural water is supplied to the brine shrimp area.

Water is manually adjusted to 80–85°F (27–29°C); thus temperature is maintained by the submersible heater. Salinity is adjusted to 18 ppt by adding non-iodized granulated salt. After loading up to 5.5 g/L of cysts into tubs, the brine shrimp solution is strongly aerated for a 24 hr incubation period.

To harvest the nauplii, the aeration, light and heat are turned off. The slurry is allowed to stand for 5–10 min so the outer shell of the cysts, unhatched cysts and nauplii separate in the water column. A valve is then opened that draws fluid from the bottom. The first gallon that contains unhatched cysts is discarded; the remaining fluid contains a nauplii suspension and is saved, except the contents at the very end of the vessel. The nauplii slurry is placed in the feeders.

### Fry culture

Gametes from wild Oneida Lake broodstock are generally collected in April. Prior to hatching, a portion of the fertilized eggs are designated for fingerling production using the intensive culture techniques. These eggs are placed on a separate egg incubation battery and allowed to hatch for 24 h. Fry hatched during this period are collected in a holding trough; eggs unhatched at the end of this period are removed from the egg battery. In this manner, only fry of known age (between 0–24 h) are used in the culture program.

Walleye fry from different genetic strains initiate feeding at different times. Oneida Lake walleye fry begin to feed around 100°F (37.8°C) temperature units (TU). A temperature unit is defined as the average daily water temperature (Fahrenheit) minus 32°F; therefore at an average water temperature of 62°F (17°C), about 30°F TU's (16.6°C TU's) are accumulated each day and walleye will initiate feeding between 3–4 d.

About 90,000 (21.4 fry/L) known age walleye fry are stocked into start tanks 24 hrs prior to first feeding. Fry are inventoried by volumetric displacement; displacement values (fry/ml) are determined by sampling and

counting of fry on the same day fry are stocked. Depending on their age, 160–210 walleye fry will displace one ml of water.

Water flow in each of the 23 start tanks is set between 10–15 gpm (37.8–56.8 Lpm) to minimize any effect of flow on fry distribution in the tank. A minimal water temperature of 55°F (12.8°C) is needed to start fry on brine shrimp. At Oneida, because ambient creek temperature can fluctuate 3–5°F (1.7–2.8°C) in a 24 hr period, water is usually heated to 58–60°F (14.4–15.6°C). Propane-fired boilers, heater exchangers, and packed columns are used in the heating process. When ambient Scriba Creek temperature remains above 55°F (12.8°C), water is not heated.

High-intensity lights, over each start tank, produce 680 lux at the water's surface. These lights are activated when fry are stocked. The increased light intensity aids in achieving even linear distribution of fry throughout the tank; since walleye are cannibalistic, dispersal of individuals is important. It also attracts fry to the surface of the tank which may aid in the process of swim bladder inflation.

Darkened sides on the rearing tanks minimizes "side-clinging behavior" of newly hatched walleye fry. If uncontrolled, this activity can result in lower swim bladder inflation and feeding rates.

### *First feeding with brine shrimp*

Nauplii production starts 24 h before walleyes are scheduled to receive their first food. Initially, a feeding rate of 800–1000 nauplii/fish/day is targeted. This requires incubating about 2.2 lb (999 g) of cysts in each of five tubs at 0800 h and the same quantity of cysts at 1800 hours.

The brine shrimp nauplii are harvested 24 h later from 5 tubs in the morning and 5 tubs in the evening. The hatched nauplii slurry, roughly 300–325 gal (1 135–1 230 L) from 5 tubs, is loaded directly into brine shrimp feeders following each harvest.

All brine shrimp nauplii put into a feeder during a 24 h period are used during that 24 h period. Usually, feeders dispense nauplii every 8 min for a 3–sec interval 24 h/d. Upon activation, the feeder dispenses a 500–600 ml slurry of brine shrimp into the feeding tube. The nauplii



are flushed from the feeding tube at 6 in (15.2 cm) intervals along the length of the tank.

Swim bladder inflation in Oneida Lake walleyes is initiated around 160°F temperature units (71.1°C TU's) (8–10 d). Usually within 2 d of this point, flow in each start tank is increased to between 20–25 gpm (75.6–94.6 Lpm). Over 90% of the fish raised at the Oneida Fish Cultural Station initiate feeding and inflate their swim bladder. Sampling to determine swim bladder inflation and feeding rates is not done anymore, and problems in these areas are not anticipated.

High-intensity lighting, darkened tanks sides, adequate prey density, and water quality (i.e., color and hardness) are probably responsible for this success.

In this system, mortality and cannibalism between day 0 and the initiation of swim bladder inflation is insignificant. However, when air is first detected in the swim bladder (8–10 d), mortality increases. The mortality is generally caused by a pectoral fin nip (attack) by another fish that results in death either immediate or slightly delayed. Uncontrolled nipping behavior can kill as much as 25% of the fish in a 24 hr period. Mortality from this source can be managed by reducing light intensity from 680 lux to 140 lux at the water's surface by turning "off" high intensity lights above the start tanks. This action allows the fry to disperse vertically and occupy the entire 18 in (45.7 cm) water column, instead of the upper 6 in (15.2 cm). This effectively reduces fry density by up to two-thirds and minimizes losses during this period of high mortality.

**Diet training period**

On day 30, brine shrimp feeding is increased to 1,300 nauplii/fish/d, based on the original number of fish, without consideration of mortality. At this point, 3 lb (1.4 kg) of cysts are incubated in each tub, which is a total of 30 lb (13.6 kg) of cysts per day. Also on day 30, water flow in each tank is increased to 35 gpm (132 Lpm) and feeding of formulated diets is started. The feed used at the fish cultural station is called the "New York State diet". It is a high quality (48% protein, 18% fat, 10% moisture, 8% ash) open formula feed (Table 1). Limited amounts (a 50:50 mixture of starter and 1 crumbles) are fed at 5 min intervals through 44 d, along with brine shrimp.

After two weeks of mixed feeding (d 44 posthatch), the feeding of brine shrimp nauplii is stopped and walleyes

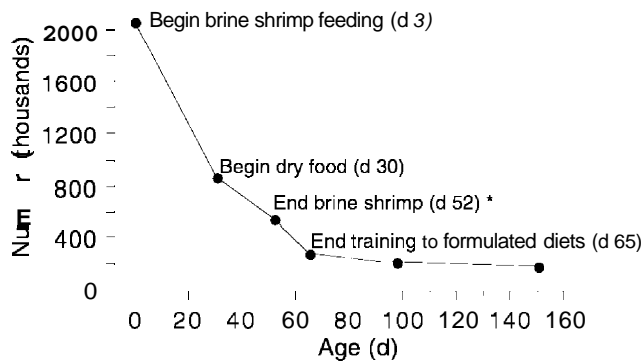
**Table 1. Ingredients used in New York State diet, No. 1.**

Ingredient	Percent
Herring-fish meal	58.0
Dried whey	8.0
Dried blood flour	5.0
Corn gluten meal	5.0
Dried brewers' yeast	3.0
Condensed fish solubles	2.5
Soybean lecithin	1.0
Tuna or herring oil	12.0
Vitamin pre-mix	3.0
Extruded wheat	remainder
Vitamin pre-mix No. 2	3.0
Choline chloride	0.58
Lignin sulphonate pellet binder	2.0
Trace mineral mix	1.5 lb/ton
Calcium propionate	2.5 lb/ton
Ascorbic acid as Stay-C	225 ppm

are only fed no.1 crumbles of the New York diet. Feeding levels of formulated feed are increased to 15% of body weight. The diet training period will generally last 2–3 weeks (44–65 d), depending upon water temperature. Fish quickly separate into two groups, those which accept the feed and those which do not (dark, listless fish). High temperatures accelerate this separation. If non-feeding fish are moved to a separate tank, significant numbers of these fish will feed. This technique is used to increase survival and to take advantage of easy removal (grading) of smaller non-feeding fingerlings.

Survival during the diet training period is affected by diet. Controlled experiments are conducted each year to evaluate formulated feeds; survival during the training period can range from 10–70% depending on the feed. Our present diet generally produces a 50% survival of fingerlings during the diet training period. In 1994, a new diet produced by Rick Barrows (of the United States Fish and Wildlife Service, Bozeman Technology Center, Bozeman, Montana) produced 70% survival during this period.

Disease outbreaks can affect survival during the diet training period. Fish being trained to accept formulated



\*Brine shrimp feeding was extended 8 d in 1993.

**Figure 1. Survival of walleye during the 1993 production season.**

diets are under considerable stress and predisposed to disease. Constant observation and prompt treatment of pathogens can be critical to success.

After being trained to formulated diets (65 d), water flow in each tank is set at 45 gpm (2.8 L/sec) to produce 2.5 exchanges of water/hr, and requirements for care and maintenance of walleye decreases. Growth after fish are trained to consume formulated diets (66–150 d) is rapid (Figure 1) and culture densities up to 2.5 lb/ft<sup>3</sup> (40.1 kg/m<sup>3</sup>) are commonly achieved with no ill effect. Survival during this period following training has ranged from 65–85% during the 2 years of production in the new hatchery.

Fish continue to be fed during this period at 5 min intervals, 24 hr/d under constant light (140 lux). Feeding rates are adjusted on a weekly basis to accommodate rapid growth; generally fish are fed at 10% of total body weight. Particle size of the New York State diet is increased as the fish grow; usually particles no larger than a 4 crumble are fed to fish stocked as fall fingerlings, 4–6 in (10.2–15.2 cm). The feed conversion averages 2.4 and ranges from a high of 5 in May (during diet training) to a low of 1.6 in August when fish are feeding on formulated diets.

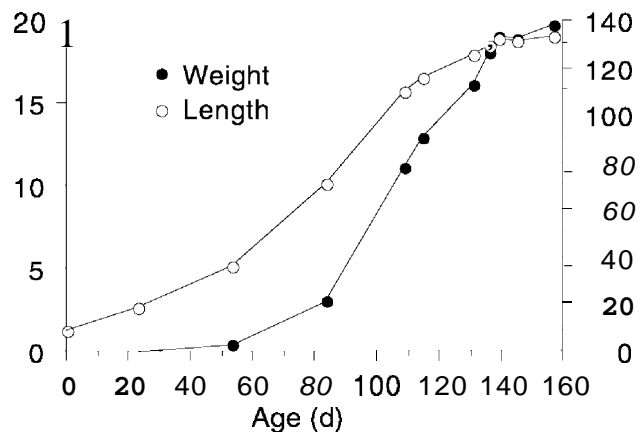
Inventory of walleye after fish have been trained to accept a pelleted ration is generally done by sampling to determine the number of fish per pound and then weighing or displacing all fish. Walleye tolerate this type of handling very well. Most fall fingerling walleye are stocked in New York between September 15–30. Walleye appear to go on a maintenance (no growth) diet when water temperatures drop below 60°F (15.6°C).

**Summary**

Production of walleye fingerlings using economical and efficient methods are goals of the New York State walleye culture program. Survival of walleye during the 1993 production season, the first year of production incorporating “new” culture techniques are encouraging (Figure 2). One hundred ninety thousand fingerlings between 4.3–5.2 in (10.9–13.2 cm), 24–41/lb (10.9–18.6/kg), were stocked; about 30,000 fish less than production goals. Overall survival for the entire 1993 production season (0–150 d) was 13.7%.

Projected walleye survival established through research and development was 57% to 30d, 50% from 31 to 65 d, and 50% from 66 to 120 d posthatch. Actual survival was 42% to 30d, 33% from 31 to 65 d, and 65% from 66 to 120d posthatch. Differences between projected and actual survival during day 0-65 are related to a NYSDEC moratorium on the use of unapproved chemicals in treating diseases of fish. As a result, diseases previously treated with chemicals are now allowed to run their course. It is expected that survival (0–65 d) will improve to projected levels when disease epizootics can be adequately controlled.

Overall, the intensive culture program for walleye fingerlings has met and exceeded expectations. Survival of fingerlings after being trained to formulated diets has been excellent; the growth of fingerlings to fall stocking has been much greater than expected. Each year of production has resulted in improvements in operational efficiency and also the future outlook for the intensive culture of walleye.



**Figure 2. Growth of walleye during the 1993 production season.**

# Intensive Culture of Walleye Fry on Formulated Feed

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## Introduction

Many resource management agencies are planning to produce substantially more large 6-8-in (15.2-20.3 cm) fingerling walleye for fisheries enhancement stocking compared with traditionally stocking of fry or small fingerlings. Currently, large fingerlings are produced in large winterkill lakes (Kinnunen 1996), and by tandem pond-tank culture methods (Held and Malison 1996). The latter production method include stocking fry in ponds, raising them to 2-in (5 cm), then training these fingerlings in tanks to accept formulated feed. Because of mortalities that occur in both pond culture and during the intensive culture phase, raising walleye from fry to fingerling on formulated feed is an attractive alternative. The two main problems of poor gas bladder inflation and low survival have slowed acceptance of this technique, however, these problems have been solved with the use of a surface spray to increase gas bladder inflation, and the Fry Feed Kyowa (FFK) B-400 to B-700 feeds (BioKyowa Inc., Chesterfield, MO) (Moore et al. 1994a, 1994b). Currently at the Rathbun Hatchery, 20,000-35,000 6- to 7-in (15.2-17.8 cm) fingerlings are produced solely on formulated feed in intensive culture environment. The objective of this paper is to summarize the walleye fry feeding techniques used at Rathbun.

## Methods

### Tanksetup

Two sizes of cylindrical tanks 73.4 and 179.3 gal (278-L and 679-L) have been used for fry walleye feeding (Figure 1). Each has a center drain and a water inflow pipe located vertically along the tank side. The inflow pipe has 1/16-in (1.6-mm) holes drilled approximately 13/32-in (10-mm) apart on the lower 12.2-in (31-cm) of the pipe. The flow is directed in a clockwise direction and is 0.8 gal/min (3.0 L/min) for the first day after stocking, and increased to 1.5 gal/min (5.7 Wmin) thereafter. To clear the surface of oil and feed to enhance gas bladder inflation, the tanks are equipped with one to four surface sprays. A single surface spray

of about 0.4 L/min is located mid-way between the tank wall and center screen of the small tanks; the large tanks have four sprayers. The tank area is covered with a black plastic curtain for the first two weeks of feeding and an incandescent light at 100 to 200 lux is recommended. The lighting helps to distribute fry evenly throughout the tank and to reduce fry congregation at the tank sides. To aid in fry dispersal, the tank sides are black, or shaded, and the bottom is a lighter color to aid in cleaning. Tanks are illuminated approximately 24 h/d.

### Fry stocking and feeding

Walleye fry, approximately 1-3-d of age, are stocked at 1,132/ft<sup>3</sup> (40 fry/L) (11,120/small tank and 27,160/large tank). We enumerate fry for stocking using a mechanical counter (Model FC2, Jentsorter Inc., Bend, Oregon), however, the volumetric method of enumeration, in which fry are allowed to settle in a graduated cylinder, may also be used. Sample counts to determine the number of fry/ml must be performed prior to using the volumetric method. Fry begin feeding when they are four to six days old, or as soon as mouth parts are developed. Feed amount and particle size is based on fish length and is dispensed as grams of food/1,000 fry/d (Table 1). Fry are fed FFKB-400 or B-700, 20-22 h a day, seven d/week. Feed is dispensed at 5-min intervals using an auger type feeder and an automatic timer to activate the feeders. One feeder is located on the small tanks and two feeders on each large tank.

Food acceptance and fry survival is greater at 65°F (18.4°C) than at 55°F (12.8°C). The ideal temperature range is 60-65°F (15.6-18.4°C) with 65°F (18.4°C) being optimum. To stimulate feeding, which increases fry survival and reduces cannibalism, a 9°F (5°C) temperature boost for 24 hours, 5 days posthatch is recommended. The temperature is then lowered to the original setting.

**Tank Cleaning and Disease**

Tanks are cleaned with a siphon on a daily basis to remove waste feed and dead fry. Screens are removed and sprayed until clean and the tank surfaces are wiped with a sponge beginning on day six.

Bacterial gill disease is the only disease problem that has been encountered during the first 25 days of feeding. A chloramine T treatment of 5.0-10.0 mg/L for 1 h for two consecutive days usually is effective with no adverse effect on the fry. An Investigational New Animal Drug permit from the Food and Drug Administration is required before the Chloramine T can be legally used.

However, bacterial gill disease starts and is not controlled, substantial mortalities may occur.

**Fry survival-large fingerling production**

Fry survival at day 25 posthatch has ranged from 35 to 75% using the methods described. The highest survival occurred at a water temperature of 65°F (18.4°C) and turbidities of 15-30NTU. Turbidity seems to allow for better fry dispersal in the tank and better food acceptance and gas bladder inflation (Bristow and Summerfelt 1995). At Rathbun, fry length ranged from 0.75-0.9-in (19-23-mm) and gas bladder inflation was >90% at 25 days posthatch. Walleye are moved to raceways for final grow-out after 25-30 d. When water temperatures range from 75-78°F (23.9-25.6°C) walleye fingerlings will grow 0.5 in/week (12.7-mm), and they will reach 6.5-7.5 in (16.5-19.0-cm) at 150 d posthatch.

**Table 1. Feeding regime (FFKB-400 and B-700) by length of walleye. The ratio of feed type and feed amount is changed when fry exceed the corresponding length.**

Fry length (mm)	Grams food/1,000 fish	Ratio of feed type (B-400:B-700)
<11	3.0	100:0
11-13	5.8	75:25
13-15	7.3	50:50
15-17	8.5	25:75
17-19	10.1	0:100
		Ratio of B-700:WG9206 <sup>1</sup>
19-21	11.9	75:25
21-23	13.6	50:50

<sup>1</sup> WG9206 is an open formula diet formulation by F.T. Barrows, US Fish and Wildlife Service Fish Technology Center, Bozeman, MT, and manufactured by Sterling H. Nelson and Sons Inc., Murray, UT.

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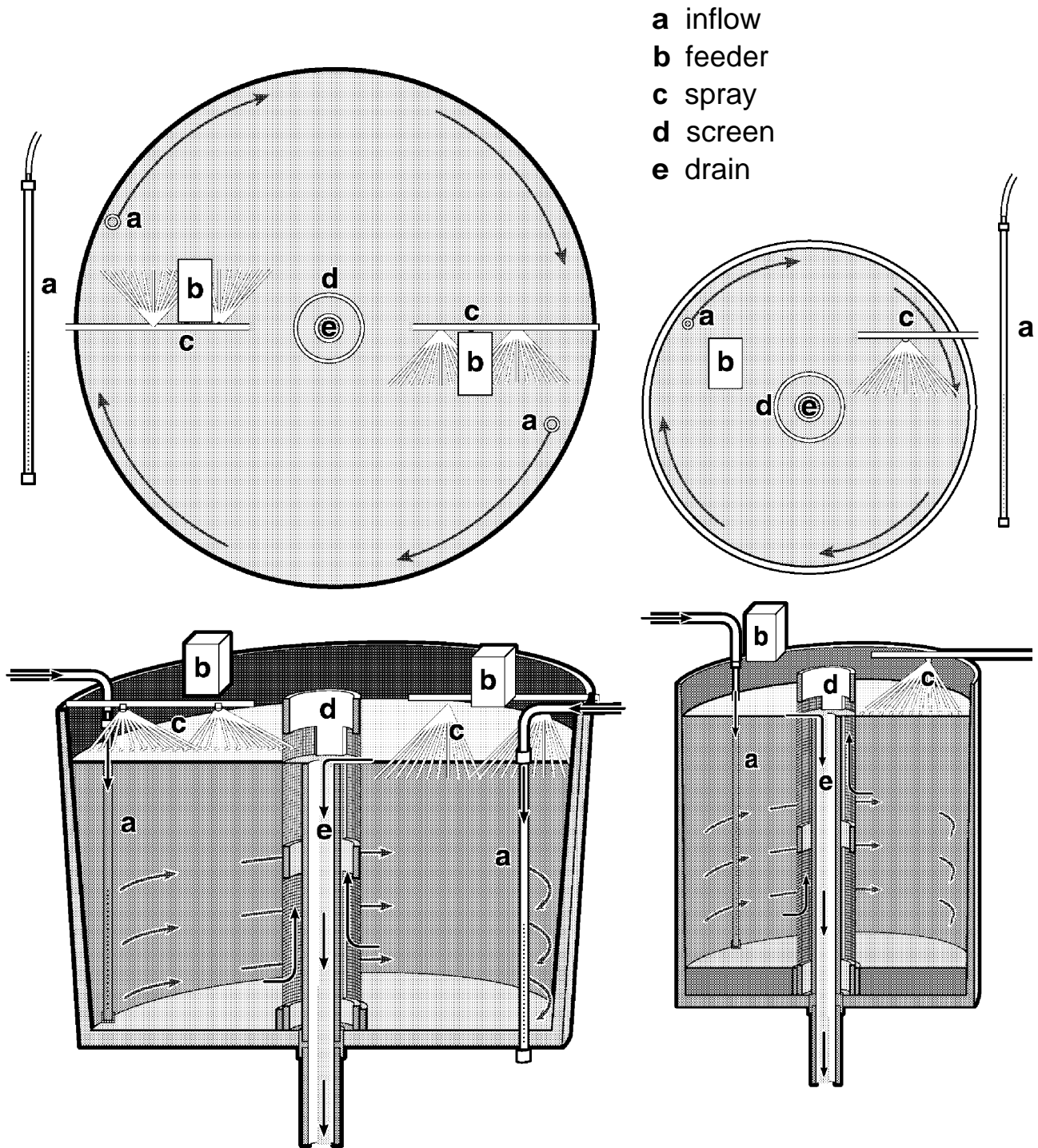


Figure 1. Top and side views of a small tank (278-L, right) and a large tank (676-L, left) used for walleye fry culture. Vertical inflow pipes (a) have been drawn next to the tanks to show inflow openings in lower third of pipe. Current direction (clockwise) is shown by arrows. (From Moore et al. 1994).

