

A review of landlocked fall chinook salmon spawning, egg incubation, and hatchery rearing

Abstract

Chinook salmon *Oncorhynchus tshawytscha* are anadromous fish native to the Northern Pacific and Arctic Oceans. Fall Chinook salmon were introduced into Lake Oahe, a completely freshwater reservoir in the state of South Dakota (USA) in 1976. This population of landlocked fall Chinook salmon is entirely hatchery maintained; natural reproduction does not occur. These landlocked salmon exhibit different natural history and hatchery-rearing characteristics than anadromous Chinook salmon in their native range. This review consolidates the existing research on Lake Oahe landlocked fall Chinook salmon life history, artificial spawning, egg incubation, and hatchery propagation.

Keywords: Landlocked Chinook salmon; South Dakota; Lake Oahe, spawning, hatchery rearing

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Introduction

Identification

Fall Chinook salmon *Oncorhynchus tshawytscha* in their native range are among the least abundant Pacific salmon. However, they are the largest Pacific salmon species, with adults frequently exceeding 45 kg.¹ Externally, large irregular spots dot the dorsal side of the fish, with roundish spots appearing more visible along both lobes of the caudal fin. Black pigment lines the bottom gum in a spotted or uniform bleed. Sexually mature individuals will turn olive brown, rich red, or dark maroon, with these color changes often more evident in males.² Mature males exhibit sexual dimorphism with a hooked jaw (kype) and bodily color change.³

Internally, two flesh colors, red and white, can be observed based on development at sea. The two forms are independent of the external color change adults undergo during the spawning season.⁴ Juveniles can be identified by the presence of a large number of pyloric caeca, while fry can be distinguished by large parr markings that extend below the lateral line.²

Landlocked fall Chinook salmon in South Dakota have silver, streamlined bodies with a bluish hue and dark spots extending from the dorsal side to near the mid-body and caudal fin.⁵ They have a long, pointed snout and a forward-facing mouth with black gums and sharp teeth. Fin rays in the dorsal and elongated anal fin are variable, at 10-to-14 and 13-to-19 rays, respectively, while the pectoral fins have 14 rays and the pelvic fins have 10 rays.⁶ Spawning adult males change to an olive-brown color and also develop a pronounced hooked kype, while females have a blunter nose.⁷ Landlocked fall Chinook salmon in South Dakota typically weigh from 2-to-5 kg, and rarely exceed 9 kg.⁸

Natural history

Native range

In their native range, Chinook salmon are anadromous, typically spending 1-to-5 years in the ocean, and semelparous, migrating up natal freshwater rivers and dying after spawning once.^{2,9} They have numerous adaptations supporting this general life history strategy, including a highly-evolved and diverse timing of spawning runs,

expression of stream-type and ocean-type life-history forms, variation in age at seaward migration, and variation in length during freshwater, estuarine, and oceanic residence.^{2,9} Because of these variations, there is ample evidence for separating Chinook salmon into two life-history sub-types defined by the geographical distribution of spawning populations, duration of freshwater inhabitants prior and post seaward migration, geographic distribution of oceanic populations, and spawning migration timing.²

Female Chinook salmon spawn in cool rivers and streams, beginning with the female making a redd, or oval shaped depression, in the gravel stream.¹¹ Eggs are deposited simultaneously during fertilization by a male. Both the male and female die after spawning, returning essential nutrients to the river as their bodies decompose.^{12,13} The fertilized eggs remain overwinter in the redd and hatch in spring. After hatching the salmon, now called alevins, are particularly vulnerable. They remain in the redd, consuming their yolk sac, a temporary, nutrient-rich organ attached to their midgut cavity.¹⁴ After yolk sac absorption, the alevins, now called fry, emerge from the gravel, with parr markings providing camouflage within the substrate and shadows of the stream environment.^{15,16}

As they migrate downstream to the ocean, juvenile salmon undergo smoltification, endocrine-induced morphological, physiological, and behavioral changes.¹⁷ Morphologically, the caudal peduncle elongates to improve swimming performance, and the body becomes more silver in color to provide cryptic coloration in pelagic waters.¹⁸ Physiologically, gill Na^+ , K^+ , -ATPase is activated to increase hypo-osmoregulatory ability¹⁹ and hemoglobin isoforms change to increase the carrying-capacity of dissolved oxygen in the blood.²⁰ Salmon behavior changes from being territorial over resources in a nutritionally low freshwater environment to schooling in oceanic conditions to decrease predation.²¹

While in the ocean, Chinook salmon are opportunistic predators, initially eating small fish, along with various euphausiid, decapod, teuthid, and pelagic amphipod prey.²²⁻²⁶ As they grow, the salmon feed primarily on fish, such as herring and anchovies.²⁷⁻²⁹ Larger prey is consumed to sustain rapid growth. After 1-to-5 years of feeding in the ocean, adult Chinook salmon return to their natal freshwater streams to spawn and die.^{9, 30-32}

South Dakota

The landlocked Chinook salmon population in South Dakota is located in Lake Oahe, a main stem Missouri River reservoir created by the construction of Oahe Dam in 1958. The Chinook salmon fishery in Lake Oahe is one of three hatchery-maintained, landlocked populations in mainstem Missouri River reservoirs, along with upstream populations in Lake Sakakawea (North Dakota) and Fort Peck Lake (Montana).³³ Unlike freshwater Chinook salmon populations in the Great Lakes, which exhibit substantial natural reproduction, these reservoir stocks rely entirely on artificial propagation.

Lake Oahe is a 372-km-long, 152,000-ha reservoir with a maximum depth of 62 m.³⁴ It extends from the middle of South Dakota into the southern third of North Dakota. The South Dakota portion contains the only permanent coldwater habitat (water temperatures ≤ 15° C) which is approximately 47,755 ha at full pool.³⁵ This suitable permanent habitat for Chinook salmon is typically located directly upstream from Lake Oahe dam, north of Pierre, to Whitlock’s Bay, west of Gettysburg.

A small number of salmon first appeared in Lake Oahe in 1979. In the early 1970s, North Dakota introduced rainbow smelt (*Osmerus mordax*) into Lake Sakakawea to create a cold-water forage base in the reservoir. In 1976, North Dakota then stocked fall Chinook salmon originating from the Abernathy and Spring Creek hatcheries in Washington, USA, into Lake Sakakawea.³⁶ By 1979, both rainbow smelt and Chinook salmon had passed through Garrison Dam and were observed downstream in Lake Oahe.³⁷ Salmon egg collections from Lake Oahe for restocking began in 1981.^{37,35} Lake Oahe was also stocked with Chinook salmon juveniles obtained as eggs from

Lake Michigan fish from 1982 to 1988.^{37,35} The original sources of the Lake Michigan Chinook salmon were a Tule strain that migrated up the Columbia River and others from a Puget Sound strain cultivated in Washington’s Green River Hatchery.³⁸ Juvenile salmon originating from the Green River in Washington were also stocked into Lake Oahe in 2023 and 2024. Natural reproduction of Chinook salmon in Lake Oahe has not been documented and is extremely unlikely to occur.³⁹ Thus, the Lake Oahe Chinook salmon population has been entirely maintained by artificial spawning and hatchery rearing of resident fish since 1989.³⁵

In 1984, Whitlock Bay Spawning and Imprinting Station was built on the eastern shore of Lake Oahe, approximately 29 km miles west of Gettysburg. The station consists of a concrete fish ladder, concrete raceways, and a building where artificial spawning takes place.⁴⁰ After 3-to-4 years in Lake Oahe, adult salmon ascend the fish ladder from October through early November.⁸ The fish are artificially spawned, and the fertilized eggs are then transported to state fish hatcheries for incubation, with most of the resulting progeny stocked back into Lake Oahe at 8 cm the following spring. A smaller number of salmon are grown to a larger size (approximately 20 cm) and stocked in late October.⁴¹

Lake Oahe Chinook salmon are considerably smaller than Chinook salmon in their native range, with the weight of spawning fish typically only 75% of that of anadromous stocks.^{6,33,42–44} Reproductive characteristics, such as fecundity, egg size, and egg survival, are also significantly reduced in Lake Oahe salmon in comparison to fish in their native range.^{33,44–54} Lake Oahe salmon spawning female size and reproductive characteristics are compared to other Chinook salmon populations in Table 1.

Table 1 Spawning female Chinook salmon ages, mean fork lengths (mm), mean total fecundity, and egg size (eggs/mL) from Lake Oahe and other populations reported in the literature. Egg sizes reported as the number of eggs/oz were converted to eggs/mL of water displaced.

Location	Female age	Female length	Fecundity	Egg size	Source
Lake Oahe, South Dakota	3-4	713 ^a	2,997	5.33	33
Klamath River, California			2,902	2.57	49
Fall Creek, California		762	3,748		46
Klamath River, California		814	3,753		442
Cowichan River, British Columbia	3	864	3,885		442
University of Washington		65-86 cm	3,975	2.23	47
University of Washington		61-94 cm	4,171	2.07	47
Robertson Creek, British Columbia		720 ^b	4,452		51
Abernathy Creek, Washington	3 ^c		4,851	3.85	48
Rakaia River, New Zealand		743 ^d	4,855		443
Waitaki River, New Zealand		778 ^d	5,202		443
Abernathy Creek, Washington			5,323	3.35	444
Sacramento River, California	4-5	837	5,449		442
Taku River, Alaska		742 ^e	5,504		51
Quinsam River, British Columbia		864 ^b	6,720		51
Kamchatka River, Russia		70-115 cm ^f	9,350		42,445
Rivers Inlet, British Columbia	3-7	941 ^b	9,790		51
Kenai River, Alaska		844 ^e	10,137		51

^a total length
^b length from posterior margin of the orbit to the end of the hypural plate
^c females less than 80 cm were not sampled
^d fork length
^e length measured from mid-eye to the fork of the tail
^f length measurement method unknown

Lake Oahe fall Chinook salmon are likely under temperature and nutritional stress, which may explain their differences with anadromous stocks.^{33,55–58} For example, adult female salmon with developing eggs are routinely subjected to water temperatures at or even above 19° C, which is well above preferred temperatures for egg development.^{9,59} Historically, the diet of Lake Oahe Chinook Salmon was primarily rainbow smelt,⁶⁰ although recently lake herring (*Coregonus artedii*) and gizzard shad (*Dorosoma cepedianum*) also have become a part of the prey base.⁴¹ During years of low rainbow smelt abundance, the salmon diet shifts to Ephemeroptera and zooplankton.⁴⁴ Food availability is likely a stressor with Lake Oahe salmon, unlike anadromous fish, where marine food supplies are not thought to be a limiting factor for salmon growth.⁶¹

Spawning

Broodstock capture

Artificial propagation of Lake Oahe fall Chinook salmon begins with feral broodstock collection. Most salmon broodstock are obtained at Whitlock Bay Spawning Station via a concrete fish ladder. If insufficient numbers return to the fish ladder for spawning, additional females are obtained by boat electrofishing.⁶²

The design of the ladder at Whitlocks Spawning Station emulates a pool and weir system, where fish use a burst of energy to swim up fast moving water over a weir and rest in a pool above.⁶³ This design allows salmon to ascend the relatively long distance from Lake Oahe to the spawning station raceways by breaking up the elevation and distance into passable increments that fish can navigate at their own pace.⁶⁴ At the upper terminal end of the ladder, the salmon swim through a funnel-shaped gate that directs the fish into a 13.7-m-long, 2.4-m-wide, and 1.2-m-deep holding raceway.⁶⁵ Approximately 1,000 salmon ascend the ladder during a given spawning season. Prior to adding a one-way gate at the top of the ladder in 2020, nearly 40% of the fish ascending the ladder subsequently left the spawning station prior to spawning by descending through an open weir.^{65,66}

Boat electrofishing is also used to collect broodstock Chinook salmon from Lake Oahe. Historically broodstock obtained by electrofishing are immobilized by electronarcosis, netted, placed into a tank on the boat, transported to a boat ramp, netted into a truck-mounted transfer tank, driven to the spawning station, and netted from the tank into one of the spawning station raceways.^{62,67–69}

Egg survival from female broodstock obtained by electrofishing is typically much lower than that of eggs obtained from females ascending the fish ladder.^{68,69} In addition, mortality prior to spawning of electrofished female broodstock is nearly twice that of female broodstock ascending the ladder.⁶² The negative effects of electrofishing have not been attributed to electrofishing per se. Rather, the relatively poor survival of eggs from electrofished females is likely because of the increased handling and physical shock to both the female and the developing eggs in vivo.^{62,68–70} In addition, all aspects of electrofishing, including the chase, electroshock, netting, and tank confinement, likely elevate physiological stress within the brood females.^{71–75}

Gamete collection

Artificial spawning at Whitlocks Station typically occurs once per week but can be as frequently as twice per week if the number of fish ascending the ladder approaches the holding capacity of the station raceways. This spawning schedule is based on the decline in egg viability after approximately one week of post-ovulation in-vivo storage in ideal water temperatures.^{76,77} In addition, Huysman et al.,⁷⁸

justified weekly spawning because egg survival was not significantly affected by a spawning delay of up to nine days post-ovulation, or if the females arrived at the station in either a pre- or post-ovulation state.

Females that return to the Spawning Station either have already ovulated (ripe) or still retain egg in the ovaries (green).⁷⁸ Ovulation status is assessed by exerting slight pressure on the abdomen, as described by Piper et al.,⁷⁹ If ovulation has occurred, eggs will be released from the genital papilla. During ovulation, the intraovarian connective tissue and the ovarian wall deteriorate, releasing the eggs into the abdominal cavity.⁸⁰ The ovulation status of the female salmon held at Whitlocks Spawning Station is assessed prior to spawning. Ripe females and males are crowded into a side channel at the station, captured in a cage, and then euthanized with a lethal dose of carbon dioxide.⁶⁹ Carbon dioxide is used so that the carcasses can be sold for human consumption after spawning.⁸¹

Females and males are processed differently during the spawning process. Males, which unlike females produce viable gametes for an extended period of time during the spawning season,⁸² are euthanized first. Milt, which contains sperm and other fluids to maintain sperm viability and motility,^{83,84} is manually removed from the male by gently squeezing the abdomen starting from the base of the belly toward the anal vent.⁸⁵ Milt is collected in plastic tubes, with the milt from one male put into one tube. The tubes are stored on ice. The milt is typically used within 60 minutes and can be safely stored on ice for up to 120 minutes.⁸⁶

After the males are processed, females are euthanized. Eggs from the females are typically removed by air-stripping. Compressed oxygen is inserted into the body cavity via a needle placed between the pectoral fins.⁸⁷ The resulting gas pressure expels ovulated eggs that are loose in the body cavity without the need for abdominal massage.⁸⁸ Air stripping is used because it is more efficient than hand stripping the relatively large females and has a lower risk of egg damage.^{89,90} Compressed oxygen pressure at 1 bar and a flow rate of 1.5 L/minute is used to maximize the number of eggs collected; higher speeds may not obtain all the eggs, while slower speeds may unnecessarily prolong the procedure.⁸⁸ Eggs are expelled from the females into a net suspended above a dry plastic pan. It is imperative that no water comes into contact with the egg to prevent premature closure of the micropyle from osmotic swelling.⁹¹ Netting is needed to decrease the physical shock and reduction in egg viability caused by eggs directly hitting a hard surface after egg expulsion.^{87,92} The netting allows for the ovarian fluid to drain. Removal of ovarian fluid prior to fertilization may be beneficial for egg survival but, more importantly, makes the spawning process much more efficient.^{93–95}

Fertilization and fertilized egg processing

Overview: One tube of milt (from one male) is added to the eggs from one female which are in the net in a plastic pan. A ratio of 1 mL milt to 1.5 L of eggs is used.⁹⁶ Enough water to completely submerge the eggs is then added to the pan to activate the sperm.^{79,97,98} In addition to activating the sperm, the water initiates egg micropyle closing, providing a very narrow window for fertilization to occur.^{91,99} Roughly after a minute, the net of eggs is removed from the milt/water solution, rinsed in fresh water, and then the eggs are placed in a plastic bag with water to complete water-hardening and for subsequent transport.¹⁰⁰

Detailed process and relevant research: Following sperm entry, the eggs undergo various structural and biochemical responses to prevent

polyspermy. Initially, intracellular calcium levels increase, triggering the release of cortical granules.¹⁰¹ This cortical reaction alters the egg envelope and creates an osmotic response due to elevated solute concentrations, which drives chorion elevation and expansion of the perivitelline space, separating the fertilized egg from the external environment.^{99,101,102} Remaining sperm in the now fertilized egg are expelled from the micropyle canal through the outward flow of perivitelline material.^{101,103} Any additional sperm attempting to enter the ooplasm are blocked by the simultaneous formation of a fertilization cone at the animal pole of the egg.¹⁰¹ This temporary physical barrier dissipates after approximately 300 seconds, narrowing the micropylar canal and creating yet another barrier at its opening to ensure that no other sperm can enter.^{101,104} These responses work cooperatively to block polyspermy while transitioning the egg into an activated developmental state.

The rapid coordination between sperm activation and micropyle closure makes fertilization highly time-sensitive. Buffered saline solutions have been reported to prevent clogging of the egg micropyle before fertilization,⁴⁹ leading to an increase in fertilization rates in some species of fish.¹⁰⁵ Theophylline, a caffeine derivative, can prolong and intensify sperm motility, thereby increasing fertilization percentages.¹⁰⁶ However, the use of a solution of buffered saline or buffered saline supplemented with theophylline during the fertilization of landlocked fall Chinook salmon eggs has not increased egg survival.¹⁰⁷

Traditionally, the entire egg/milt/water mass is stirred with a feather or finger after the addition of water.⁸⁷ Stirring is believed to minimize the swimming distance of the short-lived sperm to the micropyle before cleavage of the membrane, ultimately improving fertilization rates.^{86,108} However, Cook et al.,¹⁰⁹ contradicted this well-established tradition. They reported that stirring of eggs and milt during landlocked fall Chinook salmon spawning had no impact on fertilization success or survival and deemed it unnecessary. Eliminating stirring from the spawning process increased the efficiency of human labor.¹⁰⁹

Another traditional practice is to allow milt to remain in contact with eggs for up to 15 minutes after fluid activation in an attempt to maximize fertilization.^{44,78,110,111} Sperm collected from Lake Oahe Chinook salmon are motile for 29-to-76 seconds, raising questions about the necessity of extended residence times before rinsing.⁸⁶ The results of Shannon et al.,⁹⁶ and Stevens et al.,¹⁰⁰ indicate that both experiment-scale and production-scale spawning events required residence times as low as 20 seconds with no significant effect on egg survival to the eyed stage of development. Immediately after fertilization, egg sensitivity dramatically increases due to the water-hardening, a process of membrane separation and the rapid intake of water.⁹² It is likely that egg mortality occurs if the eggs are rinsed long after fertilization has taken place and water-hardening is occurring.⁹⁶

Gamete viability

Landlocked fall Chinook salmon eggs from Lake Oahe exhibit extremely variable, and frequently poor, survival. Several studies have been undertaken to examine gamete viability in an attempt to improve the efficiency and success of artificial propagation.

Sperm: Prior to recent research, milt was pooled from several males during landlocked fall Chinook salmon spawning in Lake Oahe. This was done to control for sperm viability and variability during spawning studies as well as to reduce the possibility of negative effects of potentially poor milt on overall egg survival.¹¹² By pooling milt, potentially problematic sperm can be diluted with that from other males and distributed to multiple batches of eggs, subsequently

improving the efficiency of spawning procedures.^{113–115} However, the use of pooled milt may instead reduce the effective number of breeders, leading to a reduction in genetic diversity and subsequent population sizes.^{113,116–118} The exceptionally small and genetically-isolated population of inland Chinook salmon in Lake Oahe, coupled with the application of the pooled milt during the spawning process likely led to potential inbreeding, which has been linked to poor embryo survival.⁴⁴ Wipf and Barnes¹¹² found no discernable male/milt effect on egg survival after spawning, indicating that Lake Oahe salmon egg survival is primarily a function of egg quality. Thus, one-to-one male-to-female spawning ratios are now the norm at Whitlocks Spawning Station.

Eggs: Maternal biological characteristics have a significant effect on eyed egg survival, and swim-up fry length and weight. These impacts vary significantly among progeny from individual females.¹¹⁹ The quality of salmonid eggs can be affected by genetics, parental nutrition and stress, water quality and temperature, time after ovulation, and culturists handling and rearing styles.^{120–122} The multifactorial aspect of egg quality has made it challenging to discover a reliable and consistent indicator of future embryo survival from landlocked fall Chinook salmon spawn. In addition, egg quality often is not apparent until much later in development, wasting considerable labor while incubating eggs with poor survival.¹²³

Egg quality tests

Numerous studies have been conducted to ascertain egg quality and future egg survival to maximize spawning and fish culture efficiencies.

Ovarian fluid turbidity: In salmonids, such as landlocked fall Chinook salmon, ovarian fluid turbidity is an indicator of egg breakage, overripening, or potential fertilization failure.^{93,123} When an egg breaks while in the female, high concentrations of proteins, lipids, and lipoproteins are released, increasing the ovarian fluid turbidity.¹²⁴ Ovarian fluid turbidity is also increased as eggs overripen within the body cavity, leading to weakened egg membranes leaking yolk and other contents into the ovarian fluid.⁹³ Suspended solids in turbid ovarian fluid can clog the micropyle or negatively affect sperm motility, leading to substantial egg mortality.^{93,94,95} In contrast to Wojtczak et al.,¹²³ turbidity of ovarian fluid is not a good predictor of future egg survival for landlocked Chinook Salmon spawns.^{125,126}

Overripe eggs: Lake Oahe Chinook salmon spawns typically contain a variable number of unviable, overripe eggs. These eggs are characterized by oil droplet coagulation, rigid outer egg membranes, and consolidation of the egg pigment into the separate globule within the egg, producing a glossy (“mooneye”) appearance.¹²⁷ Barnes and Durben¹²⁸ suggested that visually estimating the percentage of overripe eggs is a valid technique that can be used to quickly quantify overripe eggs during spawning. Barnes et al.,¹¹⁹ recommended that spawns containing more than 10% overripe eggs should be discarded to maximize spawning and egg incubation efficiencies.

Bacteria: Bacteria and other microbial pathogens can have a negative impact on salmon reproductive success.¹²⁹ Routine fish health inspections of both spawning Chinook salmon adults from Lake Oahe and salmon progeny during hatchery rearing have not resulted in the detection of any regulated bacterial pathogens. However, non-regulated pathogens may still play a role in egg survival in Lake Oahe Chinook salmon. Nero et al.,¹³⁰ surveyed bacteria present in the kidneys of landlocked fall Chinook salmon. Kidneys are a prime location to detect the presence of bacteria as they contain hematopoietic tissue and are a major blood filtration site.¹³¹ Twelve

bacteria genera were isolated from spawning female Lake Oahe Chinook salmon and identified to the genus level: *Acinetobacter*, *Aeromonas*, *Brevundimonas*, *Chryseobacterium*, *Flavobacterium*, *Acidovorax*, *Arthrobacter*, *Deinococcus*, *Enterococcus*, *Leucobacter*, *Micrococcus*, and *Oerskovia*.¹³⁰ Although several of these genera contain pathogenic species, the bacteria isolated from the kidneys did not have any apparent effect on female condition and were not correlated with subsequent egg survival.¹³⁰

Bacteria present in ovarian fluid are deemed a concern driven by the possible impacts on eggs survival and vertical disease transmission from the female to the egg.¹²⁹ Barnes et al.,¹³² identified a number of bacteria from the ovarian fluid of spawning landlocked fall Chinook salmon. These include a number of known and potentially pathogenic species: *Acinetobacter* spp., *Aeromonas hydrophila*, *Aeromonas veronii*, *Arthrobacter* spp., *Pseudomonas* spp. (including *P. putida*), *Moraxella* spp., and *Microbacterium* spp. Some of these species (*Acinetobacter* spp., *Aeromonas veronii*, *Pseudomonas putida*, *Arthrobacter* spp., *Moraxella* spp., and *Microbacterium* spp.), were isolated for the first time in any population of Chinook salmon.¹³² In contrast, Sauter et al.,¹³³ reported anadromous Chinook salmon spawned in their native range had an absence of bacteria in over 80% of ovarian fluid samples. Barnes et al.,¹³² identified a weak but significant positive correlation between bacterial density in the ovarian fluid and egg survival of Lake Oahe Chinook salmon. However, given that not all bacteria in the ovarian fluid will be able to attach to and infect unfertilized eggs, the resulting bacteria found in ovarian fluid may not accurately represent the number and species of bacteria found on the external membrane of the eggs.¹³⁴ Though collected from the same population, the bacterial community present in the kidneys of Lake Oahe Chinook salmon differs from bacteria isolated from the ovarian fluid.^{130,132} It is important to note that most bacteria cannot be cultured in the laboratory, making it likely that additional bacterial species beyond those identified are present in the ovarian fluid and kidneys of landlocked fall Chinook salmon.¹³⁵

Dietary and environmental impacts

While environmental factors, including elevated water temperatures during oogenesis and spawning,^{50,136} likely play a role in the poor reproductive success of Lake Oahe salmon, aspects of female nutrition are also important.^{44,58,137} Chinook salmon primarily feed on rainbow smelt when abundant in Lake Oahe.⁶⁰ Rainbow smelt contain thiaminases, a group of enzymes that break down thiamine (vitamin B1), leading to deficiencies when consumed in high quantities.^{138,139}

In fish, thiamine is found in three vitamers; thiamine pyrophosphate (TPP), thiamine monophosphate (TMP), and free thiamine.¹⁴⁰ TPP and TMP can be directly used for essential physiological functions without further metabolic conversion (biologically active).^{141,142} TPP and TMP facilitate the pyruvate decarboxylase complex and enzymes involved in the Krebs cycle, the primary aerobic pathway for breaking down carbohydrates and generating *NADH* and *FADH₂* for energy production.^{141,143} Thiamine deficient fish become lethargic and eventually die due to decreases in metabolism and neuron degeneration.¹⁴⁴

Doyle et al.,¹³⁹ studied the effects of maternal liver and egg thiamine levels on reproductive characteristics of Chinook salmon from Lake Oahe. Egg survival to hatch was not correlated with egg thiamine levels, but positive correlations were observed between egg size and egg thiamine levels and female size and liver thiamine levels.¹³⁹ Negative correlations were observed between the number of eggs per spawning female and egg thiamine pyrophosphate,

liver thiamine monophosphate, and liver total thiamine levels.¹³⁹ In the years sampled, Doyle et al.,¹³⁹ did not see strong indications of thiamine deficiencies Lake Oahe Chinook Salmon eggs, indicating other factors are likely responsible for poor egg survival as egg survival is still relatively low. Overall, thiamine levels in Chinook salmon eggs from Lake Oahe were much higher than those reported in the Great Lakes or the Baltic Sea, where thiamine deficiency complex is frequently observed.^{145,146} Thiamine deficiency complex may not be a problem for the salmon in Lake Oahe because the concentration of thiaminase in rainbow smelt may not be sufficient for induction of the complex¹⁴⁶ or any consumed thiaminase from rainbow trout is diluted by other prey items.¹⁴⁷

Rainbow smelt may be impacting Lake Oahe salmon reproduction in other ways than induced thiamine deficiencies. Barnes et al.,¹⁴⁸ reported the Chinook salmon fecundity was significantly and positively correlated to rainbow smelt abundance and relative weight of age-1 and older salmon collected in gill nets the year before spawning.¹⁴⁸ This is likely because more available energy allows female salmon to more efficiently convert body mass to egg mass and quantity.¹⁴⁹ Barnes et al.,¹⁴⁸ also observed significant relationships between egg survival and May inflow conditions into Lake Oahe during the spawning year and October inflows in the preceding year. May and October inflows influence the amount of cold water habitat available in Lake Oahe,¹⁵⁰ and increased habitat allows for increased fish growth of resident fish populations by reducing competition for biological and physical resources and reducing physiological stress.^{151,152} The relationship between the prior-year inflows in October and egg survival may also be because of a potential influence on rainbow smelt productivity over the winter and subsequent spring.¹⁴⁸ Nutrients can be introduced during cold-water inflows during a critical time for rainbow smelt recruitment, growth, and survival. As a primary prey from Chinook salmon, rainbow smelt abundance can be a limiting factor in determining Chinook salmon growth, gonadal development, and egg development.¹⁵³

Transportation of gametes

Delayed fertilization: Delayed fertilization may be done to increase the number of eggs available for fertilization or improve the efficiencies of spawning operations, particularly if spawning occurs far from incubating hatcheries.^{154,155} Any techniques to store or transport unfertilized gametes require that they not contact any water to prevent either sperm activation or micropyle closure.⁹¹ Eide and Barnes,¹⁵⁶ by adding oxygen and maintaining a temperature of 11°C, were the first to successfully store landlocked fall Chinook salmon eggs for 4 hours before fertilization. Subsequent research extended the egg storage period to 8 hours, although egg survival was still observed, albeit at lower levels, at 12 and 20 hours of storage.¹⁵⁷ These egg storage parameters of landlocked fall Chinook salmon are likely specific to the Lake Oahe stock. Eggs from Chinook salmon populations in their native range are able to withstand holding periods much longer than those observed from salmon in Lake Oahe,^{49,79,157} likely because the reproductive characteristics of this non-native population of freshwater Chinook salmon are completely different than those of Chinook salmon in their native range.^{44,33}

Milt can be stored for longer periods with less impact on viability compared to eggs. While Reese et al.,⁸⁶ indicated that landlocked Chinook salmon milt can be successfully stored on ice for up to 2 hours, Hunter and Barnes¹⁵⁷ maintained sperm viability in landlocked fall Chinook salmon milt stored for 20 hours. Bencic et al.,¹⁵⁸ stored milt from Chinook salmon spawning in their native range for 14 days and Stoss and Holz¹⁵⁹ stored rainbow trout milt for 34 days.

Sperm motility is influenced by the duration of milt storage and storage conditions, such as temperature, oxygen content, anesthesia, ion concentrations, and pH.^{160–162} Upon activation, sperm motility, swimming speed and period of forward motility can be influenced by pH and other water chemistry characteristics such as ion concentrations, and viscosity.^{163–166} When storing or transporting milt, lower temperatures must be used to prevent biological degradation.⁸⁶ Semen and temperature follow an inverted U-shaped relationship where an optimal temperature range maintains sperm quality, with both high and low extremes accelerating deterioration.¹⁶⁷ In addition to storage temperature, oxygen availability is crucial for maintaining sperm quality during milt storage because fish sperm cannot survive in anoxic environments.¹⁶⁸

Transportation of fertilized eggs and subsequent decontamination protocols

It is not uncommon for salmon eggs to be transported long distances from the spawning location to the incubating hatchery.^{45,50,169} In South Dakota, incubation of eggs spawned and fertilized at Whitlocks Spawning Station occurs in hatcheries up to 360 km away, with typical delivery times of up to 4 hours.¹⁷⁰ Different techniques have been used to transport water-hardened eggs, including placing eggs in water-filled containers^{49,50,171} or wrapping them in cheesecloth with just ice (no water) to maintain moist conditions.^{172,173}

Barnes et al.,¹⁷⁰ recommended the transportation of fertilized landlocked fall Chinook salmon eggs from Lake Oahe in coolers containing water volumes equal to egg volumes. They observed a 69% egg survival to hatch in eggs transported in coolers containing equal water and egg volumes, compared to 56% survival for similar eggs transported in moist air conditions. Barnes et al.,¹⁷⁰ also reported that survival of eggs transported in water for 4 hours was not significantly different than eggs incubated at the spawning station and not transported. The use of water likely provides cushioning for eggs undergoing or exiting the high sensitivity phase of water hardening, after which the eggs appear to be relatively resistant to shock and can be safely handled.^{49,171,174–179}

Zebra mussel decontamination

Decontamination of fertilized eggs and their transport water is a critical biosecurity measure to prevent the introduction of aquatic invasive species into hatchery water systems. Non-native and invasive zebra mussels *Dreissena polymorpha* were detected in Lake Oahe in 2023.¹⁸⁰ Zebra mussels are a major aquatic nuisance that can clog water intake pipes, screens, and equipment with their rapid growth.^{181,182} Edwards et al.,^{183,184} developed chemical protocols that kill both adult and larval zebra mussels to allow for the safe movement of fish and fish eggs between water bodies. Hillard et al.,¹⁸⁵ successfully evaluated and then suggested the use of 750 mg/L potassium chloride for 1 hour followed by 20 mg/L formalin for 3 hours when moving Chinook salmon eggs from waters potentially infested with zebra mussels to hatcheries for incubation.

Microbial disinfection

Hatcheries use biosecurity measures to minimize the risk of introducing new microbial pathogens.^{186,187} Disinfection is an established and routine practice when salmonid eggs are transferred between hatcheries or prior to egg introduction into a hatchery setting from non-hatchery environments.^{188–192} It is used to reduce the risk of microbial pathogen introduction, as well as to potentially decrease egg mortality due to bacteria, fungi, or viruses.^{188,193–196} Povidone-iodine is used as a standard egg disinfectant when Lake Oahe salmon

eggs arrive at a receiving hatchery. While not an approved aquaculture drug, povidone-iodine has Low Regulatory Priority status with the United States Food and Drug Administration, allowing it to be used in hatchery settings for 10 minutes in an aqueous solution at a concentration of 100 mg/L active iodine.¹⁹⁷ While other chemicals, such as hydrogen peroxide and formalin, have been evaluated as potential egg disinfectants,^{198–200} povidone iodine is safer for both the fish egg and staff administering the treatment. Iodine is relatively non-toxic to fish eggs, and its effectiveness is not heavily influenced by water chemistry or temperature.^{193,194,200–202} However, the standard bath treatment of 100 mg/L active iodine for 10 minutes does not kill all of the bacteria attached to the external egg membrane,^{198,203–205} nor does it influence future bacterial colonization during incubation.²⁰⁵ Research using Lake Oahe landlocked fall Chinook salmon eggs with povidone-iodine solutions containing 0, 100, 200, and 400 mg/L active iodine indicated that egg survival did not differ among the treatments, but the 400 mg/L treatment provided the most microbial reduction with no effect on subsequent egg survival.^{205,206}

Egg incubation

Incubation method

After disinfection, landlocked fall Chinook salmon eggs are placed into hatchery incubators. Within South Dakota, vertically-stacked upwelling trays are used, along with hatching jars. Petri dish incubation is used for experimental purposes.

Vertically-stacked upwelling trays

In vertical-stacked upwelling tray incubation, water moves through a stack of shallow, screened trays in a cascading flow. Water enters a channel at the head of the tray, upwells through the screened egg tray, and flows over the front wall into the subsequent tray below.^{207,208} This is repeated until the water exits the system as effluent.²⁰⁷ This system uses minimal floor space, uses relatively small amounts of water, introduces atmospheric gases through the transfer of water from one tray to the other, and allows for the handling of individual trays without disturbing the entire stack.^{6,79,207,209} However, regular treatments of formalin or hydrogen peroxide must be used to control fungus (water molds) until at least the eyed-egg stage,^{6,79,209,210} and are recommended for use until hatch during tray incubation of landlocked fall Chinook salmon eggs.²¹¹ Chinook salmon egg densities in the trays should be adjusted to account for oxygen consumption and metabolite production in upper trays in order to supply adequate oxygen levels to lower trays receiving spent water.²⁰⁷ Unlike other salmonid egg incubation methods, embryos cultured as eggs in vertical tray incubators are typically allowed to hatch and remain as fry in the incubators until just prior to initial feeding.^{79,178} Culturists can provide substrate to the trays to limit excess larvae movement to maximize fry size upon the completion of yolk absorption.²⁰⁷

Hatching jars

Hatching jars use continuous upward flow, introduced through a tube at the concave bottom, to keep eggs in a constant, gentle circulating motion.^{207,212} While jars are typically used for non-salmonid fish species such as walleye *Sander vitreus*,^{213–215} they can also be used with trout and salmon eggs.^{216–218} Upon hatching, larvae can be maintained within the hatching jar by closing outlets with screens, or they can be permitted to enter a rearing tank by volition.²⁰⁷ Jars can hold more eggs per unit than trays and result in more egg movement due to increased levels of upwelled water.⁶ Jars require more water than vertically stacked trays but also eliminate the need for anti-fungal chemical treatments during incubation.^{79,217–221} Flows too low lead

to proliferation of water molds, while flows too high can cause egg mortality from excessive egg movement.²¹⁷ Specific to landlocked fall Chinook salmon from South Dakota, no difference in egg survival was observed between eggs incubated in jars or upwelling trays.²¹⁸

Petri dishes

Landlocked fall Chinook salmon egg incubation in Petri dishes allows for experimentation with abundant replication and the use of treatments that may otherwise imperil large numbers of eggs in production incubation systems.²²² In addition, incubation of small numbers of eggs in static water would greatly facilitate experiments involving potential therapeutic chemicals awaiting regulatory approval.^{223,224} Smirnov and Kamishnaya (Moscow University, Russia) incubated a small number of salmonid eggs in petri dishes in domestic refrigerators, formulating the use of a static-water method described by Bevan.²²⁵ While Rojas-Beltran and Gillet,²²⁶ Wedekind et al.,²²⁷ and Wedekind²²⁸ all commented on Petri dish incubation, Barnes and Durben²²⁹ conducted the first controlled experiments validating the technique with rainbow trout. Subsequently, Neumiller et al.,²²² documented that up to 15 landlocked fall Chinook salmon eggs incubated at temperatures up to 11° C can be successfully hatched in Petri dishes with water changes every 7 days before eye-up.

Saprolegnia control

The growth of *Saprolegnia* and other water molds on dead eggs creates significant problems during hatchery incubation.^{230,231} These fungi are ubiquitous in the water supplies for all of the state hatcheries in South Dakota. For example, McNenny State Fish Hatchery sources water from the Madison and Minnelusa aquifers via high capacity artesian wells and natural springs.^{232,233} Barnes and Gabel²³⁴ identified *Saprolegnia* spp. as the prevalent fungus in the hatchery water system and reported that it was found throughout the hatchery water supply, including the hatchery well, aeration tower, and incubation head boxes. Water molds are known to survive in all types of aquatic environments and moist soils, with *Saprolegnia* spp. fungal infections on incubating salmonid eggs being common in most hatcheries.²³⁵ The growth of microscopic stages of *Saprolegnia* can weaken the chorion of salmon eggs, causing premature hatch.²¹¹ Burrows²³⁶ suggested that a living egg may survive a fungal infection, but that the chorion would become so weakened resulting in premature hatch and subsequent death of the fry.

Control of *Saprolegnia* on salmon eggs in vertically-stacked upwelling tray incubators typically involves a combination of chemical and physical treatments.^{79,210} Formalin is the primary chemical fungicide used, along with hydrogen peroxide to a lesser degree.^{237–241} Egg picking, the manual or mechanical removal of dead eggs, is predominantly used beginning at the eyed stage of egg development.^{242–244} Chemical control is optional during jar incubation, with adequate fungal control provided by egg picking and flow adjustments.²¹⁸

Chemical control

Formalin

Reddecliff²⁴⁵ developed the standard daily, 15-minute, 1,667 mg/L formalin treatment used today. These treatments typically occur from initial incubation through the eyed-stage of egg development, at which time the fungal infestation source (dead eggs) can be safely removed.^{107,246} However, landlocked fall Chinook salmon egg survival increased up to 5% when daily formalin treatments were continued until hatch, with or without the presence of handpicking.^{211,234} Barnes et al.,²⁴² recommended the use of formalin during the entire residence of

salmonid eggs and fry in vertically-stacked upwelling tray incubators.

The mechanism by which formalin is preventing *Saprolegnia* infestations and increasing egg survival is unclear. Although formalin is a potent fungicide and the 15-minute daily treatments temporarily reduces fungal populations, incoming water quickly resupplies additional zoospores for possible reinfection.^{211,224,247} Formalin likely prevents zoospore germination by potentially removing any microscopic hyphae attached to the external egg membrane²⁴⁸ or possibly changing the structure of the external egg membrane.

Hydrogen peroxide

Formalin is currently the only fungicide approved by the U.S. Food and Drug Administration for use during the incubation of salmonid eggs²⁴⁹ and while effective, there are concerns about user safety and effluent effects.²²⁴ These concerns have led to considerable research on the use of hydrogen peroxide as an alternative fungicide for fish eggs.^{224,238,250–253} The U.S. Food and Drug Administration currently designates hydrogen peroxide as a low regulatory priority drug, thereby allowing it to be used on fish eggs.²⁴⁹ However, the use of hydrogen peroxide during blastopore formation is problematic with salmonid eggs.²⁵⁴

Hydrogen peroxide has been used successfully during landlocked fall Chinook salmon egg incubation. An initial experiment indicated that daily hydrogen peroxide treatments of 700 mg/L for 15 minutes controlled *Saprolegnia* as effectively as formalin, with no negative effects on egg survival.²⁵⁵ Subsequent experiments indicated that hydrogen peroxide concentrations of 2,500 mg/L caused elevated egg mortality, even if concentrations were decreased to 500 mg/L during blastopore formation.²⁵⁶ Concentrations of 1,000 mg/L did not cause increased mortality but did not completely control fungal growth.²⁵⁶ However, these results may not be applicable to production level incubation because trays only contained 300 eggs, compared to production level loadings of 5,000 to 7,500 eggs.^{49,172,257}

Chemical control effects on egg morphology

The use of hydrogen peroxide or formalin can have effects on microscopic characteristics of external egg membranes from eyed eggs of landlocked fall Chinook salmon. The external membrane of a normal Chinook salmon egg consists of an externus, a relatively thin outer layer, and an internus, a thick inner layer of tightly packed fibers constituting the majority of the membrane.²⁵⁸ The distinct reproductive characteristics of landlocked fall Chinook salmon, compared to anadromous populations, may increase the susceptibility of their egg membrane to chemically-induced morphological impacts during incubation.²⁴⁰ Stephenson et al.,²⁵⁹ noted that just prior to hatch, the internus became significantly less differentiated in the membranes of eggs treated with hydrogen peroxide compared with those in the formalin treatments or untreated controls, but there were no significant differences in total membrane thickness, pore canal height, basal layer height, pore canal width, and the number of pore canals per 50-mm lengthwise segment along the membrane. Mean externus thickness was 0.69 mm, nearly two times that reported previously for non-landlocked Chinook salmon.²⁵⁹ The internus was similar in thickness to eggs from Chinook salmon in their native range.²⁶⁰ Quagio-Grassiotto and Guimarães²⁶¹ suggested that the external egg membrane is thicker in eggs subjected to heavy mechanical stress, while a thinner membrane could facilitate oxygen diffusion as suggested by Kjorsvik and Lønning.²⁶² Landlocked fall Chinook salmon eggs have the characteristic helicoid appearance of egg membranes in salmonids^{263,264} as well as a distinct difference in fibril orientation, that delineates between the upper portion of the internus

and the basal portion.²⁵⁹ Although unaffected by antifungal chemical treatments, landlocked fall Chinook salmon egg fibrils of the upper layer were more or less perpendicular to the egg surface, while the fibrils of the basal layer were approximately parallel to the egg surface and obscured most pore canals.²⁵⁹ Pore canals were most visible in the upper portion of the internus and emerged on the internal surface of the membrane.^{258,260}

Hops - A botanical alternative

The use of hops *Humulus lupulus* as an antimicrobial agent has been a well established practice in the brewing industry for centuries.²⁶⁵ The chemical constituents produced by strobiles (cones) in the flower of hops are an effective bacterial inhibitor against gram-positive bacteria and other microbes,^{266–270} but much less effective against gram-negative bacteria.^{271,272} Barnes et al.,²⁷³ performed an initial study that demonstrated, for the first time, the use of hops as a possible antifungal agent for eggs in aquaculture production. Results from three experiments using wild and commercial hops against *Saprolegnia diclina* suggest that hops possess potent antimycotic properties suitable for hatchery use, provided that concentrations are sufficient and application methods allow for pellets to disintegrate.

Mechanical control (hand picking)

Manual picking of the dead eggs is fungistatic, acting as a growth inhibitor by removing the potential nutrient supply for *Saprolegnia*.²¹¹ While hand picking of eggs, after the eyed stage of development, can effectively control fungal infestations,²⁷⁴ such picking can result in additional mortality.²⁷⁵ Eliminating hand picking after hatch and using formalin for fungal control significantly increased landlocked fall Chinook salmon egg survival.^{243,275} Micro-abrasions can occur from the inserting of the picking apparatus directly into the tray²⁷⁵ and excessive movement in the incubation trays, as occurs during hand picking, can result in membrane or dermal abrasions and subsequent microbial infections.^{172,276} Paradoxically, removing dead eggs to prevent fungal growth may instead be facilitating the growth of water mold on previously healthy individuals via external damage to the surface of the egg membrane.²¹⁰ It is also possible that additional light exposure during the picking process could be causing mortality.²⁷⁵ Exposure to intense and extended periods of light has been associated with increased mortality of salmonid embryos, although fry are much less susceptible than eggs before the eyed stage of development.^{277,278}

Soft-egg disease

Soft-egg disease is occasionally observed during hatchery incubation of salmonid eggs, including those of landlocked fall Chinook salmon.^{255,279,280} Characteristics of soft-egg disease include slightly-adhesive eggs that are less turgid than normal,²⁸⁰ rupture of the yolk sac upon handling,²⁸¹ and premature hatching and subsequent fry death.²⁷⁹ The onset of soft-egg disease is believed to be because of degradation of the external egg membrane (chorion) that destroys membrane permeability regulation,^{280,282} potentially allowing for the intrusion of opportunistic microbial pathogens.²⁵⁸ Soft-egg has been attributed to a number of factors, including excess ammonia in the incubation water,²⁸³ bacterial degradation of the external egg membrane,^{257,282} high incubation water temperatures,²⁵⁸ and mineral content of incubation water.²⁸⁰ Decreased resistance to microbial infection might be because of abnormal chorionic pore development leading to the extrusion of pore plugs,²⁵⁸ an increased number of complementary surface receptors for bacteria on the chorion,²⁸⁴ or some impairment of egg membrane bactericidal or chemical defenses.²⁸⁵

Landlocked Fall Chinook salmon eggs periodically exhibit the symptoms of soft-egg disease during incubation in vertical-flow incubators. Barnes et al.,¹¹⁹ hypothesized that female salmon from Lake Oahe experiencing dietary deficiencies can influence egg development, resulting in a higher susceptibility to membrane degradation and infection.^{120,262,286,287} Dietary stress can lead to a decrease in embryonic immunity or resistance to microbial attack by interfering with the maternal loading of unfertilized eggs with protective lectins and hemagglutinin.^{122,288–291} The improved survival in eggs receiving twice-daily formalin treatments also indicates that bacterial or fungal agents may have played some role in the development of soft-egg.²⁵⁵

Egg bacteria

Considerable research has been conducted on bacteria and landlocked fall Chinook salmon eggs. Trust¹³⁴ considered vertically-stacked upwelling tray incubators to be a continuous flow enrichment culture apparatus for bacteria. Throughout incubation of landlocked fall Chinook salmon eggs, bacterial abundance increases from the top to the bottom of the incubation stack.²⁷⁴ Bacteria may also benefit from chemical or mechanical treatments that reduce pathogenic competition from *Saprolegnia* and other parasitic or saprophytic fungi.²⁹² However, culture techniques, such as hand picking eggs directly from the tray, can lead to temporary increases of microbial populations.^{234,274} After picking, culturable bacterial numbers typically return to prepicking levels,²⁷⁴ likely because not all bacteria will be able to attach to the external egg membrane.¹³⁴ Attachment will be determined by temperature, water quality features, and the presence of complementary surface receptors on the external egg membrane.²⁸⁴

Bacterial levels on landlocked fall Chinook salmon eggs may be influencing egg survival. The number of bacteria observed on the eggs by Scanning Electron Microscopy (SEM) decreased and egg survival increased when formalin treatments increased from once to twice per day.²⁹³ While antifungal formalin treatments are typically conducted at the same concentration and duration throughout incubation despite fluctuations in microbial levels,^{127,134,211,294} Barnes et al.,²⁹³ recommended customizing formalin treatments based on egg bacterial numbers to maximize salmon egg survival.

Stephenson et al.,²⁹² also used SEM to compare microbial growth in eggs of landlocked fall Chinook salmon receiving daily 15-min treatments of 1,667 mg/L formalin, 700 mg/L hydrogen peroxide, or no chemical treatments during incubation in vertical-flow incubators after the eyed stage of egg development. At the end of the experiment, eggs receiving no chemical treatment had bacterial densities that were significantly greater than those on eggs receiving either of the chemical treatments, increasing 30 times over 12 days of incubation. The number of bacteria attached to the external egg membranes did not differ significantly between eggs treated with formalin and those treated with hydrogen peroxide throughout the study.²⁹² And the external membranes of only the untreated control eggs were visibly degraded over the 12-day period, and egg survival was significantly lower when the eggs did not receive either chemical treatments.²⁹²

Bergmann et al.,²⁹⁵ conducted a brief survey of culturable bacteria associated with the hatchery-reared eggs of Chinook salmon. Low numbers of bacteria were recovered from the eggs of freshly spawned Chinook salmon, with the majority of the isolates being gram-positive cocci, which were non-fermenting and oxidase and catalase positive.²⁹⁵ Similar numbers of bacteria were cultured from the ovarian fluid of landlocked fall Chinook salmon by Barnes et al.,¹³² but species composition was different. Bacterial densities on the eggs in the beginning stages of incubation, after iodophor

disinfection, were very low, and contained primarily gram positive, non-fermenting cocci.²⁹⁵ After 27 days of incubation, bacterial densities exceeded 1×10^7 CFU/egg and were dominated by slow-growing, gram-negative Coccobacilli, including *Sphingopyxis*, *Pseudomonas* spp., and *Flavobacterium*.²⁹⁵ The differing microbial populations during varying stages of egg harvesting and incubation may be attributed to the colonization of the eggs by bacteria present in hatchery water compared to other bodies of water or selection for certain taxa of bacteria as a result of differing chemical treatments.²⁹⁵ The isolation of *Sphingopyxis* later in development is not surprising as coccobacilli are common in aquatic and moist environments.^{296–298} *Pseudomonas* is another very common freshwater bacterial group²⁹⁹ and has been identified previously on stream-incubated salmonid eggs.³⁰⁰ Conversely, *Pseudomonas* and *Flavobacterium* isolates are probable pathogenic candidates inducing egg mortality through their production of extracellular proteases^{301,302} Further research is required to determine the contribution of both genera in the weakening of eggs chorionic membrane.

Thiamine hydrochloride

Feral landlocked fall Chinook salmon female broodstock consume thiaminase-containing prey, potentially leading to inadequate thiamine deposition during egg maturation. The concentration of thiamine in Lake Oahe Chinook salmon eggs vary greatly, ranging from 2.85 to 16.14 nmol/g of wet tissue.³⁰³ Treating Lake Oahe salmon eggs with standing-bath thiamine hydrochloride at 250 and 1,000 mg/L at water hardening (1 hour) and continuing during transport (4 hours) did not significantly elevate egg thiamine concentrations nor significantly improve egg survival.³⁰³ Salmonid egg survival was significantly increased by therapeutic thiamine treatments in other studies where broodstock consumed thiaminase-containing prey.^{145,146,304,305} However, the results from Barnes et al.,³⁰³ were likely influenced by unanticipated dietary shifts of adult salmon during an unusual year of very low availability of rainbow smelt *Osmerus mordax*,³⁰⁶ leading to the consumption of presumably thiamine-containing invertebrates³⁰⁷ that mitigated the effect of thiaminase-containing prey consumption.^{308,309}

Hatch

Landlocked fall Chinook salmon eggs typically incubate for 46-to-49 days before hatching at water temperatures of 10-to-11°C, although this can vary depending on water temperature and oxygen levels.^{110,310–313} Higher temperatures may cause premature hatch, while lower temperature may lead to increased egg mortality.^{312,314} Hatching time is also affected by egg size, with larger eggs taking longer to hatch in landlocked Chinook salmon¹¹⁰ and anadromous Chinook salmon in their native range.^{315,316}

The process of landlocked fall Chinook salmon egg hatching begins when larval fish gland cells release an enzyme to dissolve the inner layer of the chorion.³¹⁷ Larvae then emerge from the weakened chorion using slight physical movement.³¹² After hatch, the nutrient rich yolk sac attached to the body of the fry provides all necessary energy for initial growth and development.³¹⁸ The initiation of exogenous feeding and the introduction of artificial feeds occurs when approximately 20% of the yolk sac remains.³¹⁹ This is typically in conjunction with the “swim-up” stage, when fish rise to the surface to gulp air to fill their swim bladder.^{320–322} Upon filling, hydrostatic adjustment (buoyancy) is obtained and the larvae can maintain a position in the water column.³²³

Culture of landlocked Chinook salmon fry varies among the state hatcheries in South Dakota. After hatch, fry can be kept in vertically-

stacked upwelling tray incubators and moved to rearing tanks when an estimated 30% of the fry are free-swimming.³²⁴ Other managers prefer to move the eyed eggs to relatively small rectangular tanks a few days prior to hatch, allow the eggs to hatch in the tanks, and then start the fish on feed in the same tank. Alternatively, other managers plumb hatching jars directly into rearing tanks, allowing the fish to hatch directly into the tank where they stay until initial feeding.

Feeding

Initiation of feeding

The optimal time to begin feeding fall Chinook salmon fry was identified as 902 degree-days (1° C for 24 hours = 1 degree day) by Heming et al.,³²⁵ This timing was developed using Chinook salmon in their native range, making it unusable with landlocked Chinook salmon because of their substantially smaller eggs and other differing reproductive characteristics.⁴⁴ Rather, Barnes et al.,³²⁴ recommended starting landlocked fall Chinook salmon fry on feed at the first visible indication of free-swimming (approximately 20% yolk sac remaining). Fry started on feed at the first sign of swim-up were significantly heavier after 28 rearing days than fry started on feed at complete yolk sac absorption.³²⁴ Initial swim-up for landlocked Chinook salmon fry is 737 degree-days, or, at the 11°C incubation temperature used in South Dakota hatcheries, 67 incubation days rather than 82 recommended by Heming et al.,³²⁵ This difference further supports the influence of individual size, reproductive characteristics, and developmental rates in landlocked versus native stocks on salmon culture.^{44,56,326}

Starter feed trials

In the first study to examine commercially-available starter feeds during the initial feeding of landlocked fall Chinook salmon fry, Fletcher and Barnes³²⁷ compared Silvercup soft-moist (Nelson and Sons, Inc., Murray, Utah) and BioVita® #0 starter (Bio-Oregon, Inc., Longview, Washington). At the end of the 28 day study, fish receiving Silvercup soft-moist were significantly heavier and longer than those receiving BioVita, but total tank weights and gain were not significantly different.³²⁷ Tanks of landlocked salmon fed BioVita #0 starter experienced 28% less mortality than tanks receiving Silvercup soft-moist.³²⁷ Fletcher and Barnes³²⁷ speculated that the higher moisture content of the Silvercup diet contributed to the increased size of the fish, because increased moisture may increase diet palatability in Chinook salmon.³²⁸ They also speculated that the difference in mortality may have been because of the inclusion of brewer's yeast in BioVita. The inclusion of brewer's yeast in salmonid diets has been shown to increase both trout and landlocked fall Chinook salmon survival.^{329,330,331} Fletcher and Barnes³²⁷ stated that either diet was acceptable as a starter feed for landlocked salmon, unless survival was of the utmost concern.

The removal of Silvercup soft-moist from the market led to a subsequent landlocked fall Chinook salmon feed trial by Kientz et al.,³³² who compared Silvercup salmon starter, Silvercup 0.7 mm extruded micro-pellet, and BioVita #0 starter over a 28-day trial. Weight gain and feed conversion ratio were significantly improved in the tanks of salmon receiving BioVita compared to 0.7 mm Silvercup, with the results of Silvercup starter not significantly differing from the other two diets. Mortality was 50% lower in BioVita and 37% lower in 0.7 mm Silvercup in comparison to Silvercup starter, although none of these three means were significantly different. Based on these results, BioVita #0 was recommended to feed to landlocked fall Chinook salmon fry for the first 28 days of rearing. The original Silvercup diets manufactured by Nelson and Sons, Inc. no longer exist, with the brand being acquired in 2008 by Skretting, and new product lines and

rebranding to Skretting USA occurring in 2012.³³³

Post starter feed

Because nutritional requirements differ among life stages of the same fish species,^{334,335} commercial diets for juvenile landlocked fall Chinook salmon have also been evaluated. In 4 separate feed trials, Wipf et al.,³³⁶ compared 4 diets: Skretting Salmon Fry (Skretting Canada, Vancouver, British Columbia), Bio-Oregon Bio-Vita, Bio-Oregon Bio-Clark, and Bio-Oregon Micro-Vita. The first three diets were granulated feeds while the last was a micro-pellet. At the end of the first 28-day trial, which used #1 crumbles and salmon with a starting weight of 0.55 g, total tank weight gains were significantly lower and feed conversion ratios were significantly poorer in tanks of salmon fed Micro-Vita compared to the other three diets. Results from the second 41-day trial using #1 granules and salmon with a starting weight of 0.6 g, indicated that total tank weight gains were significantly lower, and feed conversion ratios were significantly poorer, in both Bio-Clark and Micro-Vita fed fish. The third 28-day trial used larger, 2.2 g juvenile salmon, and either #2 granules or 0.9 mm micro-pellets. In this trial, Bio-Vita produced significantly greater total tank weight gains and significantly better feed conversion ratios than the other 3 feeds. Lastly, the fourth trial, also used #2 granules and 0.9 mm micro-pellets with larger 3.6 g salmon. At the end of this 28-day trial, ending tank weights for Bio-Clark and Micro-Vita were significantly lower than those of fish fed Bio-Vita or Salmon Fry.

Wipf et al.,³³⁶ suggested that the use of poultry meal and corn gluten as a secondary protein source in Bio-Clark and the accelerated sink rate in the water column of Micro-Vita as microparticulate³³⁷ may have contributed to their relatively poor performance of these two feeds. Holt et al.,³³⁷ also noted that the texture of micro-pelleted diets, like Micro-Vita may also lead to rejection by the target fish. Based on these results, Wipf et al.,³³⁶ recommended using either Bio-Vita or Salmon Fry to maximize the growth and feeding efficiency of landlocked fall Chinook salmon during hatchery rearing.

Rearing tanks

Overhead cover

Overhead cover provided by overhanging vegetation or physical features is an essential factor for most salmonid species in natural settings, especially at juvenile sizes.^{338–342} However, during hatchery rearing tanks are typically completely uncovered to allow for periodic cleaning and observation of the fish by hatchery personnel.³⁴³

Although no studies have been conducted during the hatchery rearing of landlocked fall Chinook salmon, partial and full overhead covers are used with salmon in some South Dakota state hatcheries. The use of cover is due to the positive results observed in South Dakota when rearing other salmonid species. Specifically, Barnes and Durben³⁴⁴ reported significant increases in feral rainbow trout (*Oncorhynchus mykiss*) growth when only 29% of the open area on top of circular tanks was covered. In addition, Barnes et al.,³⁴⁵ observed a similar increase in hatchery rearing performance when using partial tank covers with feral brown trout (*Salmo trutta*). Positive behavior changes have also been observed with the use of partial covers on top of hatchery rearing tanks.³⁴⁶

Nearly completely covering tanks (full covers), with the exception of a small opening for dispensing feed, also resulted in improved growth in both rainbow trout and brown trout.^{347,348} In addition, the more recent Walker et al.,³⁴⁷ study validated the benefits of partial tank covers reported previously. Outside of South Dakota, Pickering

et al.,³⁴⁹ used a floating top that covered 67% of the upper surface of circular tanks and noted positive impacts during the rearing of wild Atlantic salmon (*Salmo salar*). The benefits of adding overhead cover during hatchery rearing are believed to correspond with the innate behavioral adaptations to respond to startle or anti-predator stimuli in natural situations.^{339,350} Cover may also be providing a refuge area within an otherwise sterile rearing environment, possibly increasing salmon growth by decreasing energy expenditures and by reducing the stress associated with the inability to find refuge in uncovered tanks.^{349,351,352}

Vertically-suspended environmental enrichment

Environmental enrichment includes techniques to increase environmental complexity in aquaculture rearing units, including introducing elements that more closely resemble natural habitats.^{353,354} In production-scale facilities, environmental enrichment can improve fish physiology and enhance behavioral responses.^{355,356} However, its implementation is often constrained by economic considerations, including labor requirements, material cost, and compatibility with routine hatchery operations. Despite these limitations, some forms of environment enrichment have been shown to provide both welfare and production benefits, improving performance metrics of fish while enhancing overall production and cost-effectiveness.^{353,354,357,358}

Vertically-suspended environmental enrichment incorporates suspended structures beneath tank covers. Although vertically-suspended structures differ from natural forms of structural complexity, they provide environmental heterogeneity that is often lacking in hatchery environments.^{359–363} In these environments, rearing systems are generally structurally barren and may limit fish behavior and enrichment potential.^{359,364,365} Vertically-suspended environmental enrichment provides the benefits of enrichment without interrupting hydraulic self-cleaning in circular tanks, interfering with routine fish culture operations, or increasing the fish health risks that occur when structures are added to the bottom of the rearing tank.^{348,356,366–375}

Considerable research on vertically-suspended enrichment has occurred in South Dakota using aluminum rods, polyvinyl chloride pipes, plastic balls, and aluminum angles.^{78,361,362,376–384} In nearly every study with salmonids, vertically-suspended environmental enrichment significantly improved hatchery rearing performance. Specific to landlocked fall Chinook salmon, Huysman et al.,³⁸³ reported significant improvements in final tank weight, gain, percent gain, specific growth rate, and feed conversion ratio in tanks of salmon containing vertically-suspended environmental enrichment. The results of Huysman et al.,³⁸³ were supported by Rosburg et al.,³⁸⁰ who observed significant improvements in landlocked fall Chinook salmon juveniles reared in tanks with vertically-suspended environmental enrichment.

Color

Color of surrounding structure in rearing tanks can affect fish growth, physiology, aggression, and stress response.^{385–391} Two studies have been conducted during the rearing of landlocked fall Chinook salmon comparing vertically-suspended environmental enrichment painted different colors. Jones et al.,³⁹² used aluminum angles painted either silver, red, black, or green. After 25 days, mean total lengths and weights of individual salmon reared in tanks with the green arrays were significantly larger than those reared with silver, red or black arrays.³⁹² Subsequently, Robidoux et al.,³⁹³ compared blue and silver environmental enrichment and observed no significant differences in salmon rearing performance with either color. Chapman et al.,³⁹⁴ and Meza et al.,³⁹⁵ also observed no effect of environmental enrichment

color during rainbow trout rearing.

It should be noted that the results of these color-preference studies could have been affected by water temperature,³⁹⁶ Chinook salmon eye anatomy and physiology,³⁹⁷ long term exposure to different colors,³⁹⁸ developmental stage,^{397,399} and the relatively small colored surface area of the suspended structures compared to the color of the entire rearing tank.^{394,395} Genetics, and the likely unique genetic background of landlocked fall Chinook salmon also likely contributes to any potential color preferences genetics.^{389,396,400–402}

Exercise

Exercise during hatchery rearing has been shown to increase growth,^{403–406} swimming performance,^{403,407} disease resistance,^{406,408} and post-stocking survival,⁴⁰⁹ as well as decrease stress,⁴¹⁰ stress recovery time,^{411–413} and agonistic behavior.^{414,415} Parker and Barnes⁴¹⁶ conducted the first experiment evaluating exercise during landlocked fall Chinook salmon rearing, using three different water velocities [0.5, 1.5 and 3.0 body length/s (BL/s)]. Following 4 weeks of feeding, they reported that fish reared in 0.5 and 1.5 BL/s had the same growth and food conversion ratio, while fish reared at 3.0 BL/s had a significant reduction in both metrics. Furthermore, fish reared at 1.5 BL/s had a significantly higher condition factor than fish reared in other treatments. Parker and Barnes⁴¹⁶ recommended exercise at a moderate velocity (1.5BL/s) for landlocked Chinook salmon, while also avoiding velocities of 3.0 BL/s. Similar results were reported for rainbow trout.⁴¹⁷

Voorhees et al.,⁴¹⁸ reported that intermittent exercise combined with vertically-suspended environmental enrichment improved the hatchery rearing performance of landlocked fall Chinook salmon. In contrast, Martling et al.,⁴¹⁹ observed negative impacts of exercise with very small salmon juveniles but also noted these results did not continue as the fish got larger. For salmon in their native range, Kiessling et al.,⁴²⁰ and Gallagher et al.,⁴¹⁴ observed decreased hatchery growth in exercised salmon, and Davison⁴²¹ suggested that Chinook salmon do not benefit from exercise.

Rearing density

Rearing density, the weight of fish per unit volume of rearing space,⁴²² is a critical consideration during fish culture. The use of increased rearing densities can maximize fish production but also negatively impact growth, feed conversion, fish health, and physiological functions.^{423–425} Rearing densities for juvenile Chinook salmon *Oncorhynchus tshawytscha* from their native range have been studied extensively to minimize the detrimental effects while maximizing production in often limited hatchery space.^{426–430}

Juvenile landlocked fall Chinook respond positively to lower rearing densities, even though such densities reduce overall yield. Over three different rearing years, Barnes et al.,⁴³¹ observed that final rearing densities ranging from 7.92 to 11.72 kg/m³ produced bigger fish with improved feed conversion ratios compared to final densities ranging from 15.02 to 25.22 kg/m³. Rosburg and Barnes⁴³² also reported a negative relationship between landlocked salmon rearing density and rearing performance. They evaluated three densities (final densities were 8.93, 16.41, 26.86 kg/m³) with specific growth rate being significantly lower, total length being significantly shorter, and feed conversion ratios being significantly greater in the fish from the highest-density treatment. Percentage of weight gain, final weights, and condition factor were also significantly reduced in fish from the highest-density.⁴³² In contrast, Cook et al.,⁴³³ who compared final rearing densities of 3.26 and 12.85 kg/m³ in landlocked fall Chinook salmon shortly after feed training, reported no significant differences

in growth or any rearing variables. However, both of the rearing densities used were relatively low, particularly in relation to the higher densities evaluated by Barnes et al.,⁴³¹ and Rosburg and Barnes.⁴³²

The Barnes et al.,⁴³¹ Cook et al.,⁴³³ and Rosburg and Barnes⁴³² landlocked fall Chinook salmon density studies used circular or semi-circular tanks. Optimal rearing densities can vary by rearing unit type used in hatchery production and may even be hatchery specific.^{422,426,427,428,430} The negative effects of elevated rearing densities, such as lower growth rates resulting in smaller fish, may be because of increased competition, increased aggression, decreased visibility, water quality degradation, and other factors.^{424,425,434–439}

The densities used during hatchery rearing can also impact the survival of hatchery-reared fish released into natural environments.^{426,431,438,440,441–445} Barnes et al.,⁴³¹ determined that the fish harvested by anglers or that returned to spawn was significantly greater from lower-density treatments. They also concluded that even if fewer landlocked salmon could be hatchery reared using the lower density, because post-stocking return was 6-times greater in the lower-density treatment, the overall return could potentially be doubled. Martin and Wertheimer⁴²⁸ and Banks⁴²⁹ also reported greater returns of Chinook salmon in their native range as a result of lower hatchery rearing densities.

Conclusions and management recommendations

Considerable research focusing on artificial spawning and hatchery techniques for landlocked fall Chinook salmon from Lake Oahe, South Dakota has occurred. While this research has produced considerable improvements in spawning and culture efficiencies, opportunities exist for additional improvement. Environmental enrichment in all of its forms, including areas such as structure, exercise, color, noise, and lighting, still need further investigation, both in relation to hatchery rearing and also post-stocking survival. Thus, the collaboration of fisheries managers and hatchery staff is essential in ensuring that the salmon are reared using proper techniques and at the appropriate densities to maximize their positive impact on the Lake Oahe fishery. Research into the impact of hatchery rearing on otolith chemistry and morphology is an emerging research area and should be conducted with landlocked fall Chinook salmon. Lastly, additional research into traditional culture practices, such as spawning techniques, egg transport, egg incubation, rearing densities, and other rearing strategies, will continue to be needed to decrease rearing costs, improve rearing performance, and increase post-stocking survival.

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None.

Conflicts of interest

The authors declare that there are no conflicts of interest.

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