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Reproductive Characteristics of Landlocked Fall Chinook Salmon from Lake Oahe, South Dakota

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ABSTRACT Lake Oahe, South Dakota, USA, landlocked fall Chinook salmon (*Oncorhynchus tshawytscha*) reproductive characteristics were examined over a 27 year period, from 1988 to 2015. Mean total lengths of spawning females ranged from 665 mm (1995) to 812 mm (2015) with considerable year-to-year variation. Post-spawn female weights varied, ranging from 2.02 kg (2000) to 5.55 kg (2015), with an overall mean of 3.04 kg. Fecundity peaked at 4,555 eggs per female in 2003, which was just 3 years after a low of 2,011 eggs per female in 2000. Relative fecundity based on female weight was greatest at 1,211 eggs/kg in 2006 and lowest at 631 eggs/kg in 2015, while relative fecundity based on female length peaked in 2003 at 5.64 eggs/mm with the lowest value of 2.93 eggs/mm in 2000. Mean egg size for all years combined was 5.33 eggs/mL of water displaced, but was extremely variable, with the smallest eggs in 1998 and largest in 2015. Survival to the eyed-egg stage of development ranged from 0 to 100% for individual spawns, with an overall mean of 31.2%. Total fecundity was significantly correlated with both length and weight, and linear relationships between fecundity and female length, fecundity and egg size, and female length and egg size were observed. Egg survival was not significantly correlated to female length, weight, fecundity, or egg size. The information from this study will increase the efficiencies of salmon spawning operations, particularly with regard to the duration and intensity of egg collection efforts, as well as provide the foundation to evaluate possible management changes to improve Lake Oahe Chinook salmon reproductive success.

KEY WORDS Chinook salmon, fecundity, Lake Oahe, South Dakota, *Oncorhynchus tshawytscha,* reproduction, spawning.

The life history and reproduction characteristics of fall Chinook salmon (*Oncorhynchus tshawytscha*) are well documented in their native range of the North American Pacific Northwest (Rounsefell 1957, Donaldson and Menasveta 1961, Fowler 1972, Leitritz and Lewis 1976, Healey and Heard 1984) and Asia (Vronskiy 1972, Smirnov 1975). However, few studies have described reproductive characteristics of Chinook salmon transplanted into novel areas; Quinn and Bloomberg (1992) report the fecundity of Chinook salmon from New Zealand. Barnes et al. (2000) identified several unique reproductive characteristics in landlocked fall Chinook salmon in South Dakota, although they only used two years of data from 48 fish.

The landlocked Chinook salmon population studied by Barnes et al. (2000) was located in Lake Oahe, South Dakota, and was one of three hatchery-maintained, completely freshwater Chinook salmon populations in North America. The other populations existed in two upstream mainstem Missouri River reservoirs (i.e., Lake Sakakawea in North Dakota and Fort Peck Lake, Montana). A small number of salmon first appeared in Lake Oahe in 1979 by downstream movement from Lake Sakakawea (Warnick 1987). The Lake Sakakawea salmon originated from the Abernathy and Spring Creek hatcheries in Washington, USA (Lee et al. 1996). Salmon egg collections from Lake Oahe for restocking began in 1981 and the reservoir also received Chinook salmon originating from Lake Michigan from 1982 to 1988 (Warnick 1987, Lott et al. 1997). Natural reproduction of Chinook salmon in Lake Oahe has not been documented and is extremely unlikely to occur (Marrone and Stout 1997); thus, the Lake Oahe Chinook salmon population has been entirely maintained by artificial spawning and hatchery rearing of resident fish since 1989 (Lott et al. 1997).

In comparison to native range stocks, Barnes et al. (2000) observed dramatically reduced survival during hatchery rearing of Lake Oahe Chinook salmon eggs. They also reported lower fecundity levels and egg sizes in salmon from Lake Oahe. Fluctuations in Lake Oahe prey fish levels (Hill 1997), water temperatures (Marrone and Stout 1997), and changes in broodstock genetics due to bottlenecks and hatchery rearing (Araki et al. 2008) have likely influenced salmon reproduction over the past 18 years. Information on Lake Oahe reproduction characteristics is not only interesting from a natural history perspective, but also is needed to plan for the spawning effort required to maintain the population. Additionally, such information also could be used to recognize reproductive impairments, allowing for potential corrective actions to be undertaken. Thus, the objectives of this paper were to document changes in Lake Oahe salmon reproduction characteristics using available historical data and to determine possible predictive relationships involving past reproductive success.

STUDY AREA

Lake Oahe is a 150,000 ha mainstem Missouri River reservoir located in North and South Dakota. The South Dakota portion contains approximately 47,755 ha of coldwater habitat (water temperatures ≤ 15° C) at full pool (Lott et al. 1997). Models predicting percent available coldwater habitat based on Lake Oahe elevation show greater than 45% of the total coldwater habitat was available to salmon during the years of our study (USACE 1994). This suitable permanent habitat for Chinook salmon is typically located directly upstream from Lake Oahe dam, north of Pierre, South Dakota, to Whitlock's Bay, west of Gettysburg, South Dakota, USA. All spawning occurred at Whitlocks Spawning Station, and all egg incubation occurred at McNenny State Fish Hatchery, Spearfish, South Dakota, USA.

METHODS

Reproductive data were collected from individual Chinook salmon spawns in October 1988, 1998–2006, 2008, 2012, 2013, and 2015 at Lake Oahe. The spawning dates were relatively consistent each year, with data collected during the middle of the run. The years during which data were collected were based on the availability of incubation space at McNenny Hatchery. Because McNenny hatchery is a production facility, the opportunity to separately incubate eggs from individual females is extremely limited and predicated on hatchery operations.

While the intent was to use only females that ascended the fish ladder, it is possible that a small number of females collected via electrofishing also were included; during some years the fish were not kept separate at the spawning station. We spawned fish using similar procedures each year. Prior to gamete collection, we anesthetized male and female salmon in carbon dioxide-saturated lake water. We collected milt from a minimum of 30 males by hand-stripping, pooled it in a container, and kept it cool until added to eggs. We injected compressed oxygen at low pressure into the body cavity of ripe females to expel their eggs into a plastic pan. We added previously collected milt to the pan and lake water (11–13° C, total hardness as $CaCO_3$ = 160 mg/L, pH = 8.2, total dissolved solids = 440 mg/L) was added to activate the milt. After approximately one minute, we washed eggs in lake water to remove excess milt, and then placed them in lake water for one-hour to allow for membrane separation (waterhardening). After water hardening, we placed eggs in plastic bags with fresh lake water, and transported them approximately 4 hours to McNenny Hatchery. We maintained each spawn discretely during the spawning process and during transportation to the hatchery.

We measured spawned females for total length (mm) and weight (0.01 kg) with the exception of 2002 when weights were not recorded. Additionally, we did not record lengths from spawning fish for 1 fish in 2000, 14 fish in 2002, and 1 fish in 2006. We dissected postspawned females to ensure that no eggs remained in the body cavities after pneumatic expulsion. The number of females spawned for this study varied across years depending on available incubation space.

At McNenny Hatchery, we disinfected eggs in a solution of 100 mg/L buffer free iodine for 10 min, inventoried them by water displacement (Piper et al. 1982), and placed them in vertical-flow incubator trays (Marisource, Payallup, Washington). We maintained each spawn discretely during disinfection and throughout incubation until the eyed-egg stage. We used well water (11° C, total hardness as $CaCO_3$ = 360 mg/L, alkalinity as $CaCO_3$ = 210 mg/L, pH = 7.6, total dissolved solids = 390 mg/L) at a flow of 12 L/min for egg incubation. We treated eggs daily for 15 min with 1,667 mg/L formalin (Parasite-S, 37% formaldehyde, 6–14% methanol; Western Chemical, Inc., Ferndale, Washington, USA). At the eyed stage of development (incubation day 28), we removed dead eggs and calculated percent egg survival as follows:

Egg survival (%) = 100 × (number of eyed eggs / initial number of eggs)

Similarly, we calculated relative fecundities based on spawning female lengths and post spawn weights as follows:

Relative fecundity weight (eggs/kg) = number of eggs / female weight (kg)

Relative fecundity length (eggs/mm) = number of eggs / female length (mm)

We analyzed data using SPSS (9.0; SPSS, Chicago, Illinois, USA). Regression and correlation analysis was used to ascertain any possible relationships among the variables. We analyzed yearly data using ANOVA, with Tukey post-hoc mean comparison procedures. We logit transformed (log (x / [1-x]) percentage data prior to analysis of variance to stabilize variances (Warton and Hui 2011). We used a predetermined significance level for all tests of $P < 0.05$.

RESULTS

While data from an average of 16 spawning females and their eggs were obtained for each year of this study, data were only available from 5 and 6 fish respectively in 1999 and 2004. Mean spawning female total lengths were significantly different ($F_{13, 220}$ = 17.304, $P < 0.001$) among years, ranging from 665 mm (1999) to 812 mm (2015), with considerable variation across years (Table 1). Year-to-year post-spawn female weights also were significantly different ($F_{12, 189}$ = 24.837, $P < 0.001$), with fish in 2003, 2004, and 2015 (mean weights of 4.44, 4.51, and 5.55 kg, respectively) significantly heavier than fish from most other years. Overall mean total lengths and weights were 713 mm and 2.43 kg.

Total fecundity was significantly different ($F_{13, 236}$ = 13.876, $P < 0.001$) among years. Fecundity peaked at 4,555 eggs per female in 2003, which was just 3 years after a low of 2,011 eggs per female in 2000. Relative fecundity based on female weight also differed ($F_{12, 189}$ = 3.205, P = 0.001)

Table 1. Mean (SE) yearly spawning and reproductive success data for landlocked fall Chinook salmon from Lake Oahe, South Dakota, from 1988, 1998–2006, 2008, 2012, 2013, and 2015. Means in a column followed by different letters are significantly different ($P < 0.05$).

Year	N	Length (mm)	Weight (kg)	Fecundity (eggs/female)	Relative Fecundity (eggs/kg)	Relative Fecundity (eggs/mm)	Egg Size (eggs/mL)	Survival (%)
1988	26	681 (10) wvu	2.73 (0.15) wvuts	2,728 (145) wvuts	1,086 (92) zyx	3.96 (0.16) yxt	4.25 (0.25) usr	37.7 (0.1) zyx
1998	22	686 (9) wvu	2.05 (0.08) ts	2,426 (183) vus	1,034 (72) zyxw	3.50 (0.24) ut	6.99 (0.35) z	50.6 (0.1) z
1999	5	665 (30) wvu	2.26 (0.34) wvuts	2,473 (294) wvuts	1,135 (135) zyxw	3.70 (0.34) yxt	4.90 (0.34) xvur	63.7 (0.2) zy
2000	20[a]	678 (13) wvu	2.02 (0.14) ts	2,011 (160) vts	1,019 (67) zyxw	2.93 (0.21) ts	6.86 (0.38) zy	36.4 (0.1) zyx
2001	21	690 (10) wvu	3.00 (0.15) wv	2,374 (161) vuts	780 (51) xw	3.41 (0.21) wt	4.59 (0.15) vr	31.5 (0.1) zyx
2002	27[b]	776 (15) zx		4,057 (181) zy		5.20 (0.35) zy	5.02 (0.24) xvr	34.4 (0.1) zyx
2003	20	810 (6) z	4.44 (0.14) y	4,555 (151) zx	1,049 (49) zyw	5.64 (0.20) z	4.38 (0.09) vur	29.1 (0.1) zyx
2004	6	791 (19) zy	4.51 (0.46) zyx	3,257 (731) yxwvuts	709 (150) zyxw	4.08 (0.89) zxwvus	5.66 (0.67) zwvu	27.5 (0.1) zyx
2005	20	722 (15) yxwv	3.49 (0.33) xw	3,311 (261) yw	1,090 (105) zyxw	4.61 (0.35) zxwvu	5.86 (0.15) zyx	25.0 (0.1) yx
2006	16[c]	733 (8) yxw	2.96 (0.13) wv	3,489 (166) yw	1,211 (67) zy	4.79 (0.23) zx	5.70 (0.12) ywv	16.1 (0.1) x
2008	16	702 (8) wvu	3.03 (0.11) wv	2,840 (163) wvuts	948 (58) zyxw	4.04 (0.22) yxt	5.22 (0.11) wvu	23.6 (0.1) zyx
2012	19	663 (14) u	2.49 (0.21) vuts	2,339 (163) s	992 (68) zyxw	3.51 (0.21) xvt	5.61 (0.33) wv	26.6 (0.1) zyx
2013	20	677 (12) uv	2.70 (0.17) wvuts	2,639 (242) wvuts	1,034 (96) zyxw	3.92 (0.35) yxt	5.24 (0.22) wvu	22.3 (0.1) x
2015	10	812 (16) z	5.55 (0.40) z	3,214 (271) ywus	631 (92) w	4.01 (0.38) yxt	3.64 (0.17) tsr	17.2 (0.1) x
Total	250	713 (4)	3.04 (0.08)	2,997 (71)	999 (24)	4.10 (0.10)	5.33 (0.10)	31.2 (0.1)

[a] N = 19 for length.
[b] N = 13 for length.
[c] N = 15 for length.

among years. Although considerable overlap existed among the means, the lowest mean values of 631 eggs/kg in 2015 and 780 eggs/kg in 2001 were significantly less than mean values from most other years. Significant differences ($F_{13, 220} = 9.972$, $P < 0.001$) in relative fecundity based on female length among years also were observed, and followed a different pattern than relative fecundity based on weight. Significant differences among means were similar to that observed from overall fecundity, with the highest values of 5.64 and 5.20 eggs/ml observed in 2002 and 2003 respectively. The lowest relative fecundity value of 2.93 eggs/mm occurred in 2000.

Mean egg size for all years combined was 5.33 eggs/mL of water displaced, and differed ($F_{13, 236} = 12.911$, $P < 0.001$) among years. Egg size was extremely variable, with the smallest eggs at 6.99 eggs/mL in 1998 compared to the largest eggs at 3.64 eggs/mL in 2015. Survival to the eyed-egg stage of development varied ($F_{13, 236} = 3.207$, $P < 0.001$) among years, with an overall mean of 31.2% for all years examined. Mean egg survival was highest in 1999 at 63.7% and 1998 at 50.6%, with mean survival in all other years below 40%. Eyed-egg survival from individual spawns ranged from 0 to 100%.

Total fecundity was significantly correlated ($P = 0.001$) with both total length ($r = 0.596$) and weight ($r = 0.106$). Egg size (eggs/ml) was also significantly correlated ($P = 0.001$) with total length ($r = –0.353$), weight (r = –0.318), and fecundity ($r = –0.223$). Egg survival was not significantly correlated to total length, weight, fecundity, or egg size. Significant regressions were observed for female total length in relation to fecundity ($P < 0.001$) and egg size ($P < 0.001$) and total fecundity and egg size ($P < 0.001$; Fig. 1).

DISCUSSION

Relatively low reproductive success observed in Lake Oahe Chinook salmon is less than that reported for Chinook salmon in their native range (Johnson and Brice 1953, Banks and Fowler 1982). In this study, approximately 31% of Lake Oahe Chinook salmon eggs reached the eyed stage, with survival exceeding 50% in only two years. In contrast, fall Chinook salmon eyed-egg survival from Snake River in the western United States exceeded 88% (Geist et al. 2006). In British Columbia, Beacham and Murray (1989) observed eyed-egg survivals of 92% from Chinook salmon eggs collected in the Kitmat River and 98% in the Bella Coola River in British Columbia. The highest reported Chinook salmon

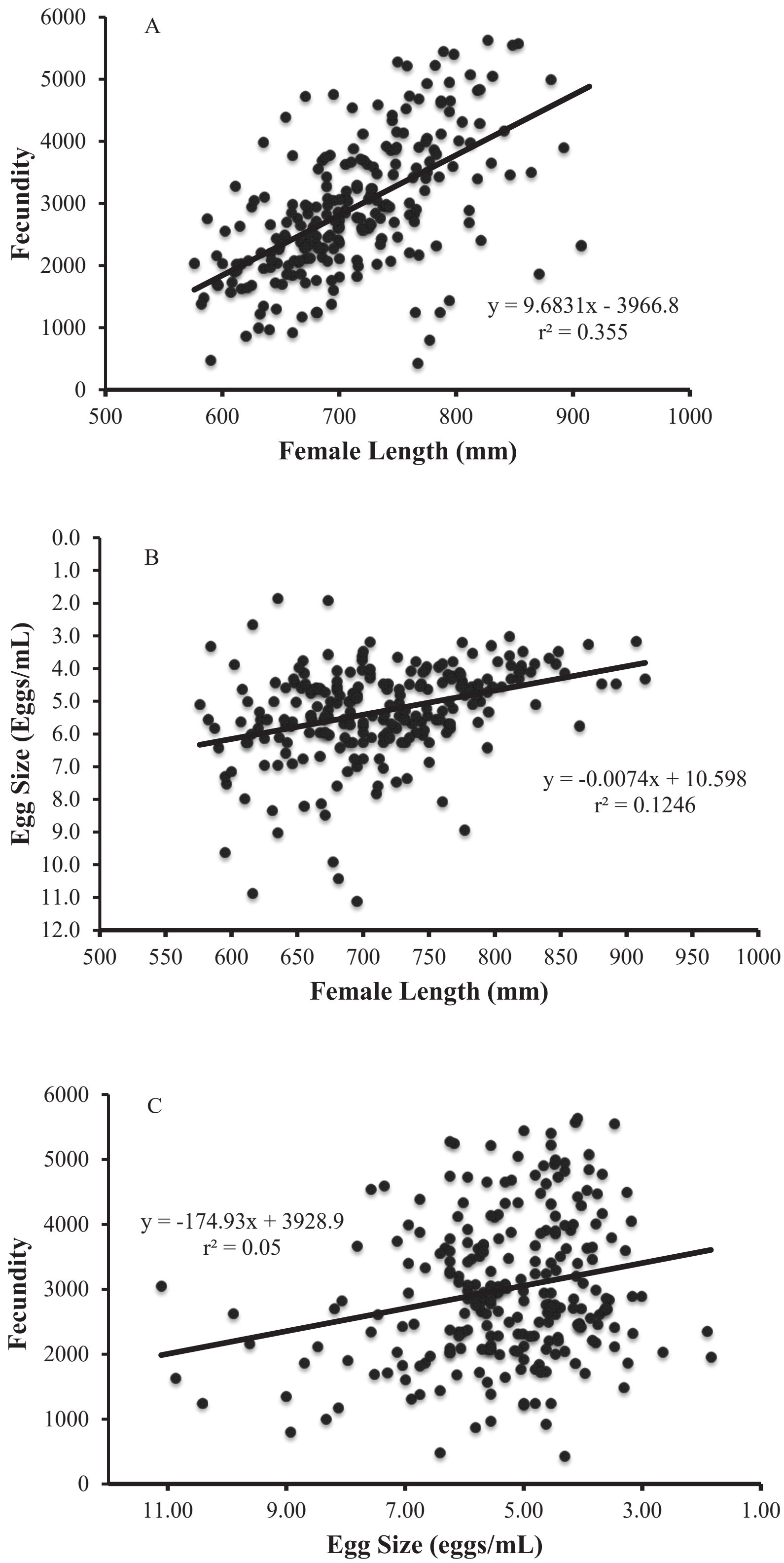

Figure 1. Regression line of (A) total fecundity (y) on female length (x), (B) total fecundity (y) relative to egg size (x), and (C) egg size (y) to female length (x) for female fall Chinook salmon from Lake Oahe, South Dakota, in 1988, 1998–2006, 2008, 2012, 2013, and 2015. The y-axis in figure B and the x-axis in figure C have been reversed because egg size was measured as eggs/mL of water displaced (as eggs/mL decreases, egg size increases).

eyed-egg survival rate was 99.4% from fish returning to the Quesnel River in British Columbia (Beacham and Murray 1989).

Major differences in water temperature and nutritional resources between Lake Oahe fall Chinook salmon and fish in their native range may possibly explain the observed differences in egg survival. Water temperature is a key factor when looking at egg survival to the eye up stage during egg development. According to Quinn (2005) egg survival is good at incubation temperatures between 5–11° C, but temperatures above 14° C lead to egg mortality. Furthermore, exposure to elevated water temperatures can adversely affect eggs during pre-spawn gonadal development (Van Der Kraak and Pankhurst 1997). While egg incubation temperature during hatchery rearing is 11° C, during the final month of egg maturation prior to spawning, broodstock females are routinely subjected to prolonged periods of water temperatures at or even slightly above 19° C. Water temperatures during spawning at Whitlocks Spawning Station, particularly during the first half of the run, often are above 16° C. Anecdotal evidence from large groups of eggs incubated at both McNenny and Cleghorn Springs State Fish Hatchery (Rapid City, South Dakota, USA) indicate that egg survival consistently increases from the start of the spawn to the end, contributing further evidence to the possible negative effects of elevated water temperatures prior to ovulation.

While the amount of available coldwater habitat fluctuates from year-to-year in Lake Oahe, it likely has little effect on egg survival. Barnes et al. (2001) found no relationship among 13° C or 15° C habitat volumes and fecundity, egg size, or egg survival. However, more recent studies have not been conducted, and while unlikely, it is possible that changes in available habitat may have some impact.

Low egg survival also may be due to dietary limitations, as parental nutrition is known to influence egg eye-up (Poston and Ketola 1989). Lake Oahe Chinook salmon are considerably smaller than their native range counterparts, at total lengths up to 300 mm shorter and spawning weights typically 25% or less than native range fish (Smirnov 1975, Laird and Needham 1988, Stickney 1991, Barnes et al. 2000). The diet of Lake Oahe Chinook Salmon in many years is primarily comprised of rainbow smelt (*Osmerus mordax*; Hill 1997). However, smelt numbers can fluctuate greatly from year-to-year (Stone and Nealson 1990). During years of low smelt abundance, Lake Oahe Chinook salmon diets consist primarily of Ephemeroptera and zooplankton (Barnes et al. 2000), although recently lake herring (*Coregonus artedi*) and potentially gizzard shad (*Dorosoma cepedianum*) also have become a part of the salmon prey base. While rainbow smelt abundance has been correlated with Lake Oahe Chinook salmon fecundity (Barnes et al. 2001), a correlation between smelt abundance and egg survival has never been observed. In comparison to Lake Oahe, Chinook salmon in the ocean consume a variety of fish species, along with various euphausiid, decapod, teuthid, and pelagic amphipod prey (Silliman 1941, Merkel 1957, Prakash 1962, Higgs et al. 1995, Wydoski and Whitney 2003). The more abundant and higher quality marine food supplies are not thought to be a limiting factor (Rothschild 1972).

Lake Oahe Chinook salmon produce smaller eggs than Chinook salmon in their native range. At 5.33 eggs/mL of water displaced, Lake Oahe eggs are approximately two-thirds the size of eggs from native range Chinook salmon which range from 2.07 to 3.60 eggs/mL (Donaldson and Menasveta 1961, Fowler 1972, Leitritz and Lewis 1976). Unlike the limited study of Barnes et al. (2000) on Lake Oahe fall Chinook salmon, this study documented a positive relationship between egg size and both spawning female length and post-spawn weight, possible due to the larger sample size of the current study. This relationship supports the hypothesis that the relatively small egg size is due to the relatively small size of Lake Oahe salmon, rather than some unidentified environmental factors (Jonsson and Jonsson 1999). Other researchers have documented a positive relationship between egg size and female size in salmonids (Pitman 1979, Springate and Bromage 1984, Fraser and Parke 1991, Estay et al. 1994, Morita and Takashima 1998).

At an average fecundity of less than 3,000 eggs per female, Lake Oahe Chinook salmon produce fewer eggs than that reported for native range populations, except for the Klamath River population in California (Leitriz and Lewis 1976). Fecundity of native range Chinook salmon populations ranges from 3,750 in Fall Creek, California (Wales and Coots 1954) to over 10,000 in Alaska (Healey and Heard 1984). Differences in food availability between Lake Oahe salmon and Pacific Ocean salmon are likely the reason for the differences in fecundity (Legget and Power 1969, Smith et al. 1979, Bagenal 1978, Luquet and Watanabe 1986). Dietary influences on fecundity are also supported by the positive relationship observed between fecundity and spawning female total length and weight in this study and in other studies (Buss and McCreary 1960, Scott 1962, Beacham 1982, Thorpe et al. 1984, Estay et al. 1997). The weak, but positive relationship between spawning female length and fecundity is similar to that observed in Lake Oahe Chinook salmon by Barnes et al. (2000) in 1998. However, Barnes et al. (2000) noted no relationship from the same population sampled in 1988.

The results of this study could be influenced by the paucity of data during certain years, as well as the complete absence of data during other years. For example, while the highest egg survival was observed in 1999, this was based on only five females. Sample size was only six females in 2004 as well. There was a complete data gap between 2008 and 2012, and the absence of spawning female weight data in 2002. Additional sampling would be beneficial, but is entirely dependent on the very limited space available and time constraints at a production hatchery.

MANAGEMENT IMPLICATIONS

Understanding typical egg survival percentages will assist managers in determining the effort required to collect female salmon to spawn to reach egg collection goals. The regression equation for fecundity and female length also should assist in this regard. In addition, the information on historical egg survival from Lake Oahe salmon can also be used to help managers decide, after spawning has been completed, if additional eggs should be sought from other Chinook salmon populations, if they were available. Salmon stocking numbers also may be adjusted to better balance stockings with available forage in an attempt to maximize spawning female size and increase the number of eggs per female.

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