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CHINOOK SALMON LENGTH/FECUNDITY: A REGRESSION MODEL FOR THE MOKELUMNE RIVER, CALIFORNIA

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ABSTRACT

From the fecundity data for Chinook salmon stocks, variability has been found both within and between populations. This variability increases the difficulty in predicting recruitment, even if numbers and sizes of returning female spawners can be estimated. We constructed length/fecundity models for fall run Chinook salmon on the Mokelumne River, a flow-regulated river in California, using 93 pre-spawn females.

Our model using non-$\log_e$-transformed data ($y = 11.137x-3065.5$; $r^2=0.54$; $n=93$) had equivalent predictive power to models using $\log_e$-transformed data ($y = 1.7x-2.7068$, $r^2=0.57$; $n=93$). In these models, fish length (x) accounted for 54-57% of the variability in fecundity (y), similar to that determined for Chinook salmon from other watersheds throughout the Pacific Northwest. These regression models should assist natural resources managers in regulating river flows and temperatures to maximize wild Chinook salmon spawning success and assist hatchery managers in improving salmon population maintenance and restoration.

INTRODUCTION

Chinook salmon, *Oncorhynchus tshawytscha,* have a wide distribution around the Pacific Rim extending from Russia to the lower latitudes of California. These stocks encompass a wide variety of life history adaptations ranging from lengthy (>1000 km) to fairly short upstream (<100 km) migrations, as well as different seasonal runs within specific watersheds. Sacramento River California Chinook salmon stocks, for example, are composed of four distinct runs: winter, spring, fall, and late-fall-run salmon (Moyle 2002). California Chinook salmon stocks are typically characterized as ocean-type although there is evidence that Sacramento River spring and winter-run Chinook salmon contain both ocean and stream-types (Healy 1994, Fisher 1994, Teel et al. 2000) and the late-fall run has been described as being stream-type (Moyle 2002). Current Mokelumne River, California, Chinook salmon stocks are fall-run, which exhibit an ocean-type life history.

A number of variables influence Chinook salmon fecundity (egg number) including, but not limited to, egg size, fish length, life-history strategy (ocean- or stream-type), latitude of natal stream, as well as the potential influence of hatchery operations on egg size evolution (Healey 1991, Moyle 2002, Heath et. al. 2003). Population density, food availability, and stream gradient also have been suggested as factors affecting fecundity in salmon as well as in other species (Wooton 1973; Dahlgreen 1979). Although fecundity generally increases with increasing female fish size when individuals uniformly produce eggs of similar size, Chinook salmon may deviate substantially from this model due to the variables listed above. This apparent deviation from life history theory has been predicted for semelparous species exhibiting high pre-reproductive survival (Bell 1980). Chinook salmon fecundity is determined from a combination of egg size and overall size of the individual (Nicholas and Hankin 1988; Healey 1991). Although larger Chinook salmon tend to produce larger eggs (Rounsefell 1957; Nicholas and Hankin 1988), fecundity estimates demonstrate large annual variances within populations with inter-population differences being even greater (Healey and Heard 1984; Nicholas and Hankin 1988). Additionally, salmon fecundity generally decreases with decreasing latitude with the exception of Sacramento River stocks, which show relatively high fecundity (Healey and Heard 1984). The observed population differences in Chinook salmon fecundity argue for the use of watershed-specific fecundity models for predictions of annual Chinook salmon ova production for use by fishery managers to manage Chinook salmon stocks

(Healey and Heard 1984).

The Mokelumne River, California, is a regulated river impacted by high temperatures, low flows, mining, multiple pollution sources (e.g., agricultural and urban runoff), dams, and water diversions that have adversely affected Chinook salmon stocks (CDFG 1959, Finlayson[1] and Rectenwald 1978). During the 1980s Chinook salmon augmentation, with ova and fry from Feather and American river stocks, represented >90% of salmon production (Estey[2] 1987). These augmentations have resulted in a Mokelumne River Chinook salmon stock of mixed origins. During their spawning migration, returning females can be identified by their morphology and their numbers and lengths estimated by staffed or video-equipped counting fences (Merz and Merz 2004). There is an approximate 12-hour to 10-day interval after passing video monitors at Woodbridge Irrigation District Dam (WIDD) fish ladders at (RKM 63, Workman[3] 2002) to when fish arrive on the spawning grounds and at the Mokelumne River Fish Hatchery (MRFH, Merz 1996). If lengths of fish passing fish-counting structures or ladders could be used to predict potential egg production, hatchery and natural resources managers could improve salmon population maintenance and restoration. For example, utilizing data on size, number, sex, and estimated fecundity, hatchery managers and biologists can estimate the proportion of salmon remaining in the river for a natural spawning in comparison to those spawned in the MRFH. In-stream estimates of ova production could provide hatchery and fisheries biologists crucial information on which management recommendations should be made concerning the timing and magnitude of water releases necessary to maintain optimal spawning conditions (i.e., temperature, flow, substrate availability, and oxygenation) during critical spawning periods. Our objective was to construct a Chinook salmon length/fecundity model specific to the Mokelumne River watershed, which could be used as a predictive tool for hatchery and fisheries management in this system.

MATERIALS AND METHODS

Fish Collection

Mokelumne River Chinook salmon were sampled, depending on availability of returning, ripe females, during scheduled spawning events at the California Department of Fish and Game (CDFG) MRFH. The number, and size, of fish selected during each sampling event was at the discretion of the MRFH manager. Since ≥40% of returning Chinook salmon in the Mokelumne River were classified as grilse in some years, grilse should be included in the sampling regime and in the length/fecundity models to provide better estimates of Chinook salmon ova production (personal communication Workman[4] 2004). To minimize time of return bias and potential differences in fecundity variability throughout the fall run Chinook salmon our objective was to select and sample 100 fish over the October to December 2003 spawning season. To this end eighty-six Chinook salmon were collected from the MRFH during 12 spawning events between 23 October and 22 December 2003, with 7 additional fish collected as trapping mortalities at the Woodbridge Dam fish ladder. Fish collection included adult females (fish > 610mm) and smaller, precociously mature fish classified as grilse, (fish ≤ 610 mm), for model construction. Electroshocking was the principle method of anesthetizing salmon broodstock at the MRFH. To minimize the impact on hatchery operations and to prevent the loss of ova during anesthesia and sorting of salmon broodstock we directed hatchery managers to select fish with eggs still bound to the ovary ("green" or unripe fish).

Fish Processing

To reduce the likelihood of ova spoilage due to blood contamination of ovaries anesthetized females were killed by a blow to the head and exsanguinated by severing the gill arches on both sides of the fish. Two length measurements were obtained prior to dissection of ova: fork length (FL) and the length from the posterior margin of the eye orbit to the end of the hypural plate (POH). Ovaries of selected fish were removed from the body cavity and placed in labeled, individual plastic bags and stored on ice prior to processing. Care was taken to account for any eggs remaining in the body cavity. Ovaries collected at Woodbridge Dam were salted and frozen prior to processing. Scale samples were taken posterior to the right pectoral fin in a subset of fish (n=55) sampled for the fecundity model to determine age (Jearld 1983).

Egg Processing

Chinook salmon ovaries were removed from storage bags, drained, and blotted dry prior to weighing. For gravimetric, sub-sampling fecundity estimates, total ovarian weight was obtained within 6 hours of collection and single, double, or triple aliquots were subsequently selected and weighed prior to brine-processing for determination of ova number. Individual aliquots contained a minimum of 20% of total ovarian weight. Accuracy and precision of the gravimetric fecundity estimates were determined by counting all ova in 27% (25/93) of fish selected for inclusion in

[1]Finlayson, B.J. and H.J. Rectenwald 1978. Toxicity of copper and zinc from the Penn Mine area on king salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Salmo gairdneri*) in the Mokelumne River Basin, California. Environmental Services Branch Report No.-78-1. California Department of Fish and Game, Rancho Cordova, California.

[2]Estey, D.F. 1987. Mokelumne River Hatchery Annual Report 1985-1986. Inland Fisheries Administrative Report No. 87-12. California Department of Fish and Game, Sacramento California.

[3]Workman, M.L. 2002. Lower Mokelumne River Upstream Fish Migration Monitoring conducted at Woodbridge Irrigation District Dam August 2001 through July 2002. Unpublished EBMUD report. Lodi Fisheries and Wildlife Division. 20pp + Appendix.

[4]Workman, M.L. 2004. Personal communication. Fisheries Biologist. East Bay Municipal Utility District, 1 Winemaster's Way, Suite K., Lodi , Ca. 95240

the fecundity model. Of these total count samples, single aliquots were analyzed in 52% (13/25) whereas double and triple aliquot estimates were determined in 32% (8/25) and 16% (4/25), respectively.

To release and preserve individual ova, a brine solution was heated to near-boiling temperatures, and the selected aliquots were placed into the solution. The brine consisted of saturated solutions of 250 ml NaCl (salt) and 250 ml $Na_2B_4O_7 \cdot 10H_2O$ (borax) added to two liters of water. Aliquots of the ovary were gently agitated in the heated brine until all ova were released (5 to 10 min) from the ovarian tissue. Ova were removed from the solution, drained of excess fluid, allowed to cool, liberally salted, and packed into labeled, Ziploc®-type plastic bags, and stored at -20° C, 30-60 days, prior to analysis.

Ova Counts and Fecundity Predictions

Salted ova were removed from storage bags, placed in a strainer, and rinsed with fresh water. Rinsed ova were placed onto acrylic boards and individually counted. Once counted, a fecundity estimate was calculated for individual fish using the following formula (Snyder 1921):

Fecundity estimate = ((Eggs in Aliquot) * (Aliquot weight)$^{-1}$) * Total ovarian weight

Age Estimates

Scale samples were collected posterior to the right pectoral fin, placed into coin envelopes, and labeled with the date, sex, and FL measurements. Six to ten non-regenerated scales were examined from each of the fish selected for aging. Scale annuli were counted using a microfiche reader (Jearld 1983). To reduce bias, the reader conducted scale reading without knowledge of length measurements. A single individual made all age estimates.

Data Analysis

Statistical analysis of the data (one-way ANOVA, $P = 0.05$) was conducted with SYSTAT SigmaStat 2.03 statistical software comparing total fecundity counts with estimates of fecundity derived from single, double and triple ova counts for our calculations. To facilitate comparisons between published literature values and models, we constructed simple linear regression models from both the total fecundity counts and estimates of fecundity using the gravimetric method (Snyder 1021, Healey and Heard 1984). Linear regression models were constructed, plotted, and analyzed for statistical significance with the use of the SigmaPlot 2000 statistical software package published by SYSTAT software, Inc.

Table 1: Sampling dates, fork lengths, and estimates of total number of ova (derived from regression model $y = 11.1\ 4x - 3066$, $R^2 = 0.54$ [Figure 2]), in 93 salmon sampled during the 2003 return of fall-run Chinook salmon on the Mokelumne River.

Collection date 2003	Fork length (mm)	Estimate of ova number	Collection date 2003	Fork length (mm)	Estimate of ova number	Collection date 2003	Fork length (mm)	Estimate of ova number	Collection date 2003	Fork length (mm)	Estimate of ova number
23-Oct	770	4666	3-Nov	610	3317	12-Nov	787	5108	4-Dec	776	4928
23-Oct	760	7025	3-Nov	762	3151	12-Nov	851	6406	8-Dec	851	6190
23-Oct	729	4463	3-Nov	641	4845	14-Nov	886	5514	8-Dec	816	6439
23-Oct	578	2233	3-Nov	768	6090	14-Nov	800	5826	8-Dec	784	5811
23-Oct	751	3973	3-Nov	625	3325	14-Nov	654	5215	11-Dec	799	5034
30-Oct	973	7126	3-Nov	794	6082	14-Nov	822	5104	11-Dec	895	7403
30-Oct	892	5380	3-Nov	889	9492	14-Nov	797	5423	11-Dec	743	5687
30-Oct	718	4837	3-Nov	657	3462	14-Nov	807	6599	11-Dec	753	5243
30-Oct	605	3955	3-Nov	699	3946	14-Nov	664	3356	11-Dec	724	4838
30-Oct	570	3978	3-Nov	641	5628	14-Nov	835	8151	11-Dec	775	6284
30-Oct	829	7686	3-Nov	794	5695	14-Nov	756	5097	11-Dec	781	5081
30-Oct	592	3227	6-Nov	768	4955	14-Nov	743	5614	11-Dec	791	6758
30-Oct	527	2841	6-Nov	845	5843	14-Nov	740	5365	16-Dec	826	6940
30-Oct	768	5518	6-Nov	883	8546	17-Nov	860	6993	22-Dec	848	5961
30-Oct	760	5127	6-Nov	953	6693	17-Nov	676	6024	22-Dec	619	3094
30-Oct	603	3288	6-Nov	641	4182	17-Nov	876	6561	22-Dec	864	5839
30-Oct	633	4940	6-Nov	752	6393	17-Nov	780	8915	22-Dec	740	3775
30-Oct	851	4910	6-Nov	651	5738	17-Nov	750	5125	22-Dec	791	6820
30-Oct	813	7319	6-Nov	629	2132	17-Nov	800	4597	22-Dec	787	4993
30-Oct	729	6495	6-Nov	927	6784	17-Nov	820	7938	22-Dec	718	5042
30-Oct	794	5917	6-Nov	767	5838	17-Nov	830	6054	22-Dec	768	5031
30-Oct	681	3986	12-Nov	800	6222	17-Nov	700	3934			
3-Nov	673	4039	12-Nov	991	6939	4-Dec	746	4354			
3-Nov	757	5582	12-Nov	781	6293	4-Dec	813	8140			

Mean fork length = 762 mm; fork length range = 527-991 mm; mean fecundity estimate = 5,423; range of fecundity estimates = 2,132-9,492.

Figure 1:

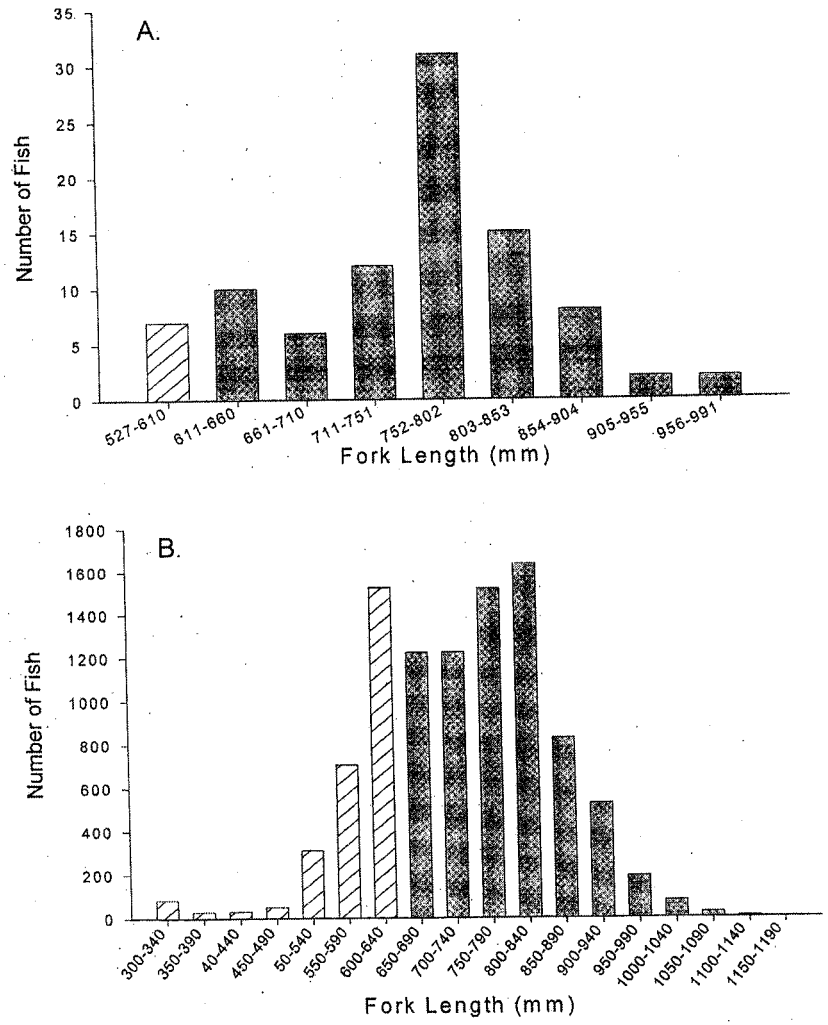

Figure 1A. Size distribution of Chinook salmon sampled during spawning events at the Mokelumne River Fish Hatchery, California. Mean fork length of Chinook salmon in our sample set was 762 mm (range: 527 – 991 mm, n=93). Grilse salmon: hatched bar. Figure 1B. Length-frequency distribution of 2003 fall-run Chinook salmon passing video monitors on the lower Mokelumne River, August 2003 to January 2004. Grilse: hatched bars. Length estimate ± 5 cm, n = 9,981

RESULTS

Fish Collection

Ninety-three individuals (527-991 mm FL [mean: 762 mm]), including 86 adults and 7 grilse were used to construct the Mokelumne River Chinook salmon length/fecundity model (Table 1, Fig. 1A). This sample is representative of the adult and grilse component of the entire 2003 run (Fig. 1B, Workman[5] 2004).

Table 2. Comparison of gravimetric sub-sampling estimates of Mokelumne River Chinook salmon fecundity versus actual fecundity counts. Reported are the results of single[a], double[b](median), and triple[c] (mean) aliquot estimates of ova counts.

Fish size (mm)	Estimated # of eggs	Actual egg count	Percent of actual count	Egg count difference[d]
800	4638[a] ± NA	5711	81.2	-1073
625	3325[a] ± NA	3951	84.2	-626
610	3316[a] ± NA	3674	90.3	-357
740	5365[a] ± NA	5685	94.4	-320
750	5125[a] ± NA	5286	97.0	-161
746	4353[a] ± NA	4425	98.4	-71
820	7937[a] ± NA	7977	99.5	-39
830	6053[a] ± NA	6079	99.6	-25
619	3093[b] ± 12	3097	99.9	-3
740	3775[b] ± 20	3776	100.0	-1
751	3973[a] ± NA	3964	100.2	9
895	7402[c] ± 85	7382	100.3	21
724	4837[b] ± 99	4820	100.4	18
753	5243[c] ± 69	5217	100.5	26
799	5033[c] ± 114	4999	100.7	35
775	6284[c] ± 123	6239	100.7	45
776	4928[c] ± 38	4882	100.9	46
826	6940[c] ± 99	6842	101.4	98
743	5686[c] ± 140	5606	101.4	81
781	5080[c] ± 50	5003	101.6	78
800	4596[a] ± NA	4468	102.9	129
768	4955[a] ± NA	4799	103.3	156
816	6438[b] ± 14	6232	103.3	207
700	3933[a] ± NA	3776	104.2	158
813	8139[a] ± NA	7103	114.6	1037
Mean # ova	5218 ± 1385	5240	99.2	-21.3
Min. # ova	3094	3097	81.2	-1073
Max. # ova	8140	7977	104.3	1037

[d]Egg count difference = Estimated count – Actual count. (Positive = overestimate and negative = underestimate).

[5]Workman, M.L. 2004. Lower Mokelumne River Upstream Fish Migration Monitoring conducted at Woodbridge Irrigation District Dam August 2003 through July 2004. Unpublished EBMUD report. Lodi Fisheries and Wildlife Division. 23pp + Appendix

Fecundity Estimation

There were no significant differences (ANOVA, $P = 0.95$) between fecundity estimates and actual counts, using the single, double, or triple aliquot method (Table 2). Egg count differences, Table 2, between gravimetric estimates and total ova counts tended to be higher in single (mean = 320) aliquot counts, but they were not statistically greater (ANOVA, $P = 0.07$) when compared to egg count differences with double (mean = 57) or triple (mean = 53) aliquot counts. Fecundity estimates varied from actual egg counts by <1% to 19%, with 84% of the estimates within 4% of the total ova counts and 44% of the estimates within 1% of total counts. Furthermore, gravimetric fecundity estimates were about as likely to overestimate (60% of the samples) ova counts as to underestimate them (40% of samples). Salting and freezing of egg masses was found to produce very fragile eggs which were subject to breakage during storage, processing, or handling. These broken eggs decreased both the accuracy and precision of ova counts for fecundity estimation. In comparison, the

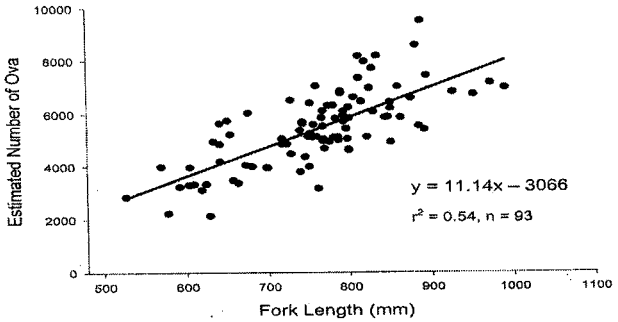

Figure 2. Regression of Mokelumne River Chinook salmon fork length and estimated number of ova, including grilse.

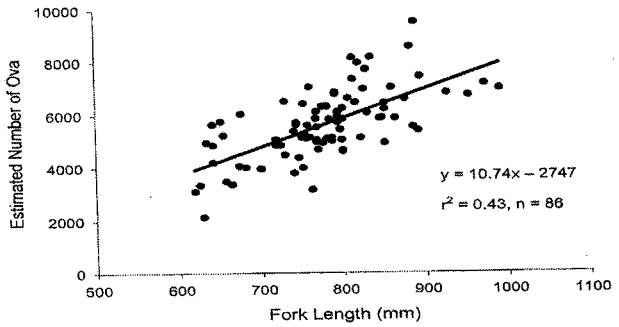

Figure 3. Regression of estimated fecundity in Mokelumne River Chinook salmon, excluding grilse (FL > 610 mm).

hot-brine preparation method produced a uniform, intact, durable egg for counting with little to no egg breakage during processing or storage.

Fecundity Estimation Models

Chinook salmon lengths were positively correlated to their fecundities, albeit

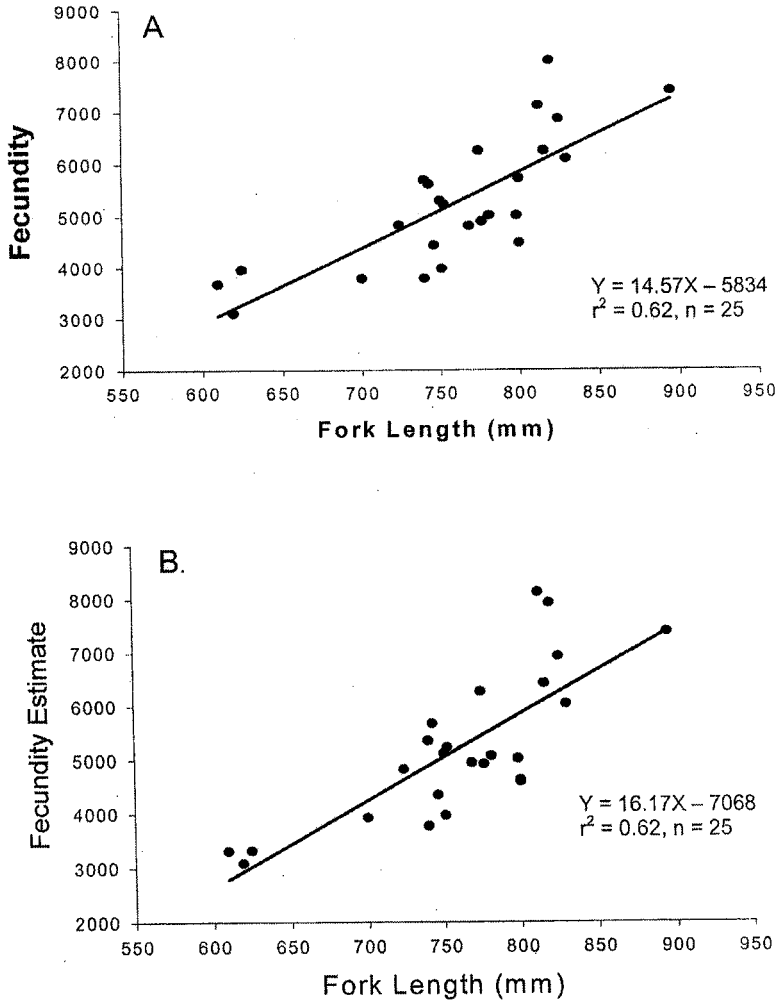

Figure 4. Regression models constructed with data from 25 individual salmon where both estimates and actual counts are known. Figure 4A shows the regression of fork length on fecundity while Figure 4B shows the regression of fork length on the estimated fecundity which was calculated by determining the proportion of eggs each aliquot represented of the total skein weight.

with substantial variability. Inclusion of grilse produced a length/fecundity model where length explains 54% (r^2=0.54) of the variability in Mokelumne River Chinook salmon fecundity with a correlation coefficient (r) of 0.75 (Fig. 2). Exclusion of grilse decreased the r^2 to 0.43 (Fig. 3). Regression analysis of FL and POH versus fecundity produced near-identical regression models (fecundity = 10.75FL - 2747; r^2 = 0.43 versus fecundity = 13.19POH - 3048; r^2 = 0.46).

Construction of three regression models showed similar predictive power (Fig. 4 A, B and Fig. 5). In the two models using the non-transformed actual and estimated fecundity data from Table 2, FL accounts for 62% (r^2=0.62) of the variability in fecundity in the fecundity estimate and actual fecundity models. This is an increase in predictive power of ≈ 6% over the length/fecundity estimate model that included grilse (Fig. 2) and 13% increase over the length/fecundity model for adult Mokelumne River Chinook salmon without grilse (Fig. 3). To compare fecundity differences among the three models, we used an average female FL of 762 mm to calculate model predictions. Estimates from all models were within 3% of each other, with 5,421 ova from the Figure 2 model and Figure 4 A and B models providing estimates of 5,268 and 5,251 ova, respectively. The $\log_e$-transformed Mokelumne River model, including both grilse and adults, show increased linearity with a slight (2%) increase (r^2=0.57) in predictive power over models constructed with non-transformed data (Fig. 5). The fecundity prediction from this model for a 762-mm Mokelumne River female Chinook salmon was 5,293 ova, which is within 2% of the estimates obtained from the non-$\log_e$-transformed models. Finally, we found no difference between the two length measurements, FL and POH, in our model predictions.

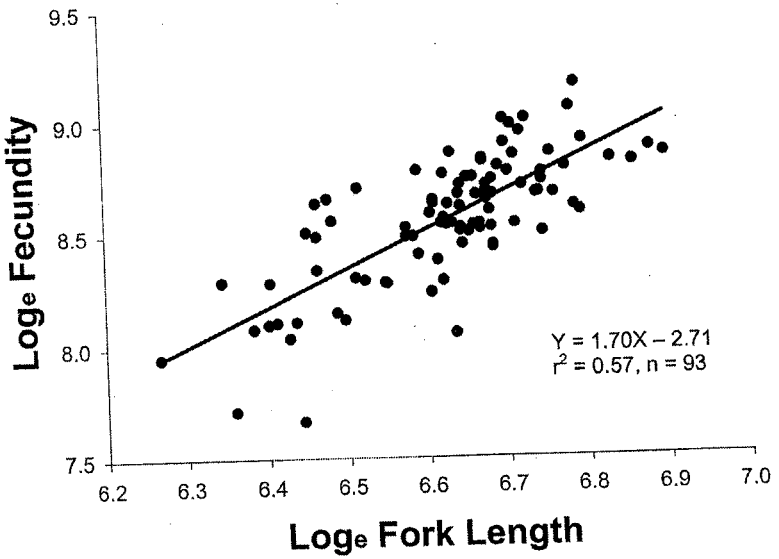

Figure 5. Regression of $\log_e$ FL and $\log_e$ fecundity data collected from the returning Fall 2003 Chinook salmon run of the Mokelumne River.

Table 3. Age structure and corresponding fecundity in Mokelumne River Chinook salmon. With a trend of increasing fecundity with age, there was a statistically significant difference in fecundity between 2 year-old fish and 3 & 4 year-old fish (ANOVA, P=0.002)

Number of eggs (500 egg interval)	Number of fish of each age			
	2 years	3 years	4 years	5 years
2,000-2,500	1			
2,500-3,000				
3,000-3,500	1	1		
3,500-4,000	2	1		
4,000-4,500		1		
4,500-5,000		4	2	
5,000-5,500		6	4	
5,500-6,000	1	5	3	
6,000-6,500	1	6	1	
6,500-7,000		2	6	
7,000-7,500		1	1	1
7,500-8,000				
8,000-8,500		2		
8,500-9,000		1		
Total Individuals	6	30	17	1
Mean number of eggs	4,185	5,838	5,994	7,403
Standard Deviation	1348	1205	784	NA

Age and Fecundity

Returning Mokelumne River Chinook salmon spawning stocks consisted of at least 4 year classes in 2003 (Table 3). Our sample set consisted of 13% 2-year-old fish, 55% 3-year-old fish, 31% 4-year-old fish, and 2% 5-year-old fish. There was a general increase in fecundity with increased age although the differences between mean ova counts in 3- and 4-year-old fish were minimal and statistically insignificant (one-way ANOVA, P = 0.63). Two-year-old fish were less fecund than either 3- and 4-year-old fish (one-way ANOVA, P = 0.003). The one 5-year-old salmon datum precluded statistical comparisons.

DISCUSSION

A paucity of fecundity data has been published regarding specific Chinook salmon stocks. Available data indicate a high degree of inter-individual variability within these Chinook salmon stocks as well as a high degree of inter-population variation among stocks examined (Healey and Heard 1984). For example, Sacramento River

Table 4: Regression parameters and coefficients for $\log_e$ transformed and non-transformed models for three California Chinook salmon populations.

Population	Sample size	Mean length	Range of length	Mean fecundity	Range of fecundity	Log_e Transformed	Regression Statistics					
							b[1]	m^2	Std error m	r	r^2	F
[1]Mokelumne	93	762	527-991	5423	2132-9492	No	-3066	11.137	1.085	0.73	0.54	105.4
[2]Mokelumne	86	776	619-991	5599	2132-9492	No	-2747	10.745	1.341	0.66	0.43	64.21
[3]Mokelumne	25	760	610-895	5218	3094-8140	No	-5856	14.599	2.394	0.79	0.62	37.2
Klamath	106	814	520-1070	3752	1718-8406	No	-1881	6.921	0.772	0.66	0.44	80.3
Sacramento	50	924	590-1100	7423	4795-11012	No	-2727	5.082	1.805	0.38	0.14	7.93
[1]Mokelumne	93	762	527-991	5423	2132-9492	Yes	-2.707	1.7	0.155	0.75	0.57	120.136
[2]Mokelumne	86	776	619-991	5599	2132-9492	Yes	-2.1	1.609	0.195	0.67	0.45	68.068
[3]Mokelumne	25	760	610-895	5218	3094-8140	Yes	-5.298	2.087	0.195	0.80	0.65	41.813
Klamath	106	814	520-1070	3752	1718-8406	Yes	-1.117	1.392	0.088	0.68	0.46	88.705
Sacramento	50	924	590-1100	7423	4795-11012	Yes	4.806	0.599	0.21	0.38	0.15	8.16

Population superscripts: 1 = fecundity estimate model with adult and grilse salmon; 2 = fecundity estimate model with only adult salmon, 3 = actual fecundity model with sub-set of Chinook salmon. b1= intercept; m^2 = slope. Statistical analysis of the data was performed using Sigma Stat 2.0 statistical software.

Chinook salmon were nearly twice as fecund as similar-size Klamath River Chinook salmon (Table 4). Whereas Klamath River Chinook stocks averaged 3,752 eggs per female (range 1,718-8,406) with 46% (r^2=0.46) of the variation in fecundity explained by salmon length, Sacramento River Chinook salmon have a mean of 7,423 eggs per female (range 4,795-11,012) with 15% (r^2=0.15) of the variability in fecundity explained by salmon length (McGregor 1922, Healey and Heard 1984). In our study, the Mokelumne River Chinook salmon stock averaged 5,423 eggs per female (range 2,132-9,492), nearly at the midpoint between Klamath and Sacramento Chinook salmon stocks with the percent variability explained by fork length ranging from 43-66% depending on which model was used. While 38-87% of the variability in Chinook salmon fecundity has been explained by length in prior studies, the remaining sources of variability have not been determined (Healey and Heard 1984). Previous fall surveys conducted on the Mokelumne River showed that size class composition of returning salmon varied greatly between yearly runs (Kano 2003 a[6] and b[7], 2004[8]). The grilse (FL ≤ 610 mm) percentage of returning salmon increased from 2.5% in 1997, to 21.5% in 1998 and 43% in 1999. Long-term-trend data collected by the East Bay Municipal Utility District (EBMUD) show 3 years where the Mokelumne run was composed of greater than 30% grilse from 1990 to 2003 (1992, 1996, and 1999, pers. communication Workman[4] 2004). In all years, even where the grilse component is high, it is typically male-dominated (60-75% male; Workman[5] 2004).

Fish Collection

McGregor (1922) found that Chinook salmon size appeared to vary with month of entry into the Klamath River system. In that study, seven salmon grouped at the extreme length range of the data set entered the Klamath River system in September. To minimize size-selection bias in our study via potential return timing differences of various size and year classes within the Mokelumne River system, we collected fish over a 60-day period, 23 October- 22 December 2003. Chinook salmon used for our length/fecundity models show a normally distributed representation of the various size classes returning to spawn in the Mokelumne River in 2003 (Fig. 1B, Workman[5] 2004). Returning fall-run salmon spawning salmon stocks on the Mokelumne River may contain a significant number of grilse in any given year. Our data show that inclusion of grilse in the regression model increases the predictive power of the model by 11 percent (r^2=0.54 with grilse versus r^2= 0.43 without grilse)

[6]Kano, R. 2003A. Annual report: Chinook salmon spawner stocks in California's central valley, 1997. Inland Fisheries Administrative Report No. 2003-1.

[7]Kano, R. 2003B. Annual report: Chinook salmon spawner stocks in California's central valley, 1998. Inland Fisheries Administrative Report No. 2003-2.

[8]Kano, R. 2004. Annual report: Chinook salmon spawner stocks in California's central valley, 1999. Inland Fisheries Administrative Report No. 2004-7.

[4]Ibid

[5]Ibid

Fecundity Estimation

Gravimetric estimation of fecundity has been reported to be accurate to about 1% of actual fecundity (Snyder 1921; McGregor 1922). These older studies utilized small (10 g) aliquots, representing approximately ≤ 1% of total ovarian weight. Our fecundity estimation procedure used larger aliquots, ≈20% of ovarian weight, to estimate total number of ova, and we found that 84% of our estimates were within 4% of total counts with 44% within 1% of total ova counts. There was no statistically significant improvement in the accuracy in gravimetric ova predictions utilizing triple or double aliquots when compared to the single aliquot estimations, nor did larger aliquot sizes improve precision of fecundity estimates. Based on these data we feel single aliquot samples, representing 1-20% of salmon ovarian tissue, provide an accurate estimation of fecundity.

Fecundity Estimation Models

Many reports on Chinook salmon fecundity use non-transformed data to construct models (Rounsefell 1957). The rationale given was that there was no improvement in prediction power between models constructed using transformed and non-transformed data. However, life history theory (Bell 1980, Healey and Heard 1984, Moyle and Cech 2004) suggests that fecundity should be proportional to the cube of fish length and that log transformation makes the data linear, stabilizing the variances in the data set (Healey and Heard 1984). In our length/fecundity analysis we compared both model construction methods and found that, while $\log_e$ transformation increased linearity, the models were comparable in predictive power. While this deviation from life history theory is predicted (Bell 1980) and observed in our and other published Chinook salmon fecundity models, the underlying mechanism remains unclear. A number of factors may contribute to this deviation, including changes in female salmon morphology with increasing size, watershed gradient, food availability, and population density as well as hatchery influence on egg size.

Our fecundity regression models show similar results to those reported for other Pacific Rim Chinook salmon. For comparative purposes we constructed regression models using $\log_e$-transformed data from literature values on fecundity for Klamath River and Sacramento River Chinook salmon stocks, as well as Mokelumne River Chinook salmon length/fecundity data (Table 4). Previous fecundity reports, based on $\log_e$-transformed data, show that length, on average, explains 62% of the variability in fecundity between populations of Chinook salmon, extending from 14% for Sacramento River stocks to 76% for Columbia River stocks (Healey and Heard 1984). Healey and Heard (1984) report that the slope of the $\log_e$-regression model on salmon fecundity is low (slope < 2) when compared to those of other species (slope > 3), probably due to both the large size of salmon eggs and that fecundity increases less with size in Chinook salmon when compared to that in other fish species (Healey and Heard 1984, Moyle 2002). In our regression model we found that the slope of the $\log_e$-transformed model was 1.7, consistent with other Pacific Chinook salmon fecundity models (Healey and Heard 1984).

Age and Fecundity Relationship

While we found a positive relationship between fecundity and age in Mokelumne River Chinook salmon, the relationship was largely driven by the high and low fecundities at the extremes of the age distribution. In contrast, Snyder (1921) found no correlation between the age and fecundity of Klamath River Chinook salmon, although he noted that the 5-year-old fish showed the highest fecundities. McGregor (1922), with a larger sample size, found a distinct increase in fecundity with increasing age among 3, 4, 5, and 6 year-old Klamath River salmon. Additionally, recent studies have found that hatcheries may accelerate the evolution of smaller egg size in salmonids by removal of selection pressures and may markedly increase fecundity (Heath et. al. 2003). These recent studies have also found that while larger egg size may facilitate greater survival of salmon fry, the evolution of small egg size and its influence on survival may be offset by the increased fecundity associated with smaller egg size (Heath et. al. 2003). In our study we found increasing fecundity from 2 year olds to 3 and 4 year olds, with no significant difference between 3 and 4 year olds.

CONCLUSIONS

In the Mokelumne River, Chinook salmon ova production is from two distinct sources, hatchery operations and in-stream spawning. By combining length/sex data from the Woodbridge fish ladder 40 rkm downstream of the MRFH with our Chinook salmon length/fecundity models, managers can make predictions of total production of Chinook salmon ova in the Mokelumne River watershed before river spawning and hatchery escapement occur. Variations among three California Chinook salmon fecundity models, with Mokelumne River fecundity estimates typically higher than those from the Klamath River and below those from the Sacramento River, underline the need for the construction of watershed-specific models to obtain accurate ova production estimates for management of Chinook salmon stocks. Prediction of potential hatchery and in-stream production of Chinook salmon ova in a given watershed has important ramifications for fishery management. These issues range from the timing and magnitude of water releases from upstream dams for management of in-stream temperatures and flows to maximize Chinook salmon spawning success, to evaluating long-term effects of environmental change (e.g., global climate change) on salmon populations. The relatively high variability observed in our data from the Mokelumne River may reflect its mixed-stock heritage as well as the potential influence from years of hatchery reproduction on egg size, hatchery-feeding regimes, as well as undetermined physiological and environmental attributes that influence the timing and age of Chinook salmon returning to this watershed. With these new models and continued fish passage monitoring of Chinook salmon sex and length, fisheries managers will be able to predict ova production, in both the hatchery and natural spawning, to better optimize salmon reproduction and escapement in the

Mokelumne River watershed.

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