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ARTICLE

The effect of reducing dietary lipid and food availability on precocious male maturation in Chinook Salmon: A production-scale hatchery experiment

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Abstract

Objective: Age of maturation in Chinook Salmon *Oncorhynchus tshawytscha* is phenotypically plastic, influenced by both genotype and environmental factors, including the availability and composition of the diet. Salmon hatchery programs often rear fish under accelerated growth regimes using high-lipid diets that can result in earlier age at maturity, including increased prevalence of age-2 males (minijacks). The goal of this investigation was to compare alternative dietary regimes to mitigate for this shift in age at maturity in hatchery-reared Umatilla River fall Chinook Salmon.

Methods: Juvenile fish were reared at Bonneville Hatchery, Oregon, under four dietary treatments across four replicate brood years. Dietary treatments included two feeding frequencies (standard [fed 7 days/week] and reduced [fed 4 days/week]) and two dietary lipid levels (standard [18%] and reduced [12%]) in a 2 × 2 factorial design. Dietary treatments were applied for approximately 9 months, beginning in March (a month after fry emergence) and lasting until December of the first year, after which all fish were reared on the standard feeding regime (7 days–18%) until the time of release the following spring as yearlings.

Result: We observed significant interannual variation in the proportion of minijacks produced among dietary treatments. For all brood years, decreasing the feeding frequency from 7 to 4 days/week reduced the proportion minijacks by 35.9%, and lowering dietary lipid from 18% to 12% reduced the proportion minijacks by 30%. The combined effects of reducing the feeding frequency and lowering dietary lipid were additive, reducing the proportion minijacks by 65.5% compared to the standard rearing regime. Growth and energetic indices were monitored throughout and confirmed findings from previous laboratory-based studies indicating that physiological status 10–12 months prior to spawn timing is important for the "decision" to mature.

Conclusion: Results of this investigation provide useful insights for optimizing rearing regimes for the Umatilla River program and other Chinook Salmon hatchery programs.

KEYWORDS

Chinook Salmon, diet manipulation, growth, hatchery, IGF-I, minijacks

Lance Clarke is retired.

†Deceased.

INTRODUCTION

Salmon hatchery programs have been implemented throughout the Columbia and Snake River basins in the Pacific Northwest to mitigate for stock losses as a result of hydropower development, urbanization, agriculture, fisheries, and forestry practices (Lichatowich 1999; Waples et al. 2007). Although some hatchery programs have successfully increased the numbers of returning adult fish (Kline and Flagg 2014; Fast et al. 2015), undesirable consequences of hatchery culture have been observed, including genotypic and phenotypic changes that have been implicated in the reduced fitness of hatchery fish when spawning in the wild (Reisenbichler and Rubin 1999; Ford 2002; Reisenbichler et al. 2004; Waples et al. 2004; Araki et al. 2008; Bowlby and Gibson 2011; Ford et al. 2012). Of particular note, several previous studies have documented the release of hundreds of thousands of male Chinook Salmon *Oncorhynchus tshawytscha* that have initiated early maturation as age-2 minijacks each year from hatchery programs throughout the Columbia River basin (range = 7.9–71.4% of males, depending on the program; Larsen et al. 2004a, 2013, 2019a, 2019b; Harstad et al. 2014, 2018; Spangenberg et al. 2014, 2015; Beckman et al. 2017). This circumstance is unfortunate, as these early maturing males do not add to hatchery program goals, including contributions to harvest of adults or supplementation of natural populations by full-size breeding adults. The high proportion of these fish in hatchery releasees has been unexpected, as minijack production in wild populations has been indirectly estimated to be 10-fold lower than that of hatchery fish (Larsen et al. 2013). Thus, hatchery culture conditions can significantly impact the age at which fish mature, highlighting the need to design rearing regimes that mitigate for these effects.

Age of maturation in salmonids has been described as a genetically set threshold trait (Piché et al. 2008; Larsen et al. 2019b, 2021) in which the condition of individual fish during a sensitive time period, set by seasonal photoperiod, influences the physiological "decision" to initiate the maturation process (Clarke and Blackburn 1994; Thorpe 1994; Silverstein et al. 1998; Beckman et al. 2007). In Chinook Salmon, this window for minijack maturation has been documented to begin during the summer–autumn period 10–12 months prior to reaching full maturity the following year at age 2 (Shearer and Swanson 2000; Campbell et al. 2003; Larsen et al. 2006; Shearer et al. 2006). Laboratory-based studies have shown that both food availability and dietary lipid levels during the critical decision window may alter rates of early male maturation in Chinook Salmon (Silverstein et al. 1998; Shearer and Swanson 2000; Larsen et al. 2006; Shearer et al. 2006). Similarly, manipulation of food availability has also been examined with production-scale hatchery studies showing that increased feed ration levels may increase early male maturation (Larsen et al. 2013; Spangenberg et al. 2014; Beckman et al. 2017). Taken together, all of these studies have demonstrated that elevated energy acquisition (via food availability and/or dietary lipid) and associated growth during this sensitive period have a significant influence on minijack maturation.

Impact Statement

This study demonstrates that altering the composition and amount of feed can generate salmon smolts with differing physiological attributes and levels of early maturation. These findings may influence hatchery programs to alter standard feeding practices to produce smolts with more desirable phenotypes and thus increase hatchery productivity. The most important implication is that hatchery programs have the ability to make choices about feeding programs that allow them to produce smolts with varying performance.

In the early 1980s, the Umatilla River fall Chinook Salmon hatchery program in northeast Oregon was established to reintroduce fall Chinook Salmon to the Umatilla River, recover lost harvest opportunities, and help reestablish a "localized" population (Figure 1). This hatchery program has experienced relatively low adult returns to the Umatilla River (Hogg et al. 2014; Oregon Department of Fish and Wildlife 2015). Confounding the program's low anadromous adult production has been very high minijack production. During return years 1995–2011, an average of 41.4% of all adults (51.5% of all males) returning to Three Mile Falls Dam (TMFD; Figure 1) on the Umatilla River consisted of minijacks (Zimmerman et al. 2003; Clarke et al. 2014; Oregon Department of Fish and Wildlife 2015). This poor performance necessitated further exploration of alternative dietary regimes for the yearling production of the Umatilla River fall Chinook Salmon hatchery program in an effort to improve survival and reduce high minijack production. The novelty of this work lies in the manipulation of both the dietary lipid level and food availability to assess the relative effect of each factor alone or in combination on early male maturation.

The objective of this study was to explore how manipulating food availability and dietary lipid levels during early rearing affects minijack production in the Umatilla River yearling fall Chinook Salmon hatchery program. Throughout the experiment, we monitored dietary treatment effects by measuring a suite of known growth and energetic indices and then conducted a census of minijack

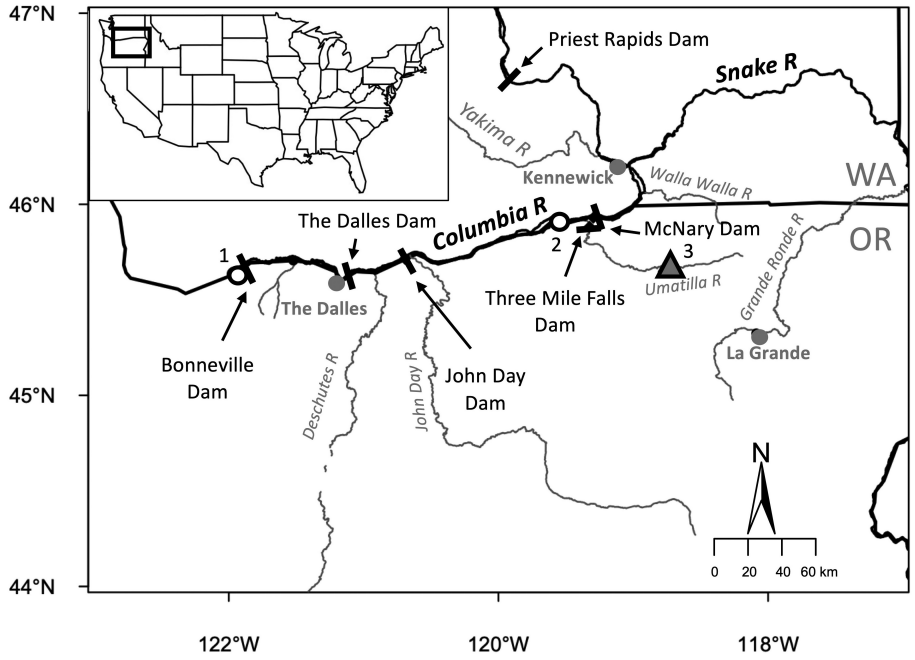

FIGURE 1 Rearing sites for the Umatilla River fall Chinook Salmon hatchery program in northern Oregon (1 = Bonneville Hatchery; 2 = Umatilla and Irrigon Hatcheries; 3 = Pendleton Acclimation Facility).

production from each feed treatment group at the end of hatchery rearing. Finally, we explored the temporal relationships between growth and energetic indices and the proportion of minijacks. The overall goal of this work is to optimize hatchery rearing regimes for the Umatilla River yearling fall Chinook Salmon hatchery program and provide guidance for other regional Chinook Salmon hatchery programs.

METHODS

Experimental design

The study used a 2 ×2 factorial design, with two food availability treatments (achieved via the number of days on which the fish were fed each week; hereafter, "feeding frequency") and two dietary lipid treatments repeated over 4 years (brood years [BYs] 2010–2013). The two feeding frequency treatments were standard (fed 7 days/week) and reduced (fed 4 days/week). The two dietary lipid treatments were standard (18% lipid; BioClark Fry Feed; Bio-Oregon) and reduced (12% lipid; a special formulation of the Abernathy Salmon Diet; Rangen, Inc.). Combined, the feeding frequency and dietary lipid treatments created four dietary treatments: standard feeding frequency and standard dietary lipid (7 days–18%); standard feeding frequency and reduced dietary lipid (7 days–12%); reduced feeding frequency and standard dietary lipid (4 days–18%); and reduced feeding frequency and reduced dietary lipid (4 days–12%). The 7 days–18% treatment represents the typical feeding regime used to rear juveniles for the Umatilla River yearling fall Chinook Salmon hatchery program and other programs throughout the Columbia River basin. This treatment essentially served as a control treatment for comparison with the other three dietary treatments. The dietary treatments began in March for all groups after initial rearing on BioVita starter feed (Bio-Oregon). Fish continued rearing on experimental dietary treatments until the beginning of December for each BY; thereafter, all groups were reared under the standard feed regime (7 days–18%) until the time of release the following spring.

The amount of feed provided per day adhered to the feed manufacturers' recommendations based on fish size and water temperature. However, fish from the different feed frequency treatments received varying amounts of feed per week. Specifically, the 4-days/week treatments only received this daily recommended amount of food 4 days/week rather than 7 days/week. This difference in feeding frequency equates to an approximately 43% reduction in feed provided per week at the onset of the treatment period. The percentage difference in feed provided changed over time as mean fish weights of the treatments diverged. Size of fish for each rearing group was measured monthly (~1% of fish per raceway via batch weights) to forecast feed schedules. The commercially available diets described above contain comparable minimum levels of protein (47% versus 45%; Fowler and Banks 1972; Lemm et al. 1988; R. Twibell, 2010–2013, memoranda to National Fish Hatchery managers,

Pacific and Pacific Southwest Regions, report on proximate composition of feed).

Fish source and rearing logistics

In all BYs, hatchery-origin broodstock (upriver bright stock was used to reestablish this population) was collected and spawned at TMFD on the Umatilla River (river kilometer [RKM] 465.005; i.e., 465 km from the mouth of the Columbia River and 5 km from the Umatilla River's confluence with the Columbia River; Figure 1). Spawning dates ranged from October 31 to December 6 across BYs. Fertilized eggs from TMFD were immediately transported to the Umatilla Hatchery (located adjacent to the Columbia River, ~20 km downstream from the Umatilla River confluence; RKM 445) for initial incubation. In January, eyed embryos were transported to Bonneville Hatchery (located adjacent to the Columbia River, ~200 km downstream of Umatilla Hatchery; RKM 232; Figure 1), where hatch, alevin incubation, and juvenile rearing occurred. Embryos were incubated in a vertical incubation system using well water at approximately 10°C.

After incubation and initial rearing in indoor Canadian troughs, fish were ponded into five outdoor concrete raceways during late May, 2 months after dietary treatments began. Each year, approximately 50,000 fish were ponded for each dietary treatment into their corresponding outdoor raceway, except the standard feed regime group, which consisted of about 100,000 fish ponded across two raceways. To ensure appropriate densities while fish were small and to maintain similar rearing densities (kg of fish/L of water) across treatments, crowder screens were used to reduce rearing space in raceways. The primary water source for Bonneville Hatchery is Tanner Creek, with annual temperatures ranging from 0°C to 13°C, and well water is used as a secondary source and to moderate temperatures in the winter and summer months (Oregon Department of Fish and Wildlife 2015). The addition of well water varied seasonally, creating a range of rearing temperatures of 3–13°C, with the warmest rearing temperatures occurring in mid-summer.

In mid-February, age-1 fish were transported for acclimation at the Pendleton Acclimation Facility (located on the Umatilla River, 90 km upstream of its confluence with the Columbia River; RKM 465.090; Figure 1) for approximately 1 month prior to release in mid-March. Because fish from dietary treatments were mixed at the acclimation site and dietary treatment groups were no longer distinguishable, a subset of approximately 300 fish from each dietary treatment was held back (sequestered) to facilitate the sampling of fish for the minijack assessments later in April. This was necessary to allow more time for differentiation of plasma 11-ketotestosterone (11-KT) levels (see below for more details) between maturing males (as age-2 minijacks) and non-maturing males. For BY 2010, fish were sequestered at Irrigon Hatchery (adjacent to the Umatilla Hatchery), where fish from each dietary treatment were held in separate 1.83-m-diameter circular tanks. For BY 2011, the fish were first sequestered at Irrigon Hatchery but then were moved to small, enclosed net-pens in the Umatilla River at TMFD for temporary holding on March 28, 2013. For BYs 2012 and 2013, fish were sequestered at Bonneville Hatchery, differentially fin-clipped for each dietary treatment (in February), and mixed in a single raceway to optimize holding density. Disease and mortality were monitored for each BY and by treatment throughout the hatchery rearing portion of the investigation. In-hatchery mortality estimates were calculated each year from the time of tagging with coded wire tags (CWTs) in late July until transfer to the Pendleton Acclimation Facility in early February, as these events allowed for the most accurate enumeration of the fish in each raceway.

To track differential survival and age at return for each dietary treatment, all fish were tagged with CWTs bearing unique tag codes for each dietary treatment and BY. In addition, a subset of fish for each dietary treatment (~2%) was tagged using PIT tags for each BY. These tags provided the opportunity to track juvenile survival during out-migration in addition to adult returns. The survival and age-at-return data are beyond the scope of this paper; as of this writing, the data are being prepared for a subsequent publication.

Sample collection

Sampling fell into two categories: (1) seasonal growth and energetic assessments (October, December, and February; see Table 1) to confirm that dietary differences created size and energetic differences between dietary treatment groups; and (2) minijack assessments (April; see Table 1). During the seasonal growth and energetic assessments, fish from each dietary treatment were sampled for the following indices: size; Fulton's condition factor (K); percentage whole-body solid (a surrogate measure of percentage whole-body lipid; Shearer 1994); and plasma insulin-like growth factor I (IGF-I), a key growth-regulating hormone (Picha et al. 2008; Beckman 2011). Twenty-five fish per dietary treatment were randomly collected from raceways or tanks via dipnetting and were individually euthanized in a buffered solution of 0.05% tricaine methanesulfonate (MS-222; Argent Chemical Laboratories). Fish were measured for FL to the nearest 1 mm and for body weight to the nearest 0.1 g; these data were then used to calculate K according to the following formula:

TABLE 1 Sample date, gender, and maturation status (females [F], immature males [M], age-2 minijacks [MD], and age-1 microjacks [MP]) of Chinook Salmon sampled during seasonal energetic and minijack assessments for brood years (BYs) 2010–2013. Dietary treatments (TREAT) are as follows: standard feeding frequency and standard dietary lipid (7 days–18%); reduced feeding frequency and standard dietary lipid (4 days–18%); standard feeding frequency and reduced dietary lipid (7 days–12%); and reduced feeding frequency and reduced dietary lipid (4 days–12%).

		Growth and energetic assessments[a–d]				Minijack assessment							Maturation (proportion of males)	
BY	Treat	F	M	MP	Total	Date	F	M	MD	MP	Total[e]	Mean FL (mm)	MD[f]	MP[g]
2010	7 days–18%	33	38	4	75	Apr 23, 2012	163	60	113	10	346	158.2	0.653	0.0622
	4 days–18%	37	38	0	75		155	44	100		299	135.2	0.694	0.0000
	7 days–12%	42	33	0	75		165	54	78	2	299	152.5	0.591	0.0120
	4 days–12%	31	44	0	75		161	84	47		292	122.9	0.359	0.0000
2010 totals		143	153	4	300		644	242	338	12	1236	142.2	0.583	0.0214
2011	7 days–18%	39	35	1	75	Apr 8, 2013	151	69	81		301	154.2	0.540	0.0054
	4 days–18%	35	40		75		135	82	83		300	125.2	0.503	0.0000
	7 days–12%	37	38		75		145	77	78		300	135.4	0.503	0.0000
	4 days–12%	38	37		75		139	115	45		299	111.8	0.281	0.0000
2011 totals		149	150	1	300		570	343	287	0	1200	131.6	0.456	0.0013
2012	7 days–18%	40	35	0	75	Apr 28, 2014	158	56	81	5	300	173.3	0.591	0.0282
	4 days–18%	39	36	0	75		159	135	7		301	124.7	0.049	0.0000
	7 days–12%	29	46	0	75		139	104	52		295	161.9	0.333	0.0000
	4 days–12%	43	32	0	75		149	142	10		301	121.7	0.066	0.0000
2012 totals		151	149	0	300		605	437	150	5	1197	145.4	0.256	0.0067
2013	7 days–18%	35	40	0	75	Apr 27, 2015	160	74	64		298	152.6	0.464	0.0000
	4 days–18%	34	41	0	75		157	116	28		301	128.9	0.194	0.0000
	7 days–12%	40	35	0	75		167	105	18		290	131.9	0.146	0.0000
	4 days–12%	33	42	0	75		147	146	11		304	118.8	0.070	0.0000
2013 totals		142	158	0	300		631	441	121	0	1193	133.1	0.215	0.0000

[a]BY 2010 sampling dates: October 19, 2011; November 31, 2011; and January 28, 2012.

[b]BY 2011 sampling dates: October 31, 2012; November 28, 2012; and February 6, 2013.

[c]BY 2012 sampling dates: October 31, 2013; December 12, 2013; and February 5, 2014.

[d]BY 2013 sampling dates: October 30, 2014; December 9, 2014; and February 4, 2015.

[e]Not including the few unidentified-sex individuals or unidentified males.

[f]MDs were only determined from minijack assessment via 11-ketotestosterone analysis.

[g]MPs were determined by visual inspection of the gonads and were observed in both growth/energetic and minijack assessments.

$$K = \left(\text{weight} / \text{FL}^3\right) \times 10^5.$$

Blood was collected by severing the caudal peduncle of each fish and collecting the whole blood from the caudal vein by using heparinized Natelson tubes (VWR International). Whole blood was centrifuged for 5 min at 3000 × *g* to separate plasma, which was then removed and stored at −80°C until laboratory analysis. Gonads were examined in each fish to determine sex. Whole fish bodies were collected for determination of percentage whole-body solid.

For the minijack assessments, all sequestered fish from each dietary treatment (~300 per treatment) were sampled in April during all years (Table 1). Fish were individually euthanized in a buffered solution of 0.05% MS-222 and measured for FL and weight; sex was determined by visual inspection of the gonads, and plasma was collected as previously described. Only plasma collected from males was retained and analyzed. Male maturation status was determined via measurement of plasma 11-KT as described by Larsen et al. (2004a). In BY 2011, the minijack assessment was conducted approximately 3 weeks early because some fish started to show early signs of stress (tail fungus *Saprolegnia* sp. and a few mortalities were observed) at the temporary holding pens in the Umatilla River. As the onset of minijack maturation is already set and bimodal 11-KT distributions are detectable about 8–9 months prior to spawn timing (Campbell et al. 2003), this earlier sampling would not change the minijack maturation outcome; it would only change the magnitude of the plasma 11-KT levels of maturing males.

Age-1 male maturation (i.e., microjacks) was occasionally observed and enumerated during the growth/energetic and minijack assessments. Microjacks were easily identified by the presence of enlarged testes throughout all sample dates; testes appear white and milt filled during the autumn but may contain gray and necrotic spots at later dates. This study was designed to quantify minijack (age-2 maturation) levels across dietary treatments and to track growth/energetics prior to minijack maturation; it was not specifically designed to accurately quantify and compare the microjack levels produced by each dietary treatment. Therefore, we are only reporting the incidental numbers we measured, as they are noteworthy, but we refrain from further in-depth comparisons and conclusions.

Laboratory analyses

Whole-body solid

Previous studies have demonstrated an inverse relationship between percentage whole-body lipid and percentage whole-body moisture in salmonids (R^2 range = 0.68–0.87; Shearer 1994; Trudel et al. 2005; Peters et al. 2007). Thus, the percentage whole-body solid (which by definition is the inverse of percentage whole-body moisture; whole-body solid = [1 – whole-body moisture] × 100) of fish can be used as a simple surrogate for determining whole-body lipid for relative comparisons. Fish bodies were kept frozen prior to analysis. To determine dry weight, thawed fish were cut into thin pieces and dried in an oven at 40°C in pre-weighed aluminum pans until weight stabilized (~48 h). The weight of fish prior to drying (wet weight) and the final dry weight were then used to calculate the percentage whole-body solid according to the following formula:

$$\text{Whole} - \text{body solid}\,(\%) = (\text{dry weight} / \text{wet weight}) \times 100.$$

Insulin-like growth factor I

Total plasma IGF-I levels were measured following acid ethanol extraction (Daughaday et al. 1980) using the time-resolved fluorescence immunoassay developed by Small and Peterson (2005) as described by Journey et al. (2018). Since gonadal steroids, including 11-KT, have been shown to affect plasma IGF-I levels in male fish (Larsen et al. 2004b; Beckman 2011), only females were used for IGF-I analyses to eliminate any variation that might have occurred in maturing male fish.

11-Ketotestosterone

Plasma 11-KT levels (ng/mL) were determined by an enzyme-linked immunosorbent assay (ELISA) adapted from the method of Cuisset et al. (1994) using acetylcholinesterase tracer and precoated (mouse anti-rabbit immunoglobulin G) 96-well plates (Cayman Chemical). To control for potential interference from steroid-binding proteins, the plasma was heat extracted and then analyzed according to the method of Schulz et al. (1994). Plasma was diluted 1:3 in sterile water and was placed in a water bath at 80°C for 1 h. Extracts were centrifuged at 13,000 rotations/min (~18,000 × *g*) for 6 min, and the supernatant was transferred to a new tube prior to ELISA. Plasma 11-KT data were $\log_{10}$ transformed to assess bimodal distributions of maturing versus non-maturing males as described by Larsen et al. (2004a).

Data analysis

All figures and statistical analyses were conducted using a combination of STATA/IC version 15.1 (StataCorp LLC) and GraphPad Prism version 9 (GraphPad Software).

Statistical significance was set at an α level of 0.05. Akaike's information criterion (AIC; Akaike 1974) and pseudo-R^2 values (Cox and Snell 1989) were used to assess model performance when multiple models were compared. Levels of factor variables within statistical models were compared with the post-test commands "test" and "lincom" in STATA.

Comparison of growth and energetic indices by dietary treatments

Two-way ANOVAs with dietary treatment and BY as factor variables were used to test for differences between dietary treatments for FL, *K*, whole-body solid, and plasma IGF-I during the October, December, and February time periods.

Minijack maturation

The incidence of minijacks among males (hereafter, "proportion minijacks") was calculated by dividing the number of minijacks by the total number of males sampled in April for each dietary treatment and BY, but we excluded any males that had previously matured as age-1 microjacks. Logistic regression analyses were used to compare dietary treatment and BY effects on the proportion minijacks. These analyses were done by categorizing the dietary treatments under one categorical variable (TREAT) with four levels or by categorizing the groups under both feeding frequency (FREQ) and dietary lipid (LIPID) categorical treatment variables with two levels each. The latter approach made it possible to test whether there was an additive effect of these two types of dietary treatments or whether there was a significant interaction between them.

Prediction of proportion minijacks by growth and energetic indices

To assess the timing and effect of energetic indices (FL, *K*, whole-body solid, and plasma IGF-I) on the decision to mature at age 2, we used beta regression to analyze the effect of population means of these metrics (measured during October, December, and February) on the proportion minijacks observed in April for each BY and treatment group. Brood year was included in the models because the between-year variation could mask the relationship between these energetic indices and the proportion minijacks.

Comparison of in-hatchery mortality rates

Beta regression analysis was used to analyze whether there was an effect of dietary treatment on in-hatchery mortality rates. Brood year was included in the model, as there was variation in observed mortality across the years of this study.

RESULTS

Growth and energetic indices

Fork length

Size differences between the dietary treatments were distinctive at the onset of sampling in October for each BY (Figure 2A–D). Fish from the standard feeding frequency treatments (7 days–18% and 7 days–12%) were the largest across BYs, with predicted FL means of 129.6 and 113.5 mm, respectively (Figure 3A). Fish from the reduced feeding frequency treatments (4 days–18% and 4 days–12%) were smaller, with predicted FL means of 91.3 and 79.1 mm, respectively, across BYs (Figure 3A). The combination of feeding frequency treatment with dietary lipid treatment created four distinctly different size-groups (4 days–12% < 4 days–18% < 7 days–12% < 7 days–18%) that were statistically different (Figure 3A; model 1 in Table 2), and this pattern held through the December (Figure 3B; model 5 in Table 2) and February (Figure 3C; model 9 in Table 2) sampling periods. There were BY differences in FL across time points (Figure 4A–C; models 1, 5, and 9 in Table 2), and there were significant interactions between BY and dietary treatment at each time point, indicating that the difference in FL between BYs did not manifest in the same way for all dietary treatments (Table 2).

Condition factor

Over the duration of the study, *K*-values were lowest during the autumn and increased until fish were moved to their acclimation site in February (Figures 2E–H and 3D–F). Dietary treatment did affect *K* across sampling dates. In October, fish from the standard feeding frequency treatments (7 days–18% and 7 days–12%) had the highest *K*-values, with means of 1.06 and 1.02, respectively. Fish from the reduced feeding frequency treatments (4 days–18% and 4 days–12%) had similar mean *K*-values of 0.99 and 0.97, respectively (Figure 3D; model 2 in Table 2). This pattern between treatments changed by December, when

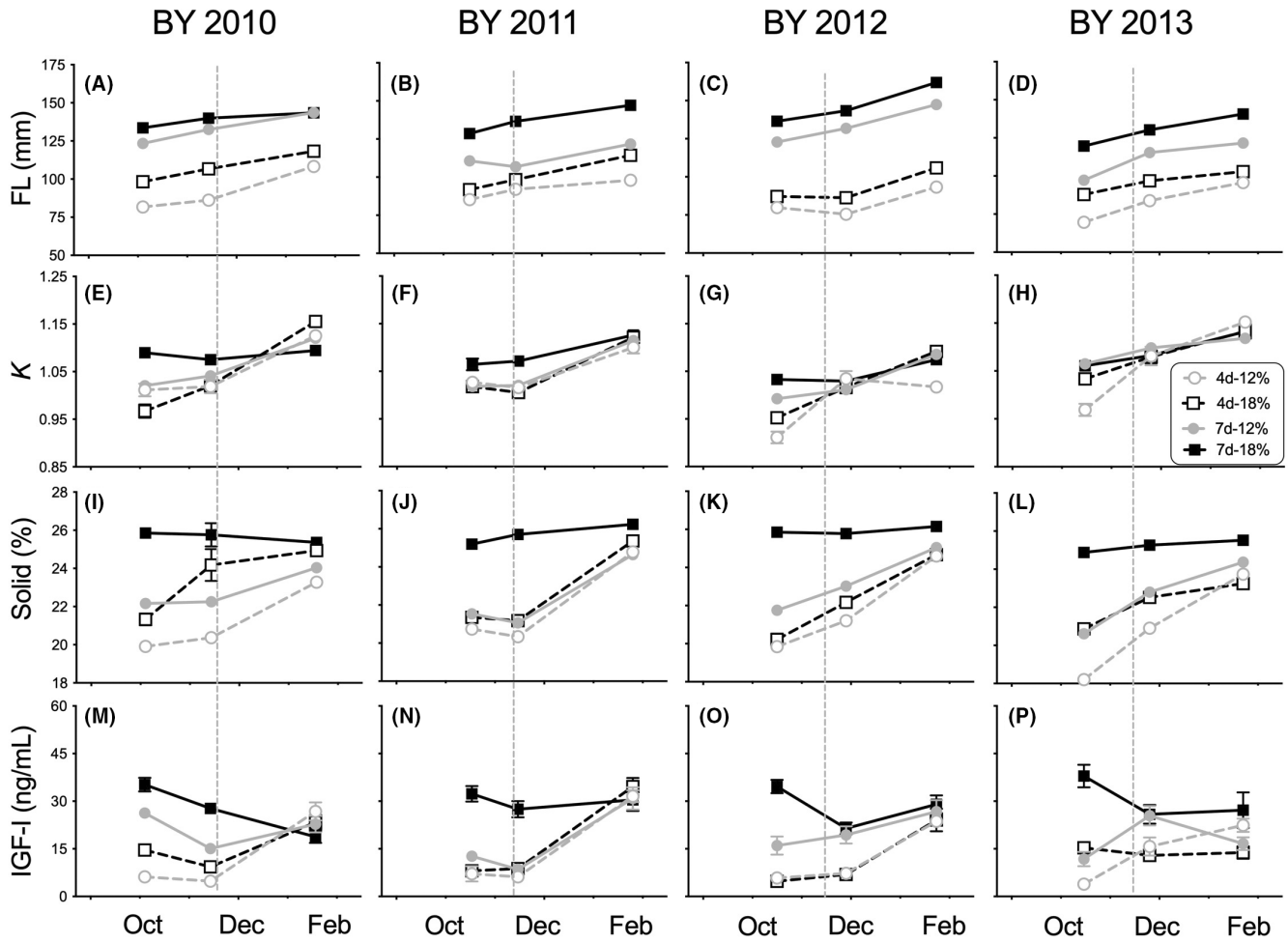

FIGURE 2 Mean values for (A–D) FL (mm); (E–H) Fulton's condition factor (*K*); (I–L) percentage whole-body solid (Solid); and (M–P) insulin-like growth factor I (IGF-I; ng/mL) for the monthly sampling until Chinook Salmon were moved from Bonneville Hatchery to the acclimation site on the Umatilla River for each brood year (BY). Sample size was 25 fish from each dietary treatment on each date, except for IGF-I, which was sampled from females only (*N* ranged from 5 to 18). Black symbols and lines represent the standard dietary lipid (18%) treatment. Gray symbols and lines represent the reduced dietary lipid (12%) treatment. Solid lines represent the standard feeding frequency (7 days) treatment. Dashed lines represent the reduced feeding frequency (4 days) treatment. Error bars represent SE (many error bars are too narrow to visualize). The vertical dotted line through each graph indicates when feeding treatments ended and all fish were put on the standard dietary regime (7 days–18%).

dietary treatment had less of an effect, as the 7 days–12%, 4 days–18%, and 4 days–12% groups had similar *K*-values (means = 1.04, 1.03, and 1.04, respectively), but 7 days–18% fish still maintained a significantly higher mean *K*-value at 1.06 (Figure 3E; model 6 in Table 2). In February, just prior to the transfer of fish to the acclimation site, mean *K*-values were higher than in December for all dietary treatments, and at this time point the 4 days–18% treatment had a higher mean *K*-value than the other dietary treatments (1.13 versus 1.10–1.11; Figure 3F; model 10 in Table 2). Mean *K* varied across BYs (Figure 4D–F; models 2, 6, and 10 in Table 2), and there were significant interactions between dietary treatment and BY for each time period (Table 2).

Percentage whole-body solid

The dietary treatments created differences in percentage whole-body solid among the groups by autumn, with some variation in rank order of dietary treatments among years (Figure 2I–L), but significant differences in predicted means across years were observed (Figure 3G). The 7 days–18% fish had higher predicted means of percentage whole-body solid than the other dietary treatments in October (25.4% versus 19.7–21.5%), with 4 days–12% fish having the lowest predicted means (Figure 3G; model 3 in Table 2). In December, this pattern changed slightly, with the two intermediate dietary treatments (7 days–12% and 4 days–18%) no longer differing in predicted percentage

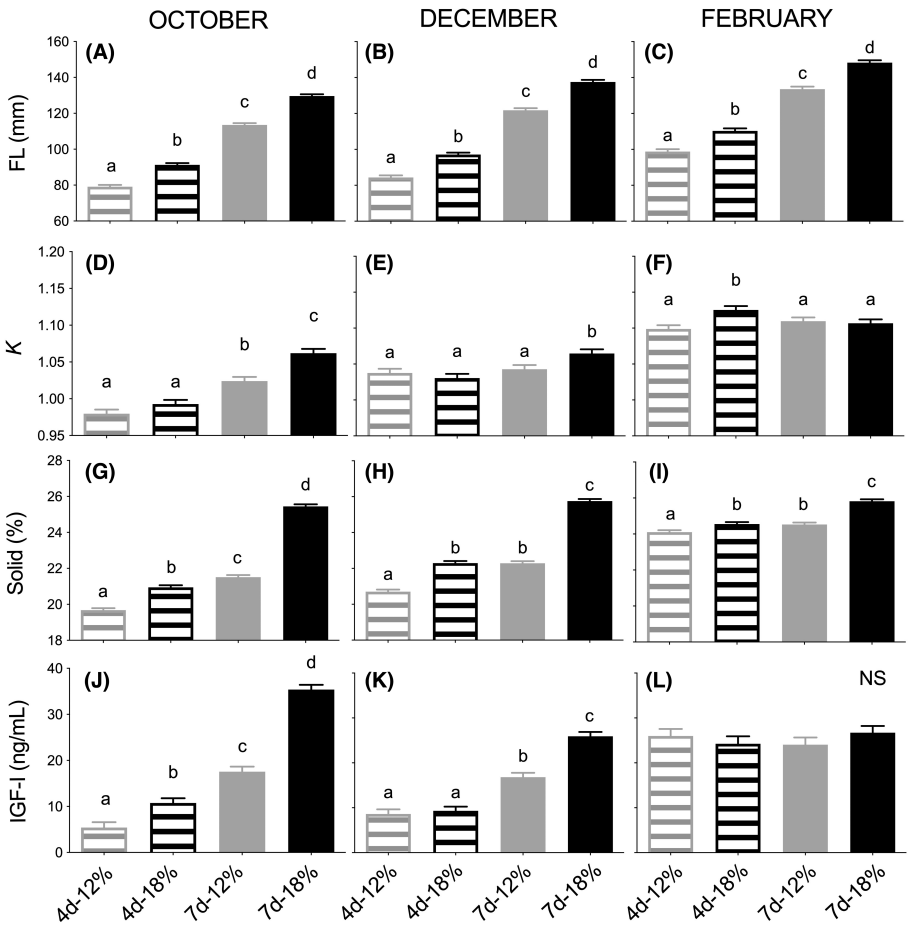

FIGURE 3 Linear prediction of means and SE for each feed treatment by using linear regression models (including the categorical variable brood year) for (A–C) FL (mm), (D–F) Fulton's condition factor (*K*), (G–I) percentage whole-body solid (Solid), and (J–L) insulin-like growth factor I (IGF-I; ng/mL) of Chinook Salmon during October (dates ranged from October 19 to October 31), December (November 28 to December 12), and February (January 31 to February 6; see Table 1 for the dates for specific brood years). Different letters represent a statistical difference ($\alpha = 0.05$) between dietary treatments from linear combinations within each regression model (model summaries are shown in Table 2). Abbreviation: NS, not significant.

whole-body solid means (Figure 3H; model 7 in Table 2). Predicted means for the three non-standard dietary treatments increased by February (as all dietary treatment groups were put on the same feeding regime at the beginning of December) but were still slightly lower than that of the standard feeding regime (7 days–18%) treatment (24.1–24.6% versus 25.8%; Figure 3I). Fish from the 7 days–18% treatment did not exhibit an increase in percentage whole-body solid from December to February. Percentage whole-body solid varied across BYs for each sample period (Figure 4G–I; models 3, 7, and 11 in Table 2). There were significant interactions between dietary treatment and BY at all time points (Table 2).

Insulin-like growth factor I

Fish from the 7 days–18% treatment had the highest mean plasma IGF-I levels in the autumn for each BY (means across BYs: 35.4 versus 5.4–17.6 ng/mL), followed by a pattern of decline into the winter (Figures 2M–P and 3J–L; Table 2). Fish from the 4 days–12% treatment had the most dynamic IGF-I profile, with the lowest levels occurring in the fall (5.4 ng/mL), followed by increases from October to December (8.6 ng/mL) and again in February (26.0 ng/mL). Fish from the 4 days–18% and 7 days–12% treatments had intermediate plasma IGF-I levels in October, but only fish from the 7 days–12% treatment were intermediate in December (Figure 3K; Table 2). By February, all dietary treatments had similar plasma IGF-I levels (Figure 3L; model 12 in Table 2). There were significant differences between BYs for IGF-I (Figure 4J–L; models 4, 8, and 12 in Table 2), and there were significant interactions between dietary treatment and BY in October and December (models 4 and 8 in Table 2).

As noted previously, placing fish from all dietary treatments on the standard (7 days–18%) dietary regime in December for each BY cohort mediated some of the

TABLE 2 Linear regression model summaries for each energetic variable run separately as the response for each sampling period (October, December, and February). Dietary treatment (TREAT; four levels: combinations of two dietary lipid and two feeding frequency treatments) and brood year (BY) were categorical predictor variables. These models correspond with the significance designations shown in Figures 3 and 4. Abbreviations: IGF, insulin-like growth factor I; *K*, Fulton's condition factor; Solid, percentage whole-body solid. Results in bold are statistically significant ($p < 0.05$).

Model	Response variable	Predictor variables	*N*	*F*	df	*p*	R^2	Test of TREAT			Test of BY		
								F	df	*p*	*F*	df	*p*
October													
1	FL[a]	BY + TREAT	400	253.94	6393	<0.0001	0.795	**464.81**	**3393**	**<0.0001**	**43.08**	**3393**	**<0.0001**
2	*K*[a]	BY + TREAT	400	33.61	6393	<0.0001	0.3391	**41.81**	**3393**	**<0.0001**	**25.42**	**3393**	**<0.0001**
3	Solid[a]	BY + TREAT	400	238.44	6393	<0.0001	0.7845	**456.26**	**3393**	**<0.0001**	**20.62**	**3393**	**<0.0001**
4	IGF[a]	BY + TREAT	170	78.39	6163	<0.0001	0.7426	**151.46**	**3163**	**<0.0001**	**7.52**	**3163**	**0.0001**
December													
5	FL[a]	BY + TREAT	401	221.76	6394	<0.0001	0.7715	**429.14**	**3394**	**<0.0001**	**14.02**	**3394**	**<0.0001**
6	*K*[a]	BY + TREAT	401	15.11	6394	<0.0001	0.1871	**6.39**	**3394**	**0.0003**	**23.82**	**3394**	**<0.0001**
7	Solid[a]	BY + TREAT	400	161.99	6393	<0.0001	0.7121	**309.24**	**3393**	**<0.0001**	**14.75**	**3393**	**<0.0001**
8	IGF[a]	BY + TREAT	177	37.59	6170	<0.0001	0.5702	**69.01**	**3170**	**<0.0001**	**11.67**	**3170**	**<0.0001**
February													
9	FL[a]	BY + TREAT	400	146.89	6393	<0.0001	0.6916	**272.97**	**3393**	**<0.0001**	**20.82**	**3393**	**<0.0001**
10	*K*[a]	BY + TREAT	400	17.28	6393	<0.0001	0.2088	**4.3**	**3393**	**0.0053**	**30.26**	**3393**	**<0.0001**
11	Solid[a]	BY + TREAT	400	34.08	6393	<0.0001	0.3422	**45.9**	**3393**	**<0.0001**	**22.26**	**3393**	**<0.0001**
12	IGF	BY + TREAT	203	5.71	6196	<0.0001	0.1488	0.68	3196	0.5632	**10.34**	**3196**	**<0.0001**

[a]The interaction between TREAT and BY was significant for this variable ($p < 0.05$).

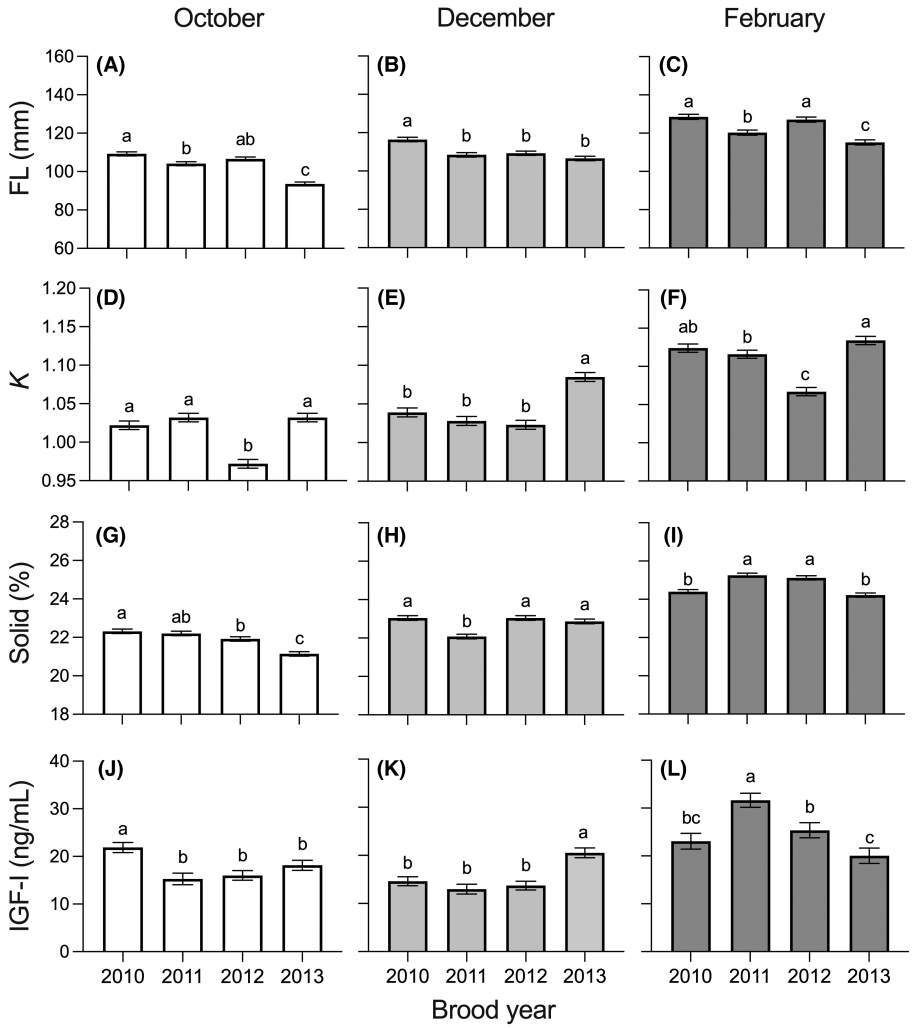

FIGURE 4 Predicted means for each brood year for the growth and energetic variables of Chinook Salmon sampled at the October, December, and February time points: (A–C) FL (mm), (D–F) Fulton's condition factor (*K*), (G–I) percent whole-body solid, and (J–L) insulin-like growth factor I (IGF-I, ng/mL). Error bars represent SE. These predictions (marginal means) are derived from the linear regression models 1–12 shown in Table 2.

differences in growth and energetic indices between dietary treatments as fish progressed into the winter (Figures 2 and 3). The change in dietary regime created increases in growth and energetic indices for fish in the nonstandard dietary treatments and reduced the differences between those groups and the fish in the standard (7 days–18%) dietary treatment group by February. The main differences that persisted across dietary treatments were the size rank of fish and, to a small degree, the ranking of percentage whole-body solid across dietary treatments (Figure 3).

Incidence of age-2 (minijack) maturation

The dietary treatments resulted in levels of minijack maturation that varied across treatments (Figure 5), and this pattern was relatively consistent across BYs (Figure 6A; Table 1). Overall, the 7 days–18% treatment had the highest proportion minijacks (mean = 0.56), the 7 days–12% and 4 days–18% treatments were intermediate (means = 0.39 and 0.36, respectively), and the 4 days–12% treatment had the lowest proportion minijacks (mean = 0.19). These results equate to a 30.0% reduction in the proportion minijacks for the 7 days–12% treatment, a 35.9% reduction for the 4 days–18% treatment, and a 65.5% reduction for the 4 days–12% treatment compared to the standard feeding regime treatment.

Brood year, feeding frequency, dietary lipid, and the combination of feeding frequency and dietary lipid treatments (equivalent to the model with the four categories of dietary treatment) were all significant predictors of proportion minijacks among males (Tables 3 and S1 [available in the Supplement in the online version of this article]). Brood year was a highly significant predictor (models 3, 5, 7, 9, and 10 in Table S1), as the mean proportion minijacks varied significantly across

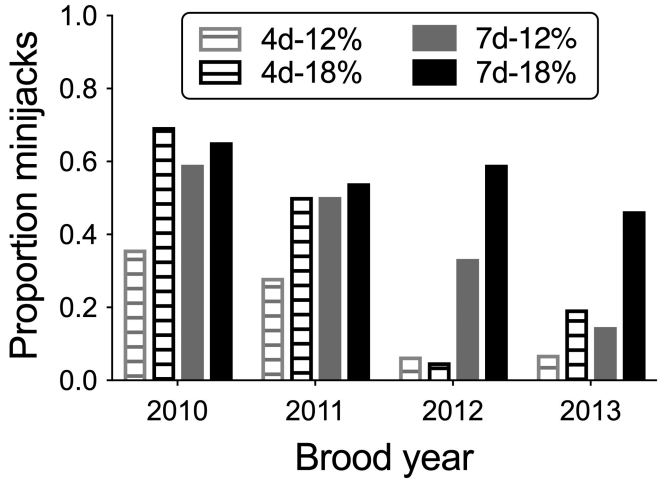

FIGURE 5 Brood year variation in the proportion minijacks among male Chinook Salmon for each dietary treatment (see Table 1 for full details).

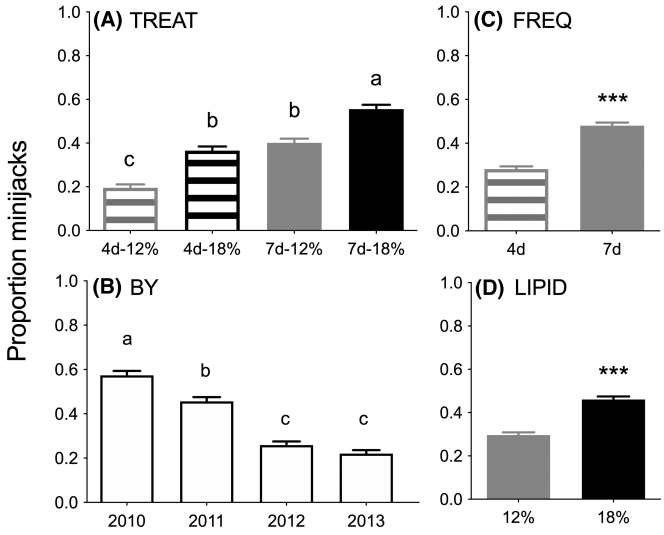

FIGURE 6 Predicted margins from logistic regression analyses for effects of (A) dietary treatment (TREAT), (B) brood year (BY), (C) feeding frequency treatment (FREQ), and (D) dietary lipid treatment (LIPID) on the proportion minijacks among male Chinook Salmon. Panels A and B are derived from Table 3, model 5 (BY + TREAT). Panels C and D are derived from Table 3, model 3 (BY + LIPID + FREQ). Error bars represent SE. Different letters represent significant differences between BYs (***$p < 0.001$).

BYs, ranging from 0.22 to 0.58 (Figure 6B; Table 1). Feeding frequency and dietary lipid treatments were approximately equal in their effects on the proportion minijacks, with odds ratios of 2.65 and 2.24, respectively (Figure 6C,D; model 3 in Table S1). Reducing the feeding frequency from 7 to 4 days/week reduced the mean proportion minijacks from 0.48 to 0.28 across dietary lipid treatments (Figure 6C; $z = 10.37$, $p < 0.001$; model 3 in Table S1), and reducing the lipid concentration in feed from 18% to 12% reduced the mean proportion minijacks from 0.46 to 0.30 across feeding frequency treatments (Figure 6D; $z = 8.62$, $p < 0.001$; model 3 in Table S1). There were substantial interactions between BY and dietary treatment ($\chi^2 = 79.4$, $p < 0.001$; Table S2) and between BY and feeding frequency treatment ($\chi^2 = 54.1$, $p < 0.001$; Table S2), whereas a lesser interaction was observed between BY and dietary lipid treatment ($\chi^2 = 11.1$, $p = 0.011$; Table S2).

Relationship between growth/energetic indices and proportion minijacks

October

Each of the growth and energetic indices (FL, *K*, percentage whole-body solid, and IGF-I), measured at about 12 months prior to age-2 maturation, was positively

TABLE 3 Logistic regression model comparisons for predicting the proportion minijacks by the variables brood year (BY), dietary lipid treatment (LIPID), feeding frequency treatment (FREQ), and overall dietary treatment (TREAT) for Chinook Salmon ($N = 2359$ for all models). See Tables S1 and S2 for further details for each model. Abbreviations: AIC, Akaike's information criterion; ΔAIC, difference in AIC between the given model and the best-performing model; LR, likelihood ratio.

		Model statistics					
Model	**Predictor variables**	**LR χ^2**	**df**	***p***	**Pseudo-R^2**	**AIC**	**ΔAIC**
1	BY × LIPID × FREQ	513.7	15	<0.0001	0.16	2650.9	0.0
2	BY × TREAT	513.7	15	<0.0001	0.16	2650.9	0.0
3	BY + LIPID + FREQ	410.1	5	<0.0001	0.13	2734.6	83.6
4	BY + LIPID × FREQ	411.8	6	<0.0001	0.13	2734.8	83.9
5	BY + TREAT	411.8	6	<0.0001	0.13	2734.8	83.9
6	BY × FREQ	400.9	7	<0.0001	0.13	2747.7	96.8
7	BY + FREQ	333.8	4	<0.0001	0.11	2808.8	157.9
8	BY × LIPID	310.2	7	<0.0001	0.10	2838.5	187.6
9	BY + LIPID	298.5	4	<0.0001	0.10	2844.2	193.2
10	BY	223.5	3	<0.0001	0.07	2917.0	266.1
11	LIPID + FREQ	188.7	2	<0.0001	0.06	2949.9	299.0
12	LIPID × FREQ	190.5	3	<0.0001	0.06	2950.2	299.2
13	TREAT	190.5	3	<0.0001	0.06	2950.2	299.2
14	FREQ	109.7	1	<0.0001	0.04	3027.0	376.0
15	LIPID	78.3	1	<0.0001	0.03	3058.4	407.4

related to the proportion minijacks in beta regression models that also included BY as a predictor variable (models 1–4 in Table 4; Figure 7A–D). The proportion minijacks was previously shown to vary significantly across BYs, and BY was again significant in these models. In the comparison of beta regression models 1–4 (Table 4), FL was the best predictor of the proportion minijacks (AIC = −21.7), followed closely by percentage whole-body solid (AIC = −20.6), whereas *K* was the least predictive, with an AIC value of −10.5.

December

By December, mean *K* for each dietary treatment was no longer predictive of the proportion minijacks, but mean FL, percentage whole-body solid, and IGF-I levels were predictive (Figure 7E–H). Fork length and percentage whole-body solid achieved the strongest relationships (AIC values of −21.5 and −16.4, respectively), followed by IGF-I (AIC = −11.5), when BY was included in the beta regression models (models 5–8 in Table 4).

February

Just prior to the transfer of fish to the acclimation site in early February, the mean FL and percentage whole-body solid were still highly related to the proportion minijacks (Figure 7I,K), but mean IGF-I values were no longer significantly related to the proportion minijacks (Figure 7L; model 12 in Table 4).

Incidence of age-1 (microjack) maturation and mortality rates

Microjacks were only observed in dietary treatments that received the standard feeding frequency treatment (7 days–12% and 7 days–18%), and the proportion microjacks ranged from 0.000 to 0.062 of the males across these treatments and BYs (Table 1). The standard dietary treatment (7 days–18%) had the highest proportion microjacks, which averaged 0.024 across years. Incidence of microjacks was highly variable across BYs: the highest proportion microjacks across dietary treatments (0.021) was observed in BY 2010, and no microjacks were observed in BY 2013.

In-hatchery mortality rates (July–February) varied across dietary treatments and BYs (Table 5), ranging from a low of 0.1% to a high of 34.3%. Overall, the reduced (12%) lipid treatments experienced higher mortality rates than the standard (18%) lipid treatments ($\chi^2 = 29.0$, $p < 0.0001$). There were also BY differences in mortality, with BY 2013 fish exhibiting significantly higher mortality than all other BYs ($\chi^2 = 19.6$, $p = 0.0002$).

TABLE 4 Beta regression models for predicting the proportion minijacks in Chinook Salmon, including brood year (BY) as a categorical variable in addition to the growth and energetic indices (continuous variables) shown in Figure 6 (**$p < 0.01$, ***$p < 0.001$). Abbreviations: AIC, Akaike's information criterion; IGF-I, insulin-like growth factor I; *K*, Fulton's condition factor; LR, likelihood ratio; NS, not significant; Solid, percentage whole-body solid.

Model	Predictor variable(s)	*N*	Full model statistics				*dy/dx*				Test of BY		
			LR χ^2	df	*p*	AIC	FL	*K*	Solid	IGF-I	χ^2	df	*p*
October													
1[a]	FL + BY	16	27.3	4	<0.0001	−21.7	0.0064***				26.3	3	<0.0001
2[a]	K + BY	16	16.1	4	0.0029	−10.5		2.37**			14.0	3	0.0029
3[a]	Solid + BY	16	26.1	4	<0.0001	−20.6			0.058***		26.1	3	<0.0001
4[a]	IGF + BY	16	25.8	4	<0.0001	−20.3				0.01***	27.7	3	<0.0001
December													
5[a]	FL + BY	16	27.1	4	<0.0001	−21.5	0.0059***				28.4	3	<0.0001
6	K + BY	16	10.5	4	0.0335	−4.9		1.28 NS			13.6	3	0.0035
7[a]	Solid + BY	16	21.9	4	0.0002	−16.4			0.061***		28.2	3	<0.0001
8[a]	IGF + BY	16	17.1	4	0.0019	−11.5				0.01**	23.2	3	<0.0001
February													
9	FL + BY	16	29.2	4	<0.0001	−23.7	0.0065***				35.4	3	<0.0001
10	K + BY	16	10.5	4	0.0326	−5.0		1.22 NS			11.8	3	0.0080
11[a]	Solid + BY	16	22.9	4	0.0001	−17.3			0.161***		32.4	3	<0.0001
12[a]	IGF + BY	16	11.2	4	0.0241	−5.7				0.01 NS	12.7	3	0.0054

[a]Significant interaction between growth/energetic indices and BY.

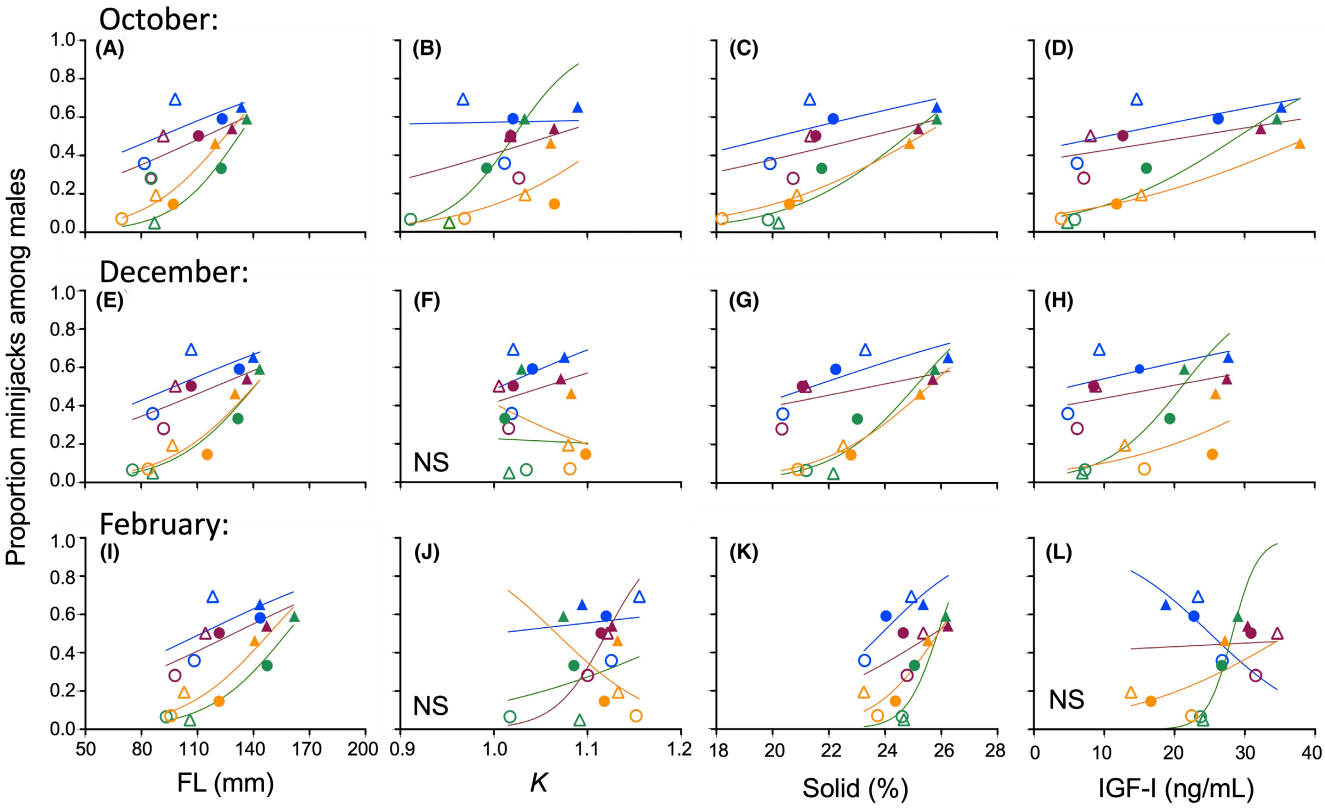

FIGURE 7 Beta regression models of the relationship between the growth and energetic indices (FL, Fulton's condition factor [*K*], percentage whole-body solid [Solid], and insulin-like growth factor I [IGF-I]) and the proportion minijacks among male Chinook Salmon for the (A–D) October, (E–H) December, and (I–L) February sampling periods. These time periods represent physiological status 8–12 months prior to full maturation as age-2 minijacks. Symbols represent dietary treatment (combination of feeding frequency and dietary lipid level; solid triangles = 7 days–18%; open triangles = 4 days–18%; solid circles = 7 days–12%; open circles = 4 days–12%). Colors represent brood year (BY; blue = BY 2010; maroon = BY 2011; green = BY 2012; orange = BY 2013). See Table 4 for beta regression models of the same data with the addition of BY as a predictor variable in each model. Abbreviation: NS, not significant ($p > 0.05$).

DISCUSSION

This is the first production-scale hatchery experiment to successfully demonstrate that relatively modest manipulations of food availability and dietary lipid during early rearing reduce minijack production in Chinook Salmon. The prescribed dietary regimes created relatively distinct treatments, as evidenced by seasonal monitoring of a suite of growth and energetic indices. Across all years, decreasing the feeding frequency from 7 to 4 days/week reduced the proportion minijacks by 35.9%, and lowering dietary lipid from 18% to 12% reduced the proportion minijacks by 30%. The combined effects of decreasing the feeding frequency and lowering dietary lipid were additive, reducing the incidence of minijack maturation by 65.5% compared to the standard dietary regime. Additionally, we observed that these dietary regimes also had an observed impact on age-1 (microjack) maturation. Microjacks were only observed in the two standard feeding frequency (7 days/week) treatments, with higher prevalence in the group that received the standard dietary lipid (18%) feed.

An important exception to the generally positive results of this study was the observation that despite significant BY and treatment variation, there were higher mean mortality rates among the reduced-lipid treatments, most notably the 4 days–12% group (Table 5). This mortality was attributed to disease outbreaks, including enteric redmouth disease (caused by *Yersinia ruckeri*) and the protozoan *Hexamita* sp. (Oregon Department of Fish and Wildlife, unpublished hatchery records); thus, there was some interaction between the low-lipid feed and disease resistance. Throughout the course of this study, the hatchery staff considered the daily mortality rates to be relatively low, and the decision was made to not treat any of the fish for disease, as such treatment would have necessitated substituting the experimental diets with therapeutic diets, thus compromising the original objective of the experiment. Under normal production hatchery protocols, fish would have been treated for disease outbreaks, likely mitigating some of the observed mortality. Moreover, it is important to realize that the different diets were made by different

TABLE 5 In-hatchery mortality rates (%) of Chinook Salmon for each dietary treatment (TREAT) and brood year (BY) of rearing at Bonneville Hatchery ($N = 16$). These mortality rates were estimated from the time of coded wire tagging (late July) until transfer to the Pendleton Acclimation Facility (early February) for each BY. Different letters represent significant differences following beta regression analysis ($p < 0.05$).

	BY				
Treat	2010	2011	2012	2013	Mean mortality (%)
4 days–12%	5.8	14.6	17.4	34.3	18.0 z
4 days–18%	2.0	1.6	0.1	1.8	1.4 x
7 days–12%	7.5	1.3	2.2	31.0	10.5 y
7 days–18%	5.7	2.8	2.8	3.5	3.7 x

companies, and any number of different components of the diet could have varied between the manufacturers. Low-lipid diets themselves may not have been the issue compromising disease resistance.

Finally, it is important to note that our experimental regimen does not represent an explicit recommendation for standard rearing at this hatchery or other hatcheries. The experiment was designed to assess whether varying dietary regimes could alter the proportion of minijacks produced during hatchery rearing. Our results suggest that through future refinement of the feed application and diet formulations established in this initial investigation, coupled with appropriate therapeutics to control pathogen outbreaks, hatchery programs may realize potential gains in smolt production through reductions in early male maturation.

Previous studies on growth and energetic effects on early male maturation

This investigation mirrors results from previous smaller-scale, hatchery- and laboratory-based experiments demonstrating that reducing food availability and/or dietary lipid can result in reductions in growth, body adiposity, and the associated prevalence of early maturation in spring Chinook Salmon (Clarke and Blackburn 1994; Silverstein et al. 1998; Shearer and Swanson 2000; Larsen et al. 2006; Shearer et al. 2006) and Atlantic Salmon *Salmo salar* (Jonsson et al. 2012, 2013; Norrgård et al. 2014). Larsen et al. (2006) found that reducing the growth rate during autumn, summer, or both created differences in fish size and body adiposity between treatments and reduced the proportion minijacks by 16, 26, and 39%, respectively, in Yakima River (Washington) spring Chinook Salmon. Silverstein et al. (1998) conducted a laboratory experiment examining the effects of reducing food availability and dietary lipid through the first autumn, and they found a striking reduction (~80%) in minijack maturation among Willamette River (Oregon) spring Chinook Salmon. Successfully demonstrating these effects at a hatchery scale is important for determining whether minijack production can be reduced, thus leading to greater production of older-aged fish if the growth/diet manipulations do not result in reduced overall survival.

To date, a relatively limited number of hatchery production-scale studies has explored the effects of diet manipulation and/or growth rate on minijack production. Spangenberg et al. (2014) monitored the Hood River (Oregon) stock of spring Chinook Salmon reared under three different hatchery environments as juveniles and found that the mean proportion minijacks varied significantly from 0.15 to 0.44 across groups; they attributed the differences to variation in seasonal rearing temperatures and associated feed rates. Larsen et al. (2013) conducted a production-scale study on spring Chinook Salmon from the Yakima River and found that lowering growth by reductions in food availability during hatchery rearing subsequently reduced the proportion minijacks by approximately 50%. Furthermore, they found a lower proportion of minijacks among out-migrating natural-origin fish compared to either the standard-growth or low-growth hatchery treatments during smolt out-migration in the lower Yakima River. This can also be interpreted as differences in diet and growth influencing minijack maturation, as this hatchery program uses natural-origin broodstock, maintaining hatchery-reared fish that are genetically similar to the wild population. Previous work by Larsen et al. (2006) confirmed that natural-origin fish in the Yakima River system have reduced energetics (both size and whole-body lipid levels) compared to the hatchery-reared fish. Finally, Harstad et al. (2014) found a relationship between size at release and the proportion minijacks among various stocks of Chinook Salmon across several hatcheries in the Columbia River basin. Taken together, results from these previous studies provide direct or indirect evidence of the effects of growth rate, body size, and whole-body lipid on early male maturation, and the results from the current investigation provide the first production-scale demonstration of the interplay among these factors.

Design of hatchery experiment: Seasonal timing

Studies of Atlantic Salmon (Thorpe et al. 1998; Thorpe 2007) suggested that maturation in salmonids is initiated during a sensitive period in the autumn, approximately 1 year prior to final maturation and spawning. During the sensitive period, animals initiate gonadal

maturation, depending on whether physiological signals related to growth and adiposity exceed a genetically set threshold. Subsequent work found that physiological mechanisms of Pacific salmon are similar; fish with relatively high growth rates or lipid reserves in the autumn will mature the following year, while fish with either reduced growth rates or reduced adiposity will remain immature (Shearer and Swanson 2000; Campbell et al. 2003). Our study design was based on this paradigm; reduced food availability and lower dietary lipid treatments extended from the first spring through the following fall and were then discontinued. In December, fish from all treatments were reared on the standard dietary treatment (7 days–18%). Our study reinforces the paradigm of an autumnal sensitive period, as the physiological indices in late October were the strongest predictors of the proportion minijacks observed in the following autumn.

Some caution is warranted when assessing physiological responses of "treatments" after December, as the feeding regime differences had been discontinued by this time. Fish from the reduced dietary treatments displayed increased values for both the percentage whole-body solid (a surrogate for adiposity) and *K* from December to February relative to the standard treatment (7 days–18%), as all fish were fed similarly during that time. Physiologically, fish essentially recovered from the reduced dietary treatments. However, even after 2 months of subsequent rearing on the standard dietary treatment, fish from the reduced dietary treatments were still smaller and had only slightly lower adiposity in February than fish reared on the standard treatment throughout. Any tradeoffs of rearing fish to a smaller size, including tradeoffs in hatchery mortality, reduced energetics in the first autumn, and small smolt size, will be determined by the final analysis of adult survival and maturation schedules when CWTs and PIT tags from all adult age-classes are reported and analyzed.

Assessment of hatchery experiment: Brood year variation

Hatcheries are not controlled laboratory settings. Generally, compromises must be made when designing hatchery experiments because resources are limited, resulting in less control and monitoring than would be feasible in a controlled laboratory setting. We designed the study with replication across years but without the added advantages of replicating treatments within years. Replication within a year was considered by the project comanagers to be too great an investment into an unproven rearing strategy compared to the standard rearing regime. Ultimately, our ability to make statistical inferences about differences between dietary treatments within BYs was less robust due to this lack of treatment replication within a year.

Despite the aforementioned limitations, we found a threefold difference in the proportion minijacks between treatments when combined across years. The 4 days–12% treatment usually produced the lowest proportion minijacks (except for BY 2012), the 7 days–12% treatment was consistently intermediate, and the 7 days–18% treatment produced the highest proportion minijacks in most years. We also found significant levels of variation across years, with mean minijack maturation being much more prevalent in BY 2010 than in BYs 2012 and 2013. There was a strong interaction between BY and dietary treatment, with relatively little variation in early male maturation of the standard (7 days–18%) dietary treatment fish across years, whereas the averages for fish from the other dietary treatments varied by more than threefold over the same period. Similarly, physiological differences between the dietary treatments in all BYs were also not consistent across years, suggesting that differences in the proportion minijacks between years were due to differential manifestation of dietary treatment on the physiology of the fish within the treatments across years.

Despite the variability in population means for energetic indices and the proportion minijacks, we were able to assess the relationships between these variables via beta regression. Across all years, we observed positive and significant relationships between all growth and energetic indices and the proportion minijacks, with the strongest relationships observed in late October. Our results are consistent with other mechanistic studies demonstrating that growth and adiposity about 1 year prior to maturation are important for the physiological decision to mature (Shearer and Swanson 2000; Campbell et al. 2003). These positive relationships confirm that our study design created energetic differences between treatments and that these differences are in fact predictive of age-2 maturation. We did observe variation between BYs in how these relationships appeared, in terms of both the intercept (height) and the slope (shape), suggesting that additional factor(s) affecting minijack maturation beyond those that we measured may have been present.

The inconsistency in how dietary treatments affected energetic indices and the proportion minijacks across years may be due to several potential sources, including variation in feed application and/or feed composition, variation in environmental factors like water temperature, unknown stress or disease (noted previously), or genetic variation in broodstock between years. Feed consumption (the proportion of feed applied to a raceway that was actually eaten by the fish) was not directly measured and could have varied across years. The composition of

the feeds with the two dietary lipid levels was also not directly measured during this study. Available reports on similar commercial feeds have shown that the lipid and protein content within feeds can sometimes vary up to several percentage points across batches (e.g., the lipid content of the BioClark Fry 2.0-mm feed ranged from 17.8% to 23.0% in batches measured during 2012–2013; Twibell, memoranda). Water temperatures may have varied across years but likely not significantly, as the hatchery mixes well water with the surface water to moderate the rearing temperatures during summer and winter months as needed. Disease differences could also have played a part in the observed variation in energetics and maturation levels for some years and treatments. Finally, we have no direct measure of genetic variation between annual broodstock collections for this study, but previous studies have shown differences in genetically set maturation thresholds between populations (Piché et al. 2008; Larsen et al. 2021) and between years within populations (Larsen et al. 2019b). Whatever the cause(s), the smaller size and reduced adiposity of BY 2013 fish in October certainly suggest some yearly difference in feeding success and growth of the fish. The observed variation in mortality, energetics, and maturation of the dietary treatments between BYs suggests that future efforts will need to direct more control over how the dietary treatments are applied before we can offer a more prescriptive direction on the design and effects of various feeding schedules and rations.

Design of hatchery experiment: Feed composition

Current commercial salmon feeds are formulated for low cost and to generate high growth rates for fish in commercial culture. These feeds contain high lipid levels to support metabolism, sparing expensive protein for growth. Fish that are reared on commercial feeds often have high body lipid levels (Mock et al. 2019). In commercial aquaculture, fish need to be grown to a sufficiently large size so that the product is attractive to the consumer; therefore, feed cost is a very important consideration. In contrast, public salmon hatcheries release small juvenile fish with the expectation that these fish will feed and grow in the ocean, thus reducing the time and cost of rearing at the hatchery facility. The expense of salmon feed is also a concern for public salmon hatcheries, but the accounting for cost and benefit differs greatly from that of a commercial salmon aquaculture program. Public salmon hatchery goals are focused on the survival of young fish after release to allow for the eventual return of full-size adult fish. Cogliati et al. (2019) examined the effects of various formulations of a "conservation diet" for use in public salmon hatcheries and found the diets to be effective for use in conservation programs seeking to release smaller, leaner, healthy Chinook Salmon. Furthermore, experiments in production-scale Atlantic Salmon grow out also suggest that altering protein/lipid ratios in feeds can produce beneficial effects on fish growth and body composition (Dessen et al. 2017; Rørvik et al. 2018; Weihe et al. 2018). Overall, we suggest that there is ample room for further evaluation of the effects of various feed formulations, seasonal growth rate, and smolt release size for public salmon hatcheries. These efforts should take a different direction than previous work on juvenile salmon rearing—for example, including a focus on the consequences of varying body size and composition on survival to adult return and maturation schedules rather than simply focusing on reducing feed costs.

CONCLUSIONS

We successfully modulated feeding frequency and dietary lipid in the first year of rearing to alter the incidence of minijack maturation among yearling fall Chinook Salmon in a production-scale hatchery program. Over the course of the 4-year study, we did observe interannual variation in growth/energetic indices and the proportion minijacks among dietary treatments, most notably in the intermediate (4 days–18%) treatment. Overall, altering the feeding frequency and dietary lipid in a 2×2 factorial design at the production scale created distinct treatment groups with differences in growth and energetics; consequently, a 65.5% reduction in the proportion minijacks was achieved when both factors were reduced. Maintaining consistency in conducting hatchery-scale experiments presents unique challenges, but relatively simple manipulations to hatchery rearing can have a potentially significant effect on the development and life history of released fish. Future analysis of CWT and PIT tag recovery information will help to refine our understanding of the efficacy of these dietary treatments and will inform hatchery management decisions for the Umatilla River program and other regional Chinook Salmon hatchery programs.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the minijack data for this study can be found online as part of a larger data set (https://doi.org/10.5061/dryad.0rxwdbrzn). The energetics data is available upon request from the corresponding author.

ETHICS STATEMENT

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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