State-dependent life history plasticity in Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate smolting and early male maturation

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Abstract: An experiment was performed to determine the relative effects of photoperiod at emergence and growth rate on smolting pattern and early male maturation rate in Sacramento River (California, USA) winter-run chinook salmon (*Oncorhynchus tshawytscha*) (listed as endangered under the US Endangered Species Act). Fry were ponded on the same day but at three different points in the seasonal photoperiod cycle (using artificial lighting) spanning the natural range of emergence timing in this population. Significant increases in gill Na^+,K^+-ATPase activity and seawater survival were found during March and April in all treatments, similar to yearling smolting patterns found in many salmonids. Fish that emerged early and grew at a relatively high rate also demonstrated signs of smolting in August–November. Male maturation was growth dependent, with HiFeed groups maturing at a rate double that found in LoFeed groups. Male maturation was also photoperiod dependent with a linear relation found between emergence date and rate of male maturation. These results demonstrate that individual life history pattern was variable and dependent on emergence timing and growth rate.

Résumé : Nous avons procédé à des expériences afin de déterminer les effets relatifs de la photopériode au moment de l'émergence et du taux de croissance sur les patterns de transformation en saumoneaux et le taux de maturation précoce des mâles chez les saumons chinook (*Oncorhynchus tshawytscha*) de la montaison d'hiver du Sacramento (Californie, É.-U.), une espèce menacée d'après la loi américaine sur les espèces menacées. Nous avons placé des alevins dans des étangs le même jour, mais soumis à trois régimes différents du cycle photopériodique saisonnier (à l'aide de lumière artificielle) qui couvrent l'étendue naturelle des périodes d'émergence chez cette espèce. Dans toutes les conditions expérimentales, il y a en mars et avril des augmentations significatives de l'activité de la Na^+,K^+-ATPase des branchies ainsi que de la survie en eau de mer, semblables à celles observées chez de nombreux salmonidés lors de la transformation annuelle des poissons d'un an en saumoneaux. Les poissons qui émergent tôt et qui croissent à un taux relativement élevé montrent aussi des signes de transformation en saumoneaux en août–novembre. La maturation des mâles est dépendante de la croissance et les groupes nourris abondamment atteignent la maturité à une fréquence double de celle des groupes moins bien nourris. La maturation des mâles est aussi reliée à la photopériode et il existe une relation linéaire entre la date de l'émergence et le taux de maturation des mâles. Ces résultats démontrent que les patrons des cycles biologiques individuels sont variables et qu'ils dépendent du moment de l'émergence et du taux de croissance.

[Traduit par la Rédaction]

Introduction

The life history of chinook salmon (*Oncorhynchus tshawytscha*) is structured by migrations between freshwater and oceanic habitats that are coupled to life stage specific developmental events (smolting and sexual maturation). Intra- and inter-population variability in age, size, and seasonal timing at which these developmental events occur are a mark of the species (Healey 1991). Smolting is a physiological process that both allows and stimulates juvenile salmonids to under-

Received 18 April 2006. Accepted 22 December 2006. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 22 February 2007.
J19277

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 doi:10.1139/F07-001

take the initial freshwater to seawater migration (Hoar 1976). Smolting is thus a key life history transition fundamental to the nature of salmon, as it allows juvenile fish to leave relatively unproductive riverine or lacustrine freshwater habitats to take advantage of relatively richer ocean feeding grounds (Gross 1987).

There are four life history groups of chinook salmon in California's Central Valley: spring, fall, late fall, and winter defined by adult migration and spawn timing (Myers et al. 1998; Yoshiyama et al. 1998; Lindley et al. 2004). Each of these groups is distinct genetically (Bartley et al. 1992; Banks et al. 2000) and they were historically located in different geographic regions of the Sacramento and San Joaquin River drainages (Yoshiyama et al. 1998; Lindley et al. 2004). Spring chinook salmon spawned earliest in the year in higher elevations, while late-fall and fall chinook salmon spawned later in lower elevation areas. Winter-run chinook salmon were found in streams with unique hydrogeographic properties as water originated from springs fed by snowmelt from lava beds on Mt. Lassen and Mt. Shasta in the Upper Sacramento River Basin (above Shasta Dam). These streams possess very stable, cool temperatures yearround. In turn, winter-run fish possess unique life history traits as compared with other chinook salmon: adults return to the Sacramento River in winter (as opposed to spring–summer–fall) and spawn in spring–summer (as opposed to summer–fall–winter) (Healey 1994; Yoshiyama et al. 1998; Lindley et al. 2004).

Descriptions of smolting in winter-run chinook salmon are vague, as most are based on the observation of downstream-migrating chinook salmon juveniles without any reference to specific population-level markers (physical tags, morphological attributes, genetic identity) or physiological status (hypoosmoregulatory ability) (Myers et al. 1998). A large proportion of the winter-run population appears to move downstream past Red Bluff Diversion Dam (located below the major spawning sites for winter-run fish) during September–October at relatively small sizes (~50 mm) (Gard 1995, cited in Myers et al. 1998; Gaines and Martin 2002). It is quite common for juvenile chinook salmon to display seasonal downstream movement prior to, and distinct from, smolting that occurs at a later time (Taylor and Larkin 1986; Bradford and Taylor 1997). To our knowledge, fish migrating past Red Bluff Diversion Dam have not been specifically assessed for physiological characters of smolting (ability to survive and grow in seawater). Juvenile chinook salmon found lower down in the Sacramento River or Delta or San Francisco Bay might come from any one of the four distinct population groups, so it has been difficult to identify winter-run smolts among the total population of juvenile salmonids (Brandes and McLain 2001). Descriptions published to date suggest that smolting occurs in October–April at sizes >70 mm (Myers et al. 1998). In contrast, Sacramento River spring and fall chinook salmon (the most abundant population groups in the Sacramento Basin) generally smolt within 1–4 months postemergence, in the spring – early summer, at sizes of 50–70 mm (Myers et al. 1998; Yoshiyama et al. 1998; Lindley et al. 2004).

The current paradigm organizing life history variability (including smolting) between chinook salmon populations is based on a dichotomy proposed by Healey (1991). In this classification, Healey suggested that that there are two "races" of chinook salmon (ocean-type and stream-type), each having distinct geographic distributions and life history characteristics (juvenile and adult). Smolting pattern is suggested to fall into two main categories: ocean-type (enter seawater in spring or summer, weeks to months after emergence, at 40–70 mm in length) and stream-type (enter seawater in the spring at an age of >1 year after spending the winter in fresh water, >70 mm in length). Healey (1991) suggested that ocean-type fish are found in the southern geographic range of chinook salmon from coastal British Columbia to California. It is not clear how, or if, the smolting pattern of Sacramento River winter-run chinook salmon relates to the ocean-type – stream-type dichotomy. Thus, we will use the term "underyearling" (fish smolt before spending a winter in fresh water) or "yearling" (smolt after spending a winter in freshwater) to describe smolting pattern for results in this paper, as these terms do not imply associated genetic population structure or intertwined juvenile and adult life history traits.

Potential smolting patterns are presumably genetically set; however, the environment modulates the endocrine and physiological status of a fish to produce a specific smolting phenotype for a given individual. The results of Clarke et al. (1992, 1994) suggest that smolting in stream-type chinook salmon may be plastic, occurring either as yearlings in the spring or as underyearlings in the preceding year. Further studies have shown that this plasticity may depend on size and growth rate of individual fish (Ewing et al. 1980; Beckman and Dickhoff 1998; Connor et al. 2005). Larger, faster growing fish have been found to smolt in the fall, while smaller, slower growing fish do not smolt until the following spring for fish exposed to normal seasonal photoperiodic schedules. Beckman et al. (2003) suggested that smolting in the autumn as an underyearling fish might be considered distinct from prototypical ocean-type smolting, as the fish were larger and older than characteristic ocean-type fish and these same fish, as a group, appeared to be able to smolt either in the autumn (as underyearlings) or in the spring (as yearlings). Smolting may thus be variable both between populations (ocean-type versus stream-type) and between individuals within populations (underyearling versus yearling). This variability and the interactions between genetic and environmental sources of this variability make it very difficult to predict either smolting pattern or the environmental control of smolting pattern in Sacramento River winter-run chinook salmon.

Juvenile male salmonids may directly mature rather than smolt. This has been termed "early male maturation", as these fish mature at a young age (1 or 2 years old) and a small size (as small as 10 g) as compared with full-size anadromous males (Healey 1991; Unwin et al. 1999). This alternative developmental pathway has been of both theoretical and practical interest and has received a great deal of attention, especially with Atlantic salmon (*Salmo salar*) (Thorpe 1986; Fleming 1998; Garant et al. 2003). Studies of Atlantic salmon have revealed that early male maturation is a conditional event occurring or not depending on seasonal growth rate and (or) fat stores. Larger, faster growing parr initiate male maturation as opposed to smaller, slower growing fish that smolt instead (Thorpe 1986, 1989). Similarly, juvenile

chinook salmon males may undertake early maturation dependent on growth and adiposity (Clarke and Blackburn 1994; Silverstein et al. 1998; Shearer and Swanson 2000). Depending on conditions (temperature and feed), up to 90% of males in an experimental population of chinook salmon may mature (Foote et al. 1991; Shearer et al. 2006). Thus, variation in the juvenile life history of chinook salmon not only includes age, size, and season of smolting but also an alternative for males to either mature or smolt.

There are specific conservation and management concerns that stimulate investigating life history in Sacramento River winter-run chinook salmon. These fish were listed under the US Endangered Species Act as threatened in 1989 and subsequently as endangered in 1994 (Yoshiyama et al. 2000). Based on this situation, hatchery and captive broodstock programs were initiated to supplement the natural winter-run population (U.S. Fish and Wildlife Service 2000). These programs might be better managed if there were a basic understanding of the range of juvenile life history variation possible within winter-run fish and the factors controlling this variation were known.

We thus designed an experiment to investigate variability of smolting and early male maturation in winter-run chinook salmon. Based on the findings of Healey (1991) and Clarke et al. (1992, 1994), we can offer several predictions: (*i*) if winter-run fish have an ocean-type life history pattern, smolting will be size dependent and photoperiod independent, (*ii*) if winter-run fish have a stream-type life history pattern, smolting will be photoperiod dependent and occur in the spring, and (*iii*) if winter-run fish have a variable smolting pattern, smolting might occur in either the autumn or the spring dependent on individual fish growth rate and photoperiod.

Accordingly, fish were reared under two feeding regimes (HiFeed and LoFeed) and three different photoperiod regimes. Eggs were obtained from crosses of captively reared adults at Bodega Marine Laboratory. Fry were ponded (first exposure to light and when feeding was initiated) on the same day but under different photoperiods matching the natural range of emergence (first-feeding) for winter-run fish (June–October). The objective was to assess life history variability among fish of the same size and age (and of the same genetic composition) emerging at different points of a seasonal photoperiod cycle.

Materials and methods

Fish and rearing

Eyed eggs from five male × female crosses (spawned on 23 July 2002) were obtained from the Sacramento River winter-run chinook salmon captive broodstock program at Bodega Marine Laboratory, Bodega, California (see Arkush et al. (2004) for a description of spawning protocols). Eggs were shipped to the Northwest Fisheries Science Center experimental hatchery in Seattle, Washington, and arrived on 23 August 2002. Egg lots were incubated separately in Heath trays, in the dark, in a recirculating-water egg incubation system maintained at 11 °C. Permits allowing these eggs to be used for research purposes were granted from both the National Marine Fisheries Service and the California Department of Fish and Game, as the eggs were in excess of broodstock program demands and considered surplus. Total egg hatch for all crosses was achieved by 4 September. Differential mortality between crosses occurred owing to incomplete hatch (fry became stuck in the egg membrane as they emerged and subsequently died). One to two hundred fry per cross (depending on availability) were placed into each of six 1.3 m diameter fiberglass tanks on 9 October for a total of 690 fry per tank. Water was supplied from a recirculating system with biofiltration, ozonation, and ultraviolet sterilization and maintained at 12 °C (±1 °C). Average fry weight at ponding varied from 0.210 to 0.265 g between crosses (n = 15 per cross). Each tank was illuminated with an incandescent light with a photoperiod set to match that of Sacramento, California (38°N), adjusted weekly. Photoperiod varied among tanks as described below. Fry were fed Biodiet Starter ad libitum through 15 November for 6 days per week, after which rations were set as described below and fed Biodiet Grower 5 days per week. Fish were maintained in their respective tanks through July of 2003 (9 months of rearing).

Experimental design

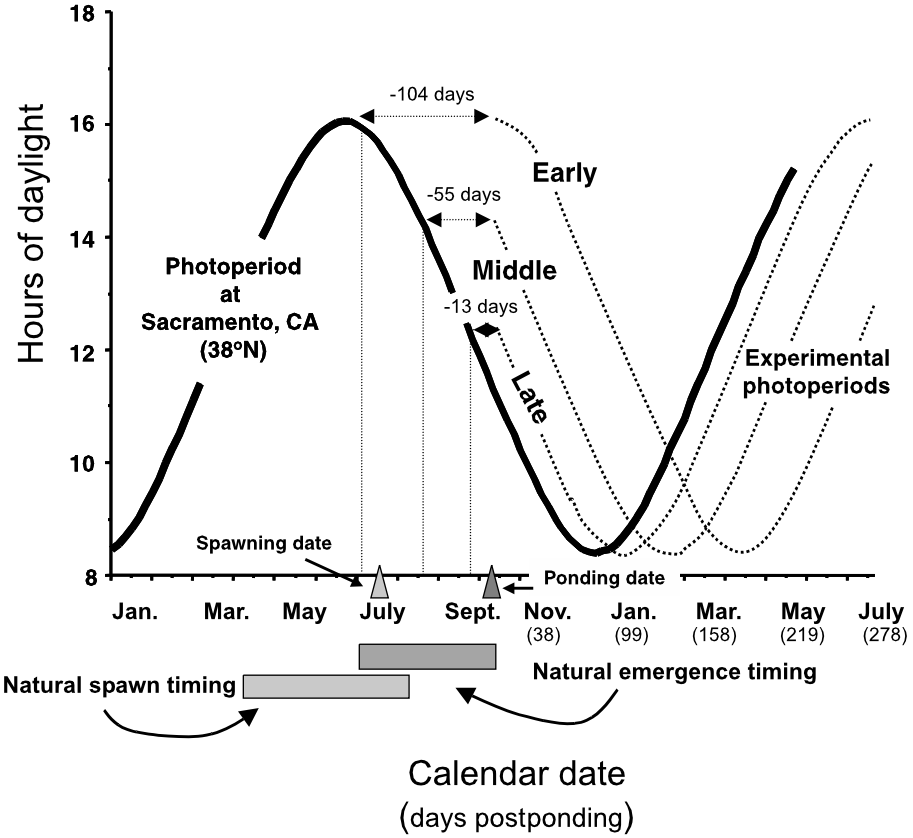
At ponding (no egg sac visible, ventral body wall nearly or completely fused), fish were placed into three separate photoperiods (two tanks per photoperiod): early (matching emergence early in the summer, 27 June, 104-day shift from the actual date), middle (matching emergence in the middle of summer, 15 August, 55-day shift), and late (matching emergence late in the summer, 27 September, 13-day shift) (Fig. 1). Photoperiod followed a normal seasonal trajectory from each respective starting date.

After a robust feeding response was established, fish from each photoperiod were fed at two different rates to cleanly establish fish with different growth histories within each photoperiod. Thus, a high- or low-feeding treatment was given to each pair of tanks for each photoperiod (two feeding treatments × three photoperiods) designed to yield fish of 10 and 25 g by a calendar date of 1 February using the delta-l method of Piper et al. (1982). Subsequently, during the experiment, fish appetite was found to decrease strongly with winter solstice photoperiods and ration was determined every 2 weeks by feeding the HiFeed tank in the photoperiod closest to solstice (displayed the poorest feeding response) to satiation. Feeding for the subsequent days for HiFeed fish was set at 80% of satiation. LoFeed tanks were fed 50% of the HiFeed ration. This feeding strategy allowed us to maintain equivalent sizes and growth rates among HiFeed or LoFeed fish, respectively, in the different photoperiod treatments and subsequently allowed us to directly assess the effects of photoperiod on smolting and maturation while removing any photoperiod-influenced difference in appetite and subsequently growth that might have compounded a direct photoperiod effect. Actual amounts fed correspond to 3.5% of body weight per day in November dropping to 1.7% of body weight per day in May for the HiFeed groups.

Fish sampling

Batch weights (three 25-fish composite samples per tank) were taken approximately monthly to facilitate ration calculations. Twelve fish per tank were sampled about every 3 weeks for gill tissue starting on 13 November. By 18 De-

Fig. 1. Experimental shift of seasonal photoperiod as compared with that found at Sacramento, California (38°N). Spawning dates of broodstock for experimental fish and actual ponding date (first exposure to light) are shown by arrows on the *x*-axis. The natural ranges of spawning date and emergence timing displayed by winter-run chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River are shown by light- and dark-shaded bars under the *x*-axis (Yoshiyama et al. 1998).



cember, fish were large enough to make blood sampling practical. Blood samples were pooled (two fish per pool) for samples obtained 18 December – 7 February; single-fish samples were obtained thereafter. Fish were sampled on a total of 11 occasions, with the last sample taken on 15 July. Sampling started with fish first netted and counted into a bucket and then netted singly into a lethal dose of tricaine methanesulfonate. Fish were then blotted dry, fork length (millimetres) and weight (grams) were measured, the caudal peduncle was severed, and blood was obtained in a heparinized capillary tube. The blood was subsequently transferred to a microfuge tube and stored on ice until all samples were obtained (<2 h). Microfuge tubes were spun at 3000*g*, plasma obtained, and samples stored at –80 °C until hormone analysis was undertaken. Gill tissue was snipped from arches, placed in a buffered solution of sucrose, EDTA, and imidazole according to McCormick (1993), and frozen at –80 °C until assayed for gill Na^+,K^+-ATPase activity.

Also, on an approximately 3-week schedule, 15 fish per treatment were placed into a 0.65 m^2 tank filled with 35 g artificial seawater·L^{-1}(Instant Ocean) aerated and maintained at 12 °C (Clarke and Blackburn 1977). Survival was monitored for 72 h after transfer to seawater. Testis size was visually assessed in all sampled fish to monitor for early male maturation. Differences in testis size between maturing and nonmaturing males may be ascertained up to 6 months prior to final maturation (spermiation) (Campbell et al. 2003; Larsen et al. 2004). Maturing males were excluded from subsequent analysis of smolting characters. At the end of the experiment, all remaining fish were sacrificed to assess gender and testis development, determined as above. In addition, up to 10 immature and 10 mature testes from male fish from each treatment were weighed as the experiment was terminated to determine gonadal somatic index (GSI).

Laboratory methods

Plasma insulin-like growth factor-I (IGF-I) levels were determined by radioimmunoassay (RIA) using components obtained from GroPep Ltd. (Adelaide, Australia) as described in Shimizu et al. (2000). Briefly, 10 µL of plasma was thoroughly mixed with acid–ethanol (87.5% ethanol and 12.5% 2 mol HCl·L^{-1} by volume) at a ratio of 1:4 and then incubated at room temperature for 30 min. The tubes were centrifuged at 3000*g* for 20 min at 4 °C. The supernatant was decanted into a new set of tubes, neutralized with 0.855 mol·L^{-1} Tris base at a ratio of 5:2, and assayed for IGF-I. Gill Na^+,K^+-ATPase activity was assessed using the method of McCormick (1993). All gill Na^+,K^+-ATPase activities are reported in units of µmol PO_4·mg protein^{-1}·h^{-1}.

Analytical methods

Neither of our experimental variables was fixed: daylength progressed through a natural seasonal cycle for each photoperiod treatment, and while feeding rates were consistently set at either HiFeed or LoFeed levels between photoperiod treatments, actual feeding rates changed temporally

with appetite and fish size. Thus, within this experiment, photoperiod, feeding rate, and fish age all varied and differences in feeding rate resulted in variation in fish size and fish growth. The experiment was purposely designed, as we expected developmental decisions for individual fish to be dependent on interactions between photoperiod, fish size, fish growth, and fish age. There are two frames of reference for this experiment: (*i*) calendar day, which refers to the actual day on which experimental events occurred, and (*ii*) photoperiod day, which corresponds to the day of the year in which a respective experimental photoperiod could be found. Thus, for each calendar day during the experiment, there were three different photoperiod days corresponding to the date 104, 55, and 13 days previous (early, middle, and late) (Fig. 1). Both frames of reference are valid and both might be considered to appreciate the results. To reduce confusion between these frames of reference, we have transformed calendar dates to days postponding for use in figures, tables, and statistical analysis. Thus, the experiment ranged from day 1 postponding (9 October 2002) to day 277 postponding (15 July 2003).

We most formally examined results by comparing fish of the same age, sampled at the same number of days postponding, using a three-way analysis of variance (ANOVA) with date, ration (HiFeed and LoFeed), and photoperiod (Early, Middle, and Late) the effects examined. If significant effects were found, a one-way ANOVA followed by Scheffé's multiple range test was conducted to assess differences between individual means. Overall, significant effects and interactions were found for all main factors for the three parameters examined (length, plasma IGF-I, gill Na^+,K^+-ATPase activities; results not shown).

Within this statistical framework, photoperiod affects were apparent as consistent differences between photoperiod treatments within a feed treatment (e.g., EarlyEmergeHiFeed different from LateEmergeHiFeed). State-dependent effects (size or growth) were apparent as differences between HiFeed and LoFeed treatments within a photoperiod (e.g., EarlyEmergeHiFeed different from EarlyEmergeLoFeed). Interactions between photoperiod and feed treatment are indicated when HiFeed and LoFeed differences are not consistent between photoperiod treatments (e.g., EarlyEmergeHiFeed different from EarlyEmergeLoFeed, while LateEmergeHiFeed not different from LateEmergeLoFeed). Significant differences between treatments for a given number of days postponding are shown in the figures. Significant differences between sampling dates within a treatment are discussed in the text. The significance level was set at $p < 0.05$.

The metric for seawater challenges was percent survival; for each treatment, for any one date, there was only one trial, so $n = 1$ for each date. On a calendar date scale, we assessed mean seawater survival for each treatment over trials conducted between days 439 and 553 postponding (five trials, $n = 5$ per treatment). The square root of the proportion of fish surviving (0–1) was arcsine transformed prior to analysis with ANOVA (Zar 1984). All subsequent percentage data were similarly transformed (percentage of males maturing, GSI). Differences in transformed means were determined by one-way ANOVA followed by Scheffé's multiple range test.

Percent early male maturation (summed over samples taken from the whole experiment) was compared simply between HiFeed and LoFeed treatments with ANOVA (two treatments, three replicates). Simple regression was used to assess percent early male maturation in all treatments with respect to photoperiod day at emergence after values were standardized to a common mean for each feed treatment (HiFeed or LoFeed): standardized mean = % maturation for a treatment – (mean % maturation for a feed group – overall mean % maturation). GSI was determined as GSI = gonad weight × body weight^{-1} × 100.

Seasonal framework for analytical analysis

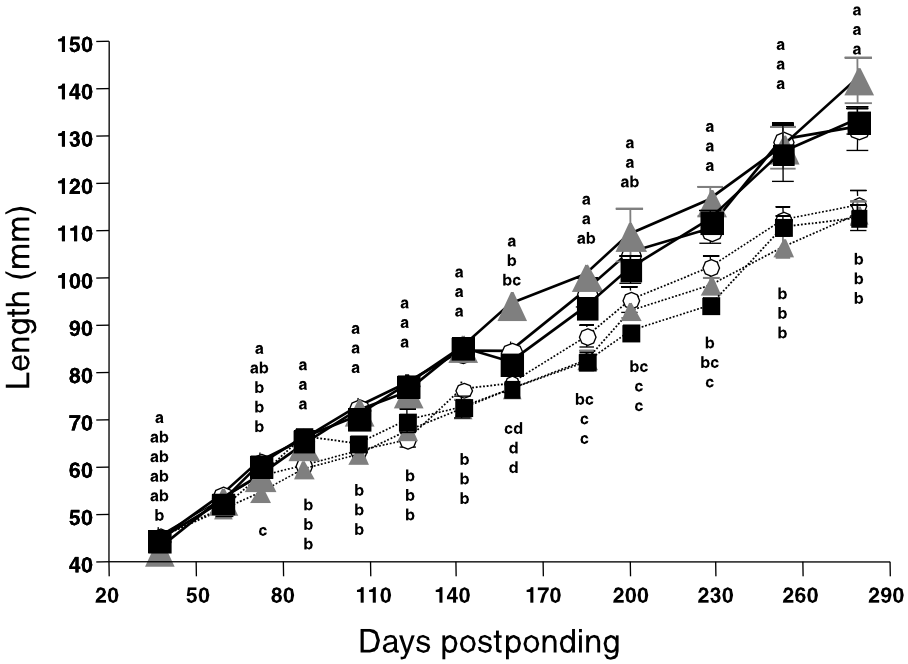
Simple regression was used to assess the relations among length and gill Na^+,K^+-ATPase activity for fish grouped into seasonal stanzas (August–September, October–November, December–January, February–March, April–May, June–July) by photoperiod date. A simple size versus gill Na^+,K^+-ATPase activity relation consistent over all dates would be indicative of an underyearling smolting pattern. A significant size versus gill Na^+,K^+-ATPase activity relation only found in the spring would be indicative of a yearling smolting pattern. Seasonal changes in the size versus gill Na^+,K^+-ATPase activity relation would indicate a variable smolting pattern. Differences in mean seasonal gill Na^+,K^+-ATPase activities were also assessed by one-way ANOVA as discussed previously, with fish binned into the same seasonal stanzas as described above. Finally, mean seawater tolerance of each treatment was also assessed on a photoperiodic scale over the photoperiod dates of 15 November – 15 January ($n = 3$ or 4 per treatment) to demarcate potential autumnal smolting.

Assessing size, growth, maturation, and smolting

Size and growth were examined, as they represent physiological pathways through which environment influences development (smolting and maturation). More directly, size and growth rate may influence the decision of individual fish to either smolt or mature. As such, we are not so much interested in the effects of feeding rate and photoperiod on size and growth; instead, we are interested in how size and growth relate to environment and the subsequent expression of smolting and early male maturation. We measured size of fish in each treatment at each sampling date and assessed differences between treatments with ANOVA (described above). We could not estimate growth rate of fish over each sampling interval, as we neither tagged individual fish nor included robust replication of tanks within our experiment; however, we did measure plasma levels of the hormone IGF-I at each sampling interval, as it has been established as an effective index of fish growth (Beckman et al. 2004). Overall, we assessed IGF-I not to ascertain growth differences between individual treatments; rather, we wished to test whether we produced two different growth trajectories (HiFeed and LoFeed). We could again assess differences in mean IGF-I between treatments with ANOVA.

Maturation represents a binary response (yes or no) and male maturation may be easily assessed visually as a thickening of the testis (Campbell et al. 2003; Larsen et al. 2004). The number of males in each treatment that initiated maturation was simply counted cumulatively over the course of

Fig. 2. Mean (±SE) length of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge (squares), MiddleEmerge (triangles), and LateEmerge (circles)) and two feeding levels (HiFeed (solid lines) and LoFeed (broken lines)). Symbols with similar superscripted letters are not significantly different frpm each other for a given date. The order of letters (top to bottom) corresponds to the order of symbols (top to bottom) on a given date.



sampling and added to the count made by terminally sampling all of the remaining fish at the end of the experiment.

Ecologically, smolting is a binary response that is represented by whether or not fish migrate downstream to the ocean (yes or no) and whether the individual can adapt to seawater when they reach that destination (live or die). Functionally, smolting thus includes both behavioral (migration) and physiological (seawater tolerance) traits that are seasonally correlated but represent distinct organismal responses. Assessing smolting in an experimental context is difficult, as there is no one character that represents the overall biological response. Investigators have used behavioral, morphological, endocrine, and physiological traits to index smolting (Hoar 1976; Folmar and Dickhoff 1980; McCormick and Saunders 1987). All of these traits display gradual quantitative changes that occur over a period of weeks to months within both individuals and populations that are difficult to transform into a simple binary smolt index (smolt or nonsmolt). In addition, smolting is reversible (Shrimpton et al. 2000). Thus, any one sample of a population may include individuals that are initiating smolting, fish fully within the smolting process, and fish readapting to fresh water. Thus, we cannot simply count individual smolts within a treatment over the course of time.

We assessed smolting by marking the development of seawater tolerance, a key characteristic for animals successfully making a freshwater to seawater transition. Two measures of seawater tolerance were conducted: measuring the activity of the enzyme Na^+,K^+-ATPase found in the gill (Zaugg and Wagner 1973) and survival in a seawater challenge (Clarke and Blackburn 1977). It is tempting to interpret the results of seawater challenge (live or die) as a binary indicator of smolting (yes or no). However, again, smolting is reversible, so a given seawater challenge can not determine whether a fish has not yet smolted (dies) or has smolted and subsequently readapted to fresh water (dies). We interpret differences in the mean value of either gill Na^+,K^+-ATPase activity or proportion of individuals surviving a seawater challenge as differences in the tendency of individuals within an experimental population to smolt during a given period. Given that smolting is a temporally extended process (weeks to months), we expect diagnostic differences in seawater tolerance to extend through at least two sampling periods. Furthermore, note that changes in the results of seawater challenges tend to lag changes in gill Na^+,K^+-ATPase activity in captive populations and these indicators are thus not expected to display exact temporal equivalence (Beckman et al. 1999).

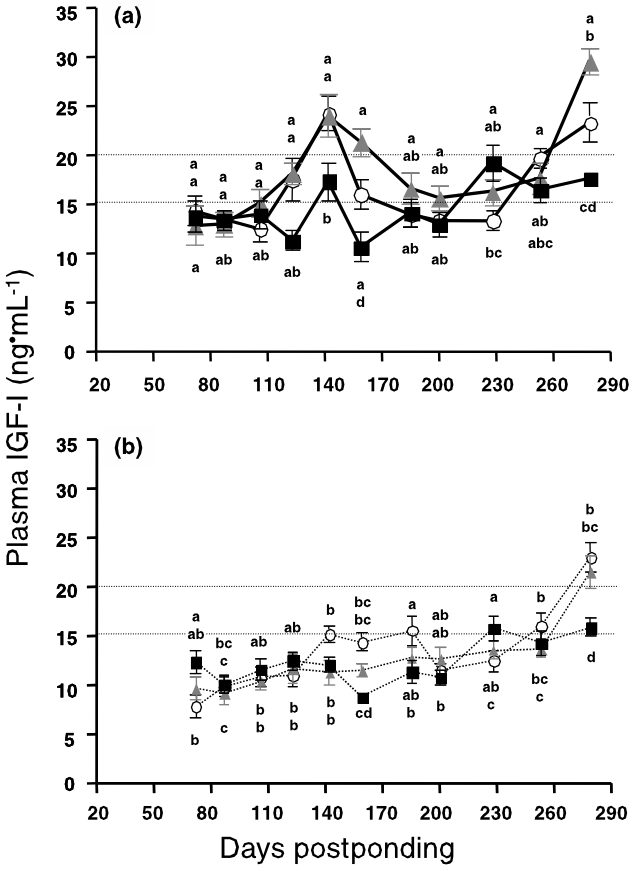
Results

Length and growth

Consistent, significant differences in length were found between feeding treatments by 90 days postponding and these continued throughout the experiment, with fish from HiFeed treatments being larger than fish from LoFeed treatments (Fig. 2). Samples obtained from day 160 to day 230 postponding diverged somewhat both within and between feeding treatments, with fish from the EarlyEmergeHiFeed and the LateEmergeLoFeed groups not significantly different from each other on several sampling occasions. Subsequently, all HiFeed groups were significantly different from all LoFeed groups day 230 through day 277.

Significant differences in plasma IGF-I levels for fish in different feeding treatments (HiFeed versus LoFeed) were found on nine of the 11 dates that blood was obtained, dem-

Fig. 3. Mean (±SE) plasma IGF-I level of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge (squares), MiddleEmerge (triangles), and LateEmerge (circles)) and either (*a*) HiFeed (solid lines) or (*b*) LoFeed (broken lines) level. Symbols with similar superscripted letters are not significantly different from each other for a given date for each panel. The order of letters (top to bottom) corresponds to the order of symbols (top to bottom) on a given date.



onstrating a strong effect of ration on plasma IGF-I level (statistical analysis not shown) (Fig. 3). Photoperiod effects were also found within feeding treatments. Plasma IGF-I levels in MiddleEmergeHighFeed and LateEmergeHiFeed fish increased from ~12 ng·mL^{-1} to a peak of ~25 ng·mL^{-1} before declining to ~15 ng·mL^{-1} between days 110 and 200 postponding (Fig. 3*a*). Plasma IGF-I levels in the EarlyEmergeHiFeed group were significantly less than found in the other two HiFeed groups during this period (days 110–200). Similarly, IGF-I levels found in fish from the EarlyEmergeLoFeed group were significantly less than found in fish from the LateEmergeLoFeed group days 140–185 postponding (Fig. 3*b*). Photoperiod for the EarlyEmerge fish matched that of the winter solstice at approximately day 188 postponding (Fig. 1); thus, the period of relatively low IGF-I levels in EarlyEmerge fish matches the period during which the fish received the least photoperiodic stimulation.

Smolting

Gill Na^+,K^+-ATPase activities increased significantly from day 170 to day 260 postponding in all treatments (Figs. 4*a* and 4*b*). Gill Na^+,K^+-ATPase activity increases occurred later in both EarlyEmerge groups (HiFeed and LoFeed) as compared with the other photoperiod groups. This difference corresponds to the 100-day delay in the spring increase in daylight as defined by differences between the EarlyEmerge and LateEmerge photoperiod treatments and directly translates into a photoperiod effect on the increase in gill Na^+,K^+-ATPase activities. There were no significant differences between feeding groups within a photoperiod treatment from day 170 to day 260 postponding, suggesting that there was no effect of size or growth on smolting during this period.

Differences between both feeding and photoperiod treatments were found from day 50 to day 110 postponding. LateEmergeHiFeed fish had lower gill Na^+,K^+-ATPase activities than found in other HiFeed groups between day 50 and day 110. In addition, fish from both EarlyEmergeHighFeed and MidEmergeHiFeed groups had significantly higher gill Na^+,K^+-ATPase activities than fish from EarlyEmergeLowFeed and MidEmergeLoFeed groups for at least three sampling dates from day 50 to day 110 (Figs. 4*a* and 4*b*), suggesting a state-dependent effect (size or growth) on smolting in the EarlyEmerge and MiddleEmerge photoperiod treatments during this time period.

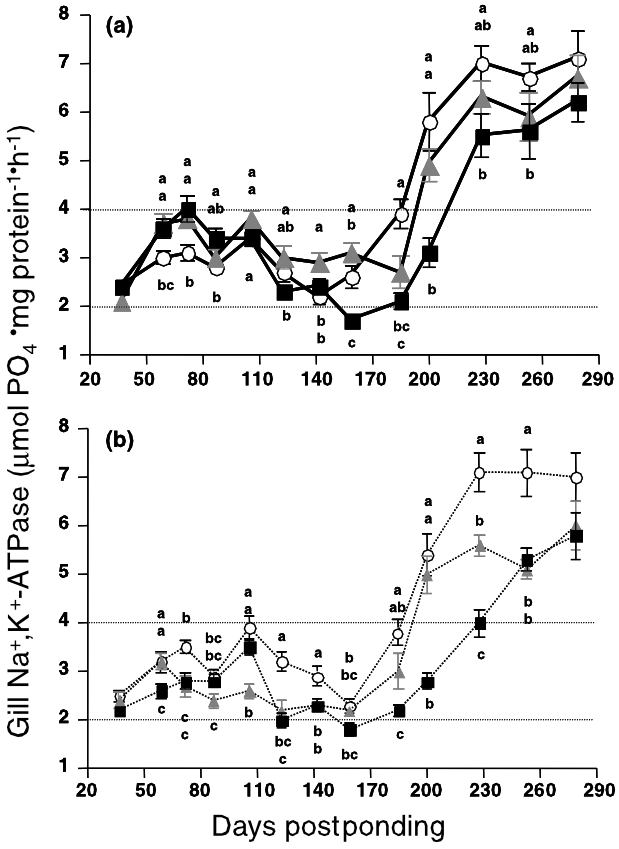
Seawater survival increased from 0% day 36 through day 110 postponding to 100% in all groups by day 285 (Fig. 5). Photoperiod at emergence had a stronger effect than feeding rate on seawater survival (two-way ANOVA: photoperiod, $F = 7.2$, $p = 0.005$; feeding rate, $F = 2.2$, $p = 0.16$; interaction, $F = 0.3$, $p = 0.77$, $n = 30$) over days 143–248 postponding.

Seasonal size–smolting relations

In general, bigger fish had high gill Na^+,K^+-ATPase activity (Fig. 6*a*), with only fish >80 mm possessing gill Na^+,K^+-ATPase activities >6. However, fish of this size were not found until February–March (photoperiod dates), with bigger fish and higher gill Na^+,K^+-ATPase activities found at even later dates (April–July, photoperiod dates, gill Na^+,K^+-ATPase activities 6–10). Physiological condition of fish altered the general size – gill Na^+,K^+-ATPase activity relation, as maturing males (visibly enlarged testis) had gill Na^+,K^+-ATPase activities significantly less than found in fish of a similar size (for fish >100 mm, mature male gill Na^+,K^+-ATPase = 3.8, not mature male gill Na^+,K^+-ATPase = 6.0; $F = 69$, $p < 0.0001$). Seasonal photoperiod also appeared to influence the size – gill Na^+,K^+-ATPase activity relation, as some fish of a size of ~60 mm had gill Na^+,K^+-ATPase activities >4.25; these fish were sampled in the autumn period (August–November, photoperiod date).

Size–smolting relations were not consistent through season. Simple regression showed significant, positive relations in August–September, February–March, and April–May. No relation was found in October–November and a negative relation was found in December–January. This later finding may be due to some relatively large males (90–100 mm) that had physiologically initiated maturation prior to the beginning of visually discernable enlargement of the testis. Nevertheless, there was no sign of increased gill Na^+,K^+-ATPase activities during the December–January period. Finally, a seasonal comparison of mean gill Na^+,K^+-ATPase activities was made (Fig. 6*b*). Average gill Na^+,K^+-ATPase values

Fig. 4. Mean (±SE) gill Na^+,K^+-ATPase activity of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge (squares), MiddleEmerge (triangles), and LateEmerge (circles)) and either (*a*) HiFeed (solid lines) or (*b*) LoFeed (broken lines) level. Symbols with similar superscripted letters are not significantly different from each other for a given date. The order of letters (top to bottom) corresponds to the order of symbols on a given date (top to bottom).



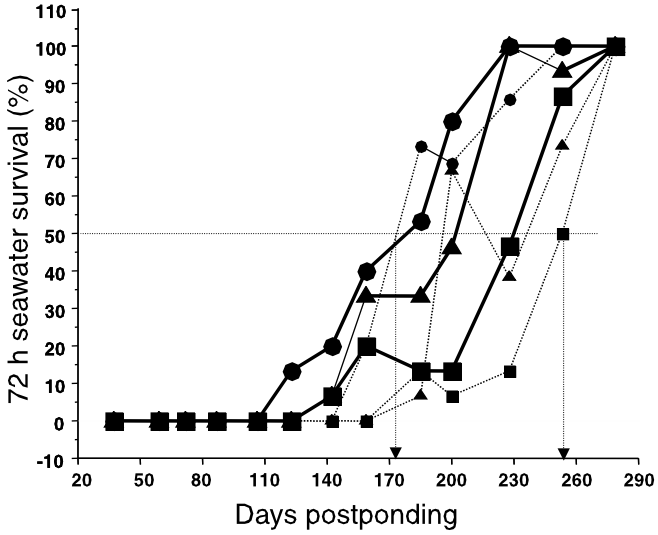
found in December–January were significantly lower than found during any other period, while strong increases were found from February through July. These analyses demonstrate a seasonally variable smolting pattern in winter-run chinook salmon.

When examined with regard to photoperiod date, increases in seawater tolerance were tightly coupled to photoperiod, with date of achieving 50% survival in seawater spanning less than 6 weeks between treatments (mid-February to late March), regardless of size or age (Fig. 7). All fish survived the 72-h seawater challenge in May (photoperiod date). In contrast, date of achieving 50% seawater survival spanned 3 months (early March – late June) when examined by calendar date (fish of the same age) (Fig. 5).

Early male maturation

Male maturation was significantly higher in HiFeed groups (31.5%) as compared with LoFeed groups (9.3%) ($F = 28.7$, $p = 0.006$, $n = 6$) (Fig. 8*a*). In addition, a significant linear relation was found between photoperiod at emergence and feed treatment standardized percent male maturation ($F = 1184$, $p = 0.02$, $r^2 = 0.96$, $n = 6$) (Fig. 8*b*).

Fig. 5. Percent survival of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge (squares), MiddleEmerge (triangles), and LateEmerge (circles)) and two feeding levels (HiFeed (solid lines) and LoFeed (broken lines)) subjected to a 72-h 35 ppt seawater challenge plotted versus days postponding. Broken-lined arrows indicate the period over which different treatment groups first achieved 50% survival.



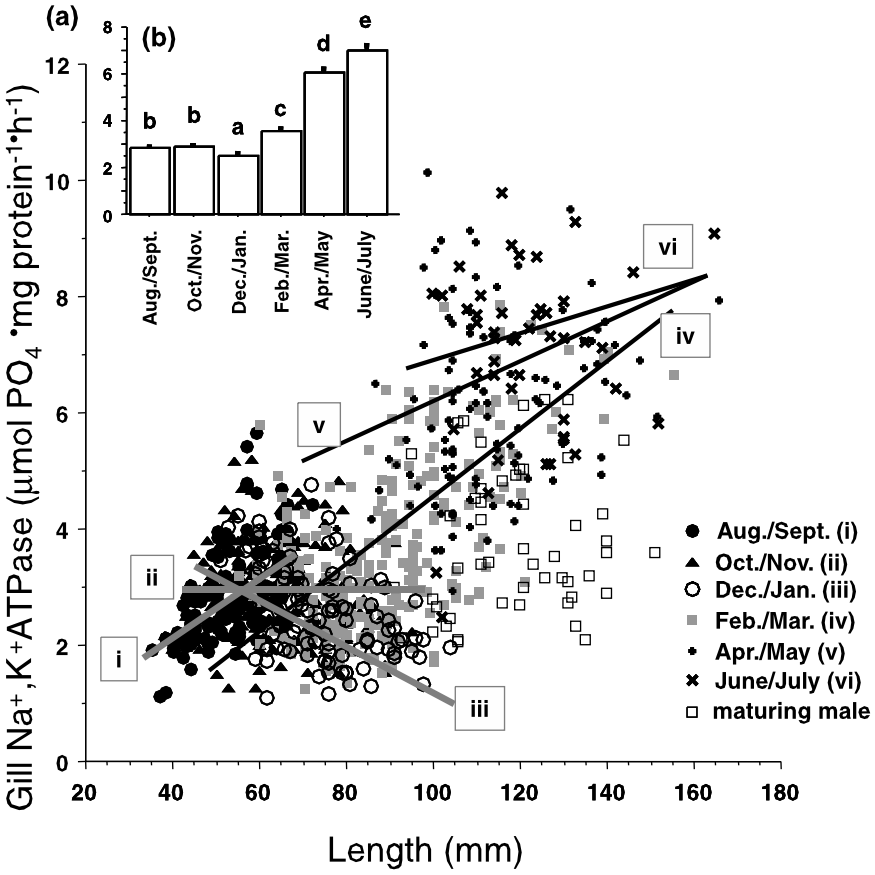
There were no differences in GSI among immature males at the termination of the experiment in July ($F = 1.5$, $p = 0.19$) (Fig. 9*a*). In contrast, GSI of maturing males was significantly higher in LateEmerge and MiddleEmerge fish than in EarlyEmerge fish ($F = 26.1$, $p < 0.0001$) (Fig. 9*b*). Spermiating males were found in both the MiddleEmerge and LateEmerge groups.

Discussion

Sacramento River winter-run chinook salmon displayed a variable juvenile life history dependent on photoperiod at emergence and subsequent growth rate. Two different smolting patterns were found: the first, a distinct seasonally defined, photoperiod-driven, spring smolting pattern typical of chinook salmon that smolt as yearlings (Beckman et al. 1998, 1999, 2000); in addition, autumnal smolting occurred (Ewing et al. 1980; Beckman and Dickhoff 1998; Beckman et al. 2003). Autumnal smolting appeared to be both size (growth) and photoperiod dependent, as (*i*) EarlyEmerge-HiFeed fish appeared to smolt, while EarlyEmergeLoFeed fish did not and (*ii*) LateEmergeHiFeed fish did not smolt when they were the same age and size as EarlyEmerge-HiFeed fish but were experiencing a different photoperiodic signal. Both smolting patterns were clearly seasonal (photoperiod driven), as spring smolting and autumnal smolting were separated by the December–January period (photoperiod date) during which there was little evidence of smolting regardless of fish size or growth rate.

Precocious male maturation was growth dependent, as has been demonstrated previously in chinook salmon (Clarke and Blackburn 1994; Silverstein et al. 1998; Larsen et al. 2006), as HiFeed groups had higher maturation rates than photoperiod-matched LoFeed groups. In addition, there was

Fig. 6. (*a*) Scatterplot of length and gill Na^+,K^+-ATPase activity for individual Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*). Different symbols indicate season (photoperiod) under which fish were sampled. Maturing males are depicted by separate discrete symbol regardless of season. Regression relations between length and gill Na^+,K^+-ATPase activity are plotted for each season; the length of each line encompasses the range of fish length for each season (August–September: $p < 0.0001$, $r^2 = 0.34$, $n = 119$; October–November: $p = 0.6$, r^2 not significant, $n = 215$; December–January: $p < 0.0001$, $r^2 = 0.22$, $n = 118$; February–March: $p < 0.0001$, $r^2 = 0.37$, $n = 283$; April–May: $p = 0.008$, $r^2 = 0.07$, $n = 102$; June–July: $p = 0.28$, r^2 not significant, $n = 45$). (*b*) Mean seasonal gill Na^+,K^+-ATPase activity (regardless of treatment); columns with similar superscripted letters are not significantly different from each other ($p > 0.05$).



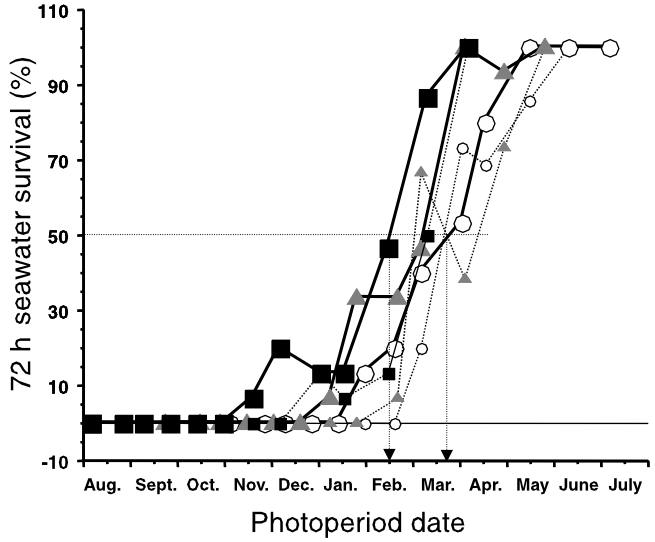
a linear relation between emergence date and maturation, as EarlyEmerge fish matured at a higher rate than LateEmerge fish. This photoperiod effect suggests that there is a growth × photoperiod interaction involved in the early maturation "decision" (see below).

Photoperiod, seasonal windows, emergence timing, and quantitative threshold traits

Key to this experimental design was the exposure of first-emerging fry to different photoperiods. Exposing salmonids to altered experimental photoperiods is not novel. In many cases, investigators have used a constant short-day photoperiod (simulating emergence during the winter or early spring) in an effort to produce "zero-age" coho (*Oncorhynchus kisutch*), Atlantic, or chinook salmon smolts that might be transferred to seawater at a younger age, thus increasing the efficiency of aquaculture operations (Clarke et al. 1989; Duston and Saunders 1995; Duncan and Bromage 1998). For chinook salmon, Clarke et al. (1989, 1992, 1994) compared the smolting response of individuals from ocean-type and stream-type populations from British Columbia exposed to constant short-day (9.5 h, photoperiod equivalent to emerging prior to the spring equinox) and long-day (14.5 h, photoperiod equivalent to emerging after the spring equinox) photoperiods for 2 months postemergence prior to placing them on the same natural photoperiod. He found that fish from ocean-type populations smolted as underyearlings regardless of photoperiod. In contrast, fish from stream-type populations smolted as underyearlings when exposed to a short-day photoperiod at emergence but did not when exposed to a long-day photoperiod. These experiments demonstrated both that there were genetic differences between chinook salmon populations with regard to the photoperiod dependence of smolting and the physiological fact that smolt timing was sensitive to the photoperiod during early development. Placed into an ecological context, these data suggest that fry that emerge relatively late in a growing season (long-day photoperiod) suppress the initiation of smolting until the following spring regardless of their growth rate.

Similarly, Clarke and Blackburn (1994) exposed fry from a stream-type chinook salmon population to short-day (10 h of light) and long-day (14 h of light) photoperiods for 2 months postemergence and then examined the effect of this photoperiod treatment on early male maturation. They

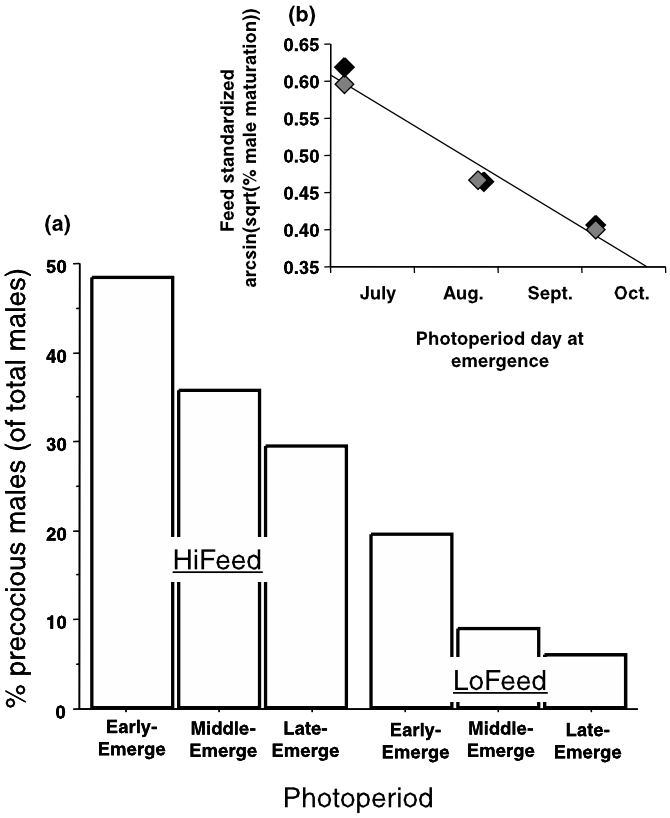
Fig. 7. Percent survival of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge (squares), MiddleEmerge (triangles), and LateEmerge (circles)) and two feeding levels (HiFeed (solid lines) and LoFeed (broken lines)) levels subjected to a 72-h 35 ppt seawater challenge plotted versus photoperiod date. Broken-lined arrows indicate the period over which different treatment groups first achieved 50% survival.



found no maturing males in the long-day group but 7.8% of the short-day males were mature at age 1. Subsequently, at age 2, 83% of the short-day males were found to be mature, while only 40% of the long-day males matured. Berrill et al. (2003, 2006) have developed additional evidence for the effect of photoperiod on early male maturation in Atlantic salmon. Fish were placed into several different compressed photoperiod schedules with first-emergent fry first placed into a constant 24-h light environment for 6 or 8 weeks (simulated summer) followed by 8 or 12 weeks of short-day photoperiod (simulated winter) and then returned to constant 24-h light (simulated summer) in an attempt to provide fish the proper seasonal sequence of photoperiod changes to promote smolting (normally in the second spring of life) at an early age. Male maturation at age 1 ranged from 4.3% to 20.9% varying by photoperiod treatment, again demonstrating a physiological interaction between photoperiod and development. Once again, placing these data on the photoperiod effect on early male maturation into an ecological context suggests that fry that emerge early (short-day photoperiod) in a growing season are more likely to mature at age 1 than fry that emerge later. This strongly suggests that individual developmental decisions are made with reference to season as delineated by photoperiod.

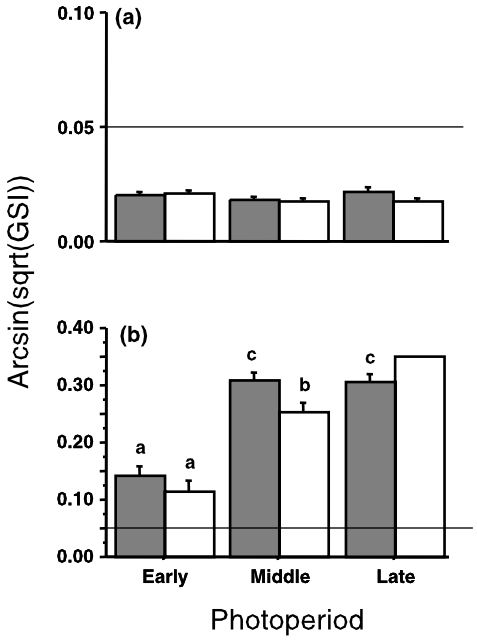
Relations among emergence timing and life history variation have also been examined using a correlational approach. Several investigators have found positive relations among emergence timing, metabolic rates, behavioral dominance, growth rate, and tendency to either smolt or mature at a relatively early age (Metcalfe and Thorpe 1992; Metcalfe et al. 1995; Cutts et al. 1999). However, these experiments do not strictly test for an effect of photoperiod at emergence; rather, they really demonstrate an overall correlation between developmental rate and metabolic rate, as photoperiod was not directly manipulated. Instead, the traits of naturally early-emerging fish were compared with fish naturally emerging later. Moreover, the differences in emergence timing in these experiments ranged from a few days to several weeks, and thus, the differences in photoperiod experienced by fry emerging at different times did not approach the 4-month difference in photoperiod experienced by fish in the present experiment.

Fig. 8. (*a*) Percentage of male Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge, MiddleEmerge, and LateEmerge) and either HiFeed or LoFeed conditions determined to be maturing at age 1 based on visual assessment of testis size. (*b*) Scatterplot of standardized (to the mean maturation rate) arcsine square root transformed percent maturation data plotted against day of the year for photoperiod at emergence ($F = 107.8$, $p < 0.001$, $r^2 = 0.96$, $n = 6$). Shaded diamonds represent HiFeed and open diamonds represent LoFeed treatments.



The experiment detailed herein differed from these other approaches. All fish were exposed to the same seasonal photoperiod; fish just entered the seasonal photoperiod cycle (emergence) at different points. Thus, fish from different photoperiod treatments received seasonal photoperiod signals at different ages (i.e., autumnal equinox occurred at 86 days postemergence for EarlyEmerge fish, 37 days postemergence for MiddleEmerge fish, and 5 days preemergence for LateEmerge fish) but they received exactly the same photoperiod signal. Thus, we were not testing for an effect of photoperiod, but rather, we were testing for the effect of emergence at seasonally different dates as defined

Fig. 9. Average arcsine square root transformed GSI of (*a*) immature male and (*b*) maturing male Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge, MiddleEmerge, and LateEmerge) and either HiFeed (shaded bars) or LoFeed (open bars) conditions and sampled at termination of the experiment. Bars with similar superscripted letters are not significantly different. The horizontal line indicates the 0.05 level for both panels.



by photoperiod. We directly compared fish of the same age and size and inferred a photoperiod effect by differences between treatments. However, our primary objective was to infer how a range of seasonal emergence timings, coupled to different growth rates, would alter life history patterns in these fish as they progressed through seasonal periods with differing conditions.

HiFeed fish were the same age and size throughout the experiment (days postponding), but some EarlyEmerge fish smolted in the autumn and a greater percentage of EarlyEmerge males matured as compared with LateEmerge fish, suggesting that photoperiod at emergence did alter life history pattern. It is an important point to note the GSI differences in maturing males from EarlyEmerge and LateEmerge treatments at the termination of the experiment. While maturing, the EarlyEmerge fish were not yet mature (as indicated by the lower GSI and the lack of spermiating fish) and the seasonal photoperiod cue had not yet advanced to the point that stimulates Sacramento River winter-run chinook salmon to spawn, while photoperiod had passed this point for the LateEmerge fish (as indicated by the higher GSI and the presence of spermiating fish). Again, because these fish were the same age, seasonally changing photoperiod was synchronizing maturation. In addition, fish from the MiddleEmerge and LateEmerge treatments were mature (spermiating) at the "correct" seasonal time, in synchrony with naturally breeding winter-run chinook salmon (Myers et al. 1998; Yoshiyama et al. 1998). This suggests that fish in this experiment were "correctly" interpreting the photoperiod signals given to them.

McNamara and Houston (1996) developed the concept that life history variation may be "state dependent". This formalized the observation that an animal's reproductive decisions (to reproduce (yes or no), fecundity (how many), and offspring size (big or little)) were dependent on the actual physiological status of the animal (size or energy reserves), not just on an animal's age. Among salmonids, this concept has been explored most thoroughly in Atlantic salmon. A series of studies has demonstrated that the "decisions" on early maturation (yes or no) and smolting (yes or no) are dependent on growth rate and (or) adiposity, with bigger, faster growing, fatter fish initiating development and smaller, slower growing, leaner fish delaying development (Thorpe 1986, 1989; Metcalfe 1998). Based on these studies, theoretical models predicting life history trajectory for Atlantic salmon have been developed (Metcalfe 1998; Thorpe et al. 1998). These models explicitly recognize that development is dependent on an individual salmon's condition.

A number of experiments in salmon have suggested that there is a period of initiation and commitment to male maturation that occurs in the autumn–winter, up to a year prior to spawning (Thorpe 1994; Silverstein et al. 1998; Campbell et al. 2003). This work underlies models of Atlantic salmon life history variability (Metcalfe 1998; Thorpe et al. 1998), which recognize that developmental decisions are made within photoperiod-circumscribed seasonal periods. Thus, development is dependent on condition surpassing a threshold during a certain seasonal period. Recent work by Aubin-Horth and Dodson (2004) and Baum et al. (2004) supports the theoretical construct of this model by demonstrating variable size- and growth-dependent thresholds for maturation. Together, this work on Atlantic salmon provided the basis for our experimental design. There was good reason to believe that juvenile life history of winter-run chinook salmon was variable, but because of the unique run and spawn timing of these fish, it was hard to predict when seasonal periods for commitment to developmental decisions might occur. Thus, we needed to produce cohorts of juvenile fish of different condition progressing through different, photoperiod-defined seasonal periods.

Ecologically, the best way to view these data is size (growth) plotted against season in association with photoperiod (photoperiod date) (Fig. 10). Based on this, one can infer the interactions between photoperiod, size, and age. Two important points are illustrated by this approach. (*i*) LateEmergeHiFeed fish emerged after EarlyEmergeHiFeed fish had already developed elevated gill Na^+,K^+-ATPase activities, suggesting that LateEmergeHiFeed fish had missed the seasonal period for autumnal smolting by emerging near the autumn equinox. It is not clear whether these recently emerged fry were not old enough or not large enough to respond to the photoperiod at emergence, whether they were not growing fast enough to trigger development, or whether the fish emerged late enough in the season that the photoperiod cuing autumn smolting had already passed. Regardless of whether the fish did not receive the "correct" cue or whether the fish were not developed enough to perceive the cue, LateEmerge fish did not smolt in the autumn. (*ii*) LateEmergeHiFeed fish were smaller than EarlyEmergeLoFeed in late December and January (photoperiod date). Enlarged testes were first observed during this same winter

Fig. 10. Mean length of juvenile Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*) reared under three differing photoperiods (EarlyEmerge (squares), MiddleEmerge (triangles), and LateEmerge (circles)) and two feeding levels (HiFeed (solid lines) and LoFeed (broken lines)) plotted versus photoperiod date. Dates when enlarged testis and spermiation first observed are indicated by arrows. Dates over which Sacramento River winter-run chinook salmon naturally spawn are indicated by a shaded bar on the *x*-axis. The broken line and shaded area indicate the timing of autumn gill Na^+,K^+-ATPase activity increase in the EalyEmergeHiFeed treatment.

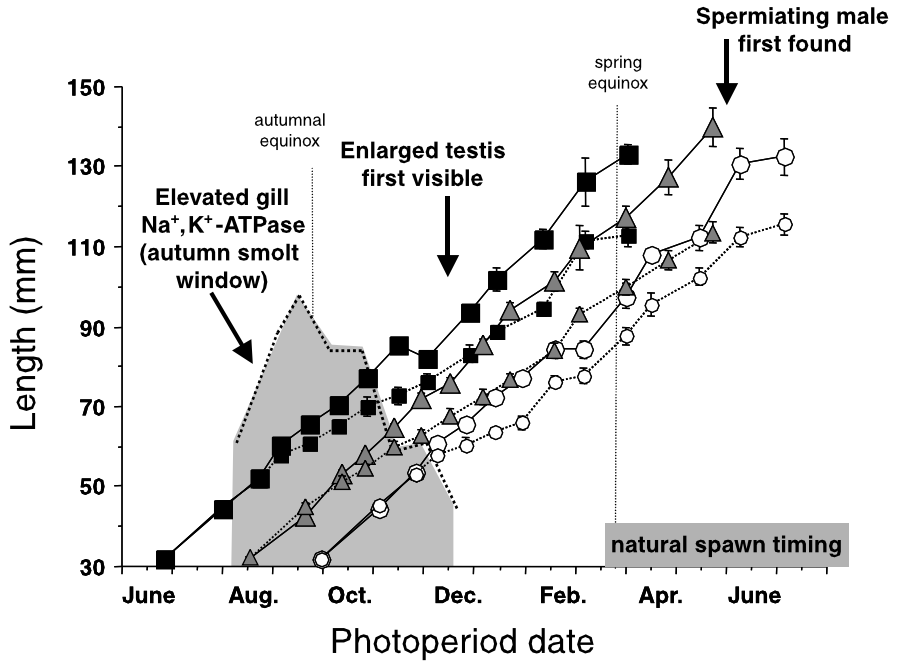
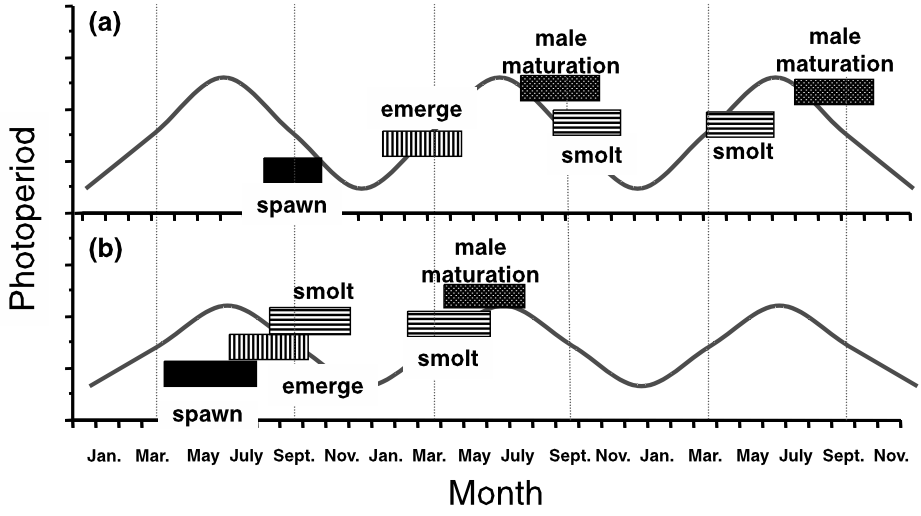


Fig. 11. Seasonal timing of selected life history events (spawning, emergence, smolting, and early male maturation) comparing (*a*) Columbia River spring-run and (*b*) Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*). The solid line depicts seasonal photoperiod change on an arbitrary scale. Vertical broken lines indicate spring and autumn equinoxes.



solstice period. Clearly, fish must have initiated maturation sometime prior to this point to allow testis development to visibly occur in December. Given that the size of EarlyEmergeLoFeed fish was greater than that of LateEmergeHiFeed fish through December, size was unlikely to be the factor determining male maturation, given that the rate of maturation was greater in LateEmergeHiFeed fish than in EarlyEmergeLoFeed fish. Instead, we suspect that differences in growth rate within seasonal period may have triggered the maturational decision (Rowe and Thorpe 1990; Larsen et al. 2006; Morita and Fukuwaka 2006).

The data presented herein suggest that emergence timing may play a role in life history variability of chinook salmon. Emergence timing is dependent on adult spawn timing, incubation temperature, maternal effects (egg size), genetic effects (individual differences in development rate), and interactions among all of these (Beacham and Murray 1990; Robison et al. 1999; Berg et al. 2001). Variation in emergence timing has been a little-explored axis promoting life history variation in salmon, as there is a general dogma that there is very strong stabilizing selection for emergence timing in a local area (Brannon 1987; Brannas 1995; Letcher et

al. 2004) owing to interactions between seasonal flooding and predation (selection against early emergence; Jensen and Johnsen 1999) and territorial dominance and rapid growth by first-colonizing fry (selection against late emergence; Einum and Fleming 2000). Whether this dogma is operational on a basin scale (such as the Sacramento River) is unknown. Certainly, there may be enough environmental variability in this region to result in variations in emergence timing. Moreover, it is uncertain if a dogma generated for territorial juvenile salmonids applies to winter-run chinook salmon, as they presently spawn in mainstem habitats and may rear in the mainstem or even delta habitats that may not be conducive to establishing and maintaining individual feeding territories. Thus, it is possible that significant differences in emergence timing may occur in the Sacramento River Basin (or other large river systems) that may result in ecologically relevant life history variation among chinook salmon.

Comparative juvenile chinook salmon life history

The life history of Sacramento River winter-run chinook salmon is apparently unique among chinook salmon populations (Healey 1994). However, this uniqueness is most readily apparent through the seasonal timing of life history events (adult migration and spawn timing); individual variation in life history pattern within the population and the photoperiodic regulation of these patterns appear to have been maintained. Among chinook salmon populations, smolting and early maturation of spring-run fish from the Fraser and Columbia rivers have been relatively well studied (Healey 1991; Myers et al. 1998). Three differences stand out between Fraser and Columbia River spring-run and Sacramento River winter-run chinook salmon juvenile life histories (Fig. 11). First, the juvenile period is temporally compressed in winter-run fish. Only weeks separate spawning and emergence instead of a 3- to 6-month period found in spring-run fish. In addition, the period between emergence and smolting is also compressed, with at most 1 year separating the two events in winter-run fish. A minimum of 12 months separates these events in naturally rearing Columbia River spring-run fish and 18–20 months is standard. One might speculate that this is simply the consequence of water temperature. Winter-run fish emerge relatively quickly after spawning, as water temperature is relatively warm; in contrast, spring-run eggs and alevins experience a rapidly decreasing water temperature as eggs are deposited in the fall as winter approaches. Nevertheless, fish from each population appear to be sensitive to and respond to photoperiodic signals that occur at emergence, even though these signals may be different (see below). Thus, salmon are capable of maintaining a photoperiodic cuing for developmental events, even though the temporal duration of life history expression is compressed.

Second, the temporal order in which developmental decisions are manifested is switched. Winter-run fish may smolt either in the autumn or in the succeeding spring before any male maturation is apparent. In contrast, spring-run males have an opportunity to mature in the late summer or fall prior to or simultaneous with the first autumnal smolting period. Note that just because smolting was apparent before early male maturation in Sacramento River winter-run chinook salmon, this does not necessarily imply either that (*i*) the smolting "decision" was made prior to the early maturation "decision" or that (*ii*) there are two distinct "decisions" (smolt (yes or no) or mature (yes or no) during two distinctly different occasions) or (*iii*) there is one decision with three "choices" (mature, smolt, wait). We did not directly determine whether there were large, fast-growing males in the fall, which we would predict might have smolted, that instead had "made the decision" to mature the following spring–summer and thus did not smolt. These observations on the timing of smolting and early male maturation imply some plasticity in the interactions between age, photoperiod, and developmental decisions in the evolutionary history of chinook salmon.

Third, smolting and maturation decisions in both populations appeared to occur during equinoxes; however, the direction of photoperiod change stimulating development appears to be reversed between the populations, early male maturation occurring at the spring equinox (increasing photoperiod) for winter-run fish and at the autumnal equinox (decreasing photoperiod) for spring-run fish. Fish from either population appear to be capable of smolting in either the autumn or the spring, synchronized by either increasing or decreasing photoperiods.

Together, these differences suggest that chinook salmon have a great deal of flexibility (at least in an evolutionary sense) with regard to the photoperiodic signals that key development and the order in which developmental events occur. Given the great variability in chinook salmon life history, this last statement might seem simplistic; however, the statement does point out the comparative opportunities available to investigate the mechanism(s) that allow this plasticity to occur.

Acknowledgements

This research was conducted in collaboration with the US Fish and Wildlife Service and the California Department of Fish and Game under permits from the National Marine Fisheries Service and the California Department of Fish and Game and was supported by funds from the US Bureau of Reclamation and the California Department of Water Resources (contract 4600001540). We thank Anne McBride and Holly Mendonca for assistance with fish spawning and shipment of eggs and Correigh Greene, Joe Cech, Scott Foott, Steve Lindley, and two anonymous reviewers for providing constructive critical comments that improved the manuscript. Finally, we thank Penny Swanson for making the introductions that initiated this work. Reference to trade names does not imply endorsement by the National Marine Fisheries Service or the National Oceanic and Atmospheric Administration.

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