

# Exceptions to semelparity: postmaturation survival, morphology, and energetics of male chinook salmon (*Oncorhynchus tshawytscha*)

M.J. Unwin, M.T. Kinnison, and T.P. Quinn

**Abstract:** Between 2.1 and 6.8% of fall-run male chinook salmon (*Oncorhynchus tshawytscha*) reared in two New Zealand hatcheries matured as yearling parr, of similar size to immature siblings. The incidence of mature parr in 58 half-sib families ranged from 0 to 69% of the available males. Although chinook salmon are normally semelparous, about 80% of mature parr survived to mature again at age 2, and all fish held for another year matured again at age 3. All three ages produced milt that successfully fertilized eggs. Morphological development in mature parr and repeat-maturing males was consistent with that of older, first time maturing males. The gonadosomatic index for mature age-2 males was 11.7, 7.2, and 5.4% for repeat-maturing males, freshwater-reared males, and sea-run males, respectively. Muscle energy density for repeat-maturing males (4.45 kJ/g) was lower than for normal males (5.20–5.45 kJ/g) and negatively correlated with the gonadosomatic index. Although we think it unlikely that repeat maturation occurs regularly in the wild, our results indicate that under favorable conditions, chinook salmon can exhibit some iteroparous traits. We hypothesize an evolutionary continuum between semelparity and iteroparity in salmonids, primarily characterized by modifications in a few key energetic and physiological thresholds.

**Résumé :** De 2,1 à 6,8% de la remonte d'automne de quinnats (*Oncorhynchus tshawytscha*) mâles élevés dans deux écloséries de la Nouvelle-Zélande ont atteint la maturité sexuelle alors qu'ils étaient des tacons d'un an de taille similaire à leurs congénères immatures issus des mêmes géniteurs. La proportion de tacons matures dans 58 familles à demi-apparentées était de 0 à 69% des mâles existants. Bien que le quinnat soit normalement sémelpare, environ 80% des tacons matures ont survécu pour atteindre une seconde maturité sexuelle à l'âge de 2 ans, et tous les poissons gardés pour une autre année ont atteint une nouvelle maturité à l'âge de 3 ans. Les poissons de ces trois âges ont produit une laitance qui a pu féconder des oeufs avec succès. Le développement morphologique des tacons matures et des mâles qui ont atteint plusieurs maturités sexuelles était semblable à celui des mâles plus vieux qui ont atteint leur première maturité à un âge plus avancé. Les indices gonadosomatiques des mâles matures de 2 ans étaient de 11,7, 7,2 et 5,4% chez les mâles à maturation multiple, les mâles élevés en eau douce et les mâles anadromes, respectivement. La densité énergétique des muscles chez les mâles à maturation multiple (4,45 kJ/g) était inférieure à celle observée chez les mâles normaux (5,20–5,45 kJ/g) et corrélée négativement avec l'indice gonadosomatique. Bien que nous jugions improbable que la maturation multiple se produise régulièrement dans la nature, nos résultats indiquent que, dans des conditions favorables, le quinnat peut montrer certains caractères d'itéroparité. Nous formulons une hypothèse suivant laquelle il y aurait un continuum évolutionnaire entre la sémelparité et l'itéroparité chez les salmonidés, principalement caractérisé par des modifications de quelques seuils énergétiques et physiologiques importants.

[Traduit par la Rédaction]

## Introduction

Salmonid fishes display a variety of interrelated life history traits (Scott and Crossman 1973; Groot and Margolis 1991). Key traits include variation in age at first maturation,

the proportion of each population that survives to spawn more than once (iteroparity), frequency of spawning events for given individuals, and migration between freshwater spawning and incubation sites to marine feeding areas (anadromy). Anadromy is generally associated with high growth rate, early age at maturation, and lower probability of repeat spawning. These life history traits vary within the family, ranging from fully freshwater, iteroparous, long-lived species such as lake trout (*Salvelinus namaycush*) to invariably semelparous, short-lived, anadromous species such as pink salmon (*Oncorhynchus gorbuscha*). There is also great variation among populations within species and between males and females in life history patterns and the degree of anadromy (e.g., Groot and Margolis 1991; Jonsson and Jonsson 1993). Such variation presumably reflects evolutionary adaptations to the fact that marine waters occupied by salmonids provide greater opportunities for growth than

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M.J. Unwin, National Institute of Water and Atmospheric Research, Box 8602, Christchurch, New Zealand.

M.T. Kinnison<sup>1</sup> and T.P. Quinn, School of Fisheries, Box 357 980, University of Washington, Seattle, WA 98195, U.S.A.

<sup>1</sup>Author to whom all correspondence should be addressed:  
Department of Biological Sciences, Dartmouth College,  
Gilman Hall, Hanover, NH 03755, U.S.A. e-mail:  
mike.kinnison@Dartmouth.EDU

freshwater habitats, but exploitation of these rich feeding areas exposes them to a higher mortality rate and a sometimes arduous return migration to the spawning site.

Chinook salmon (*Oncorhynchus tshawytscha*) are generally considered to be entirely semelparous and anadromous within their natural range but vary widely in timing of migrations and age at maturity, both between and within populations. Age at maturation is most commonly between 3 and 5 but ranges from 2 to 8 (Healey 1991; Roni and Quinn 1995). The species is often divided into ocean-type populations, in which juveniles spend a few months in freshwater prior to seaward migration, and stream-type populations, in which juveniles migrate after a full year or more in the river (e.g., Healey 1983). Modal age at maturity tends to be younger for ocean-type populations, and in many populations, some males (termed "jacks") mature at a younger age than the youngest females in the population (Healey 1991; Roni and Quinn 1995). Age at maturation in chinook salmon is partially subject to genetic control (Hankin et al. 1993; Heath et al. 1994a), but as in most salmonids (see Thorpe 1986) is also strongly influenced by growth rate. For example, age at maturity tends to be younger for hatchery-produced chinook salmon than for related wild fish (e.g., Unwin and Glova 1997).

In a number of chinook salmon populations, a small proportion of male parr mature at the end of their first year of life, while still resident in freshwater, in a phenomenon often termed "precocious" maturation. Unlike jacks, which have gone to sea and returned at a younger age than females of their population, mature parr have remained in freshwater throughout their first year of life. However, because the term "precocious" could apply to jacks as well as to mature parr, and also because it implies some abnormality (cf. Thorpe 1986), we avoid it in this paper. To remove any possible ambiguity, we use the term "mature male parr" to refer specifically to stream- or hatchery-resident male chinook salmon maturing towards the end of their first year of life, with both a total age (measured from the date of fertilization) and a freshwater age of about 12 months. (An exception to this definition would be stream-type populations in which some individuals rear in streams for 2 years prior to seaward migration (e.g., Beacham et al. 1989); such mature parr might be 2 years old.)

Parr maturation has been reported in populations of both natural and hatchery origin in many river systems (e.g., Robertson 1957; Flain 1970; Taylor 1989; Bernier et al. 1993). These fish produce viable sperm (e.g., Robertson 1957) and can survive into their second year and reinitiate gonad development under hatchery conditions (Flain 1971) or after transfer to seawater (Bernier et al. 1993). Understanding the processes that underlie parr maturation and repeat maturation may provide important insights into the evolution of salmonid life histories, particularly with regard to semelparity and iteroparity. However, some important questions remain unanswered. Is parr maturation necessarily associated with stream-type populations (e.g., Taylor 1989; Healey 1991) or can it occur more generally? To what extent do the physical changes associated with parr and repeat maturation mirror the normal maturation process in older fish? Is repeat maturation limited to fish transferred to seawater after first maturing as parr (cf. Bernier et al. 1993) or can it occur en-

tirely in freshwater? If so, how many times can individual males mature? How do energetic and physiological influences affect early and repeat maturation? Taking these issues into account, is repeat maturation of chinook salmon likely under natural conditions, and what does the process reflect about the evolutionary association between semelparity and iteroparity?

The objectives of this study were to document the incidence of mature male parr among hatchery-reared chinook salmon in New Zealand and test the hypotheses that (i) ocean-type parents as well as stream-type parents can produce mature male parr, (ii) mature parr are larger than immature fish at the time of maturation, (iii) mature parr are unevenly distributed among families, (iv) the offspring of mature parr show a higher incidence of mature parr than offspring sired by older males, and (v) mature parr necessarily die at the end of the spawning season. The last hypothesis was falsified and many such mature parr survived the first spawning season, allowing us to test the additional hypotheses that growth, gonad size, energy density, and morphology of repeat-maturing individuals are similar to those traits in mature male parr and males maturing for the first time at age 2 or greater.

## Methods

### Study populations

New Zealand's chinook salmon populations are derived from fall-run (ocean-type) Sacramento River stock (McDowall 1994; Quinn et al. 1996) and are primarily confined to the large, glacier-fed rivers on the east coast of the South Island where spawning typically occurs from mid-April to early June (Quinn and Unwin 1993). Fish in this study were mostly derived from Glenariffe Stream (43°18'S, 171°22'E), a spring-fed headwater tributary of the upper Rakaia River, in which chinook salmon have been studied since 1965 (Unwin 1986, 1997). Prior to 1979, this population was maintained by natural spawning, with some hatchery supplementation during the 1980's after hatchery facilities were developed in the late 1970's (Unwin and Glova 1997). During the latter period, maturing male parr were frequently encountered during routine husbandry operations or coded-wire tag (CWT) application. Mature parr were distinguishable from immature fish by their darker, less silvery body color compared with immature parr, a greenish pigmentation in the fins, and a less-streamlined body (cf. Taylor 1989). The mature parr tended to expel milt freely when handled, and their musculature was noticeably less firm to the touch than that of immature parr.

There were two large-scale experimental programs on chinook salmon, conducted from 1982 to 1984 and from 1994 to 1998. They allowed us to collect data on mature male parr to test our hypotheses but were not designed expressly for that purpose. Consequently, some characteristics of our data were constrained by the design and (or) logistic requirements of the main programs. When presenting our data, these constraints are noted only when they are relevant to interpretation of our results.

Between April 1982 and November 1984, 923 000 fry from the 1982 and 1983 brood years were raised at Glenariffe Stream as part of a study of the effects of date and size at release on survival of chinook salmon smolts. All fry were reared in concrete hatchery raceways at ambient stream temperature (7–14°C) and were fed a standard OMP diet. The date and size protocol was to divide the fish into 102 groups (over 2 years), representing predetermined size ranges (range of mean weights 10–150 g), and release them at selected monthly intervals to include a range of sizes on each

release date. Each group was marked with CWT's and released from March to November, corresponding to ages of 10–18 months postfertilization (Unwin 1997). About 100 fry from each CWT group were sacrificed 1 day before release for measurement of fork length (FL) and weight and recovery of CWT's. All fish were sexed by dissection and examination of the gonads, and any maturing parr were identified.

In addition, an intensive experimental program was initiated at Glenariffe Stream in 1994 to determine whether New Zealand chinook salmon have developed into genetically distinct populations over the 90 years since their introduction (Kinnison et al. 1998a). We collected gametes from 108 mature adults in two study streams, Glenariffe Stream and the Hakataramea River (44°43'S, 170°30'E), a tributary of the Waitaki River 150 km southwest of the Rakaia River. The gametes were taken to the Silverstream Research Station (44°43'S, 170°30'E) on the lower Waimakariri River and used to establish a total of 72 full-sib families nested within 36 half-sib families by crossing each male with two females. These were subsequently culled to 58 full-sib families within 29 half-sib families, evenly divided between the two populations. Unless otherwise specified, the term "family" refers to one full-sib family. We determined the age and life history type (i.e., ocean, stream, or hatchery) for all adults by scale pattern analysis (Unwin and Lucas 1993). When culling families, we tried to retain those for which both parents were of natural (ocean or stream) rather than hatchery origin. Families were individually incubated, hatched, and reared in ambient (12.4°C) well water (Kinnison et al. 1998a). At about 6 months postfertilization, each family was randomly assigned to one of 29 3000-L circular tanks, with two families (one marked by excision of the adipose fin) sharing each tank.

### Incidence, size, and growth of mature male parr

For each family, we estimated mean fry weight on 12 occasions between 10 August 1994 and 18 April 1995 (Kinnison et al. 1998b). We examined about 300 fish from each family for the presence of mature male parr between 24 April and 4 May 1995 (about 12 months postfertilization) as a prelude to tagging and further experimental protocols. We calculated the incidence of mature male parr on the assumption that 50% of the fish examined were males. We used a nested ANOVA on arcsine square root transformed proportions, with sires nested within populations, to determine if there were significant population and sire effects that would suggest heritable influences on incidence.

### Fertilization trials and postmaturation survival

We used the combined pool of mature parr from all experimental families to initiate several further experiments. First, we tested the viability of milt from six mature parr by fertilizing six samples of 100–200 ova (collected from two mature females) and incubating these at Silverstream under standard hatchery conditions. We estimated fertilization rates for each male by counting the number of live and dead ova after shocking (by brief physical agitation) 29 days after fertilization. All surviving ova were hatched and reared for a further 12 months, initially at Silverstream (to a weight of about 5 g) and then at Glenariffe. In April 1996, these fish were individually examined to determine the incidence of mature male parr.

We retained about 150 of the mature parr collected in April and May 1995 in a 6-m-diameter circular holding pond at Glenariffe, where they were reared (under standard hatchery procedures) to determine whether they could survive for a second year. At age 2 (26 April 1996), 118 surviving fish were collected. All of these had matured a second time, and milt from six mature individuals was used in another fertilization trial at Silverstream, using the same protocol as in 1995. Most of the remaining fish were sacrificed for collection of ancillary data (see next paragraph), but 10 fish were reared for another year. All survived and matured for a third time

(at age 3) in April 1997, at which time, we used milt from six individuals to conduct a third fertilization trial.

### Reproductive output and energy density

Representative individuals from all experimental groups (i.e., the mature parr collected in April 1995, their survivors in 1996 and 1997, and the age-1 progeny of the 1995 fertilization trial) were sacrificed for measurement of FL, weight, and gonad weight. We measured gonad weight by removing the testes from the body cavity and weighing the total mass, taking care to include any expressed milt. We calculated the gonadosomatic index (GSI) for each fish, where GSI is the wet gonad weight as a percentage of the total body weight (including gonads), to compare gonad development and relative gonad size between groups, excluding any individuals visually assessed as underripe (i.e., with testes not fully developed) or overripe (i.e., with testes partially or wholly spent).

To provide additional comparisons with "normal" fish (i.e., those maturing no earlier than the end of their second year), we drew on two parallel experimental groups established in April 1995 from siblings of the Glenariffe and Hakataramea families. One group consisted of 2900 fish (50 from each of 58 families), individually marked with passive integrated transponder (PIT) tags and subsequently reared in captivity at Glenariffe. A second group (totaling 141 000 fish marked with CWT's) was released from Glenariffe Stream in July 1995, thereby gaining access to the South Pacific Ocean via the Rakaia River and returning as sea-run fish from 1996. Mature 2-year-old fish from both groups were examined at Glenariffe in April and May 1996, allowing for measurement of size and GSI using the same protocols as above. We used a somatic condition factor ( $CF_{\text{som}} = 10^5 \times W_{\text{som}}/FL^3$ , where  $W_{\text{som}}$  = total body weight – testes weight) to provide a measure of body robustness independent of gonad development. For most groups of fish, we also dissected about 10 g of tissue from the dorsolateral muscle, anterior to the dorsal fin. After oven drying this tissue at 95°C for 24 h, we calculated the ratio of dry weight to total weight (each measured to  $\pm 0.0001$  g) and used the general nonlinear model for energy density (ED, joules per gram) given by Hartman and Brandt (1995) ( $ED = 45.29 \times (\% \text{ dry weight})^{1.507}$ ) to estimate specific ED for each individual. To obtain ED estimates for yearling parr (which was not measured in autumn 1995), we collected additional tissue samples from two yearling groups held at Glenariffe in April 1996 and May 1998.

### Body morphology and salinity tolerance

We analyzed morphology based on a series of landmark points (Table 1) to characterize morphological differences between immature parr, mature parr, mature 2-year-old males, and 2-year-old repeat-maturing males. Parr were placed on a sheet of paper and a pin was used to mark each landmark point for subsequent data capture via a digitizing pad. To characterize morphological development in normal males, we collected similar data for 109 PIT-tagged fish sampled in November 1995 (at an age of 18 months) from the captive freshwater group at Glenariffe and later (as mature 2-year-old males) in April 1996. The morphology of these fish at maturation was also compared with that of 78 repeat-maturing males collected at the same time and age. For these (and all subsequent fish), morphometric data were obtained by placing each fish on its left side (alongside a 40-cm ruler), taking a photograph from a camera mounted directly overhead, and digitizing all points of interest from the resulting print.

In most cases, we compared landmark arrangements via relative warps analysis (Rohlf 1993). To allow for the substantial size difference between repeat- and first time maturing age-2 males, and possible allometric effects in this comparison, we calculated four univariate measures likely to differ between groups (snout length: point 1 to point 17; hump size: point 14 to point 19; belly depth: point 4 to point 20; anal region depth: point 12 to point 5) from the

**Table 1.** Landmark points used for morphometric and relative warps analysis.

Point	Description
1	Tip of snout
2	Outline point directly ventral to posterior end of maxilla
3	Outline point directly ventral to pectoral fin insertion
4	Outline point directly ventral to pelvic fin insertion
5	Anterior insertion of anal fin
6	Posterior insertion of anal fin
7	Ventral insertion of caudal fin
8	Central point of hypural flexure
9	Caudal fork
10	Dorsal insertion of caudal fin
11	Posterior insertion of adipose fin
12	Anterior insertion of adipose fin
13	Posterior insertion of dorsal fin
14	Anterior insertion of dorsal fin
15	Outline point directly dorsal to point 16
16	Dorsal insertion of gill plate
17	Center of eye socket
18	Insertion of pectoral fin
19	Vertical projection of point 14 onto lateral line
20	Vertical projection of point 4 onto lateral line

landmark points. The groups were then compared relative to body length using ANCOVA of logged trait values versus logged mid-eye to hypural length.

We assessed the salinity tolerance of maturing male parr by including 10 individuals in a hypersalinity trial conducted on the main group of 58 families in May 1995. The challenge was implemented by placing the fish to be tested into water at a salinity of 45 ppt and recording time to death, FL, and weight for each fish. Full details of the experimental protocol and results of family- and population-level comparisons are given in Kinnison et al. (1998b).

## Results

### Incidence of mature male parr

Of 4624 male parr examined between 5 March and 1 November in 1983 and 1984, 96 (2.1%) were sexually mature. Mature parr were recorded in all months except November (when only 18 males were examined) but were most common in March (nine out of 288 fish; 3.1%) and April (38 out of 883 fish; 4.3%). They were less prevalent from June to October but still comprised 1.2% (30 fish) of 2590 parr examined over this period. Mature male parr were relatively more common in the 1995 families, comprising 572 of 16 853 parr examined (3.39% of the total, or 6.79% of the males).

The incidence of mature male parr within families varied greatly. Of the 58 families examined (all but four of which had between 293 and 304 individuals), 12 had no mature parr and another 16 families had fewer than five. By contrast, 15 families produced more than 15 mature males, including one family (of Glenariffe origin) that yielded 97 mature parr from the original 300 fish (69% of the estimated males). The family sharing the same tank yielded only two such fish out of 297 examined, indicating that the unusually high proportion of mature parr in the other family was not an artifact of the rearing regime in that particular tank. Despite family variation in the incidence of mature parr, nested

ANOVA on transformed proportions did not indicate significant sire ( $p = 0.23$ ) or population ( $p = 0.12$ ) effects. Moderate deviations from a 50:50 sex ratio within each family would have relatively little effect on the estimated incidence of mature male parr and could not account for the observed level of variation. Even if the imbalance were as much as 2:1, so that a sample of 300 individuals could include between 100 and 200 males (much greater than the estimated 95% confidence interval of  $\pm 17$  males for 300 fish per family), a count of five or fewer mature parr out of 300 fish would represent a lower incidence of maturation (0–5%) than a count of 15 or more (at least 7.5%).

Scale pattern analysis of the parents indicated that mature male parr were descended from parents with an ocean-type life history. In 40 families for which both parents were positively identified as ocean-type individuals (including the family with 97 mature males), the incidence of mature parr was 445 out of 11 475, or 7.8% of the assumed males. The only family derived from a stream-type parent (crossed with an ocean-type individual) produced seven mature parr out of 300 (2.3%; similar to the average for all families combined).

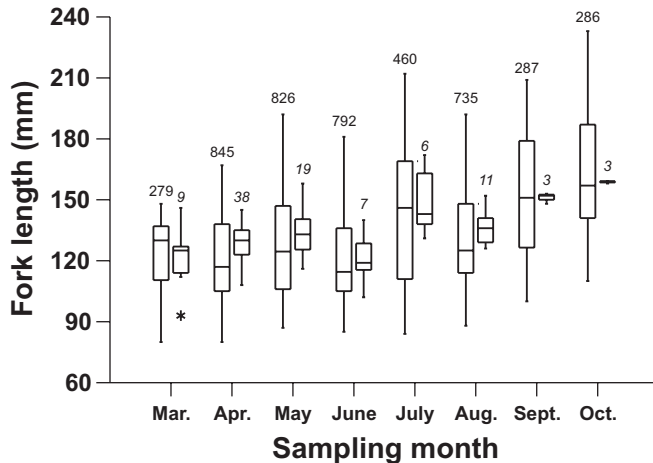
### Size and growth

Size differences between mature and immature parr were apparent in both 1983–1984 and 1995 but were inconsistent between seasons and were generally small compared with the size range within each cohort. Mature parr recorded in 1983–1984 were slightly longer than normal parr (nested ANOVA of log FL by month and maturity: all fish,  $p = 0.001$ ; males only,  $p = 0.006$ ). However, the size difference was small in absolute terms (mature males: FL = 132.5 mm; immature males: FL = 131.2 mm) and the significance of this result is primarily attributable to the large sample size ( $N = 4510$ ) for immature male parr. By contrast, mature male parr recorded in 1995 were smaller than immature parr of unknown sex (mature: 161.5 mm,  $N = 97$ ; immature: 167.7 mm,  $N = 278$ ;  $t$  test,  $p < 0.001$ ). Mature parr recorded in 1983–1984 lay within a much more restricted length range than immature male parr (Fig. 1). Only six (6%) of the 96 mature parr were smaller than 110 mm or larger than 160 mm FL whereas 41% of immature males fell outside this size range. However, no difference in variance was apparent in 1995.

Mature parr were heavier for their length than immature parr. ANCOVA of log  $W$  on maturity, with log FL as the covariate, showed no interaction between maturity and slope ( $p = 0.23$ ) but a difference in elevation of the regression line for mature and immature parr ( $p < 0.001$ ). This was equivalent to an average weight difference of 15.2% between mature and immature parr of the same length. Mean condition indices (unadjusted for gonad weight) were 1.33 for mature parr compared with 1.13 for immature parr.

The incidence of mature parr in each family was uncorrelated with mean weight within the family, as measured on 18 April 1995 ( $p = 0.92$ ) or at any of the 11 earlier weigh-ups ( $p > 0.05$  in all cases), with mean alevin weight ( $p > 0.16$  for all four weigh-ups), and with mean ova weight ( $p = 0.83$ ). We looked for evidence of a family-level correlation between the incidence of mature parr and growth rate by considering all possible pairs of dates for the 12 successive fry weigh-ups, estimating mean specific growth rate

**Fig. 1.** Box and whisker plots showing variation in FL between mature and immature parr by month for combined 1983 and 1984 data. Sample sizes (mature parr in italics) are shown above each box. Each plot shows the median, the upper and lower quartiles, the upper and lower inner fences, and any outlying points (asterisk). Variations in mean FL between months are an artifact of the 1982–1983 time and size at release protocol.



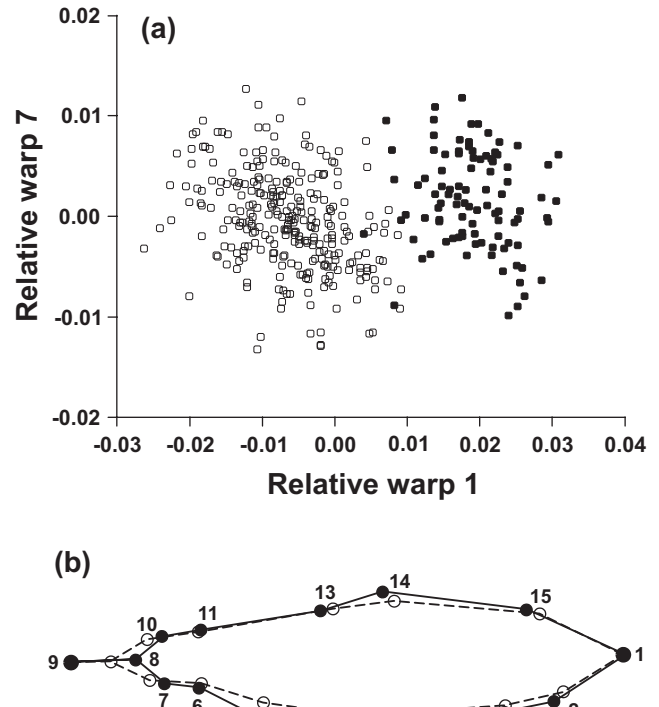
(percent weight gain per day) for each family over the 132 (12 × 11) date intervals, and calculating the Pearson correlation coefficient. Only three of these coefficients (ranging from  $-0.27$  to  $-0.30$ , all corresponding to intervals from September 1994 to March 1995) were significant at  $p < 0.05$ , and none were significant at  $p < 0.01$ . Because this result is more or less what would be expected by chance in a set of 132 randomly generated correlation coefficients, we conclude that our data show no evidence of a correlation between growth rate and maturation.

### Body morphology

Differences in body morphology between 278 immature and 97 mature male parr were clearly apparent via analysis of relative warps. The first relative warp (analogous to a principal component of geometric shape) described 32% of the morphometric variation in the two groups combined. This relative warp also best described the morphometric difference between mature parr and their immature relatives ( $p < 0.001$ ) (Fig. 2a). Physically, this warp describes increased development of the hump and snout in mature parr, together with a “deepening” of the anal region (Fig. 2b). By contrast, their immature relatives had a more streamlined body with a longer and shallower caudal peduncle more typical of fish undergoing smolt transformation. Relative warp 7 also differed slightly between the immature and mature parr, but it explained only 4.0% of variation in shape, did not have a clear biological interpretation, and contributed much less to group separation than warp 1 (Fig. 2a).

The pattern of development in mature male parr strongly resembled the morphological development that we observed, from 18 to 24 months of age, in repeated measures of 109 of their individually tagged male siblings that matured at age 2. The first relative warp captured 34% of the morphometric variation and best described the difference between fish before and after maturation ( $p < 0.001$ ) (Fig. 3). Development of the snout and hump and deepening of the anal region

**Fig. 2.** Relative warps analysis results for mature male parr (solid symbols) and immature fish of the same age (open symbols) in terms of (a) relative warp 1 versus relative warp 7 scores and (b) extremes of relative warp 1 (exaggerated for clarity) along the axis best describing shape differences between the groups. Landmark points are numbered as in Table 1 and are aligned relative to points 1 and 9.

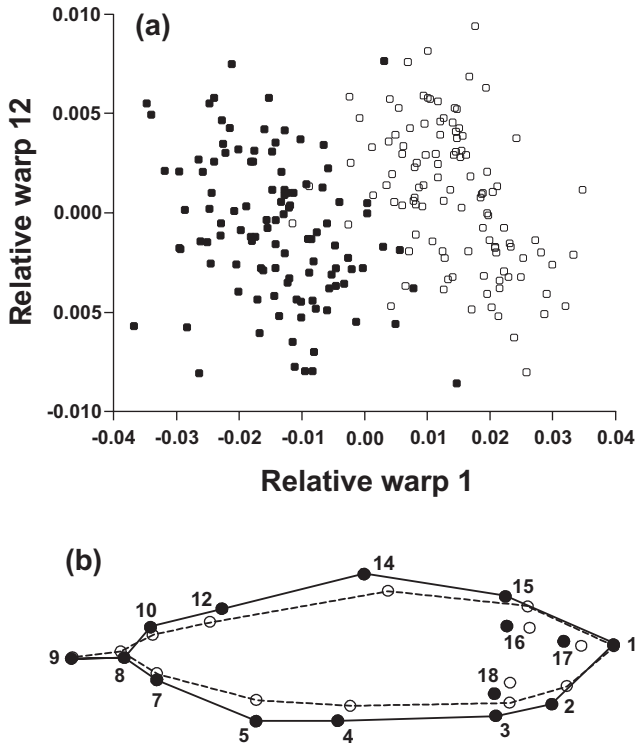


were again characteristic and were slightly more pronounced than in mature male parr. Warp 12 showed a relatively small amount of group separation compared with warp 1 (Fig. 3) but explained only 1.6% of the variation in shape and lacked a clear biological interpretation. Comparison of univariate size-adjusted traits indicated that repeat-maturing fish were 13.9% greater in belly depth and 6.6% greater in anal region depth ( $p < 0.001$  in both cases) than males reared in freshwater and maturing for the first time at age 2.

### Fertilization trials

All six mature yearling parr tested in April 1995 produced viable milt. Of 1030 ova shocked, 986 were fully viable and survived at least until hatching, 35 had weak or malformed embryos, and only nine showed no evidence of successful fertilization. Mean fertilization rate (for the fully viable ova) was 95.5%, ranging from 87 to 98% for the six individual males. Similar results were obtained for six freshwater-reared fish spawning a second time in April 1996 (mean 87.2%, range 71–94%) and for a final group of six of these fish maturing for the third successive year (at age 3) in April 1997 (mean 93.3%, range 92–95%). The fertilization rate exceeded 90% for 14 of the 18 individuals tested over the three seasons. This compares with rates of 75–85% for routine hatchery operations at Silverstream, based on delayed (4–6 h) fertilization (National Institute of Water and Atmospheric Research, unpublished data).

**Fig. 3.** Relative warps analysis results for 109 individually marked males that matured at age 2, at 18 months (6 months prior to maturation) (open symbols), and at 24 months (fully mature) (solid symbols) in terms of (a) relative warp 1 versus relative warp 12 scores and (b) extremes of relative warp 1 (exaggerated for clarity) along the axis best describing shape differences between the groups. Landmark points are numbered as in Table 1 and are aligned relative to points 1 and 9.



Of 728 progeny from the April 1995 fertilization trial (using mature parr as sires) examined in April 1996, 27 (3.7%) were mature male parr, representing 7.4% of the assumed male half of the population. This proportion did not differ from the 6.79% incidence of mature parr among their parent stock, as determined in April 1995 ( $\chi^2 = 0.22$ ,  $p = 0.64$ ).

#### Postmaturation survival, growth, and reproductive output

Survival of mature parr to the end of their second year was high (118 out of about 150 individuals, or about 80%), but growth during this period was extremely poor. By April 1996, their mean weight had increased from 57 g (in April 1995) to 333 g, but they were well under half the weight of their freshwater-reared male siblings maturing for the first time at age 2 and less than 30% as heavy as mature sea-run age-2 males (ANOVA with post hoc Bonferroni tests,  $p < 0.001$  for all paired comparisons) (Table 2). Examination of stomach contents from repeat-maturing males in April 1996 suggested that they were feeding actively at that time, with nearly all fish examined having undigested food in their gut. However, in most individuals the gut wall showed signs of partial degradation, appearing thinner and less muscular than in immature parr.

Reproductive output for mature male parr was high relative to body weight (Table 2). Mean GSI for parr maturing

in April 1995 (9.14%) was substantially greater than for either of their sibling groups maturing for the first time at age 2 (freshwater reared: 7.23%; sea-run: 5.39%; ANOVA with post hoc Bonferroni tests,  $p < 0.001$  for all paired comparisons). Mean GSI for age-2 repeat-maturing fish was higher still, averaging 11.67% and ranging from 4.7 to 16%. The 10 males maturing for a third successive year had a mean GSI of 7.9% (range 4.8–10.3%). We retained 10 mature parr (collected in April 1996 from a 1995 spawning) at Glenariffe until 26 November 1996, at which time, nine surviving fish were sacrificed to determine the state of their gonads midway through the second year of life. Their testes were greatly reduced in size compared with the previous autumn, with a mean GSI of 1.2% (range 0.8–1.7%). However, all individuals retained the general appearance of mature male parr (including enlarged fins and dark coloring) and still exuded a small quantity of milt (of unknown viability) when squeezed gently around the vent.

Specific ED for 2-year-old males varied among the three sibling groups maturing in 1996, being highest for freshwater-reared males, slightly lower for sea-run males, and lowest for the repeat-maturing males (ANOVA with post hoc Bonferroni tests,  $p < 0.001$  for all paired comparisons) (Table 2). Specific ED was negatively correlated with GSI for all three groups combined ( $r = -0.62$ ,  $p < 0.001$ ) (Fig. 4), although when each life history type was considered separately, only the repeat-maturing males exhibited the same trend ( $r = -0.59$ ,  $p < 0.001$ ). The loss in energy with increasing GSI for this latter group was substantial, predicted ED (based on linear regression of ED on GSI) declining from 4.33 kJ/g for a fish with a GSI of 10% to 3.47 kJ/g for a GSI of 15%. This trend was partially confounded by a negative correlation between  $CF_{\text{som}}$  and GSI ( $r = -0.55$ ,  $p < 0.001$ ) and a positive correlation between  $CF_{\text{som}}$  and ED ( $r = 0.70$ ,  $p < 0.001$ ), both of which are consistent with an energetic trade-off between gonad development and production of somatic tissue. However, regression analysis and examination of residuals confirmed a tendency for ED to decline with increasing GSI independent of  $CF_{\text{som}}$  ( $r = -0.29$ ,  $p = 0.014$ ).  $CD_{\text{som}}$  did not differ between 2- and 3-year-old repeat-maturing fish ( $t$  test,  $p = 0.07$ ) despite their differences in mean ED (Table 2). Mean ED's for yearling parr were 5.81 kJ/g (April 1996 immature: mean FL = 224 mm,  $N = 30$ ), 5.23 kJ/g (April 1996 mature: FL = 212 mm,  $N = 10$ ), and 4.60 kJ/g (May 1998 mature: FL = 133 mm,  $N = 47$ ), respectively. ED for both groups of mature parr was less than for immature parr but also differed between seasons for the two groups of mature parr (ANOVA with post hoc Bonferroni tests,  $p < 0.001$  for all paired comparisons).

Mature male parr were less able to withstand hypersaline conditions than their immature counterparts. Mean survival time for the 10 mature parr subjected to the hypersalinity challenge was 11 h 8 min compared with 29 h 53 min for immature parr ( $p < 0.001$ ).

#### Discussion

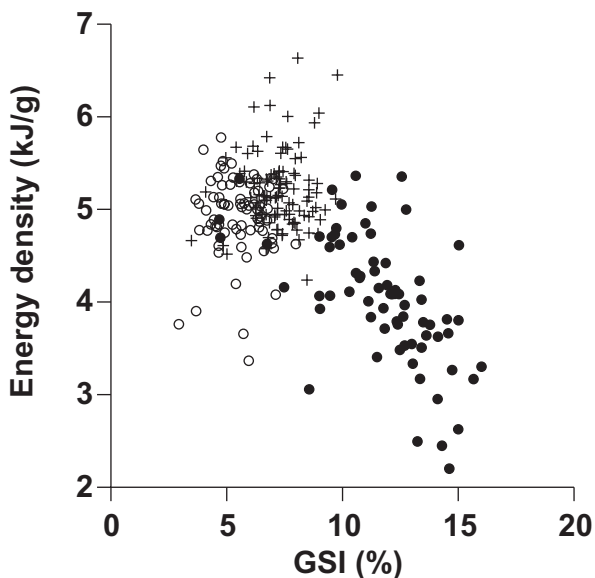
Based on our observations at Glenariffe and Silverstream, maturation of male chinook salmon parr was a common (although not routine) occurrence in the populations that we examined. Such males were able to survive and mature

**Table 2.** Mean ( $\pm 1$  SE) size (FL and weight), reproductive output (testes weight and GSI), and muscle ED for five groups of sibling chinook salmon maturing over three consecutive seasons (1995–1997).

Maturation number	First	First	First	Second	Third
Age at first maturation	1	2	2	1	1
Age at this maturation	1	2	2	2	3
Rearing environment	Hatchery	Sea-run	Hatchery	Hatchery	Hatchery
<i>N</i>	81	87	126	78	10
FL (mm)	161 $\pm$ 9	454 $\pm$ 6	373 $\pm$ 5	278 $\pm$ 7	342 $\pm$ 7
Weight (g)	57.0 $\pm$ 1.0	1177 $\pm$ 45	796 $\pm$ 37	333 $\pm$ 47	645 $\pm$ 62
Testes weight (g)	5.21 $\pm$ 0.14	63.6 $\pm$ 3.6	57.8 $\pm$ 3.0	37.7 $\pm$ 3.8	50.5 $\pm$ 6.2
GSI (%)	9.14 $\pm$ 0.18	5.39 $\pm$ 0.32	7.23 $\pm$ 0.27	11.67 $\pm$ 0.34	7.87 $\pm$ 0.56
ED (kJ/g) <sup>a</sup>	—	5.20 $\pm$ 0.12	5.45 $\pm$ 0.10	4.45 $\pm$ 0.12	5.15 $\pm$ 0.24

<sup>a</sup>*N* = 73–108 for 2-year-old groups.

**Fig. 4.** Muscle ED versus GSI for three sibling groups of 2-year-old male chinook salmon maturing in autumn 1996. Individual groups are sea-run fish maturing for the first time (○), hatchery-reared fish maturing for the first time (+), and hatchery-reared fish maturing for the second time (●).



again for at least two more seasons while remaining in a freshwater hatchery environment. Our studies also suggest that parr maturation is not limited to stream-type populations but can occur under some conditions in ocean-type populations (e.g., when juveniles were held in freshwater for a year). Taken together, these results suggest that the phenomena of parr and repeat maturation in male chinook salmon occur under a wider range of conditions than has been recognized to date.

Maturation of chinook salmon parr is generally regarded as a characteristic of stream-type populations (Healey 1991; Mullan et al. 1992), which are, in turn, traditionally associated with spring-run adults (Healey 1983, 1991). In a laboratory study of four British Columbia chinook salmon populations, Taylor (1989) found that mature parr comprised 12–29% of the males in two stream-type populations (Slim Creek and Bowron River) but did not occur in two ocean-type populations (Harrison River and Nanaimo River). New Zealand chinook salmon are descended from fall-run Sacra-

mento River stocks (McDowall 1994; Quinn et al. 1996), and both the seasonal timing of the adult spawning migration (Quinn and Unwin 1993) and the migration patterns of newly emerged fry (Unwin 1986) are consistent with fall run/ocean-type behavior. The mature parr in this study therefore appear to be derived from an ocean-type population.

Because maturation in salmon commences some months before external signs become apparent (Silverstein et al. 1997), the time of year when individual male parr begin to mature and the processes that trigger this development are unclear. Under natural conditions, parr maturation and smolting are usually incompatible (cf. Thorpe 1986); parr from ocean-type chinook salmon populations generally smolt and migrate to sea within 3–6 months of emergence, excluding any prospect of maturing in freshwater. Morphological differences between immature and mature parr, particularly the lengthening of the caudal region in immature (apparently smolted) fish compared with their mature siblings, also suggest that the developmental trajectory leading to maturation began before the onset of smolt transformation in the remainder of the cohort. Our observations of mature parr in March, together with Flain's (1970) records of mature parr from Lake Heron (in the upper Rakaia catchment) in February, are consistent with Robertson's (1957) finding that mature parr first appeared at about 10 months.

Age at maturity in most salmonid species is inversely related to growth rate (Thorpe 1994). The onset of maturation in Atlantic salmon (*Salmo salar*) has been linked to increased mesenteric fat reserves during the previous spring (Rowe et al. 1991), and similar mechanisms may apply to chinook salmon. Silverstein et al. (1997) found that amago salmon (*Oncorhynchus masu ishikawai*) that matured at 12 months of age had higher triacylglycerol levels than immature controls as early as 1 week after the beginning of exogenous feeding. We found no correlation between the incidence of mature parr in the 1994 experimental families and their mean size or growth rate at any time during their first year, although analysis of individual growth trajectories would provide a more sensitive method for detecting such correlations. Our finding that mature parr were either of similar length (in 1983–1984) or smaller (in 1995) than immature parr from the same cohort, and (in 1983–1984) less variable in size, also contrasts with previous studies. For example, Gebhards (1960) and Taylor (1989) found that mature chinook salmon parr were larger than immature parr,

and Silverstein et al. (1997) noted that mature amago salmon yearlings were more variable in size than immature parr. Nevertheless, the virtual absence of mature parr among the lower quartile of the populations sampled in 1983 and 1984 (Fig. 1) suggests that the slowest growing fish in these cohorts were unable to mature and is consistent with a minimum size or growth threshold for maturation (Rowe et al. 1991). Whether mature parr are larger or smaller than their immature counterparts may depend on a number of factors, including how much initial growth advantage maturing parr had at the onset of maturation and when sampling occurs relative to when maturing parr reduce their food consumption.

Maturation of male parr was subject to strong family-level variability. However, the lack of significant sire or population effects and the absence of any increase in maturation rate among the progeny of the mature parr spawned in 1995 (cf. Robertson 1957) suggest that any additive genetic effects (and consequently, heritability) are weak. These findings differ from those of Heath et al. (1994a), who reported significant sire effects and heritability for the incidence of jacks in chinook salmon. However, jack maturation does not necessarily reflect the same trait as parr maturation, which occurs at a younger life history stage and without any marine phase. Indeed, Heath et al. (1994b) found no evidence for genetic family contributions to parr maturation in chinook salmon but did find evidence for genetic contributions to jack maturation. Our results are also consistent with the low additive genetic variation and heritability for parr maturation in coho salmon (*Oncorhynchus kisutch*) (Silverstein and Hershberger 1992).

By making use of relative warps, our results provide a more comprehensive depiction of body development in mature parr than previously presented (Taylor 1989). In addition to being consistent with previous observations of deeper bodies and increased snout development in mature male parr (Taylor 1989), we were also able to graphically depict development of the hump and anal region in mature fish as well the lengthening of the caudal region in immature fish. While the morphological changes associated with parr maturation are subtle to the naked eye, we were able to determine that they are similar to those occurring in older and larger males, suggesting that their subtle development represents a lower endpoint along an allometric gradient. The tendency for deepening of the body and enlargement of the anal region to be more pronounced in repeat-maturing males than in first time maturing males is consistent with their high GSI's.

A striking feature of our results was the negative correlation between ED and GSI for 2-year-old repeat-maturing fish. We interpret this as reflecting the energetic costs associated with gonad production in a situation where energy reserves prior to the onset of maturation were severely limited, probably due to incomplete recovery after initial maturation. Fish spawning for a third successive season had condition indices similar to those of their 2-year-old counterparts, with lower GSI's and higher energy reserves, indicating a reduced investment in gonad development during their third year. The substantially lower ED for 2-year-old repeat-maturing males, compared with sea-run males maturing for the first time, is equally striking given that the latter group would

have had to allocate some of their energy reserves to upstream migration (Glenariffe Stream is 100 km upriver at an elevation of 430 m). The discrepancy in ED between 2-year-old sea-run fish and their freshwater-reared siblings that first matured at age 2, although somewhat smaller, is also consistent with an energetic trade-off between gonad production and return migration.

Whether naturally occurring mature male parr could survive for a second year outside the hatchery environment is uncertain. Twenty-five mature male chinook salmon returning to the University of Washington hatchery at 1 year of age in autumn 1995 were held (with food provided) in freshwater, but all died within a week of capture (M. Kinnison, unpublished data). At 12 months the mature parr in our study performed poorly in a hypersalinity challenge compared with normal parr, although Bernier et al. (1993) found that mature parr reared in freshwater for 21 months (i.e., until late summer) were generally seawater tolerant. In naturally spawning populations, however, stream-type or yearling juveniles migrate to sea somewhat earlier than this, about 16–17 months postfertilization (i.e., early spring), both in the Pacific Northwest (Healey 1983) and in New Zealand (Unwin 1986; Unwin and Lucas 1993), and the seawater tolerance of mature parr at this age is unknown.

Even if smolt transformation and migration do not occur, energetic considerations weigh against postmaturation survival under all but highly favorable circumstances. Although specific ED's for mature parr varied widely, they were generally lower than for 2-year-old first time maturing males. Thus, mature parr would have had to overcome a significant energy deficit if they were to survive in the wild during their second year. This energy deficit (and perhaps some further nutritional effects related to gut atrophy) is evidenced by the large discrepancy in mean weight (at age 2) between previously mature parr and fish maturing for the first time at age 2 in our study. Despite much higher growth than encountered in the wild during their first year (hatchery FL: 132–212 mm; wild FL: 92–131 mm; Flain 1970) and an abundant food supply during their second year, repeat-maturing fish were incapable of allocating as much energy to growth. Their ability to survive for a third year, despite their low ED's, indicates that in the absence of other factors, low energy reserves do not inevitably result in death. Nonetheless, natural environments are likely to be much less conducive to postmaturation survival than hatchery environments, and this energy deficit might be a particularly important barrier to repeat maturation in stream-type chinook salmon populations within their natural range. Such populations are usually in regions with comparatively poor growing conditions, especially in the postspawning (winter) period (Taylor 1990).

Taking these factors into account, we think that mature male parr of natural origin might occasionally survive for a second (or even third) year if they remained in freshwater and obtained enough energy but would be extremely unlikely to survive downriver migration, seawater entry, and a return spawning migration up the Rakaia River within a 6- to 12-month time span. A nil return from a 1986 brood year release of 501 CWT-marked mature male parr from Glenariffe in July 1987 (National Institute of Water and Atmospheric Research, unpublished data) further supports this

conclusion. Although marine survival for the 1986 brood was poor (Unwin 1997), this group remains the only one of 247 CWT groups released from Glenariffe between 1978 and 1993 that failed to generate any adult returns.

The ability of some individuals to mature in up to three consecutive seasons confirms and extends previous findings that semelparity in male chinook salmon is not inevitable (Robertson 1957; Flain 1971; Bernier et al. 1993). However, four considerations suggest that the physiological changes associated with parr maturation were never fully reversed: (i) the persistence of mature male parr in samples collected over at least 8 months of the year, at ages ranging from 10 to 18 months, (ii) the ability of at least some such fish to express milt as late as the end of November (19–20 months, viability unknown) despite a significant decrease in GSI, (iii) the fact that, without exception, all mature male parr that survived for a second year matured again at age 2, and (iv) the extremely high GSI's for the age-2 repeat-maturing males. Thus, although mature parr in this study clearly exhibited one iteroparous characteristic (i.e., the ability to survive after spawning), it is unclear whether maturation reversal and subsequent redevelopment of the testes occurred to the same degree as in nominally iteroparous salmonids such as rainbow trout (*Oncorhynchus mykiss*).

The appearance of some iteroparous tendencies in male chinook salmon suggests an intermediate state in a continuum from fully semelparous Pacific salmonids (*O. gorbuscha*, chum salmon (*O. keta*), sockeye salmon (*O. nerka*), and *O. kisutch*) to more strongly iteroparous species such as brown trout (*Salmo trutta*) and char (*Salvelinus* spp). This intermediate state approaches a life history variant that occurs in some populations of masu salmon (*Oncorhynchus masou*), in which males sometimes mature in freshwater at the end of their first year before migrating to sea to return and spawn again (Tsiger et al. 1994). Females of this species less commonly mature in freshwater and are apparently always semelparous (Kato 1991). The most strongly iteroparous species within the genus *Oncorhynchus* are steelhead (*O. mykiss*) and cutthroat trout (*O. clarki*), both of which are capable of repeat spawning after successive return migrations between their freshwater and marine habitats (e.g., Scott and Crossman 1973). By contrast, repeat maturation in chinook salmon (and *O. masou*) appears to occur only after initial maturation in freshwater (i.e., parr maturation), suggesting a link between anadromy and semelparity.

Although mature male chinook salmon parr are unlikely to represent more than a minority of any population, we believe that they should be more widely acknowledged. Within naturally spawning New Zealand populations, mature male parr are probably about as common (in a demographic sense) as 2-year-old females and 5-year-old fish of either sex (Quinn and Unwin 1993). More generally, their small size would make them difficult to sample in the larger rivers often used by chinook salmon, so they are probably underrepresented in spawner surveys. The incidence of mature parr in our study was not correlated with size or growth rate at any time during the first year of life, and the mechanisms that trigger maturation of individual parr remain unclear. Nevertheless, given the apparent ease with which iteroparous male chinook salmon developed within a hatch-

ery environment, in an intrinsically "ocean-type" population, the distinction between semelparous and iteroparous species of *Oncorhynchus* may not represent a large evolutionary gulf. Our results suggest that such a difference could evolve through small changes in a few key energetic and physiological thresholds.

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