**Scott D. Patterson**[1], Oregon Department of Fish and Wildlife, 107 20th Street, LaGrande, Oregon 97850

**Dennis L. Scarnecchia,** Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho 83844-1136

and

**James L. Congleton,** U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, Idaho 83844-1141

# Sexual Maturation in Kokanee *Oncorhynchus nerka*

## Abstract

We used observational and experimental approaches to obtain information on factors affecting the timing of maturation of kokanee *Oncorhynchus nerka*, a semelparous, landlocked salmon. Gonadal staging criteria were developed and applied to three kokanee populations in Idaho lakes and reservoirs. Testes were classified into three stages: immature (stage one, S1), maturing (S2), and mature (S3). Ovaries were classified into eight stages: immature (S1-S3), transitional (stage S4), maturing (S5-S7), and mature (S8). Males entered the maturing stage (S2) in February through April of the spawning year. Females entered maturing stage (S5) as early as July of the year before the spawning year, and as late as March of the spawning year. Three hatchery experiments demonstrated that attainment of a larger body size 10 to 16 months before spawning increased the likelihood of initiation of maturation in both sexes. No gonads in a state of regression were observed. A gonadosomatic index above 0.1 by early July was a good indicator of a maturing male, and a gonadosomatic index above 1.0 by early July was a good indicator of a maturing female. Instantaneous growth rates were not good predictors of maturation, but attaining a size threshold of 18 to 19 cm in the fall was a good predictor of maturation the following year. This improved knowledge of kokanee maturation will permit more effectively management of the species for age, growth and size at maturity as well as for contributions to fisheries.

## Introduction

Numerous studies have indicated that age at maturity of salmonids is in part genetically based (Bailey et al. 1980; Thorpe et al. 1980; Naevdal 1983; Sutterlin and MacLean 1984) and in part a response to the environment (Silverstein et al. 1998; Healey et al. 2000). As evidence for a genetic basis, younger-maturing fish produced a significantly higher proportion of younger-maturing progeny in Atlantic salmon *Salmo salar,* (Thorpe et al. 1983; Glebe and Saunders 1986), coho salmon *Oncorhynchus kisutch*, (Iwamoto et al. 1984), and kokanee *Oncorhynchus nerka* (Kato 1980). As evidence for an environmental basis, a higher proportion of early maturing salmonids has resulted when growth rate increased as a result of high feeding rates (Crandell and Gall 1993) or high water temperatures (Saunders et al. 1983). Photoperiod also affects the completion of sexual maturation (Lam 1983). Thorpe (1986) concluded that rapid growth in spring was important for initiation of maturation, and hypothesized that salmon were physiologically aware of their spring (increasing day length) growth rate through their rate of acquisition of surplus energy. Rowe et al. (1991) suggested that fat reserves, stored as visceral fat or in muscle, influence maturation in that a high spring condition factor was associated with maturing fish (Rowe and Thorpe 1990b). An individual fish's developmental history, therefore, is influenced by interacting genetic and environmental factors that affect age at maturity and ultimate body size (Ricker 1972; Gardner 1976; Scarnecchia 1983).

An understanding of the genetic and environmental factors affecting age at maturity of kokanee, a semelparous, freshwater form of sockeye salmon, is essential for effective species management. The age at maturity directly affects the number and size of fish available for harvest: an older age at maturity often yields larger fish (Holtby and Healey 1986; Grover 2005), whereas earlier maturation results in death before fishes have reached a size desirable to anglers. An understanding of the interactions among fish age, sex, size, growth rate and gonadal development is essential to identifying the physiological "window" (Thorpe 1986) in which the fish begins to mature. The objectives in this study were to determine 1) when kokanee maturation

[1]Author to whom correspondence should be addressed, E-mail: Scott.D.Patterson@state.or.us

is initiated, and 2) the influence of age-specific size and growth rate on maturation.

## Methods

Both observational and experimental approaches were used. Observationally, we followed the development of gonads through the life history of both wild and hatchery-reared fish. This approach included assessment of age, growth and maturity of individual kokanee from three wild stocks as well as from hatchery-reared fish. Experimentally, we assessed the effects of altering the growth rates of hatchery-reared fish during the first, second and third years of life on the percentages of maturing and immature fish.

### Observational

*Fish collection*—Kokanee were sampled from three northern Idaho (USA) lakes: Coeur d'Alene (CDA; area 12,899 Ha) which contained primarily age-3 spawners, Lake Pend Oreille (LPO, area 34,788 Ha), which contained primarily age-4 spawners; and Dworshak Reservoir (DWOR; area 8,023 Ha), which contained primarily age-2 spawners. Monthly samples of 25 fish each of ages 0, 1, 2 and 3 were collected from CDA from May to October 1992, March and October 1993, and in March 1994. Annual samples were collected in 1992 and 1993 from four ages in LPO (in September) and two ages in DWOR (in July).

Fish were captured by a mid-water trawl 13.7 m in length with a 3 m x 3 m (9 $m^2$) mouth. The trawl nets had graduated mesh sizes ranging from 32 mm (stretch mesh) at the mouth to 6 mm at the cod end.

Captured fish were measured for fork length (FL) to the nearest mm, weighed to the nearest g, and tentatively assigned an age and cohort based on FL. Otoliths (sagittae) were removed for age determination and for back-calculation of length at age. The quantity of visceral fat was estimated for each fish in 1993 using categorical ratings of 0-9%, 10-49%, 50-89%, 90-100% coverage of pyloric caeca (modified from Goede 1993). Both gonads were surgically removed and fixed in either 10% buffered formalin or Bouin's solution.

*Histological Procedures*—Gonads were blotted dry and weighed to the nearest mg. Following fixation and weighing, gonads were trimmed, oriented, dehydrated in alcohol, and infiltrated with paraffin. Longitudinal sections were cut from gonads less than 1.0 g; transverse sections were cut from the anterior portion of gonads 1.0 g and larger. Sections were cut 6 to 8 μm in thickness and stained with hematoxylin and eosin. Stained sections were studied using a compound microscope at powers ranging from 40X to 450X to determine maturity stage.

Testes were classified into three stages (S): immature (S1), maturing (S2), or mature (S3; Table 1). Ovaries were classified into eight stages: immature (S1, S2, and S3), transitional (S4), maturing (S5, S6, and S7), or mature (S8; Table 1). Stages were identified and characterized based on studies by van den Hurk and Peute (1979), Forberg (1982), Bromage and Cumaranatunga (1987), West (1990),

TABLE 1. Testicular and ovarian stages and distinguishing characteristics.

| Testis Stage | Distinguishing Characteristic |
|---|---|
| 1 | Spermatogonia in cysts; thick layers of connecting tissue surround cells. |
| 2 | Spermatids increase in numbers creating an organized appearance. |
| 3 | Spermatozoa with flagella appear. |
| **Ovary Stage** | |
| 1 | Small nested germ cells. |
| 2 | Germinal vesicle (nucleus) occupies most of the cell. |
| 3 | Nucleoli appear on germinal vesicle periphery. |
| 4 | Nucleus becomes more acidophilic and irregular shaped. |
| 5 | Zona radiata (red staining inner membrane) appears. |
| 6 | Distinct theca and granulosa cells develop on periphery of ova. |
| 7 | Red staining oil drops (H&E) appear. |
| 8 | Germinal vesicle migrates toward pole. |

and observations from the present study. A detailed description of the characteristics of each stage is provided in Patterson (1998).

*Age, growth, condition factor, and gonadosomatic index*—We determined the age of fish by counting annuli on the sagittal otolith using a Biosonics Optical Pattern Recognition System (OPRS). Otoliths were measured for back calculations of size at age from the sulcus nucleus of the otolith to each annulus at an angle of 25 ± 5° from the sulcus acusticus radius. Fish length at age was estimated by back calculation (Carlander 1981; Ricker 1992) using the Fraser-Lee equation:

$$L_n = a + (L - a)\,(V_n) / (V_r)$$

where $L_n$ = FL at year n

a = 20 mm (intercept from our regression; approximate length of fish at otolith formation)

L = fish length at time of capture

$V_n$ = otolith radius distance from the sulcus nucleus to the nth annulus, and

$V_r$ = otolith radius from the sulcus nucleus to otolith edge.

For CDA fish, growth rates, condition factors, and gonadosomatic indices were also calculated. The instantaneous growth rate (G) was calculated as $((\ln W_t - \ln W_o) / t) \times 100$, where $W_t$ = mean weight (g) at time t (d) and $W_o$ = initial mean weight (Ricker 1975). Condition factor (K) was estimated as $(W / L^3) \times 10^5$, where L = FL (mm) and W = weight (g) (Ney 1999). The gonadosomatic index (GSI) was calculated as ((gonad weight (g) / body weight (g)) x 100) (De Vlaming et al. 1982).

## Experimental

Experiments were conducted using LPO-stock fish reared at Cabinet Gorge, Clark Fork, and Sandpoint hatcheries (Idaho) to determine the effects of differential growth rates at ages 0, 1 and 2 on maturation schedules.

*Differential growth rate at age 0*—The first hypothesis tested was that the physiological decision to mature occurs (or does not occur) during the spring and summer of the first year of life (age 0). Growth rates were manipulated as three treatments, slow, medium or fast, in two groups (replicates) per treatment. The slow fish were reared in two groups at Sandpoint Hatchery at 7° C, fed to satiation for the first 60 d, then alternately fed one week at satiation and one week unfed for the remaining 62 d. The medium fish were reared in two groups at Clark Fork Hatchery on natural water temperatures (5° C in March, increasing to 12° C in mid-July) and fed to satiation. The fast fish were reared in two groups at Cabinet Gorge Hatchery at 11° C and fed to satiation. Fish were raised under similar densities (less than 0.2 density index), flow indices (0.8 flow index; Piper 1970), and diets. Fish from all six groups were initially fed on 10 March 1992.

On 17 July 1992, after 122 d of rearing, 2,000 fish from each treatment (1,000 fish per group) were consolidated in equal numbers into two 1,200-L tanks (3,000 fish/container) at Clark Fork Hatchery. Fish from the three treatments were identified by tagging (at this time) with fin clips: no fin removal (slow growth rate), right ventral fin removal (medium), and left ventral fin removal (fast). The fry were reared under natural temperatures and photoperiod (minimum winter water temperature 3° C, maximum summer water temperature 17° C). To estimate growth rates, each month 30 fish per treatment from each of the two tanks were sacrificed, weighed and measured. To determine maturation and gonadal development, 20 to 50 fish per treatment were examined quarterly starting 8 November 1992. In May 1994, approximately 100 fish from each treatment were examined, and the remaining fish were sampled in November 1994.

An epizootic of bacterial kidney disease (BKD) in both Clark Fork hatchery containers in June 1993 killed 13-17% of the fish. Mortality rates were similar for each of the three treatments.

*Differential growth rate at age 1*—The second hypothesis tested was that the decision to mature occurs (or does not occur) during the summer and fall of the second year of life (age 1), 10 to 16 months prior to spawning. Growth rates were manipulated in two treatments, slow and fast, in two groups (replicates) after 15 months of identical rearing at the Cabinet Gorge Hatchery. Beginning 15 June 1993, the fast fish were reared in two groups (12,500 fish per group) and fed to satiation. The slow fish were reared in two groups (1,000 fish per group) and fed intermittently (one week at satiation and three weeks unfed). All groups were reared below 0.5 density index and 1.0 flow index (Piper 1970). Water temperatures ranged from 10 to 12° C. The two feeding regimes were continued until 2 January 1994, when routine hatchery feed-

ing practices were resumed. The two groups of slow-treatment fish were transferred to Sandpoint Hatchery in February 1994, and the two groups of fast-treatment fish remained at Cabinet Gorge Hatchery. In May 1994, approximately 100 healthy fish from each treatment were examined.

An epizootic of BKD killed a combined 42% of fish in the two groups of fast-treatment fish and a combined 65% of the fish in the two groups of slow-treatment fish. Fish with clinical BKD signs (bloated appearance, body fluids, kidney lesions) were excluded from analysis.

*Differential growth rate at age 2*—The third hypothesis tested was that the decision to mature occurs (or does not occur) during the mid-spring and summer of the third year of life (age 2), six to seven months prior to spawning. Growth rates were manipulated in two treatments, slow and fast, in two groups (replicates) after 22 months of identical rearing at the Sandpoint Hatchery. Beginning 1 May 1993, the fast fish were reared in two groups (198 and 190 fish) and fed to satiation. The slow fish were reared in two groups (183 and 191 fish) and fed intermittently (one week at satiation and three weeks unfed). All groups were reared below 0.5 density index and 1.0 flow index (Piper 1970). Water temperature was 7° C. Thirty fish were sampled monthly for length and weight. Feeding stopped 1 November 1993.

*Fecundity and egg size*—In November and December 1993, ripe fish were spawned and fecundity estimated. Eggs were handled at 60 min post fertilization. Eggs from each female were drained and weighed. A subsample of eggs were weighed and counted to estimate the number of eggs/g. Fecundity was estimated as the total weight of eggs multiplied by the number of eggs/g. Immature fish were euthanized and their sex determined.

*Analysis*—We tested the null hypothesis that the percentage of mature or maturing fish were equal to immature fish using multiple comparisons of two binomial proportions ($H_a$: $p_1 - p_2 > 0$). Significant differences were identified using a Z-test. Multiple student t-tests were used to test for differences in lengths, weights, egg sizes, and fecundities. Tests were evaluated at the alpha $\leq 0.05$ level of significance (Snedecor and Cochran 1967).

## Results

### Observational

Although the target sample size of 25 fish per age was met in most instances, in LPO only 23 age-4 fish were collected in 1992 and 17 age-4 fish in 1993. Similarly, in DWOR only 19 age-1 fish and 11 age-2 fish were collected in 1992.

### *Coeur d'Alene Lake*

*Age at maturity*—Age-3 fish were the primary spawners from 1992 to 1994. (Table 2).

*Testicular development*—All 151 age-1 males examined in 1992 and 1993 were S1, as were nearly all age-2 fish (66 of 69 in 1992; 113 of 115 in 1993; Table 3). Five fish had progressed into S2 (Table 3). Age-3 males were primarily in S2 (50 of 57 in 1992; 49 of 62 in 1993; Table 3). From June through October 1993, S2 testes for

TABLE 2. Age at maturity of kokanee spawners determined histologically from Coeur d'Alene Lake (CDA), Lake Pend Oreille (PDO), and Dworshak Reservoir (DWOR)) in 1992 and 1993. Data for CDA also extend through 1994.

| | | Male | | | | | Female | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Number by age | | | | Mean age at | Number by age | | | | Mean age at |
| Lake/Reservoir | Year | 1 | 2 | 3 | 4 | maturity (yr) | 1 | 2 | 3 | 4 | maturity (yr) |
| CDA | 1992 | | 3 | 50 | 1 | 3.0 | | 3 | 55 | 3 | 3.0 |
| | 1993 | | 2 | 49 | 5 | 3.1 | | 3 | 67 | 3 | 3.0 |
| | 1994 | | 2 | 12 | | 2.9 | | 3 | 16 | 1 | 2.9 |
| LPO | 1992 | | | 3 | 10 | 3.8 | | | 1 | 10 | 3.9 |
| | 1993 | | | 4 | 11 | 3.7 | | | 7 | 11 | 3.6 |
| DWOR | 1992 | | 3 | | | 2.0 | | 4 | | | 2.0 |
| | 1993 | 2 | 18 | | | 1.9 | 1 | 8 | 1 | | 2.0 |

TABLE 3. Mean fork lengths (and standard deviation) and testicular stages for ages one, two, and three male kokanee sampled from CDA in 1992 and 1993.

| Year | Age | Date | Number of Fish | Mean fork length (mm) | Testicular stages 1 | 2 |
|---|---|---|---|---|---|---|
| 1992 | 1 | 2 Jul | 16 | 110 (5) | 16 | |
| | 1 | 28 Jul | 13 | 124 (8) | 13 | |
| | 1 | 26 Aug | 3 | 120 (7) | 3 | |
| | 1 | 24 Sep | 13 | 116 (11) | 13 | |
| | 1 | 29 Oct | 13 | 118 (7) | 13 | |
| | 2 | 27 May | 8 | 157 (14) | 8 | |
| | 2 | 2 Jul | 9 | 172 (16) | 8 | 1 |
| | 2 | 28 Jul | 13 | 194 (11) | 12 | 1 |
| | 2 | 26 Aug | 13 | 194 (13) | 12 | 1 |
| | 2 | 24 Sep | 16 | 190 (10) | 16 | |
| | 2 | 29 Oct | 10 | 207 (9) | 10 | |
| | 3 | 2 Jul | 11 | 203 (8) | 3 | 8 |
| | 3 | 28 Jul | 14 | 221 (10) | 1 | 13 |
| | 3 | 26 Aug | 15 | 221 (8) | 1 | 14 |
| | 3 | 24 Sep | 11 | 227 (11) | 2 | 9 |
| | 3 | 29 Oct | 6 | 246 (7) | | 6 |
| 1993 | 1 | 17 Mar | 10 | 73 (5) | 10 | |
| | 1 | 23 Apr | 10 | 73 (4) | 10 | |
| | 1 | 27 May | 15 | 89 (6) | 15 | |
| | 1 | 1 Jul | 12 | 108 (5) | 12 | |
| | 1 | 16 Jul | 14 | 117 (13) | 14 | |
| | 1 | 26 Aug | 3 | 120 (7) | 3 | |
| | 1 | 20 Sep | 12 | 144 (10) | 12 | |
| | 1 | 15 Oct | 17 | 152 (10) | 17 | |
| | 2 | 17 Mar | 13 | 137 (7) | 13 | |
| | 2 | 23 Apr | 15 | 140 (10) | 15 | |
| | 2 | 27 May | 12 | 139 (6) | 12 | |
| | 2 | 1 Jul | 12 | 154 (6) | 12 | |
| | 2 | 16 Jul | 20 | 164 (5) | 20 | |
| | 2 | 26 Aug | 9 | 178 (5) | 9 | |
| | 2 | 20 Sep | 18 | 186 (13) | 16 | 2 |
| | 2 | 15 Oct | 16 | 179 (7) | 16 | |
| | 3 | 17 Mar | 13 | 201 (8) | 1 | 12 |
| | 3 | 23 Apr | 3 | 205 (13) | | 3 |
| | 3 | 27 May | 12 | 211 (8) | 2 | 10 |
| | 3 | 1 Jul | 5 | 217 (4) | | 5 |
| | 3 | 16 Jul | 15 | 209 (16) | 8 | 7 |
| | 3 | 26 Aug | 1 | 215 | | 1 |
| | 3 | 20 Sep | 13 | 238 (16) | 2 | 11 |

the 1990 cohort increased in weight exponentially (Figure 1).

The 1990 cohort moved from S1 to S2 during the period from 29 October 1992 to 17 March 1993. All ten age-2 fish sampled at the beginning of the period were S1, but by the period's end, as age-3 fish, 12 of 13 fish sampled had progressed to S2 (Table 3).

The 1991 cohort moved from S1 to S2 between 15 October 1993 and 29 March 1994. All sixteen

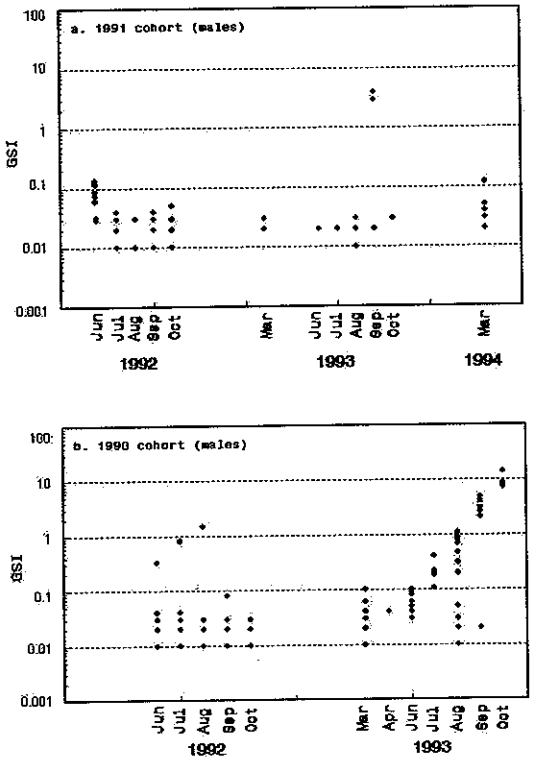


Figure 1. Gonadosomatic index (GSI) of male kokanee from Coeur d'Alene Lake in 1992, 1993, and 1994 for a) 1991 cohort and b) 1990 cohort.

age-2 fish sampled at the beginning were S1, but by the end, as age-3 fish, 12 of 15 fish sampled had progressed to S2.

*Ovarian development*—Ovaries of age-1 females were S3 in 120 of 121 fish examined in 1992 and 1993. The remaining ovary was S2 (Table 4).

Ovaries of age-2 females (1990 cohort) moved from S3 to S4 to S5 between May and October 1992 (Table 4). All ten fish sampled in May were S3, but by 2 July, two of seven fish sampled were S4. S4 frequency remained nearly the same (3 of 11) by 28 July. The incidence of S4 declined to 8.3% (1 of 12) by 26 August and 11.1% (1 of 9) by 24 September. None of nine fish sampled on 29 October were S4. As the frequency of S4 declined in August and September, the frequency of S5 increased (Figure 2).

In contrast, age-2 females (1991 cohort) showed an increasing incidence of S4 through the summer, but no progression to S5 in fall. Nearly all (16 of

TABLE 4. Mean fork lengths (and standard deviation) and ovarian stages for ages one, two, and three female kokanee sampled from Coeur d'Alene Lake in 1992 and 1993. An asterisk * indicates that one fish was in Stage 2.

| Year | Age | Date | Number of fish | Mean fork length (mm) | Ovarian stage 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|---|
| 1992 | 1 | 2 Jul | 12 | 113 (6) | 12 | | | | |
| | 1 | 28 Jul | 15 | 125 (12) | 15 | | | | |
| | 1 | 28 Aug | 3 | 127 (7) | 3 | | | | |
| | 1 | 24 Sep | 5 | 119 (4) | 5 | | | | |
| | 1 | 29 Oct | 8 | 113 (6) | 8 | | | | |
| | 2 | 27 May | 10 | 155 (8) | 10 | | | | |
| | 2 | 2 Jul | 7 | 169 (5) | 5 | 2 | | | |
| | 2 | 28 Jul | 11 | 193 (11) | 3 | 3 | 4 | | 1 |
| | 2 | 26 Aug | 12 | 191 (11) | 3 | 1 | 8 | | |
| | 2 | 24 Sep | 9 | 196 (22) | 4 | 1 | 2 | | 2 |
| | 2 | 29 Oct | 9 | 207 (19) | 3 | | 5 | | 1 |
| | 3 | 2 Jul | 12 | 203 (8) | | | 3 | | 9 |
| | 3 | 28 Jul | 13 | 220 (8) | | | | | 13 |
| | 3 | 26 Aug | 8 | 218 (8) | | | | | 8 |
| | 3 | 24 Sep | 10 | 229 (6) | | | | | 10 |
| | 3 | 29 Oct | 15 | 243 (8) | | | | | 15 |
| 1993 | 1 | 17 Mar | 11 | 72 (5) | 11 | | | | |
| | 1 | 23 Apr | 14 | 75 (4) | 14 | | | | |
| | 1 | 27 May | 11* | 88 (6) | 10 | | | | |
| | 1 | 1 Jul | 7 | 109 (7) | 7 | | | | |
| | 1 | 16 Jul | 10 | 120 (5) | 10 | | | | |
| | 1 | 26 Aug | 1 | 132 | 1 | | | | |
| | 1 | 20 Sep | 14 | 142 (11) | 14 | | | | |
| | 1 | 15 Oct | 10 | 149 (11) | 10 | | | | |
| | 2 | 17 Mar | 9 | 138 (9) | 8 | | 1 | | |
| | 2 | 23 Apr | 20 | 139 (8) | 20 | | | | |
| | 2 | 27 May | 22 | 138 (8) | 21 | 1 | | | |
| | 2 | 1 Jul | 17 | 150 (8) | 16 | 1 | | | |
| | 2 | 16 Jul | 12 | 166 (16) | 10 | 1 | | | 1 |
| | 2 | 26 Aug | 21 | 174 (4) | 19 | 2 | | | |
| | 2 | 20 Sep | 15 | 182 (16) | 10 | 3 | 1 | 1 | |
| | 2 | 15 Oct | 17 | 178 (4) | 11 | 6 | | | |
| | 3 | 17 Mar | 20 | 206 (9) | | 1 | 19 | | |
| | 3 | 23 Apr | 7 | 203 (12) | | | 7 | | |
| | 3 | 27 May | 13 | 206 (9) | | | 1 | 12 | |
| | 3 | 1 Jul | 7 | 217 (3) | | | | | 7 |
| | 3 | 16 Jul | 9 | 207 (17) | 1 | | 3 | | 5 |
| | 3 | 26 Aug | | | | | | | |
| | 3 | 20 Sep | 12 | 240 (8) | | | | | 12 |
| | 3 | 15 Oct | 4 | 238 (10) | | | | | 4 |

17, 94.1% ) had progressed to S6 by 29 March of the next year, however, Both the 1990 and 1991 cohorts matured primarily at age 3 despite their different progressions of ovarian development (Table 4).

Ovaries of age-3 females sampled in late winter and early spring of 1993 were primarily S5 before progressing to S6 by late May (Table 4). Age-3 females sampled in 1992 (1989 cohort) and in 1993 (1991 cohort) showed a clear transition from S6 into S7 by early July (Table 4).

*Gonadosomatic index*—The GSI for males ranged between 0.01% and 14.2%, remaining below 0.1% until six to seven months prior to spawning. Testicular growth occurred largely in S2. Even without histological examination, a GSI above 0.1% by early July was a good indicator of a maturing fish of that season (Figure 1). The GSI of all immature fish remained below 0.1% throughout the late summer and fall.

The GSI for females ranged between 0.06% and 18.0%. For maturing fish in S5 and S6, the

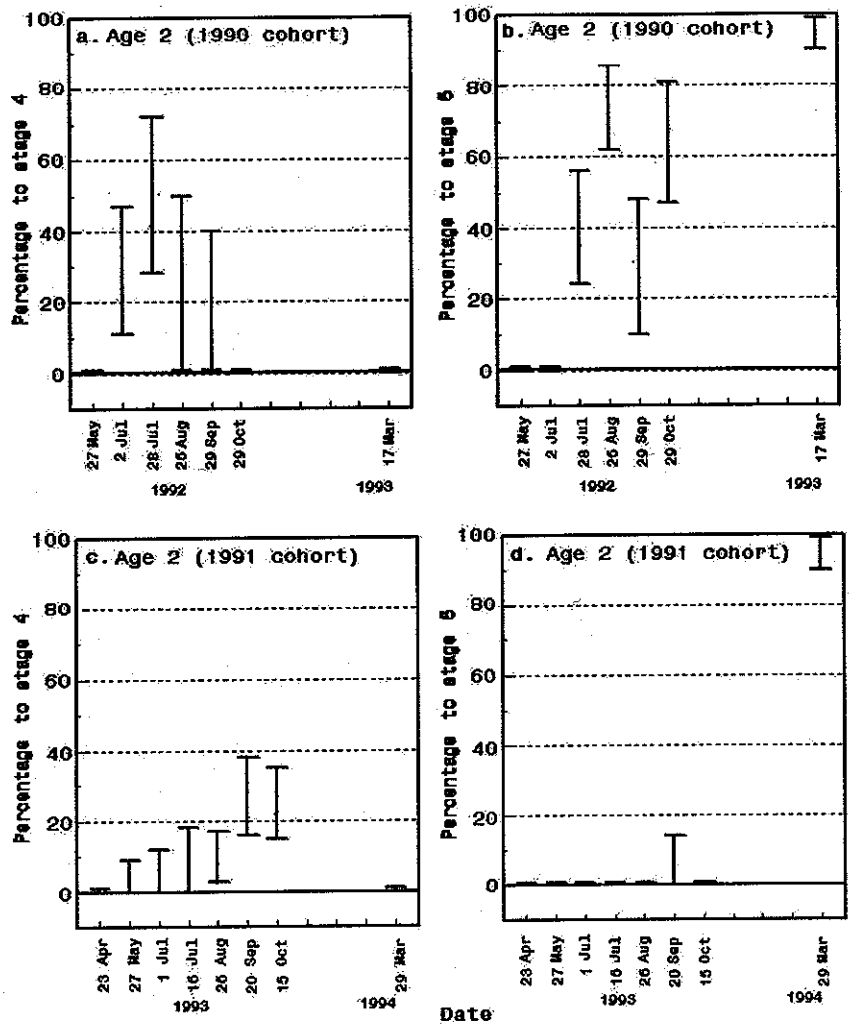


Figure 2. Mean percentage (and standard deviation) of kokanee from Coeur d'Alene Lake having a) Stage 4 ovaries in age-2 fish, 1990 cohort, b) Stage 5 ovaries in age-2 fish, 1990 cohort, c) Stage 4 ovaries in age-2 fish, 1991 cohort, and d) Stage 5 ovaries in age-2 fish, 1991 cohort.

GSI was between 0.3% and 2.0%. The GSI did not begin to increase rapidly until vitellogenesis began during S7, four to five months prior to spawning. A GSI value above 0.5% by early June and 1.0% in early July indicated a maturing fish (Figure 3). After August, the GSI values of S5 fish, which were not spawners of that year, remained between 0.5% and 1.0%.

*Condition factor and visceral fat index*—For the 1990 cohort, the fork lengths and condition factors of both male and female age-2 fish increased from July through October 1992 (Figure 4a). By March 1993, as age-3 fish, the mean condition factor had declined over winter and fish showed little increase in length (Figure 4a). In April, visceral fat content was high, covering more than 90% of the pyloric caecae. From April through October 1993, when most fish in the cohort were preparing for spawning, visceral fat declined, covering less than 10% of the caeca by October (Table 5).

For the 1991 cohort, as for the 1990 cohort, the fork lengths and condition factors in both male and female age-1 fish increased from July through October 1992. By March 1993, as age-2 fish, the condition factor had declined, even

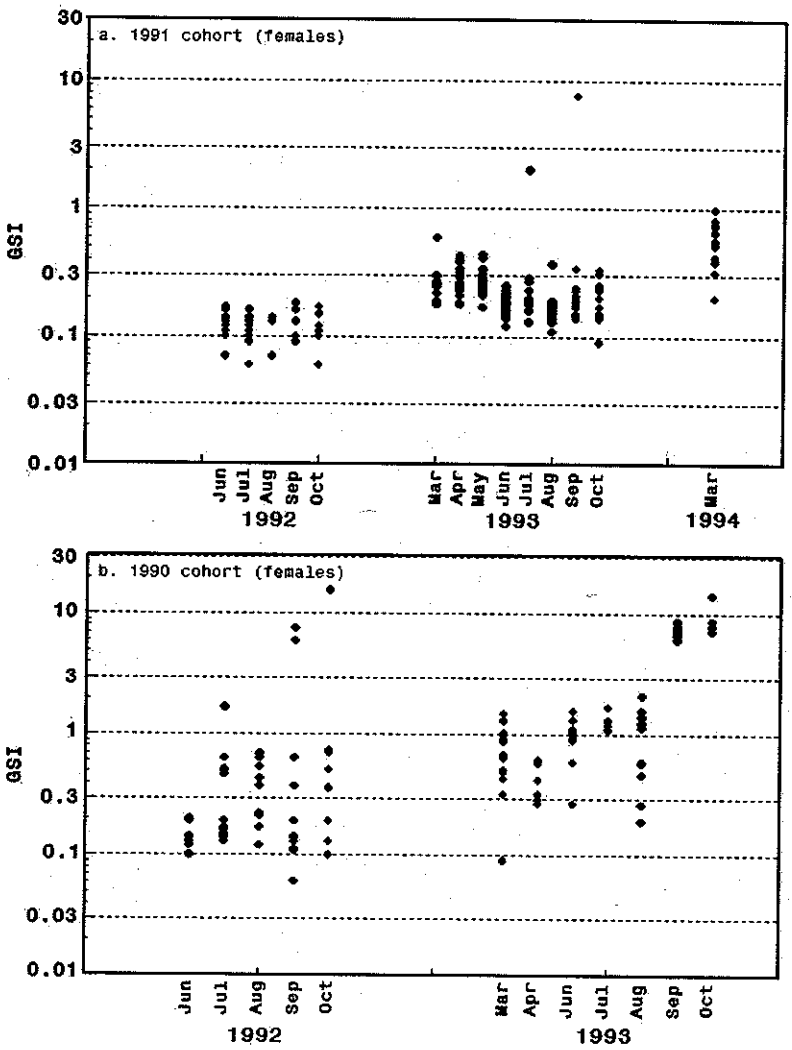


Figure 3. Gonadosomatic index (GSI) of female kokanee from Coeur d'Alene Lake in 1992, 1993, and 1994 for a) 1991 cohort and b) 1990 cohort.

though the fish had increased in length (Figure 4b). In April, visceral fat covered less than 10% of the caecae in 68.6% (24 of 35) of the fish, and between 10 and 50% of the caecae in 8 of the remaining 11 fish. From April through October, visceral fat increased, covering over 90% of the caecae. Maturing fish had less than 50% visceral fat coverage of pyloric caecae by September. By March 1994, as age-3 fish, visceral fat covered over 90% of the pyloric caecae. As with the 1990 cohort, a decline in visceral fat occurred in maturing fish in the months preceding spawning in the fall of 1994 (Table 5).

### *Lake Pend Oreille*

*Age at maturity*—Age-4 fish of both sexes were the primary spawners in 1992 and 1993 (Table 2).

*Testicular development*—All 56 age-1 and age-2 fish sampled in September 1992 and 1993 were S1. At age-3, 78% (25 of 32) were S1 and 22% (7 of 32) were S2. S2 males were considered future age-3 spawners. More than 90% (21 of 23) of age-4 males were S2 and were considered future age-4 spawners. Although 9% of the age-4 males were immature, no age-5 fish were sampled.

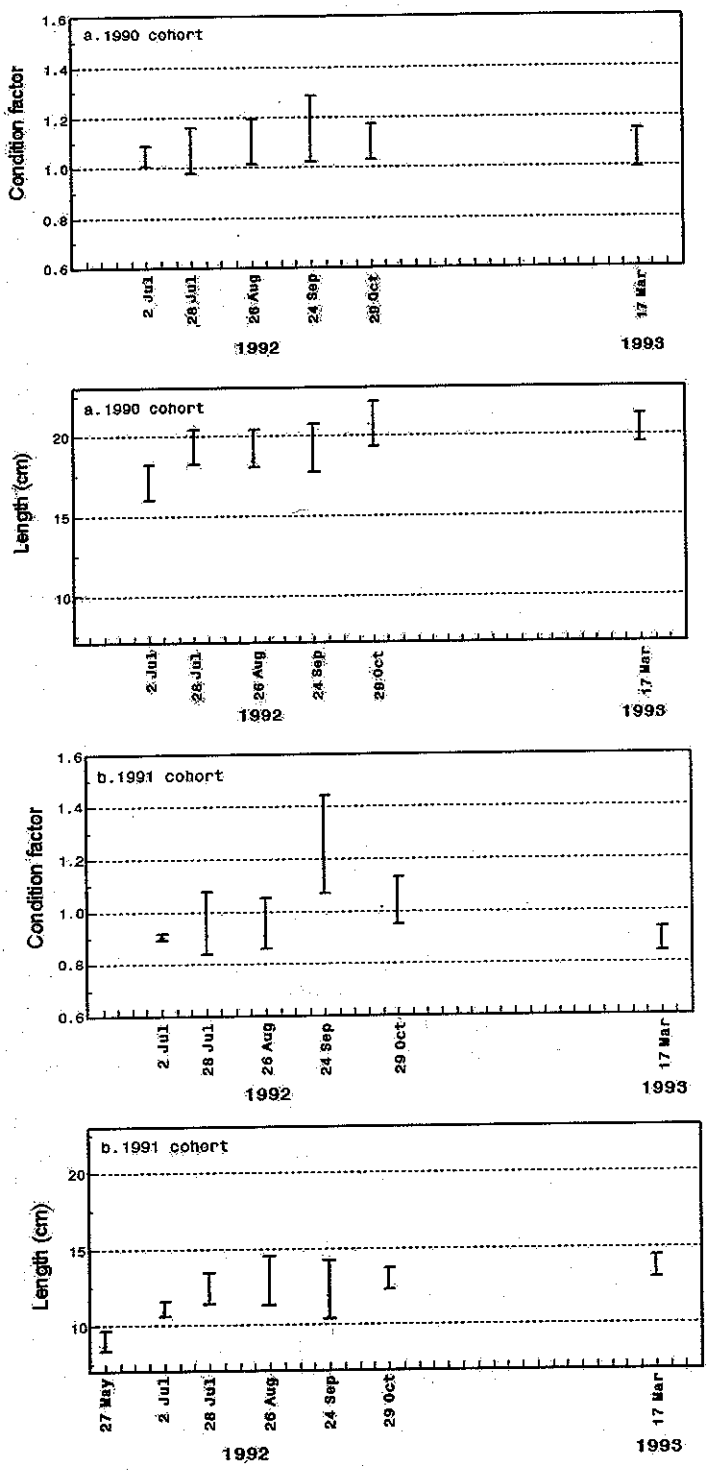


Figure 4. Condition factor and fork lengths (and standard deviations) of kokanee from Coeur d'Alene Lake during maturation in 1992 and 1993 for a) 1990 cohort and b) for 1991 cohort.

TABLE 5. Mean fork lengths (and standard deviation) and fat index for ages one, two, and three kokanee (both sex) sampled from Coeur d'Alene Lake in 1993.

| Year | Age | Date | Number of fish | Mean fork length (mm) | Fat Index 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|---|---|---|
| 1993 | 1 | 17 Mar | 21 | 73 (5) | 21 | | | |
| | 1 | 23 Apr | 24 | 74 (4) | 24 | | | |
| | 1 | 27 May | 26 | 89 (6) | 25 | 1 | | |
| | 1 | 1 Jul | 19 | 109 (6) | 3 | 16 | | |
| | 1 | 16 Jul | 24 | 119 (9) | 1 | 22 | 1 | |
| | 1 | 26 Aug | 3 | 120 (7) | | 1 | 2 | |
| | 1 | 20 Sep | 26 | 143 (11) | | 12 | 11 | 3 |
| | 1 | 15 Oct | 27 | 151 (11) | 1 | 6 | 17 | 3 |
| | 2 | 23 Apr | 35 | 139 (9) | 24 | 8 | 2 | 1 |
| | 2 | 27 May | 34 | 138 (7) | 30 | 4 | | |
| | 2 | 1 Jul | 29 | 152 (7) | | 28 | 1 | |
| | 2 | 16 Jul | 32 | 165 (12) | | 29 | 3 | |
| | 2 | 26 Aug | 30 | 176 (5) | | | 25 | 5 |
| | 2 | 20 Sep | 33 | 184 (15) | | 3 | 7 | 23 |
| | 2 | 15 Oct | 33 | 179 (6) | | | | 33 |
| | 3 | 23 Apr | 10 | 204 (13) | | | | 10 |
| | 3 | 27 May | 25 | 209 (9) | | | 6 | 19 |
| | 3 | 1 Jul | 12 | 217 (4) | | | 5 | 7 |
| | 3 | 16 Jul | 24 | 208 (17) | | 6 | 10 | 8 |
| | 3 | 26 Aug | 1 | 215 | | | 1 | |
| | 3 | 20 Sep | 25 | 239 (12) | 3 | 20 | | 2 |
| | 3 | 15 Oct | 4 | 238 (10) | 4 | | | |

*Ovarian development*—All age-1 and age-2 fish sampled in September were S3. At age 3, 26.3% (5 of 19) of the 1989 cohort were in S3, 68.4% (13 of 19) were in S5, and 5.3% (1 of 19) were in S7. At age 3, results were similar for the 1990 cohort: 29.2% (7 of 24) in S3, 41.7% (10 of 24) in S5, and 25.9% (7 of 24) in S7. A high fraction (10 of 11 in 1992; 12 of 15 in 1993) of age-4 fish sampled were S7 and presumed to be spawners of that season. Fish not in S7 were considered immature and potential age-5 spawners. However, no age-5 fish were sampled.

### Dworshak Reservoir

*Age at maturity*—Age-2 fish were the primary spawners in both 1992 and 1993 (Table 2).

*Testicular development*—Nineteen of 21 age-1 males sampled in 1992 and 1993 were S1; two fish were S2 and were considered future spawners of that year. Twenty-one of 24 age-2 males were S2; the other three fish remained at S1, although no age-3 fish were sampled in 1992 or 1993.

*Ovarian development*—Nearly all (24 of 26) age-1 females sampled in 1992 and 1993 were S3, and nearly all (12 of 13) age-2 fish were S7. One age-1 fish had progressed to S5 and another to S7.

### Growth (CDA, LPO and DWOR stocks)

Instantaneous growth rates were highest in summer and lowest in winter for all three stocks. For the CDA stock, the highest instantaneous rates (expressed on a daily basis) occurred in age-0 fish (3.8% of weight per day) during summer. As age-1 fish, growth rates also increased to their maximum (2.0% of weight per day) in the summer (July), but were less than as age-0 fish. The time of otolith annulus formation in CDA fish varied over several months. First formation was detected as early as 29 October 1992 (the last sample of the year). When sampling resumed on 17 March 1993, we observed new growth beyond the annulus in about 70% of the fish, and by 23 April, in 84 of 85 fish. We therefore used 1 April as the date of annulus formation and back-calculated lengths for all stocks.

The faster growing stocks matured at younger mean ages (Table 6), and the fastest growing individuals within a cohort matured earlier than slower growing individuals (Figure 5). The DWOR stock, which matured at the youngest age, had the highest mean back-calculated (BC) lengths at age 1 and age 2 (Figure 5). The LPO stock, which matured at the oldest age, had the lowest mean BC lengths at age 2 and age 3 (Figure 5).

TABLE 6. Back calculated lengths (and standard deviation) at age for kokanee from Coeur d'Alene Lake (CDA), Lake Pend Oreille (LPO) and Dworshak Reservoir (DWOR). An asterisk* denotes an immature fish sampled at that age.

| Lake/Reservoir | Cohort | Number of fish | Age at maturity | Length (mm) at age 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|---|---|
| CDA | 1989 | 105 | 3 | 79 (11) | 170 (15) | 223 (10) | |
| | | 8 | 4 | 76 (9) | 152 (13) | 192 (15) | |
| | 1990 | 7 | 2 | 76 (10) | 169 (19) | | |
| | | 117 | 3 | 75 (9) | 156 (16) | 205 (14) | |
| | | 17 | 3* | 75 (7) | 144 (12) | 186 (12) | |
| | 1991 | 5 | 2 | 90 (13) | 167 (9) | | |
| | | 28 | 3 | 73 (8) | 146 (7) | 183 (8) | |
| | | 4 | 3* | 69 (10) | 140 (9) | 177 (4) | |
| LPO | 1988 | 20 | 4 | 74 (15) | 131 (25) | 172 (21) | 204 (14) |
| | | 3 | 4* | 79 (26) | 141 (13) | 171 (8) | 196 (8) |
| | 1989 | 4 | 3 | 96 (23) | 164 (7) | 204 (4) | |
| | | 23 | 4 | 87 (25) | 150 (18) | 185 (13) | 212 (8) |
| | | 2 | 4* | 79 (7) | 130 (15) | 161 (11) | 186 (10) |
| | 1990 | 11 | 3 | 118 (16) | 169 (12) | 196 (12) | |
| | | 33 | 3* | 84 (19) | 138 (15) | 170 (10) | |
| DWOR | 1990 | 7 | 2 | 109 (10) | 212 (19) | | |
| | | 4 | 2* | 98 (18) | 203 (2) | | |
| | 1991 | 26 | 2 | 124 (13) | 214 (14) | | |
| | 1992 | 2 | 1 | 143 (na) | | | |
| | | 27 | 1* | 122 (11) | | | |

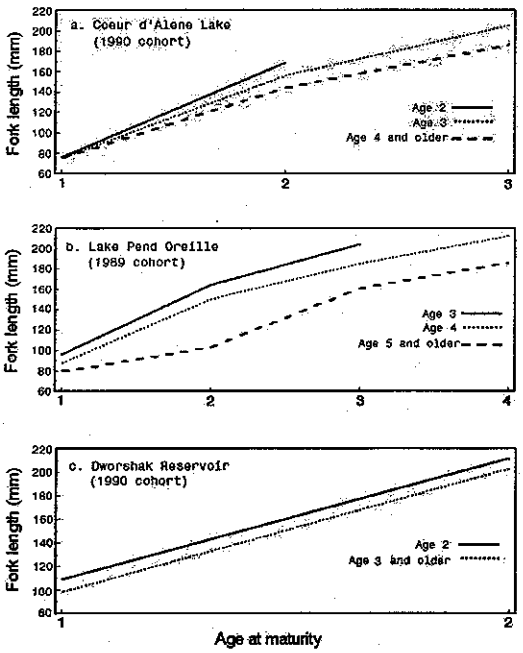


Figure 5. Relationship between kokanee growth rate, expressed as mean length at age, and age at maturity for a) Coeur d'Alene Lake, b) Lake Pend Oreille, and c) Dworshak Reservoir.

The DWOR stock had mean BC lengths over 200 mm at the second annulus (Figure 5), and produced nearly 100% age-2 spawners. In contrast, the LPO and CDA stocks, with mean BC lengths of 140 mm and 170 mm at the second annulus, produced few age-2 spawners. The LPO and CDA stocks had mean BC lengths of 180 mm and 220 mm at annulus-3 (Figure 5) and the CDA stock produced nearly 100% age-3 spawners. The age-4 LPO spawners had mean BC lengths over 200 mm at the fourth annulus.

## Experimental

### *Differential growth rate at age 0*

*Length and weight*—The three treatments (slow, medium and fast) produced highly significant ($P<0.01$) differences in mean lengths and weights after 122 d. No significant differences in mean length or weight were found between the two groups of fast fish (combined mean length, $63.0 \pm 5.2$ mm, mean weight $1.82 \pm 0.51$ g), nor between the two groups of slow fish (combined mean length, $36.3 \pm 5.5$ mm, mean weight $0.33 \pm 0.16$ g; $P>0.10$). However, we found a highly significant difference in lengths and weights between the two

groups of medium fish (lengths, 54.2 ± 5.2 mm, 58.5 ± 5.5 mm; mean weights 1.13 ± 0.3 g; 1.36 ± 0.4 g; $P<0.01$).

*Males*—From three treatments (slow, medium and fast), all 69 age-0 fish sampled in November 1992 were S1, as were all 78 age-1 fish sampled in March 1993.

The first indication of maturation was found in June 1993, when 3 of 108 (3%) fish had S2 testes. In October 1993, 3% (3 of 114) fish were S2, and in December 5% (4 of 84) were S3. Two additional age-2 spawners were detected in February 1994. Overall, an estimated 4% (12 of 303) of the fish were age-2 spawners. Maturing fish were represented in all three treatments: slow 3.5% (3 of 85); medium 4.3% (5 of 117); and fast 4.0% (4 of 101). There was no significant difference in the percentage of mature males among the three treatments (pairwise Z-test; $P>0.10$).

Males that would mature at age 2 were found as early as February 1994: 53.1% (26 of 49) of the fish were S2. By May, 91.4% (339 of 371) were maturing and in November 90.4% (85 of 94) had matured. Maturing fish were represented in all three treatments: slow 90.2% (203 of 225); medium 92.6% (113 of 122); and fast 91.5% (108 of 118). There was no significant difference ($P>0.01$) in the percentage of mature males among the three treatments. The decision by age-0 males to mature did not occur during the first 122 d of feeding.

*Females*—From the three treatments, all 74 age-0 fish sampled in November 1992 were S3, as were all 116 age-1 fish sampled in March and June 1993. By October 1993, 28.1% (18 of 64) had progressed to S4; by December 1993, 52.5% (32 of 61) were S4, with percentages of fish progressing not significantly different ($P>0.10$) among the three treatments. By February 1994, 89% of the fish had progressed past S4; by May more than 99% had progressed to S5 and S6. The transition from S4 to S5 and S6 showed a clear progression with 0% in S5 and S6 in December 1993, 41.0% (16 of 39) by February 1994, and 49.1% (145 of 295) by May.

Ovaries of maturing age-2 females were S5 and S6 in May, including 56.0% (47 of 84) from fast, 56.5% (52 of 92) from medium, and 38.7% (46 of 119) from slow fish. By November 1994, maturing age-2 females were S7, including 54.5% (12 of 22) from the fast fish, 55.5% (10 of 18) from the medium fish, and 33.0% (7 of 21) from the slow fish. There was a significantly lower percentage of maturing females between the slow fish (37.8%) and both the medium fish (56.4%) and the fast fish (55.7%; pairwise Z-tests; $P<0.01$), but no significant difference (Z-test; $P>0.10$) between the medium and fast fish.

Ovaries of immature age-2 females remained in S3 in May, but by November, ovaries in non-spawning females had developed into S5 in 90.0% (9 of 10) of the fast fish, 87.5% (7 of 8) of the medium fish, and 85.7% (12 of 14) of the slow fish. The decision to mature in females may have occurred during the first 122 d of feeding, in late winter and early spring.

### *Differential growth at age 1*

*Length and weight*—The two treatments (fast and slow) produced different sizes of fish by February 1994. The two groups of fast fish averaged 196.5 ± 22.7 mm and 199.3 ± 20.3 mm in length and 98.2 ± 37.1 g and 102.2 ± 21.1 g in weight. The two groups of slow fish averaged 152.9 ± 18.0 mm and 154.4 ± 15.7 mm in length and 33.4 ± 16.2 g and 36.6 ± 11.8 g in weight. Both fast and slow fish produced a few mature age-1 males in 1993. However, their maturation rate was not examined.

*Males*—Many males were maturing in May 1994 at age-2: 77.4% and 84.0% were maturing (S2) in the two groups of fast fish, and 43.1% and 46.0% were maturing (S2) in the two groups of slow fish. There was no significant difference ($P=0.35$) between the two groups of fast fish nor between the two groups of slow fish ($P=0.74$). A significant difference ($P<0.001$) was found, however, between the two combined groups of fast fish and the two combined groups of slow fish. The growth rate of age-1 males in the summer and fall strongly affected the percentage of fish spawning the following year, i.e., 10 to 16 months later.

*Females*—Many females matured or were maturing in May 1994 at age 2: 68.1% and 62.5% were maturing (S5) in the two groups of fast fish, whereas only 22.0% and 27.9% were maturing (S5) in the two groups of slow fish. There was no significant difference ($P=0.57$) in percentage of maturation between the two groups of fast fish nor between the two groups of slow fish ($P=0.51$).

A significant difference ($P<0.001$) was found, however, between the two combined groups of fast fish and the two combined groups of slow fish. A higher growth rate of age-1 females in the summer and fall significantly increased the percentage of fish spawning the following year, i.e., 10 to 16 months later.

### *Differential growth at age 2*

*Average lengths and weight produced by treatments*—The two treatments (fast and slow) produced significantly different ($P<0.001$) sizes of fish by December 1993. The two groups of fast fish averaged 307 ± 26 mm and 316 ± 29 mm in length and 360.3 g and 378.3 g in weight. The two groups of slow fish averaged 243.0 ± 27.0 mm and 245.0 ± 25.0 mm in length and 148.4 g and 149.8 g in weight.

*Males*—Many males matured in December 1993 at age 2: 65.0% and 56.5% matured (S3) in the two groups of fast fish and 60.2% and 58.3% matured (S3) in the two groups of slow fish. No significant difference ($P>0.10$) was found in maturation rate between the two groups of fast fish nor between the two groups of slow growth fish. No significant difference was also found ($P>0.10$) between the two combined groups of fast fish and the two combined groups of slow fish. The growth rate of age-2 males six to seven months prior to spawning did not affect the percentage of fish spawning that fall.

*Females*—Many females matured at age 2: 25.9% and 38.8% matured in the two groups of fast fish and 38.7% and 43.2% in the two groups of slow fish. One group of fast fish had a significantly ($P=0.001$) lower incidence of maturation (25.9%) than the other group of fast fish and both groups of slow fish. Overall, these data indicated that the growth rate of age-2 females six to seven months prior to spawning did not strongly affect the percentage of fish spawning that fall.

### *Egg size and fecundity*

The fast fish produced significantly more eggs per female (overall treatment means, 1285 ± 203 eggs/female, than the slow fish (overall treatment means, 697 ± 165 eggs; $P<0.001$)). Fast fish also produced significantly larger eggs (19.7 ± 2.7 eggs/g) than slow fish (23.9 ± 2.4 eggs/g; $P<0.001$). We found no significant difference in fecundity between the two groups of fast fish, nor between the two groups of slow fish ($P>0.10$). We also found no significant difference in egg size between the two groups of fast fish, nor between the two groups of slow fish ($P>0.10$).

## Discussion

### General pattern of maturation

The general pattern of kokanee maturation observed in this study was that males remained in S1 throughout most of their life, progressed to S2 in late winter, and matured the next fall (Figure 6). This maturation sequence by season was similar regardless of whether the fish matured at ages 2, 3, or 4. The first measured indications of maturation in males were in February (age-0 differential growth experiment) and March (1990 and 1991 CDA cohorts) of the spawning year. The transition

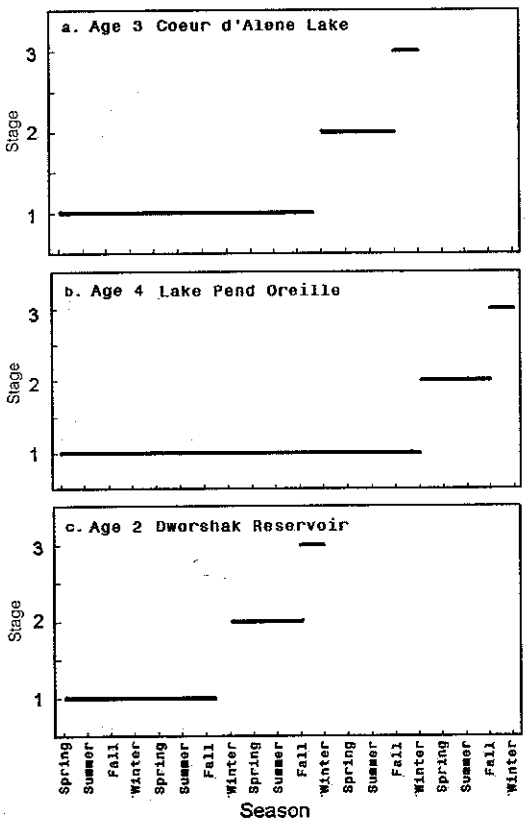


Figure 6. Typical testicular development of kokanee spawners for a) age-3 fish in Coeur d'Alene Lake, b) age-4 fish in Lake Pend Oreille, and c) age-2 fish in Dworshak Reservoir.

from S1 to S2 was characterized by an increase in the GSI due to testicular enlargement, organization of the testes, and an increase in spermatids.

Results for females were not as straightforward, although the overall sequence was similar for fish maturing at ages 2, 3, or 4 (Figure 7). Females remained in S3 throughout most of their life; progression into transitional (S4) and maturing (S5) stages occurred at different seasons. Some females progressed to S4 in summer and to S5 later in the fall; others did not progress to S4 until fall, and then to S5 in late winter or early spring. After progression to S4 and S5, progression to S6 and S7 (vitellogenesis) during the summer and fall preceding spawning occurred regardless of age at maturity. The first indicators of maturation in females were observed as early as July of the year preceding spawning (1990 CDA cohorts), i.e., 16 months before spawning, and as late as March of the spawning year. Ovaries in Stage 5 showed the first translocation of proteins derived from the liver

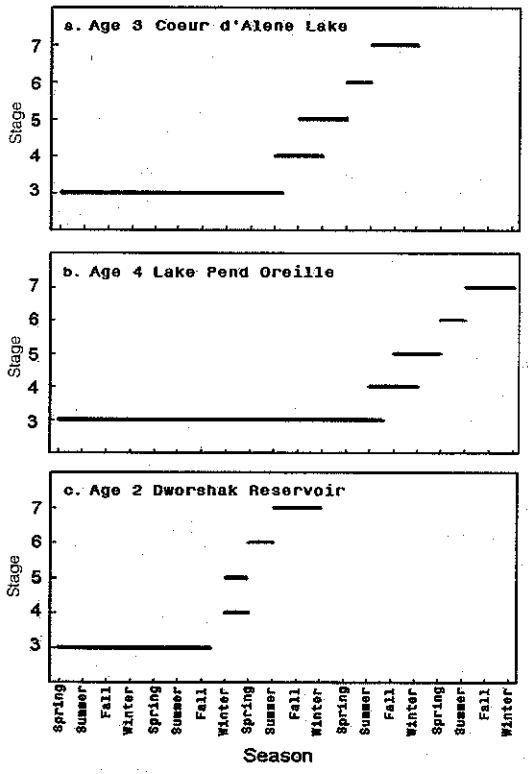


Figure 7. Typical ovarian development of kokanee spawners for a) age-3 fish in Coeur d'Alene Lake, b) age-4 fish in Lake Pend Oreille, and c) age-2 fish in Dworshak Reservoir.

and deposited inside the ova for the construction of the zona radiata or eggshell (Oppen-Berntsen 1990). Because these proteins are synthesized outside the ova, and in cells unrelated to the gonad, S5 strongly suggests initiation of maturation and energy allocation towards reproduction. Ovaries in Stage 5 quickly progressed into S6, which we distinguished by a metamorphosis of follicular cells surrounding the ova into two distinct layers and cell types. These cells contain distinct hormone receptors for gonadotropin I and gonadotropin II (Yan et al. 1992), which have a controlling influence on maturation (Swanson 1991). The development of these specific cells implies increased responsiveness to endocrine control.

The progression from S3 to S4 was not a reliable predictor of spawning in that year, even though S4 showed the first subtle change, an irregular shaped nucleus, in the ova. For example, a fish with S4 ovaries in February progressed to S5 and S6 by March or April and subsequently spawned later that year. However, a fish developing S4 ova in June progressed into S5 and S6 by October (Table 4; Figure 7) but did not spawn until the following year. Development of S5 and S6 was thus the most reliable histological predictor of final maturation.

## Critical decision period

Results of this study (gonadal development, GSI, visceral fat observations, hatchery experiments) indicate that the critical decision period for maturation was in the summer and fall 10 to 16 months before spawning. Sometime during this period, the maturation decision was made even if measurable indicators of the decision were first detected later. For experimental fish growing at slow, medium and fast rates early in life (first 122 d), only the slow females showed a lower maturation rate, a possible result of their smaller mean length throughout the experiment. On the other hand, for fish growing relatively slowly at age 1, the percentage of males and females maturing the following year, 10 to 16 months later, was significantly decreased. Testes of slow fish remained in S1 and ovaries remained in S3, resulting in a reduced percentage of fish developing maturing gonads by the following May. In the wild stocks, ovaries developing into S4 and S5 were observed from July through October in the CDA 1990 cohort and in August and September from the 1989 and 1990 LPO cohorts. For these fish, the decision to mature must have preceded

these changes. These results on maturation are consistent with general results from other studies indicating that maturation decisions are not made early in life (e.g., age 0), but later (Peterman 1985; Scarnecchia et al. 1989; 1991).

There was no evidence that growth during the last year of life (i.e., the spawning year) influenced the decision to mature. Experimental fish growing relatively slowly at age 2 matured at the same rate as fish growing relatively rapidly. In addition, no significant differences were found in the percentages of maturing fish (S5 and S6) in mid-May compared to the percentages of mature fish (S7) in November for wild CDA stock fish. Once the decision to mature was made, there was no indication that it was reversible, regardless of growth during the spawning year.

### Fecundity and egg size effects

Although slow growth of age-2 fish in the spawning year did not affect maturation rates, it did result in reduced egg size, fecundity, and length ($P$ <0.0001). Dickhoff and Swanson (1990) hypothesisized that for semelparous species, maturation is set in motion and modulated by gonadotropins I and II. Under severe ration limitations, maturation would then be expected to involve trade-offs between different reproduction investments such as egg size, number (Quinn et al. 1995), and body size. In contrast, iterparous species are able to physiologically switch off the maturation process as a result of inadequate spring growth (e.g., male Atlantic salmon parr; Rowe and Thorpe 1990a).

### Indicators of maturation

In this study, of the several factors (including fish size, growth rates, and visceral fat) considered as possible indicators of incipient maturation, the best indicator was the size attained by late summer. For example, the CDA 1990 cohort (mean length 193 ± 11 mm on 28 July 1992) had a higher incidence of age-2 females in S5 compared with the CDA 1991 cohort (mean length 166 ± 16 mm on 16 July 1993), even though the latter cohort had a higher instantaneous growth rate (Patterson 1998). Minimum size thresholds have been proposed for smolting (Elson 1957; Refstie et al. 1977; Bailey et al. 1980) and maturation (Myers et al. 1986) in male salmon parr. Some researchers have argued that a minimum-size hypothesis is too simplistic, and have proposed an alternative developmental threshold hypothesis (Saunders et al. 1982). In this study, however, late-summer size was a better indicator of maturation than instantaneous growth rates during summer.

Instantaneous growth rate was not a reliable indicator of maturation in all cases. For example, in the experiment of differential growth at age 0, instantaneous growth rates for age-1 fish were about 1.0 in June, July, and August, and 91% of the males and 49% of the females spawned the following year. In contrast, few (no females and <10% of males) wild age-1 fish from CDA with instantaneous growth rates of about 1.0 between May and July spawned the following year (Patterson 1998). Growth rates in the CDA stock were low or decreasing during late summer and fall, a critical decision period for maturation (Patterson 1998).

The relation between fish size and the process of maturation is complex. The size of the fish may, for example, indicate the status of gonadal development and rate of growth may indicate the rate of gonadal development. For example, in the experiment of differential growth at age 3, as the fish grew in length, the S3 ovary also grew in weight ($r^2 = 0.82$; $P<0.01$). Fish length, a measure of past performance, was thus also indicative of developmental progress. Since allocation of energy is critical for specific physiological processes, growth rates may indicate developmental rates, and body size may indicate when the gonad is receptive to endocrine stimulation. When the gonad has developed sufficiently to receive hormonal signals, the initiation and completion of maturation can be controlled by the photoperiod (Lam 1983; Duston and Saunders 1992) or other factors. The size threshold to receive signals, in turn, is likely under genetic control. Results from the study indicate that if a size threshold exists for maturation of kokanee, the threshold may be 18 to 19 cm by late fall, 10 to 16 months before maturation. In any case, fish reaching this length by that time typically spawned the following year.

Arguments opposing size as a predictor of maturity often attempt to correlate body size at the spawning event, rather than size during an earlier maturation decision period to maturation (Jonsson et al. 1984). Our results indicated that growth after the initiation of maturation varied greatly and ultimately affected the size a fish attained at spawning. For example, in the experiment on

differential growth at age 2, fast fish weighed more than twice as much (400g) as slow fish (178g) at spawning, although the incidence of maturation was similar. Size at the spawning event, *after* the energy expenditure associated with maturation, is therefore not indicative of the size threshold needed *before* the maturation process begins.

In this study, we observed that maturing fish had considerable visceral fat stored in the spring. The CDA 1991 cohort had high visceral fat content in the fall of the year preceding spawning, and maturing fish maintained high levels of visceral fat through the winter. Researchers have assumed that spring fat reserves are important for gonadal growth because the depletion of visceral fat has often coincided with an increasing GSI (Rowe et al. 1991). Shulman (1974) suggested that fish must have a minimum fat content in the spring before maturation is initiated, whereas Rowe et al. (1991) suggested that fat levels must be increasing during April of the spawning year for maturation to occur in Atlantic salmon. It is probable that the presence of fat through the winter is merely associated with the maturation process rather than a cause of it, which is consistent with our conclusion that the maturation decision occurred before winter.

### Stock management implications

In this study, the faster growing stocks matured earlier than the slower ones, similar to results described by Grover (2005). Within a particular stock and cohort, the faster growing fish matured earlier than the slower growing ones (Figure 5; Table 8). The relative importance of genetic versus environmental contributions to growth rates and size attained was not quantified in our study. Genetic effects on maturation have been documented in field studies for Bristol Bay sockeye salmon (Rogers 1987) and in laboratory studies with Atlantic salmon (Naevdal 1983). Wood and Foote (1990) reported that growth rates of sockeye and kokanee were influenced by genetic factors. Idaho kokanee stocks vary greatly in mean age at maturity (Tables 2), and differences in age at maturity are undoubtedly partly under genetic control.

Although differences in age at maturity among stocks may be to some degree determined by genetic factors, managers can nevertheless influence recruitment and harvest of kokanee by altering environmental factors affecting mean age at maturity. In lakes such as CDA, LPO and DWOR, manipulation of fish densities can substantially influence growth and consequently the mean age at maturity. Similarly, harvest management can also affect variance around the mean age at maturity. In our study, a high fraction of fish within a stock had the same age at maturity: 89.9% (CDA), 73.7% (LPO), and 89.1% (DWOR) (Table 2). The liberal harvest rates of 25 salmon per day and 50 in possession at the time of this study (Idaho Department of Fish and Game, unpublished) may have contributed to the lack of variation around mean age at maturity. Sport fisheries are often biased toward larger fish and inasmuch as larger (and hence older) kokanee are more vulnerable to anglers (Rieman and Myers 1990), exploitation may have selectively removed them (Ricker 1980). Knowledge of factors affecting maturation of kokanee, including genetic characteristics of the individual stocks, the influence of habitat and other environmental factors (including fish density), and fishery characteristics are all important in the effective conservation of this species.

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