Exxon Valdez Oil Spill
Restoration Project Annual Report

Restoration of Coghill Lakes Sockeye Salmon:
1994 Annual Report on Nutrient Enrichment

Restoration Project 94259
1994 Annual Report

Jim A. Edmundson
Gary B. Kyle
Stan R. Carlson

Alaska Department of Fish and Game
Commercial Fisheries Management and Development Division
34828 Kalifornsky Beach Road
Soldotna, Alaska 99669

May 1995

Restoration of Coghill Lakes Sockeye Salmon: 1994 Annual Report on Nutrient Enrichment

Restoration Project 94259
Annual Report

Study History: The project effort was initiated in the 1993 detailed study plan as Restoration Project 93024 (Restoration of the Coghill Lake Sockeye Salmon Stock). The project effort continued in 1994 with Restoration Project 94259 (Coghill Lake Sockeye Salmon Restoration), the subject of this annual report.

Abstract: Coghill Lake has been an important sockeye salmon (*Oncorhynchus nerka*) producer in western Prince William Sound. Despite the unavailability of limnological and juvenile fisheries data prior to its recent decline, indications are that consecutive years of high escapements adversely impacted the forage base (zooplankton), reducing the lake's rearing efficiency. The Coghill Lake system was selected for sockeye salmon restoration to replace fishery stocks damaged by the *Exxon Valdez* oil spill. A 5-year plan was implemented in 1993 to fertilize Coghill Lake and increase lake productivity. Nutrient treatment has resulted in a 20% increase in seasonal mean phosphorus concentration, a nearly 3-fold increase in algal biomass (chlorophyll *a*), and a greater biomass of cladocera (*Bosmina*) zooplankters, particularly in fall 1994. Increases in primary and secondary production benefitted rearing sockeye juveniles, exemplified by a positive (0.8) electivity index for *Bosmina* and by the large number of *Bosmina* found in sockeye fry stomachs. As a result, the 1994 fall (age-0) fry were 17% larger in size and better conditioned compared with 1993. Increasing sockeye production in Coghill Lake is contingent upon adequate fry recruitment. Recently adopted management strategies are in place to reduce the interception of Coghill sockeye in the commercial fishery to ensure escapement into Coghill Lake.

Key Words: Coghill Lake, glacial, meromictic, nutrient enrichment, *Oncorhynchus nerka*, Prince William Sound, restoration, sockeye salmon, zooplankton.

Citation:

Edmundson, J.A., G.B. Kyle, and S.R. Carlson. 1995. Restoration of Coghill Lakes sockeye salmon: 1994 annual report on nutrient enrichment restoration, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 94259), Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Soldotna, Alaska.

TABLE OF CONTENTS

Section Page

LIST OF TABLES

LIST OF TABLES (continued)

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Overview

Historically, Coghill Lake produced the largest sockeye salmon returns within the Coghill District of the Prince William Sound (PWS) commercial fishery. In 1982, over one million sockeye returned to Coghill Lake. Since 1987, however, sockeye returns have steadily declined to < 10,000 in 4 of the last 5 years. Several hypotheses have been proposed as causes for the decline in sockeye production. Edmundson et al. (1992) suggested that the decline was caused by a decrease in macrozooplankton from excessive planktivory by rearing fry. In particular, juvenile recruitment from the 1980-82 escapements (mean 160,000), which were nearly 3 times the 30-year mean escapement (65,000), most likely reduced zooplankton densities which adversely affected the lake's rearing capacity. Such top-down control by planktivorus fish and subsequent changes in fish production have been documented in other lakes (Carpenter et al. 1985; Kyle et al. 1988; Schmidt et al. 1994; Koenings and Kyle 1995). In addition, Willette et al. (1995) suggested that the *Exxon Valdez* oil spill (EVOS) in 1989 may have exacerbated the decline in sockeye production because juvenile salmonids migrated through oil-contaminated habitats in western PWS. However, there is no documented evidence that this occurred. It has also been speculated that climatic effects (e.g., temperature) on freshwater and/or marine survival may have contributed to the rapid decline of the Coghill sockeye run. While we recognize the importance of broad-scale temperature or energy variables to lake productivity (Brylinsky and Mann 1973) and salmonid production (Plante and Downing 1993), there is insufficient data to suggest that climatic effects are a primary cause for the observed rapid decrease in sockeye production. In addition, the interception of sockeye in the commercial harvests of adults returning to the Main Bay Hatchery in PWS has been proposed as a mechanism for this decline. While the specific cause(s) for the decline in sockeye returns remain unknown, limnological sampling revealed that Coghill Lake is a nutrient-limited system that supports a relatively low standing stock (biomass) of macrozooplankton (Edmundson et al. 1992).

The plan to restore Coghill sockeye includes nutrient enrichment as a means to increase productivity. Specifically, the restoration plan is to expand the forage base (zooplankton biomass) and to gradually increase the fry recruitment (commensurate with the forage base) by increasing the escapement through management techniques or hatchery stocking. Nutrient enrichment is a proven technique to increase a lake's capacity to produce forage (zooplankton) for rearing sockeye juveniles, which results in greater smolt biomass and higher adult returns (LeBrassuer et al. 1978; Stockner and Hyatt 1984; Stockner and Shortreed 1985; Kyle 1994; Kyle et al. 1995).

In considering the nutrient enrichment program for Coghill Lake, concern initially arose regarding the meromictic nature (monimolimnion) of this system and its effect on nutrient recycling. That is, the trapping of metabolites derived from the decomposition of organic matter within the monimolimnion, and the lack of recirculating nutrients into the trophogenic zone (Hutchinson 1957; Wetzel 1975). In addition, as Coghill Lake is glacially influenced, the presence of elevated turbidity derived from increased glacier melt, could counteract primary production through decreased light penetration, i.e., a reduced euphotic volume (Koenings et al. 1986; Grobbelaar 1989; Lind et al. 1994). These concerns are warranted as both phenomena affect lake productivity. However, two other meromictic lakes in Alaska have been treated with nutrients and have demonstrated positive results. For example, in Redoubt Lake (McCoy 1977) located near Sitka, increases in primary and secondary production resulted in larger smolts and higher adult returns (Kyle et al. 1995). Similarly, increased primary production and zooplankton biomass was observed in treated Hugh-Smith Lake located near Ketchikan (Peltz and Koenings 1989). Nutrient enrichment also increased productivity in glacially-turbid Owikeno and Kitlope lakes in British Columbia (Stockner 1987). Finally, current management plans (Donaldson 1994; PWSAC 1995) aimed at restricting the commercial harvest of Coghill sockeye in PWS when runs are weak are in place to ensure escapement into Coghill Lake.

In 1993 the EVOS Trustee Council approved restoration of Coghill Lake through a nutrient enrichment program to supplant fishery resources damaged by EVOS. The Alaska Department of Fish and Game (ADF&G), in cooperation with the U.S. Forest Service (USFS), initiated a 5-year nutrient enrichment project in 1993. During the first year (1993) of nutrient treatment, total phosphorus concentration increased by 13% and algal biomass (chlorophyll *a*) levels exhibited a 3-fold increase compared with the pre-fertilization years (Willette et al. 1995). In addition, macrozooplankton (*Cyclops* and *Bosmina*) densities and biomass more than doubled in comparison with the previous 4 years. As a result, continued fertilization of Coghill Lake was recommended for 1994 to further increase primary production and zooplankton biomass in conjunction with balancing fry recruitment (via escapement or fry stocking) with available forage. This report describes the results of the second year (1994) of nutrient treatment and discusses the effects of the treatment program on lake productivity and juvenile sockeye production.

Objectives

The primary objectives of the Coghill Lake restoration project are: 1) apply liquid fertilizer to the lake to increase nutrient concentrations, primary production (chlorophyll *a*), and zooplankton biomass; 2) determine the water residence time of Coghill Lake; 3) determine the responses of primary and secondary production to nutrient enrichment; 4) determine the effect of fertilization on the food consumption, growth, and condition of rearing sockeye fry; and 5) determine overwinter survival, age, size, and condition of sockeye smolts emigrating from the lake. In addition, we assess adult escapements and the escapement goal relative to the current forage base and historical return-per-spawner data.

Description of Study Area

Coghill Lake (61° 4' N, 147° 54'W) is located ~130 km northwest of Cordova in PWS at an elevation of 18 m (Figure 1). This lake has a surface area of 12.7 km^2, a mean depth of 46.3 m, and a total volume of 587×10^6 m^3 (Figure 2). Coghill Lake is a meromictic lake that possesses a dense (saline) and permanently stagnant water mass referred to as a monimolimnion (Hutchinson 1957; Wetzel 1975). This layer extends from a depth of about 30 m to the bottom of Coghill Lake, and comprises 45% of the total lake volume (Edmundson et al. 1992). In contrast, the lake mixes freely from the surface to a depth of ~20 m. This layer or mixolimnion is separated from the monimolimnion by a steep concentration gradient or chemocline (20-30 m).

METHODS

Fertilizer Application

Supplemental nutrient (phosphorus) loading rates for Coghill Lake were estimated using models developed by Vollenweider (1976). Based upon a spring total phosphorus (TP) concentration of 5 $\mu g\ L^{-1}$, the supplemental loading rate for 1994 was estimated to be 260 $mg\ m^{-2}\ yr^{-1}$. As a result, a total of 49,000 kg of pharmaceutical-grade liquid fertilizer containing 20% nitrogen and 5% phosphorus (20-5-0) was applied to the lake. In addition, 6,700 kg containing 32% nitrogen (32-0-0) was applied to correct for a summer depletion of nitrogen and to raise the nitrogen to phosphorus ratio. Application occurred in the middle third (5.5 km^2) of the lake (Table 1). In 1994, about 3 times more 20-5-0 fertilizer was applied than in 1993 in order to treat a larger portion of the lake and to further supplement nutrient loading. The fertilizer was dispensed via a fixed-wing aircraft on a weekly basis (a 2-3 day period) and consisted of 6 to 9 passes over the fertilization zone each day of application (Figure 2). Fertilizer was applied from about the end of June or early July, dependent upon weather conditions, to about the third week of August.

Limnological Sampling

During 1994, comprehensive limnological surveys were conducted seven times: 16 June, 20 July, 02 August, 18 August, 01 September, 29 September, and 13 October. Three limnetic sampling stations were established (Figure 2). Stations A and B represented the same survey sites as in previous years (1986-1993). Station D was first established in 1993 and is located between A and B in the middle of the fertilizer application zone (Figure 2). For each survey, light penetration (foot candles) was measured with an International Light photometer at 1-m increments from the surface to a depth of 27 m or to the light extinction (0 foot candles) depth. The vertical extinction coefficient (*Kd*), or the amount of light retained per meter, was equivalent to the slope derived via a 0-intercept linear regression for each set of photometer readings using the equation:

$$ln(I_Z/I_0) = KdZ \qquad (1)$$

where I_Z = light intensity (foot candles) at depth, I_0 = light at subsurface, Kd = extinction coefficient, and Z = depth. The euphotic zone depth (EZD), the depth at which 1% of the subsurface light (400-700 nm) penetrates, was calculated by substituting ln(100) into the regression equation ($EZD = 4.6052/Kd$). Water clarity was measured with a standard 20-cm Secchi disk. Temperature and dissolved oxygen concentration were measured at the surface and at 2-m increments to a depth of 10 m, and then at 5-m increments from 10 to 60 m.

Stream discharge was used to estimate lake water residence time, or conversely the flushing rate. Discharge was measured in Coghill River (outlet) twice during low, medium, and high flow periods. Water depth and current speed were measured at 10-m intervals along a transect perpendicular to the river length. The cross-sectional area of each segment and the current speed were used to estimate the discharge within each segment. Total discharge was calculated as the sum of the discharges for each segment (Koenings et al. 1987). Lake level was also measured using an electronic pressure recorder at the time discharge was estimated. Regression analysis was used to develop a relationship between stream discharge and lake level.

Water Sampling

Water samples were collected from 1 and 20 m at 3 stations (Figure 2). For each depth sampled, ~8 L of water were collected using a non-metallic Van Dorn sampler and placed in pre-cleaned polyethylene carboys. The samples were then transported to Cordova and filtered/preserved for laboratory analysis. Each sample was partitioned into three types: 1) refrigerated for general water-quality testing; 2) frozen for analysis of total phosphorus and total Kjeldahl nitrogen; and 3) filtered through a Whatman GFF glass-fiber filter and frozen for analysis of dissolved nutrients. Samples were stored in acid-cleaned polyethylene bottles and shipped to the limnology laboratory in Soldotna for analysis.

In the laboratory, conductivity (compensated to 25° C) was measured using a YSI conductance meter, and pH (@ 25° C) was measured with a Corning pH/ion meter. Alkalinity was determined by acid (0.02 N H_2SO_4) titration to pH 4.5 (AHAP 1985). Turbidity, expressed as nephelometric turbidity units (NTU) was measured with a HF meter, and color was determined on a filtered sample by measuring the spectrophotometric absorbance at 400 nm and converting to platinum-cobalt (Pt) units (Koenings et al. 1987). Calcium and magnesium were determined from separate EDTA (0.01N) titrations after Golterman (1969), and total iron was analyzed by reduction of ferric iron with hydroxylamine during hydrochloric acid digestion as described by Strickland and Parsons (1972). Filterable reactive phosphorus (FRP) was analyzed by the molybdenum-blue/ascorbic acid reduction of Murphy and Riley (1962) as modified by Eisenreich et al. (1975). Total phosphorus was determined using the FRP procedure after acid-persulfate digestion. Nitrate + nitrite was analyzed as nitrite following cadmium reduction of nitrate, and total ammonia was determined using the phenylhypolchlorite methodology (Stainton et al. 1977). Total Kjeldahl nitrogen (TKN) was determined as total ammonia following block digestion (Crowther et al. 1980). Finally, reactive silicon was determined using the method of ascorbic acid reduction to molybdenum blue after Stainton et al. (1977).

Algal Biomass and Zooplankton Sampling

Samples used for algal biomass (chlorophyll *a*) analysis were collected from 1 and 20 m at the 3 stations. These samples were prepared by filtering 0.5-1.0 L of lake water through a Whatman GFF glass-fiber filter, to which 1-2 ml of saturated magnesium carbonate solution were added just prior to completion of the filtration. The filters were stored frozen in individual plexislides for later analysis. Pigment was extracted after homogenizing glass-fiber filters in 90% acetone using a tissue grinder and pestle. Chlorophyll *a* concentrations (corrected for phaeophytin) were determined using the fluorometric procedure of Strickland and Parsons (1972). The low strength acid addition recommended by Reimann (1978) was used to estimate phaeophytin.

Zooplankton samples were collected from the 3 sampling stations. Vertical zooplankton tows were taken from the 25-m depth to the surface using a 0.2-m diameter, 153-μm mesh, conical net. The net was pulled manually at ~0.5 m sec^{-1}. The contents were rinsed into a polybottle and preserved with buffered formaldehyde to a final 10% formalin-sample solution. Cladocerans and copepods were identified using taxonomic keys by Brooks (1957), Pennak (1978), Wilson (1959), and Yeatman (1959). Enumeration consisted of counting the animals in triplicate 1-ml subsamples taken with a Hansen-Stempel pipet in a 1-ml Sedgewick-rafter cell. Zooplankton body length was measured to the nearest 0.01 mm for at least 10 individuals along a transect in each of the 1-ml subsamples (Koenings et al. 1987). Zooplankton biomass was estimated from species-specific regression equations derived between zooplankter body length and weight (Koenings et al. 1987).

Sockeye Fry Investigations

Juvenile sockeye salmon fry samples were collected during 16-18 August and 27-29 September for stomach content analysis, food electivity indices, food consumption, growth rates, and condition factor. Juvenile fish were collected along several randomly selected transects using a 7.5-m long mid-water trawl with a 2 x 2 m opening. Diel samples of fry, which were collected approximately every 3-6 hours at a single site over 24 hours, were used to evaluate feeding periodicity and estimate daily food ration. Fish were preserved in 10% buffered formaldehyde for at least 6 weeks (to stabilize shrinkage) before being measured to the nearest millimeter and weighed to the nearest 0.1 g. A scale smear was taken from each fish, affixed to a glass slide, and aged using a microfiche projector. Stomachs were eviscerated and preserved in 10% buffered formalin. Stomach contents were identified and enumerated to the lowest possible taxonomic level. Zooplankton were measured to the nearest 0.01 mm and prey (zooplankton) body weight was estimated from empirical regression formulae between zooplankter body length and dry weight (Koenings et al. 1987). Insects or insect body parts were placed on a glass slide, dried, and then weighed directly.

A hydroacoustic survey was conducted in September 1994 to estimate juvenile sockeye abundance and distribution. The survey was conducted at night when the fry are uniformly dispersed using a 420-khz dual-beam echo sounder. The data were collected along randomly selected transects, and the data are currently being analyzed under contract with the Prince William Sound Science Center. Results of this survey were not available at the time this report was prepared but will be provided in a future report.

Sockeye Smolt Sampling

Four inclined-plane traps (Todd 1994) were used to estimate the population of smolts and to collect smolts for size and age information. The traps covered an area that was approximately 50% of the river surface area (Figure 3). All 4 traps were installed on 24 April, and three traps were fished until 3 July; one of the traps was removed on 23 June due to a poor catch rate. Trap efficiencies were estimated from a mark-recapture technique (Rawson 1984; Todd 1994). A total of 8 mark-recapture experiments were conducted between 05 May and 18 June. Bismark brown dye was used to mark (dye) the smolt. All smolts captured were examined for dye coloration. Results of trap efficiency trials were applied to their respective time periods to estimate weekly abundance. Population estimates were adjusted for the number of mortalities in the traps. Methods described by Rawson (1984) were used to estimate the smolt population and variance. During the trapping operation all smolts were individually enumerated, and 40 per day were sampled for age, weight, and length (AWL) information. Stratified random sampling methods (Cochran 1977; Scheaffer 1986) were used to estimate age-class proportions and their respective variances; daily strata were established and stratum weights were based on smolt abundance estimates. Mean weight and length of each age-class and associated variances were estimated using stratified sampling methods for subpopulations (Cochran 1977).

Sockeye Escapement and Harvest

Adult sockeye salmon returning to Coghill Lake were enumerated with the use of a weir by the ADF&G Commercial Fisheries Management and Development (CFMD) Division as part of its management of this run. Returning adults were enumerated and sampled for age, size, and sex following procedures described by Crawford and Simpson (1991). The commercial harvest of Coghill sockeye takes place in several distinct areas in PWS including the Eshamy and Coghill Districts. However, the entire Coghill District was last open to commercial fishing in 1989. Since then, the commercial gillnet fleet has been restricted to fishing in either the Esther Subdistrict, a reduced subdistrict, or in the hatchery terminal harvest area in an effort to reduce the harvest of Coghill Lake sockeye. Similar restrictive measures have been incorporated in the Eshamy District. In 1994, the Crafton Island Subdistrict remained closed the entire season to protect weak Coghill and Northwest

District stocks which move through the Eshamy District. Closures of the Crafton Island Subdistrict to protect Coghill sockeye occurred in 1993 as well.

Age class and run timing differences between Coghill and Eshamy stocks were used to distinguish commercial harvest reported on fish tickets. While it is generally known that some Coghill sockeye are intercepted in fisheries in the Southwest, Eshamy, and Unakwik Districts (Merritt and Donaldson 1995), most of the catch in the Coghill District is assumed to be primarily Coghill sockeye.

Data Analysis

The effect of nutrient enrichment on general water chemistry, nutrient concentration, algal biomass (chlorophyll *a*), and secondary (zooplankton) production were assessed using analysis of variance (ANOVA) to test for differences between pre-enrichment (PE) and enrichment (E) years. These analyses were accomplished using a randomized complete block design to test for overall year effect, followed by a contrast statement to compare the PE and E years. We also tested for spatial (station) differences. Because station D was not established until 1993, only stations A and B were included in these analyses. All tests were conducted at the $\alpha = 0.05$ significance level. Statistical analysis was facilitated using SYSTAT version 5 (Wilkinson 1990) or SAS/STAT version 6 (SAS Institute 1990).

The effect of the fertilization on sockeye salmon fry was evaluated by testing for changes in condition factor between months and years. Two approaches were used to assess changes in fry condition. A relative weight index was computed based on the length-weight regression model:

$$W = aL^{b} e^{\varepsilon} \tag{2}$$

which can be written in linear form as: $\ln(w) = \ln(a) + b\ln(L) + \varepsilon$, where ln(a) is the intercept and b is the slope of the model. Regression analysis was used to estimate the relationship between ln(w) and ln(L). The condition factor (K) of individual fish was estimated by:

$$K = \frac{W}{\hat{W}} \tag{3}$$

where $\hat{W}$ is the predicted weight based on the fitted length-weight regression equation (LeCren 1951). Seasonal and yearly changes in the condition index were then evaluated using 1-way ANOVA followed by pairwise comparisons. The second approach used a separate-slopes analysis of covariance (ANCOVA) model to compare length-adjusted weights between groups of fry (ln-ln transformed data). With this approach, mean weight was compared after removing the effect of length, thus providing an alternative evaluation of condition. Comparisons of length, weight, and dry weight were evaluated using 1-way ANOVA followed by pairwise mean comparisons.

The electivity index (Ivlev 1961) was calculated to determine the active selection of prey items by rearing sockeye fry. This index has a range of -1 to +1; negative values indicate either avoidance or inaccessibility of a prey item, zero indicates random selection, and positive values indicate preference. The electivity index was estimated as:

(4)
$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

where E_i is the electivity measure for prey species *i* in the stomach of the predator expressed as a proportion or percentage of the total stomach contents, and p_i represents the relative abundance of the same prey item in the lake expressed as a proportion or percentage of the total density.

The diel feeding study was used to estimate food consumption utilizing temperature-specific gastric evacuation rates from Brett and Higgs (1970). Gastric evacuation is described by:

(5)
$$V_t = V_0 e^{-bt}$$

where V_t is the mean fullness (stomach content weight as a percent of fry dry weight) at time t (hours), V_0 is the initial mean fullness, and b is the temperature-specific gastric evacuation rate (Fange and Grove 1979). Daily ration (I) was estimated by:

(6)
$$I = \sum_i V_i (1 - e^{-bt})$$

where V_i is the mean fullness at the beginning of each time interval and t is the length of the time interval in hours.

Fry diet analysis included mean abundance (number fry^{-1}) and biomass (μg fry^{-1}) of each diet item for samples collected in August and September of 1994. These data were compared by month using a 2-stage nested design (townets within sampling period) after Montgomery (1984). Comparisons of fry diet for August and September between rearing years (1993 and 1994) were performed using a factorial-nested design.

Spawner-recruit analyses used Ricker's (1975) model to examine historical spawner-return data (1962-88) relative to assessing the escapement goal. Residuals from the model were analyzed for autocorrelation (Hilborn and Walters 1992) using the Durbin-Watson statistic; if warranted, autoregressive (AR) parameters were added to the model as a corrective measure. We also evaluated average return-per-spawner (R/S) and yield (returns minus escapement) for various escapement ranges.

RESULTS

Physical Features

Although Coghill Lake is glacially influenced, turbidity levels in 1994 were relatively low (Figure 4A). Within the 1-m stratum, turbidity ranged from 1.8 to a maximum of 4.6 NTU, and averaged 2.6 NTU. Maximum turbidities occurred in the fall (29 September) which corresponded with the time of peak glacier runoff. Analysis of variance (ANOVA) indicated no significant difference ($p = 0.202$) in turbidity levels between stations (Table 2). Seasonal mean turbidity exhibited a 3-fold decrease in 1994 compared to 1993 (mean 7.2 NTU). Correspondingly, the euphotic zone depth (EZD) was much deeper ($p < 0.001$) in 1994 (13.8 m) compared with 1993 (6.6 m) (Figure 4B). However, conditions of reduced turbidity and greater light penetration did not translate into warmer water temperatures in 1994, as the maximum surface temperature (~15° C) was comparable to previous years (Figure 4C). ANOVA indicated a significant ($p < 0.001$) decrease in color during enrichment but the 2 Pt unit difference is within natural variation of non-stained lakes (Koenings and Edmundson 1991). Nonetheless, based upon field observations, it appeared that the 1994 growing season was shorter compared to 1993, as ice out occurred in early June and the lake began to freeze by early October. Finally, a significant relationship was derived between stream depth (SD) and discharge (DIS). The relationship was DIS ($m^3\ sec^{-1}$) = -41.4 + 1.19SD (cm), ($r^2 = 0.85$; $p < 0.05$). Based on summer (May-August) discharge estimates, the hydraulic residence time for this period was estimated at 56 days (0.15 yr).

Water Chemistry and Nutrient Concentrations

Summaries of water chemistry and nutrient concentrations for Coghill Lake for 1986-94 are presented in Appendices A and B. Results of ANOVA on seasonal mean values derived from the epilimnetic (1 m) samples (Table 2) revealed no significant spatial (station) differences in general water chemistry; however, pH was significantly ($p < 0.001$) lower during enrichment (mean 7.0 units) compared to pre-enrichment (mean 7.2 units). However, the 0.2 unit difference in pH is not biologically significant. Conductivity (mean 75 μmhos cm^{-1}) nor alkalinity (mean 19 mg L^{-1}) differed significantly between the two periods. There were no significant ($p > 0.05$) spatial or treatment differences for calcium, magnesium and iron concentrations. For all years sampled, calcium averaged 7.4 mg L^{-1}, magnesium 1.4 mg L^{-1}, and iron 212 mg L^{-1}.

In contrast, there were significant spatial and treatment differences in seasonal mean TP and TKN concentrations. In particular, TP concentrations were higher (21%; $p = 0.013$) at station A (9.1 μg L^{-1}) compared with station B (7.5 μg L^{-1}) (Table 2). Over all years (1986-94), TP was highest in 1989 (11 μg L^{-1}), lowest in 1988 (6.4 μg L^{-1}), and averaged 8.3 μg L^{-1} (Appendix A). During enrichment (1993-94), TP concentrations (mean 9.6 μg L^{-1}) were significantly higher (20%; $p = 0.05$) compared to pre-enrichment (mean 8.0 μg L^{-1}). In addition, TKN concentrations were significantly higher (15%; $p = 0.023$) at station A (mean 61 μg L^{-1}) compared with station B (mean 53 μg L^{-1}). Moreover, in

1994 TKN concentrations (mean 97 μg L^{-1}) were the highest on record, and represented a 2-fold increase compared to pre-enrichment years. Inorganic phosphorus (TFP and FRP) concentrations were quite low and for all years averaged 3.7 and 2.4 μg L^{-1}, respectively (Appendix A); there were no significant differences by station (spatially) or after treatment (Table 2). Inorganic nitrogen (ammonia and nitrate + nitrite) levels were also very low and averaged <3 μg L^{-1} and 17 μg L^{-1}, respectively for all years. During enrichment ammonia, nitrate + nitrite, and reactive silicon concentrations were significantly lower (Table 2), but lower concentrations during treatment reflected higher assimilation by phytoplankton.

Algal Biomass

During 1994, chlorophyll *a* (chl *a*) concentrations within the epilimnion ranged from 0.2 to 3.9 μg L^{-1}, and averaged 1.73 μg L^{-1} (Figure 5A). Relatively high (~2 μg L^{-1}) concentrations occurred from mid-July through September. In addition, higher than average chl *a* concentrations occurred at all 3 stations (at the 1-m stratum), and no significant spatial (station) differences were observed (Table 2). The mean chl *a* concentration in 1994 was nearly identical to that observed in 1993 (1.75 μg L^{-1}) (Figure 5B). In comparison, chl *a* concentration prior to enrichment averaged only 0.66 μg L^{-1}. This 2.5-fold significant increase ($p = 0.001$) in chl *a* during enrichment appeared to be consistent with an increase in TP concentration (Table 2; Figure 5B).

Zooplankton

A summary of zooplankton density, biomass, and size is presented in Appendix C. The macrozooplankton community in Coghill Lake is comprised primarily of *Cyclops* and *Bosmina*. Two other species of cladocera, *Daphnia* and *Chydorinae* occur sporadically in very low densities. In 1994 *Cyclops* density (number m^{-2}) increased from 12,239 m^{-2} in June to a maximum density of 48,450 m^{-2} in July, and averaged 25,677 m^{-2} over the season (Figure 6A). By late summer, *Cyclops* began to decline and densities decreased to a seasonal low of 5,066 m^{-2} by mid-October. Seasonal mean *Cyclops* densities were slightly higher at station B (~45,000 m^{-2}) compared to station A (~35,000 m^{-2}), but not significantly ($p = 0.079$) (Table 3). *Bosmina* populations did not appear in large numbers until late summer, and by late September *Bosmina* reached a maximum density of 23,700 m^{-2} ; over the entire season *Bosmina* averaged 4,758 m^{-2}. The total macrozooplankton (TMZ) density averaged 34,200 m^{-2} in 1994. Thus, in 1994 *Cyclops* comprised nearly 100% of the TMZ density in July and August, whereas *Bosmina* comprised the largest proportion (60%) of the density in September and October.

The mean *Cyclops* density (24,318 m^{-2}) in 1994 was about 50% lower compared to 1993 (49,899 m^{-2}) (Figure 6B). In contrast, seasonal mean cladoceran (*Bosmina* and *Daphnia*) densities in 1994 (5,044 m^{-2}) exhibited more than a 50-fold increase compared to 1993 (mean 90 m^{-2}), and were the highest ever observed for this lake. Both *Cyclops* and cladoceran biomass levels followed the same temporal trends as density (Figure 6C). The 1994 TMZ biomass equaled 42 mg m^{-2}, of which *Cyclops* comprised 87% (36 mg m^{-2}), *Bosmina* 13% (5.5 mg m^{-2}), and *Daphnia* <0.1% (0.02 mg m^{-2}). *Cyclops* biomass in 1994 was less than half that in 1993. In contrast, *Bosmina* biomass increased from 0.05 to 5.5 mg m^{-2}, which represents more than a 100-fold increase compared to 1993.

For testing of spatial and treatment effects (ANOVA), we excluded the 1986 zooplankton data because only a single station was surveyed (see Appendix C). During the two years of treatment (1993-94), seasonal mean *Cyclops* density (37,108 m^{-2}) was not significantly different ($p = 0.442$) compared to all pre-enrichment years (1988-92) (Table 3). However, if the exceptionally high density of 1988 is excluded from this analysis, the mean *Cyclops* density for the 2 treated years exceed the 4-year (1989-92) pre-enrichment mean by 69% ($p = 0.05$). The seasonal mean density of *Daphnia* was also not significantly different ($p = 0.084$) during enrichment compared to all pre-enrichment years, and comparing the mean of the 2 treated years with the mean excluding 1988 revealed the same. This is not unusual given that the presence of *Daphnia* has been sporadic in this lake (Appendix C), which is typical for semi-glacial systems (Koenings et al. 1990). In contrast, mean *Bosmina* density (2,562 m^{-2}) exhibited a 20-fold increase ($p < 0.001$) during enrichment compared to all the pre-enrichment years (mean 131 m^{-2}). While the mean body size of *Cyclops* was not significantly different ($p = 0.202$) during enrichment (0.69 mm) compared to pre-enrichment (0.73 mm), both *Bosmina* and *Daphnia* were significantly (p = 0.001 and 0.002) smaller during enrichment (*Bosmina*; 0.35 mm, *Daphnia*; 0.71 mm) compared to pre-enrichment (*Bosmina*; 0.46 mm, *Daphnia*; 0.80 mm). Although mean *Bosmina* biomass was significantly higher ($p < 0.001$) during enrichment (2.8 mg $m\text{-}^{2}$) compared to pre-enrichment (0.3 mg m^{-2}), both *Cyclops* and *Daphnia* biomass was not (Table 3). Finally, ANOVA indicated no significant spatial (station) differences in average macrozooplankton density, body size, or biomass (Table 3).

Sockeye Fry Diet, Condition, and Size

A total of 213 sockeye fry were collected in August and September of 1994 for stomach content analysis (Table 4). Stomach foregut samples from August contained an average of 270 *Cyclops* fry^{-1} which represented 91% (numerically) of the total contents and 96% (mean 1,008 μg) of the total biomass. *Bosmina* represented <9% (mean 26 fry^{-1}) of the contents and 4% (mean 44 μg) of the contents biomass. Together, *Chydoridae*, *Harpacticoid* and *Chironomid* represented < 0.01% (numerically) of the total stomach contents. In contrast, samples from September contained an average of 1,984 *Bosmina* fry^{-1} which represented 96% of the total contents and 90% (mean 2,749 μg) of the contents biomass. *Cyclops* represented only 4% (mean 85 fry^{-1}) of the total contents and 10% of the contents biomass in September. *Chydoridae*, *Harpacticoid* and *Chironomid* were also found in the fry stomachs during September, but these species represented < 0.03% (numerically) of the total stomach contents. Although *Bosmina* represented a significantly larger component of the fry diet (by abundance and biomass) in September, ANOVA indicated no significant difference in the abundance or biomass of *Cyclops* in the stomachs between August and September (Table 4).

The fry diet in August and September of 1994 differed from that found in the same months of 1993 (Table 5). During August and September of 1993 the fry diet consisted primarily of *Cyclops*; however, in 1994 the fry diet switched from predominantly *Cyclops* in August to mostly *Bosmina* in September. In addition, sockeye fry stomach samples in 1994 contained a significantly larger ($p < 0.05$) number and greater biomass of *Cyclops* compared to those in 1993. Moreover, while > 90% of the stomach contents (and biomass) was comprised of *Bosmina* in September of 1994, this taxon represented only ~1% of the stomach contents in September of 1993. Finally, while *Chydoridae* were a very minor component of the fry diet in 1994 (at least in August and September), they comprised ~10% of the stomach content biomass in August of 1993.

Estimated daily ration in September (2.17%) exceeded the August estimate (1.14%) by nearly two times (Table 6). This corresponded to higher mean stomach fullness values in September (1.2-2.8%) compared to August (0.6-1.2%), while water temperatures differed by only 0.5° C. Peak stomach fullness occurred at 2130 hours (9:30 pm) in September and at 0430 hours (4:30 am) in August. These results should be viewed with caution, however, since afternoon and evening samples of fry were not obtained in August.

In 1994, prey selection based on Ivlev's (1961) index of electivity (E) indicated a strong preference by rearing sockeye fry for ovigerous *Cyclops* in August (Table 7). Ovigerous *Cyclops* represented 0.1% of the lake's TMZ density in August, but comprised nearly 2% of the fry stomach contents ($E = 0.88$) and biomass ($E = 0.61$). In August, there was a slight positive selection for non-ovigerous *Bosmina*, but ovigerous *Bosmina* and non-ovigerous *Cyclops* were randomly selected. In contrast, there was a strong preference for ovigerous *Bosmina* ($E = 0.79$ by abundance and $E = 0.82$ by biomass) in September. While *Bosmina* comprised ~50% of the September TMZ density in the lake only ~10% were ovigerous; however, ovigerous *Bosmina* accounted for ~80% ($E = 0.79$) of the fry stomach contents (numerically and based on biomass). In contrast, there was strong avoidance of both non-ovigerous *Cyclops* ($E = -0.85$ by abundance and $E = -0.73$ by biomass) and *Bosmina* ($E = -0.51$ by abundance and $E = -0.44$ by biomass).

In 1994, age-0 fry were larger and in better condition in September compared to August (Table 8). Mean age-0 fry size increased significantly ($p < 0.05$) from 45 mm and 904 mg in August to 48 mm and 1,040 mg in September. Mean dry weight also increased significantly ($p = 0.017$) from August to September. Fry condition based on wet and dry weights increased from 0.98 to 1.01 ($p = 0.016$) and 0.97 and 1.03 ($p = 0.004$), respectively between August and September. Length-adjusted dry weight also increased significantly ($p = 0.011$) from August to September. Although average length-adjusted wet weight increased from 909 to 931 mg, this 2% increase was not significant ($p = 0.074$). The 1994 fall (age-0) fry were also larger (Figure 7A) and in better condition (Figure 7B) compared to 1993. In particular, mean age-0 fall fry length increased by 10% and the average weight increased by 17% compared to the 1993 mean size (44 mm; 763 mg). Fry condition based on wet weight increased from 0.86 in 1993 to 0.97 in 1994.

Smolt Abundance, Size, and Age Composition

Trap efficiency ranged from 1.3% to 18% and averaged 9% (Table 9). The peak outmigration occurred during the week of 22-28 May when a total of 38,917 smolts were trapped. Between 05 May and 18 June the 4 traps caught nearly 89,000 smolts. The total estimated smolt outmigration in 1994 was 1,272,500 ± 259,850 (95% C.I.). Age-1 smolts comprised 97.4% (1,239,400) of the total outmigration and age-2 comprised 2.6% (33,100). The 1994 outmigration was the largest since sampling began in 1989, and represents a 4-fold increased in estimated smolt abundance compared to 1993 (Figure 8A). The 1994 smolt outmigration exceeded the 1993 fall estimate (610,000) of rearing fry by 2 fold. In 1994, a total of 2,342 smolts were sampled for AWL. Age-1 smolt size (Figure 8B) averaged 56.7 mm and 1.40 g, whereas age-2 smolts averaged 79.6 mm and 4.23 g (Figure 8C). The 1994 mean smolt sizes were relatively consistent with the average size for previous years except for 1989 in which the age-1 smolts were the smallest (51.8 mm; 1.04 g) for the 5 years sampled and the age-2 smolts were the largest (91.1 mm; 5.95 g).

Sockeye Escapement and Return-Per-Spawner

The 1994 sockeye escapement of 7,264 was well below the targeted escapement goal of 25,000. In 4 of the last 5 years, sockeye escapements averaged <10,000. The 1992 escapement equaled ~30,000, but this escapement was still lower than the 30-year mean escapement (65,000). For escapements below 30,000, brood year returns (escapement + harvest) averaged 114,000 fish for a return-per-spawner (R/S) of 8.1 (Table 10). R/S estimates were slightly higher (9.1) for escapements between 30,000 and 50,000. Escapements of less than 30,000 resulted in an average yield of 96,500 and escapements between 30,000 and 50,000 yielded about 270,000 sockeye. For escapements ranging from 40,000-60,000, 50,000-70,000, and 60,000-90,000 the average R/S ranged from 1.2 to 3.3, and the yield ranged from 14,300 to 119,100. When escapements exceeded 90,000, the R/S was 2.1 and the yield was 165,900. Although R/S for the high escapements (140,000-180,000) of 1980-82 was about average (3.3), subsequent higher-than-average escapements for brood years 1985-88 (mean 124,000) resulted in R/S < 1.0 (Figure 9).

DISCUSSION

Trophic Responses to Nutrient Treatment

Nutrient additions to Coghill Lake had positive effects on both nutrient concentration, algal biomass, and zooplankton biomass. Specifically, TP and chl *a* concentrations (Figure 5B), as well as macrozooplankton density and biomass (Figure 6) were higher during the 2 years of enrichment compared to pre-enrichment (Tables 2 and 3). We believe the higher TP and chl *a* levels were not attributed to a general increase in nutrient input from the surrounding watershed nor increased glacier melt. In particular, reactive silicon, an element contained in the surrounding watershed, but not in the fertilizer, was found to be in a lower concentration during enrichment compared to previous years which would suggest a decrease in terrigenous loading (Dillon and Rigler 1974). Moreover, although TP concentration is highly correlated with glacial turbidity (Edmundson and Koenings 1985; Koenings et al. 1986), TP levels in 1994 (mean 8.5 μg L^{-1}) were higher compared to the pre-enrichment years (mean 7.9 μg L^{-1}), yet turbidity exhibited nearly a 3-fold decrease (Figure 4B). This implies that the increased phosphorus concentration in 1994 was a direct result of nutrient additions. The mean TP concentrations were lower than expected (10 μg L^{-1}) based on nutrient loading calculations; however, this may be due to a faster flushing rate or shorter water residence time than the original estimate of 0.9 years (Edmundson et al. 1992). Based on discharge measurements during the summer, the water residence time was estimated at 51 days during the summer months of 1993 (Willette et al. 1995) and 56 days (0.15 years) in 1994. Although the phosphorus loading rate is based on annual discharge (Vollenweider 1976), the original annual residence time of 0.9 years may be overestimated. Thus, supplemental phosphorus loading may have been underestimated if the actual water residence time is shorter, and a shorter residence time would contribute to not achieving 90% of the theoretical critical loading rate (i.e., 10 μg L^{-1}).

We question the validity of the 1988 zooplankton data, which appears as a dominant outlier (Appendix C) and consequently influences the comparison of zooplankton density and biomass between enrichment and pre-enrichment periods (Table 3). Specifically, we suggest that there is a strong possibility of sampling error for the 1988 surveys because the seasonal mean *Cyclops* density and biomass (Figure 6; Appendix C) are about 3 times higher compared to the 4 immediate years before treatment (1989-92). In addition, we would expect the 1988 zooplankton, which comprises mainly of *Cyclops*, to be one of the lowest given the 1987 record escapement of ~190,000 and the apparent high preference for *Cyclops* (Table 7). If the 1988 data are in error and excluded from analysis, *Cyclops* densities were significantly higher (69% increase) during enrichment compared to pre-enrichment. However, as this cannot be confirmed, we did not exclude 1988 data from ANOVA testing (Table 3). Although mean zooplankton density and biomass were ~50% less in 1994 compared to 1993, the production of *Bosmina* increased significantly (Table 3) compared to previous years (Figure 6). In particular, *Bosmina* densities increased steadily during September-October as *Cylcops* densities decreased (Figure 6A). Cladoceran density and biomass are known to increase under enriched conditions (Brooks 1969; Allen 1976; Vanni 1986), and these animals are a preferred prey item for foraging sockeye juveniles as exemplified by the large numbers of *Bosmina* (mean 1,984 fry^{-1}) found in the fry foreguts (Table 4), and a strong positive electivity index (Table 7). The fact that *Bosmina* populations remained low during the initial year of enrichment may reflect a very low recruitment since *Bosmina* densities were severely depressed for several consecutive years (Figure 6B). It is known that collapsed zooplankton populations resulting from heavy grazing by juvenile sockeye may take several generations to recover (Kyle et al. 1988; Koenings and Kyle 1995).

We suggest that in 1993 ovigerous *Bosmina* were too few in number for these populations to immediately increase under the first year of nutrient additions. The decrease in seasonal mean *Cyclops* density (and biomass) in 1994 compared to 1993 (Figure 6) is most likely a result of increased planktivory due to the relatively high fry densities in the lake during 1993 (Willette et al. 1995), and as evidenced by the high 1994 smolt outmigration (1.3 million smolt). Moreover, the escapement that produced the 1994 smolts (1992; 30,000) and subsequent potential fry recruitment was the largest in the past 5 years (Willette et al. 1995). Thus, as sockeye fry in Coghill Lake are highly selective for ovigerous *Cylcops* (Table 7), the lower densities in 1994 are likely attributed to low recruitment and the protracted reproduction of copepods, which typically produce a single generation annually (Carter 1965; Pennak 1978).

As an apparent result of an improved forage base extending through the fall, rearing sockeye fry were larger in size and of better condition in 1994 (Figure 7) compared to 1993. This is attributed not only to higher nutrient additions (Table 1), but also to a relatively low fry density in the lake compared to 1993. That is, though we currently lack the 1994 fall fry hydroacoustic estimate, presumably fry densities were low based on juvenile recruitment from the 1993 adult escapement (9,200). In contrast, the smaller mean size and lower condition factor exhibited by the 1993 fall fry may have indicated increased interspecific competition for a limited forage base. Unlike 1994, when *Bosmina* densities increased dramatically during September (Figure 6A), a fall cladoceran bloom did not occur in 1993 (Figure 6B). Thus, the 1994 rearing fry population foraged (Tables 4, 7) on higher densities of *Bosmina* (Figure 6A) prior to overwintering, whereas the 1993 fry population did not (Table 5). Nonetheless, despite a paucity of cladocerans in the lake in 1993, *Cyclops* density and biomass were higher compared to 1994.

Under density-dependent conditions, a significant relationship has been developed between smolt biomass and zooplankton biomass (smolt biomass in kg km^{-2} = 2.1 x zooplankton biomass in mg m^{-2}) (Koenings and Kyle 1995). Based on the 1993 seasonal mean zooplankton biomass (86 mg m^{-2}), this model would predict the production of about 1 million threshold sized (~2 g) smolts which is nearly equivalent to the 1994 smolt outmigration estimate of 1.3 million. The weight of age-1 smolts in Coghill Lake (Figure 7B) are less than the average threshold size of smolts in other sockeye nursery lakes (Koenings and Burkett 1987), and consequently there may be some genetic control (advantage) of small smolts in this system. However, smolt size has dramatically increased in fertilized lakes of Alaska (Kyle 1994; Kyle et al. 1995).

Since we lack juvenile sockeye information and limnological (zooplankton) data for Coghill Lake prior to the decline in sockeye production, the specific cause(s) for this decline is unknown. Nonetheless, current production levels are the result of a very low return-per-spawner, very low nutrient pool, and small standing stock of zooplankton (Edmundson et al. 1992). Thus, the restoration project for Coghill sockeye focuses on increasing lake productivity through nutrient enrichment, which has been demonstrated as a successful tool to increase sockeye production (LeBrasseur 1978; Stockner and Hyatt 1984; Stockner and Shortreed 1985; Kyle 1994; Kyle et al. 1995). In addition, the restoration project incorporates balancing fry recruitment via management regulations of the escapement and/or fry stocking based on available forage.

Escapement Goal Assessment

Although the effects of nutrient enrichment in Coghill Lake are positive, achieving adequate escapement has been problematic due to the possible interception of sockeye in the commercial gillnet fisheries within the Eshamy and Coghill Districts. These fisheries target enhanced sockeye and chum salmon stocks returning to Main Bay and Noerenberg hatcheries. However, current management strategies have restricted the gillnet fishery in order to reduce the harvest of Coghill Lake sockeye and to ensure escapement (Donaldson 1994; PWSAC 1995). Nonetheless, the current escapement goal (25,000) has been met only once (1992) in the past 5 years. In that year, juvenile recruitment from the adult escapement (30,000) was likely at or near rearing (forage) capacity as the 1994 smolt outmigration produced 93% age-1 smolts of sub-threshold size (~2 g) (Koenings and Burkett 1987). Thus, the targeted escapement goal is consistent with the escapement levels (30,000-50,000) which historically produced the highest return-per-spawner (9.1) and maximum sockeye yield (270,000) (Table 10). Although the very high escapements (> 100,000) during 1980-82 resulted in a similar R/S, subsequent (1985-87) high escapements did not (Figure 9). When the 1980-82 escapements were omitted from a classic Ricker (1975) analysis (Table 11), the escapement (40,000) required to produce maximum sustained yield (195,000) was similar to the current escapement goal (25,000). These results indicate that the effect of overescapement on freshwater rearing capacity offers at least a partial explanation for the collapse of the Coghill sockeye run. Therefore, we would caution against fry stocking at levels that, when combined with escapement, would exceed natural fry recruitment from escapements of about 30,000 as in 1992. Fry recruitment in excess of the forage base (zooplankton biomass) could undermine the benefits of nutrient enrichment and delay the restoration of the Coghill sockeye run.

AUTHORS

Jim A. Edmundson is the limnologist in charge of the Statewide Limnology laboratory for the Alaska Department of Fish and Game, Limnology Section, Division of Commercial Fisheries Management and Development, 34828 Kalifornsky Beach Road, Suite B, Soldotna AK 99669.

Gary B. Kyle is the southcentral Regional Limnologist for the Alaska Department of Fish and Game, Limnology Section, Division of Commercial Fisheries Management and Development, 34828 Kalifornsky Beach Road, Suite B, Soldotna AK 99669.

Stanley R. Carlson is a biometrician for the Alaska Department of Fish and Game, Limnology Section, Division of Commercial Fisheries Management and Development, 34828 Kalifornsky Beach Road, Suite B, Soldotna AK 99669.

ACKNOWLEDGMENTS

Mark Willette and Greg Carpenter of ADF&G in Cordova coordinated collection of field data. Limnology Laboratory staff provided timely analysis of nutrient, zooplankton, and fish samples. Funding for this project was provided by the *Exxon Valdez* Oil Spill Trustee Council, and the United States Forest Service administered some of this funding for the purchase and application of fertilizer in 1994.

LITERATURE CITED

Allen, J. D. 1976. Life history patterns in zooplankton. Amer. Naturalist. 110:165-180.

American Public Health Association (AHPA), American Water Works Association and Water Pollution Control Federation. 1985. Standard methods for the examination of water and wastewater. 16th edition. New York. 1268p.

Brooks, J. L. 1957. The systematics of North American *Daphnia*. Mem. Conn. Acad. Arts Sci. 13:1-180.

Brooks, J. L. 1969. The effects of prey size selection by lake planktivores. Syst. Zool. 17:273-291.

Brylinsky, M. and K. H. Mann. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. 18:1-4.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience 35:634-639.

Carter, J. C. H. 1965. The ecology of the calanoid copepod (*Pseudocalanus minutus*) in Kroyer in Tessiarsuk, a coastal meromictic lake of northern Labrador. Limnol. Oceanogr. 10:345-353.

Cochran, W. G. 1977. Sampling Techniques. John Wiley & Sons, New York.

Crawford, D. and E. M. Simpson. 1991. Catch and escapement statistics for Copper River, Bering River, and Prince William Sound. 1988. Ak. Dept. Fish and Game Regional Information Report 91-06. 193p.

Crowther, J., B. Wright, and W. Wright. 1980. Semi-automated determination of total phosphorus and total Kjeldahl nitrogen in surface waters. Anal. Chem. Acta. 119:313-321.

Dillon, P. J. and F. H., Rigler. 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. J. Fish. Res. Bd. Canada 31:1771-1778.

Donaldson W. 1994. Prince William Sound salmon summary. Memorandum to Jeffery Koenings, October 21, 1994. 18 p.

Edmundson, J. A. and J. P. Koenings. 1985. The effect of glacial silt on primary production through altered light regimes, and phosphorus levels in Alaska lakes. Pages 3-19 *in* L. P. Dwight [chairman] Proceedings of Resolving Alaska's Water Resources Conflicts. Report IWR-108. Univ. of Alaska-Fairbanks, USA.

Edmundson, J. A., G. B. Kyle, and M. Willette. 1992. Limnological and fisheries assessment of Coghill Lake relative to sockeye salmon (*Oncorhynchus nerka*) Production and lake fertilization. Ak. Dept. Fish and Game FRED Division Report 118:42 p.

Eisenreich, S. J., R. T. Bannerman, and D.E. Armstrong. 1975. A simplified phosphorus analysis technique. Environ. Letters 9:43-53.

Golterman, H. L. 1969. Methods for analysis of freshwater. IBP Handbook 8. Blackwell Scientific Publications, Oxford. 166 p.

Grobbelaar, J. U. 1989. The contribution of phytoplankton productivity in turbid freshwaters to their trophic status. Hydrobiologia 173:127-133.

Hilborn, R. and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman & Hall, New York.

Hutchinson, G. E. 1957. A treatise on limnology: Vol. I. Geography, physics and chemistry. John Wiley and Sons, New York. 1015 p.

Ivlev, V. S. 1961. Experimental ecology of feeding fishes. Yale Univ. Press, New Haven Ct.

Koenings, J. P. and R. D. Burkett. 1987. The production patterns of sockeye salmon (*Oncorhychus nerka*) smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan lakes. Pages 216-234 *in* H. D. Smith, L. Margolis, and C. C. Woods, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci.

Koenings, J. P. and J. A. Edmundson. 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. Limnol. Oceanogr. 36(1):91-105.

Koenings, J. P. and G. B. Kyle. 1995. Collapsed populations and delayed recovery of zooplankton in response to intense foraging by juvenile sockeye salmon (*Oncorhynchus nerka*). Proceedings: International Symposium on Biological Interactions of Enhanced and Wild Salmonids. *In* review. Spec. Publ. Can. J. Fish. Aquat. Sci.

Koenings, J. P., R. D. Burkett, and J. M. Edmundson. 1990. The exclusion of limnetic cladocera from turbid glacier-meltwater lakes. Ecology 71(1):57-67.

Koenings, J. P., R. D. Burkett, G. B. Kyle, J. A. Edmundson, and J. M. Edmundson. 1986. Trophic levels response to glacial meltwater intrusion in Alaska lakes. Pages 179-194 *in* D. L. Kane, editor. Proceedings: Cold Regions Hydrology American Water Resources Assoc. Bethesda, MD.

Koenings, J. P., J. A. Edmundson, G. B. Kyle, and J. M. Edmundson. 1987. Limnology field and laboratory manual: methods for assessing aquatic production. Ak. Dept. Fish and Game FRED Division Report 71:212 p.

Kyle, G. B. 1994. Nutrient treatment of three coastal Alaskan lakes: trophic level responses and sockeye salmon production trends. Ak. Dept. Fish and Game Alaska Fishery Research Bulletin 1(2):153-167.

Kyle, G. B., J. P. Koenings, and B. M. Barrett. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. Can. J. Fish. Aquat. Sci. 45:856-867.

Kyle, G. B., J. P. Koenings, and J. A. Edmundson. 1995. An overview of Alaska lake-rearing salmon enhancement strategy: nutrient enrichment and juvenile stocking. *In* A. Milner and M. Oswood editors. Alaska Freshwaters. *In* press. Springer-Verlag. New York.

LeBrasseur, R. J., C. D. McAllister, W. E. Barraclough, V. O. Kennedy, J. Manzer, D. Robinson and K. Stephens. 1978. Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report. J. Fish. Res. Board Can. 35:1580-1596.

LeCren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20:201-219.

Lind, O. T., L. O. Davalos-Lind, T. H. Chrzanowski, and J. G. Limon. 1994. Inorganic turbidity and failure of fishery models. Int. Revue Ges. Hydrobiol. 79:7-16

Merritt, L. and W. Donaldson. 1995. PWS Management Area Commercial Salmon Fishery Harvests, 1969-1994. Ak. Dept. Fish and Game Regional Information Report 2A95-18.

McCoy, G. A. 1977. A reconnaissance investigation of a large meromictic lake in southeastern Alaska. Jour. Res. U. S. Geol. Survey 5:319-324.

Montgomery, D. C. 1984. Design and analysis of experiments. John Wiley & Sons, New York.

Murphy, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta. 27:31-36.

Peltz, L. and J. P. Koenings. 1989 Evidence for temperature limitation of juvenile sockeye salmon, *Oncorhynchus nerka*, growth in Hugh Smith Lake, Alaska. Ak. Dept. Fish and Game FRED Division Report 90:26 p.

Pennak, R. E. 1978. Fresh-water invertebrates of the United States, 2nd edition. John Wiley and Sons. New York. 803 p.

Plante, C. and J. A. Downing. 1993. Relationship of salmonid production to lake trophic status and temperature. Can. J. Fish. Aquat. Sci. 50:1324-1328.

Prince William Sound Aquaculture Corporation (PWSAC). 1995. Annual management plans for the Main Bay and Noerenberg hatcheries.

Rawson, K. 1984. An estimate of the size of a migrating population of juvenile salmon using an index of trap efficiency obtained by dye marking. Ak. Dept. Fish and Game FRED Division Report 28:23 p.

Reimann, B. 1978. Carotenoid interference in the spectrophotometric determination of chlorophyll degradation products from natural populations of phytoplankton. Limnol. Oceanogr. 23:1059-1066.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191:382 p.

SAS Institute Inc. 1990. SAS/STAT user's guide version 6. 4th edition, vols. 1 & 2. SAS Institute Inc., Cary, NC.

Scheaffer, R. L., W. Mendenhall, and L. Ott. 1986. Elementary survey sampling. Duxbury Press, Boston

Schmidt, D. C., J. P. Koenings, and G. B. Kyle. 1994. Predator-induced changes in copepod vertical migrations: explanations for decreased overwinter survival of sockeye salmon. Pages 187-209 *in* D.J. Stouder, K. L. Fresh and R. J. Feller editors. Theory and application in fish feeding ecology. Belle W. Baruch library in marine science number 18.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of fresh water. 2nd edition. Fish. Mar. Serv. Misc. Spec. Publ. 25:166 p.

Stockner, J. G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon *Oncorhynchus nerka* production. Pages 198-215 *in* H. D. Smith, L. Margolis, and C. C. Woods, editors. Sockeye salmon *Oncorhynchus nerka* population biology and future management. Can Spec. Publ. Fish. Aquat. Sci.

Stockner, J. G. and K. D. Hyatt. 1984. Lake fertilization: state of the art after 7 years of application. Can. J. Fish. Aquat. Sci. 1323:33 p.

Stockner, J. G. and K. S. Shortreed. 1985. Whole-lake fertilization experiments in coastal British Columbia lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. Can. J. Fish. Aquat. Sci. 42:649-658.

Strickland, J. D. H. and T. R. Parsons. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167:310 p.

Todd, G. L. 1994. A lightweight inclined-plane trap for sampling salmon smolt in rivers. Ak. Dept. Fish and Game Alaska Fishery Research Bulletin 1(2):179-186.

Vanni, M. J. 1986. Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. Limnol. Oceanogr. 31:1039-1056.

Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33:53-83.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co, Philadelphia, Pa.

Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Inc.

Willette, M., G. Carpenter, S.R. Carlson, and G. B. Kyle. 1995. Restoration of the Coghill Lake sockeye salmon stock. Restoration project 93024. 1993 annual report. Ak. Dept. Fish and Game Regional Information Report. *In* review.

Wilson, M. S. 1959. Calanoida. Pages 738-794 *in* W. T. Edmondson, editor. Freshwater biology. 2nd edition. John Wiley and Sons, New York.

Yeatman, H. C. 1959. Cyclopoida. Pages 795-815 *in* W. T. Edmondson, editor. Freshwater biology. 2nd edition. John Wiley and Sons, New York.

Table 1. Fertilizer composition, application schedule and amount applied to Coghill Lake, 1993-94.

	No. of Barrels Applied		Amount (gal)		Amount (kg)	
Date	20-5-0	32-0-0	20-5-0	32-0-0	P	N
07/01/93	9	0	495	0	51	0
07/08/93	6	0	330	0	34	0
07/09/93	9	0	495	0	51	0
07/15/93	8	0	440	0	45	0
07/16/93	9	0	495	0	51	0
07/23/93	13	0	715	0	74	0
07/24/93	10	0	550	0	57	0
07/25/93	0	10	0	550	0	886
07/31/93	0	14	0	770	0	1,240
08/01/93	0	10	0	550	0	886
08/08/93	0	3	0	165	0	266
08/09/93	0	12	0	660	0	1,063
08/10/93	0	3	0	165	0	266
08/17/93	0	19	0	1,045	0	1,682
08/27/93	0	19.5	0	1,073	0	1,727
Total	64	91	3,520	4,978	363	8,014
06/23/94	8	0	440	0	45	0
06/26/94	8	0	440	0	45	0
06/29/94	8	0	440	0	45	0
06/30/94	14	0	770	0	79	0
07/05/94	7	0	385	0	40	0
07/07/94	7	0	385	0	40	0
07/10/94	7	0	385	0	40	0
07/12/94	15	0	825	0	85	0
07/13/94	8	0	440	0	45	0
07/16/94	8	0	440	0	45	0
07/19/94	8	5	440	275	45	443
07/25/94	16	0	880	0	91	0
07/26/94	8	0	440	0	45	0
07/27/94	8	0	440	0	45	0
07/28/94	7	5	385	275	40	443
07/29/94	16	0	880	0	91	0
08/08/94	0	7	0	385	0	620
08/09/94	7	7	385	385	40	620
08/12/94	14	0	770	0	79	0
08/13/94	14	0	770	0	79	0
Total	188	24	10,340	1,320	1,065	2,125

Table 2. Mean values for selected water chemistry parameters, nutrient concentration, and algal pigments derived from the 1-m stratum at stations A and B (1986-94), and mean values for the pre-enrichment (PE) and enrichment (E) periods. Also shown are the results of ANOVA using a randomized complete block design to test for differences between stations and between PE and E periods. Probability (*p*) values < 0.05 indicate a significant difference.

		Station		ANOVA	Treatment		ANOVA
Variable	**Units**	**A**	**B**	**A vs B**	**PE**	**E**	**PE vs E**
General Chemistry							
Conductivity	(µmhos cm^{-1})	75	75	0.860	75	74	0.731
pH	(Units)	7.1	7.2	0.170	7.2	7.0	<0.001
Alkalinity	(mg L^{-1})	19	20	0.378	20	18	0.210
Turbidity	(NTU)	4.9	4.4	0.020	4.6	4.9	0.505
Color	(Pt Units)	6.7	6.5	0.217	7.2	4.8	<0.001
Calcium	(mg L^{-1})	7.7	7.6	0.582	7.3	7.6	0.364
Magnesium	(mg L^{-1})	1.3	1.5	0.140	1.4	1.5	0.825
Iron	(µg L^{-1})	234	185	0.086	214	197	0.560
Nutrients							
Total-P	(µg L^{-1})	9.1	7.5	0.013	8.0	9.6	0.050
Total Filterable - P	(µg L^{-1})	3.5	3.9	0.612	3.7	3.5	0.782
Filterable Reactive - P	(µg L^{-1})	2.2	2.6	0.398	2.4	2.1	0.876
Total Kjeldahl - N	(µg L^{-1})	61	53	0.023	47	87	<0.001
Ammonia	(µg L^{-1})	3.0	2.6	0.131	3.0	1.9	0.007
Nitrate/Nitrite	(µg L^{-1})	18.8	15.4	0.154	18.8	10.9	0.028
Reactive Silicon	(µg L^{-1})	690	664	0.125	726	527	<0.001
Algal Pigments							
Chlorophyll	(µg L^{-1})	0.83	1.01	0.314	0.64	1.73	0.001
Phaeophytin	(µg L^{-1})	0.26	0.41	0.349	0.35	0.30	0.773

Table 3. Mean values for selected macrozooplankton variables for stations A and B (1988-94), and mean values for the pre-encrichment (PE) and enrichment (E) periods. Also shown are the results of ANOVA testing for significant difference between stations and between PE (excluding 1986) and E periods. Probability (*p*) values < 0.05 indicate a significant difference.

	Station		ANOVA	Treatment		ANOVA
Taxa	**A**	**B**	**A vs B**	**PE**	**E**	**PE vs E**
			Density (number m^{-2})			
Cyclops	35,173	45,211	0.079	41,431	37,108	0.442
Bosmina	696	954	0.351	131	2,562	<0.001
Daphnia	93	103	0.864	136	5	0.084
			Body size (mm)			
Cyclops	0.72	0.71	0.872	0.73	0.69	0.202
Bosmina	0.43	0.38	0.509	0.46	0.35	0.001
Daphnia	0.73	0.79	0.435	0.80	0.71	0.002
			Biomass (mg m^{-2})			
Cyclops	64.7	747.0	0.496	73.0	61.0	0.458
Bosmina	1.1	0.9	0.383	0.3	2.8	<0.001
Daphnia	0.2	0.3	0.794	0.3	0.0	0.122

Table 4. Mean abundance (number fry^{-1}) and biomass (µg fry^{-1}) of stomach contents found in sockeye fry collected from Coghill Lake in 1994. The data were analyzed as a 2-stage nested design, and probability (*p*) values < 0.05 indicate a significant difference.

Variable	Taxa	August	September	*p*-value
Abundance	Cyclops	270	84	0.089
	Ovig. Cyclops	5	1	0.088
	Bosmina	24	276	0.022
	Ovig. Bosmina	2	1707	<0.001
	Chydoridae	0.0	0.2	0.421
	Harpactacoid	0.0	0.4	0.146
	Chironomid	0.0	0.1	0.228
Biomass (µg)	Cyclops	992	298	0.096
	Ovig. Cyclops	16	2	0.091
	Bosmina	41	336	0.033
	Ovig. Bosmina	3	2413	<0.001

Table 5. Comparison of stomach contents of fry collected in August and September of 1993 and 1994 in Coghill Lake. Mean abundance (number fry^{-1}) and biomass (μg fry^{-1}) of each taxa that share the same letter do not significantly ($p > 0.05$) differ.

		1993		1994	
Variable	**Taxa**	**August**	**September**	**August**	**September**
Abundance	**Cyclops**	8.0^{a}	18.3^{a}	274.9^{b}	84.7^{a}
	Bosmina	0.6^{a}	0.6^{a}	25.8^{a}	1983.7^{b}
	Chydoridae	1.4^{a}	1.0^{ab}	0.0^{b}	0.2^{b}
Biomass (μg)	**Cyclops**	19.5^{a}	54.4^{a}	1007.7^{b}	299.9^{a}
	Bosmina	1.0^{a}	0.8^{a}	44.0^{a}	2749.0^{b}
	Chydoridae	2.5^{a}	1.3^{ab}	0.0^{bc}	0.0^{c}

Table 6. Estimated daily ration (I; percent dry weight) of sockeye fry in Coghill Lake for August and September, 1994. Estimated mean (initial) stomach fullness (V_i) and mean food consumption (I_i) for each time interval are given. Diel comparison of stomach fullness was accomplished using 1-way ANOVA followed by pairwise t-tests. Means that share the same letter do not significantly ($p > 0.05$) differ.

Date	°C	Time Interval	Hours	Mean V_i (%)	Mean I_i (%)	Daily Ration (I)
17-Aug	6.5	0030-0130	1.0	0.68^{a}	0.049	
		0130-0430	3.0	0.55^{a}	0.110	
		0430-0900	4.5	1.23^{b}	0.350	
		0900-1200	3.0	0.89^{b}	0.179	
		1200-0030	12.5	0.74^{ab}	0.451	1.14%
28-Sep	6.0	2400-0630	6.5	1.33^{ab}	0.472	
		0630-1230	6.0	1.17^{a}	0.390	
		1230-1830	6.0	1.97^{bc}	0.656	
		1830-2130	3.0	1.21^{ab}	0.222	
		2130-2400	2.5	2.77^{c}	0.430	2.17%

Table 7. Ivlev's electivity index based on in-lake and fry stomach content abundance and biomass of the major zooplankton taxa in Coghill Lake, 1994. The index ranges from -1 to +1, with negative values indicating avoidance and positive values indicating preference.

		Abundance			Biomass		
Month	Taxa	Lake(%)	Fry(%)	Electivity	Lake(%)	Fry(%)	Electivity
August	Cyclops	95.3	89.7	-0.03	96.8	94.3	-0.01
	Ovig. Cyclops	0.1	1.7	0.88	0.4	1.5	0.61
	Bosmina	4.0	8.0	0.33	2.4	3.9	0.23
	Ovig. Bosmina	0.6	0.6	0.02	0.5	0.3	-0.16
September	Cyclops	48.8	4.1	-0.85	63.3	9.8	-0.73
	Ovig. Cyclops	0.0	0.0	na[a]	0.0	0.1	1.00[b]
	Bosmina	41.1	13.4	-0.51	28.2	11.0	-0.44
	Ovig. Bosmina	9.8	82.5	0.79	8.0	79.2	0.82

[a] Lake and fry gut abundance is zero.

[b] Based on zero biomass measurement in the lake.

Table 8. Mean fry wet weight, dry weight, fork length, fry condition (K) based on wet and dry weights, and length-adjusted wet and dry weights for Coghill Lake sockeye sampled in 1994. Also shown are probability values (*p*) for comparison tests of significant differences between August and September 1994 samples.

Variable	August	September	*p*-value
Wet weight (mg)	904.3	1,040.1	0.021
Dry weight (mg)	132.6	156.7	0.017
Fork Length (mm)	45	48	0.005
Wet weight condition factor (K)	0.980	1.011	0.016
Dry weight condition factor (K)	0.973	1.025	0.004
Length-adjusted wet weight	908.7	931.2	0.074
Length-adjusted dry weight	129.8	136.7	0.011

Table 9. Summary of smolt mark-recapture trials, smolt trap efficiency, and population estimates by weekly period for Coghill Lake, 1994.

Date	Number of Smolt					Trap	Population	
	Live	Dead	Total	Marked	Captured	Efficiency (%)	Estimate	Variance
01-07 May	3,159	66	3,225	248	45	18.1	18,031	5.83E+06
08-14 May	26,359	1,032	27,391	511	61	11.9	231,736	7.62E+08
15-21 May	11,428	1,520	12,948	507	42	8.3	158,194	5.35E+08
22-28 May	32,303	6,614	38,917	504	52	10.3	377,087	2.46E+09
29-31 May	8,396	49	8,445	500	28	5.6	155,839	7.69E+08
01-04 June	1,995	11	2,006	160	2	1.3	239,706	1.27E+10
05-11 June	3,369	184	3,553	264	14	5.3	71,347	3.05E+08
12-18 June	1,822	299	2,121	267	28	10.5	20,573	1.32E+07
Total							1,271,513	1.76E+10
						95% C.I. =	1,012,668 - 1,532,358	

Table 10. Mean number of adults, return-per-spawner, and yield of sockeye salmon for various escapement ranges in Coghill Lake for brood years 1962-88. Yield is defined as brood-year returns minus adult escapement.

Escapement	n	Returns	Return-per-Spawner	Yield
<30,000	6	114,374	8.05	96,498
30,000-50,000	7	306,254	9.08	268,545
40,000-60,000	4	168,242	3.33	119,100
50,000-70,000	5	159,391	2.79	100,170
60,000-90,000	7	85,717	1.24	14,322
>90,000	5	331,741	2.07	165,884

Table 11. Results of Ricker analyses of Coghill Lake sockeye salmon for brood years 1962-88 to estimate maximum sustainable yield (MSY) and the escapement to produce MSY (S_{msy}). The first model is the classical Ricker, which exhibited first order autocorrelation of the residuals ($p < 0.05$; D-W statistic). The second model includes a lag 1 autoregressive (AR) parameter that corrects the autocorrelation problem. The third model is the classic Ricker without the high (>100,000) 1980-82 escapements.

		Parameter Estimate	
Model	**R^2**	**MSY**	**S_{msy}**
1. Classic Ricker	**0.33 (p=0.002)**	**236,000**	**58,500**
2. Ricker AR(1)	**0.41 (p=0.005)**	**210,000**	**61,900**
3. Ricker (w/o 1980-82)	**0.52 (p<0.001)**	**195,000**	**40,000**

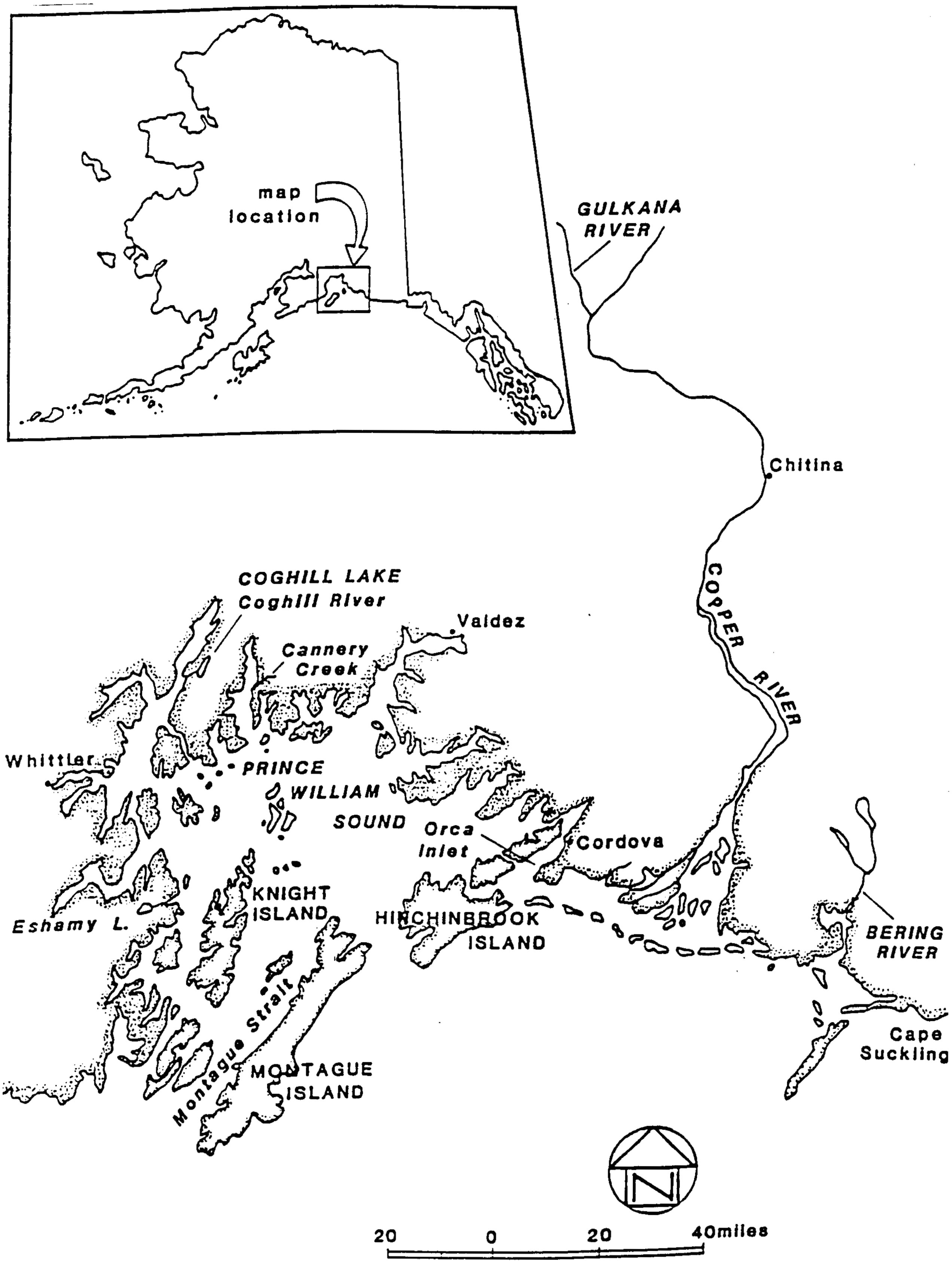


Figure 1. Geographical location of Coghill Lake in Prince William Sound.

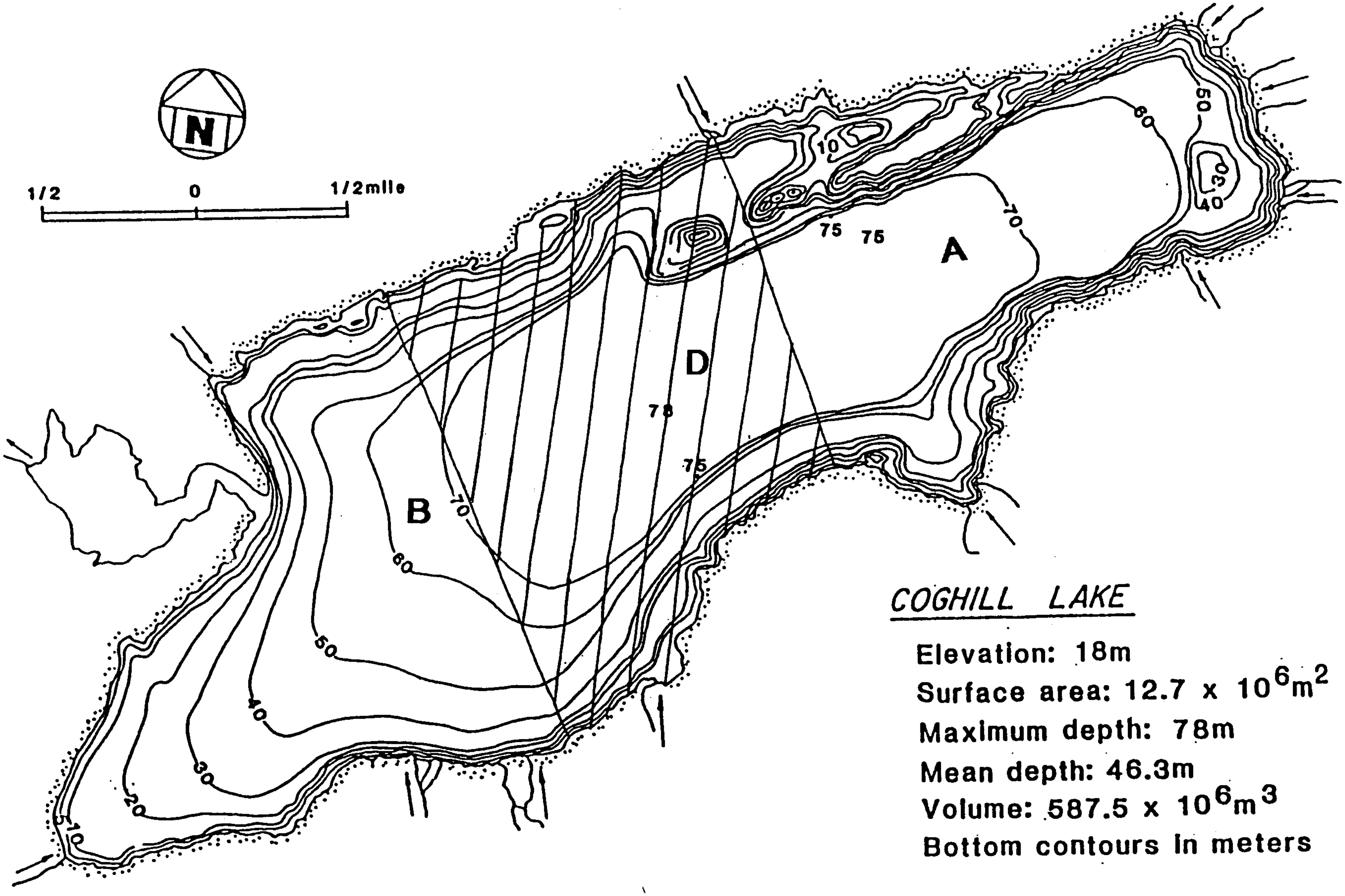


Figure 2. Morphometric map of Coghill Lake showing the location of the limnological sampling stations and the fertilizer application zone.

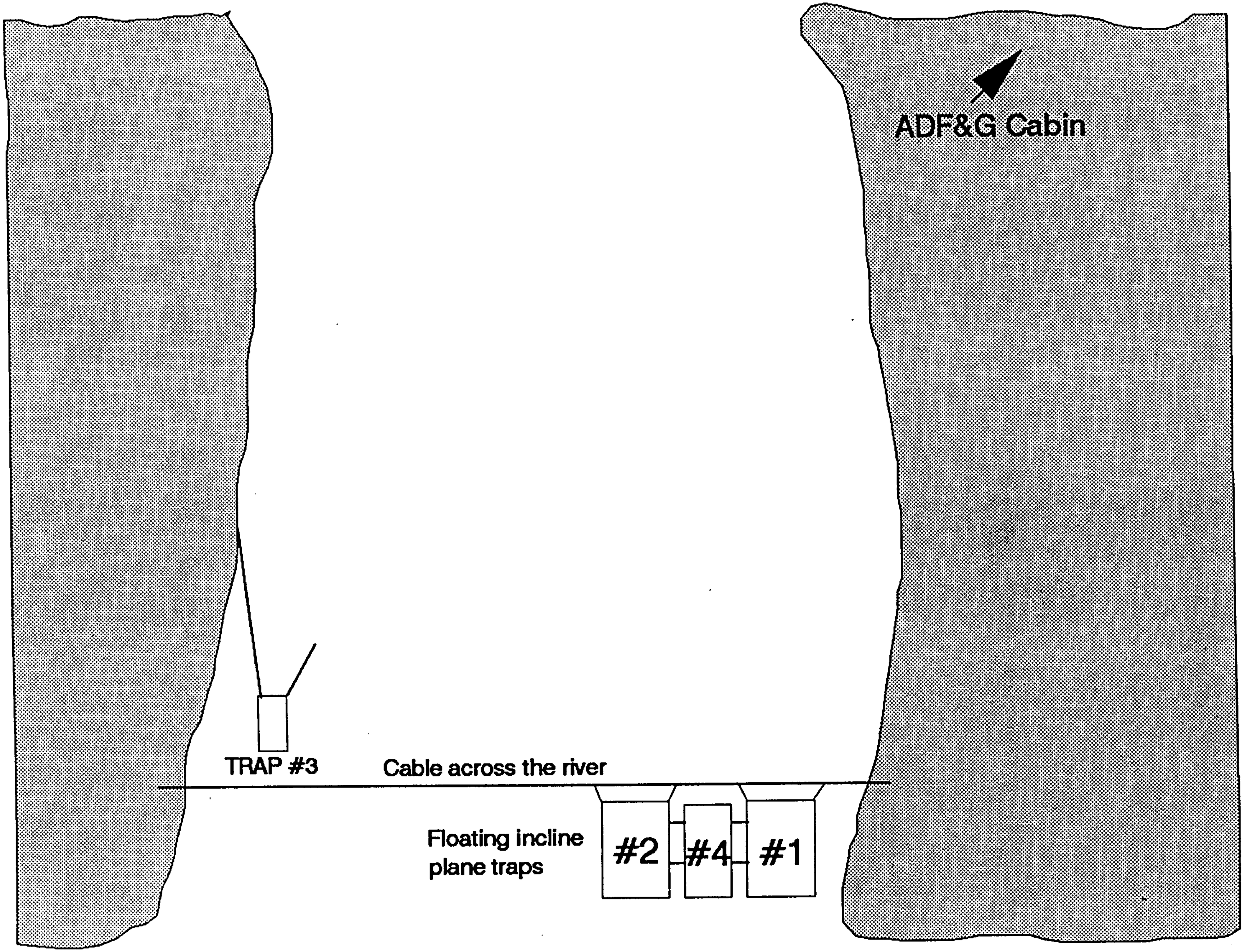


Figure 3. Configuration of the four inclined-plane (smolt) traps in Coghill River, 1994.

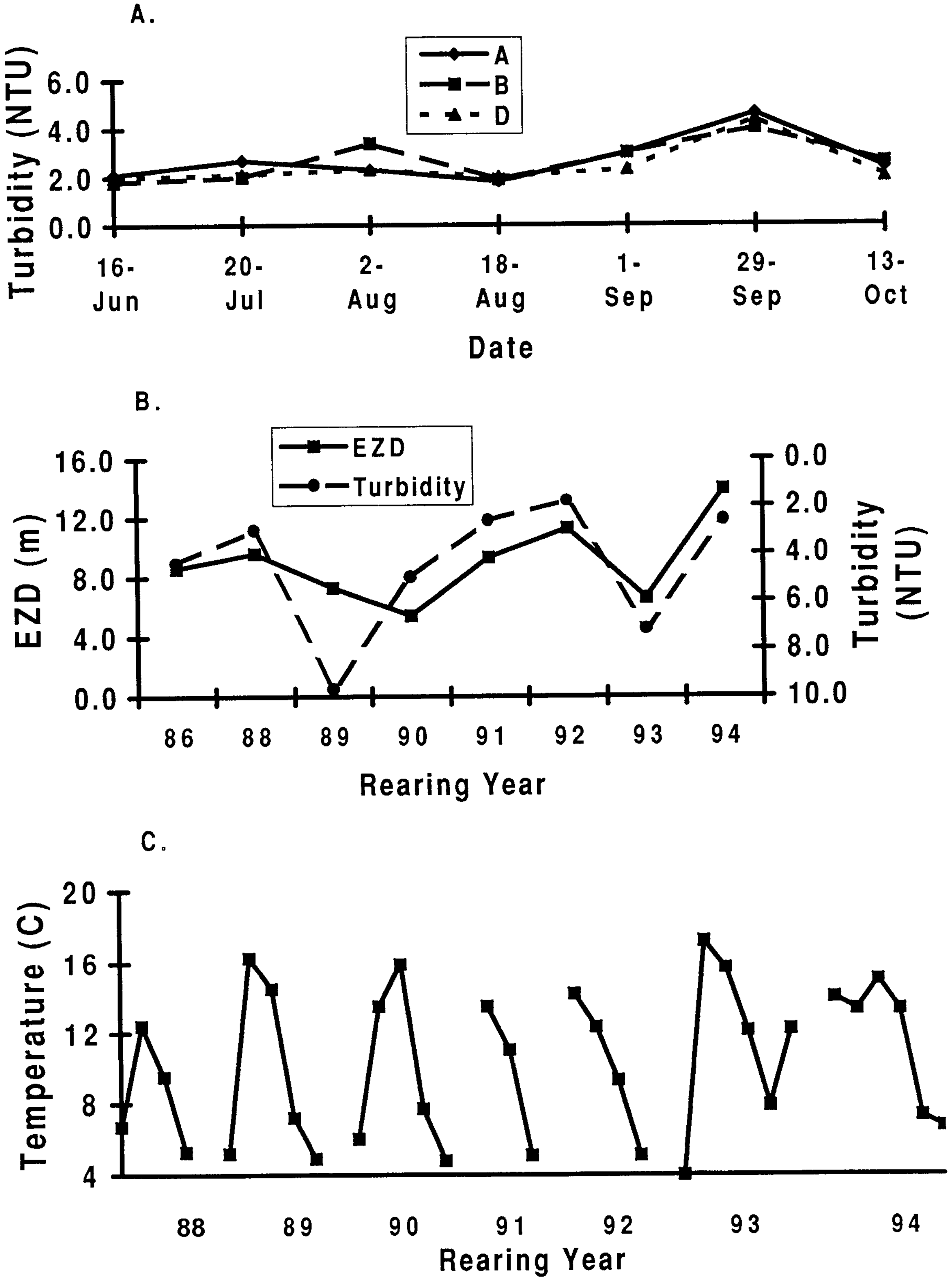
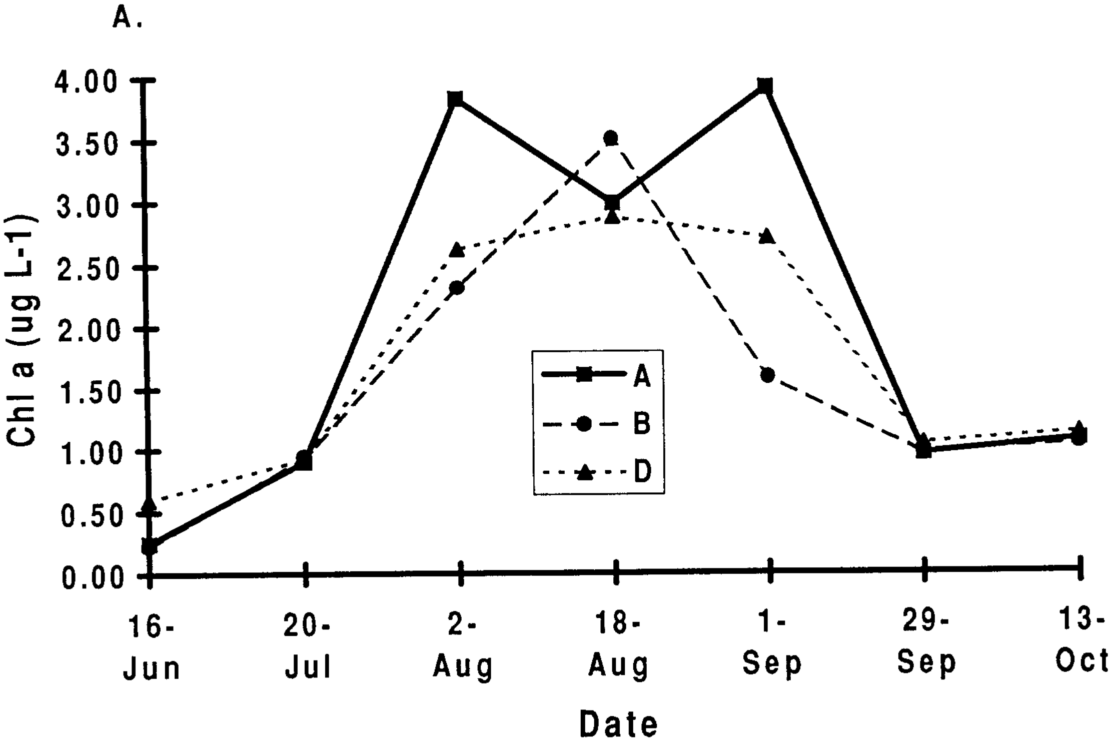


Figure 4. Seasonal changes in turbidity at 3 stations during 1994 in Coghill Lake (A), seasonal mean turbidity and euphotic zone depth (EZD) for 1986-94 (B), and comparison of water temperatures of the 1-m stratum for 1986-94 (C).



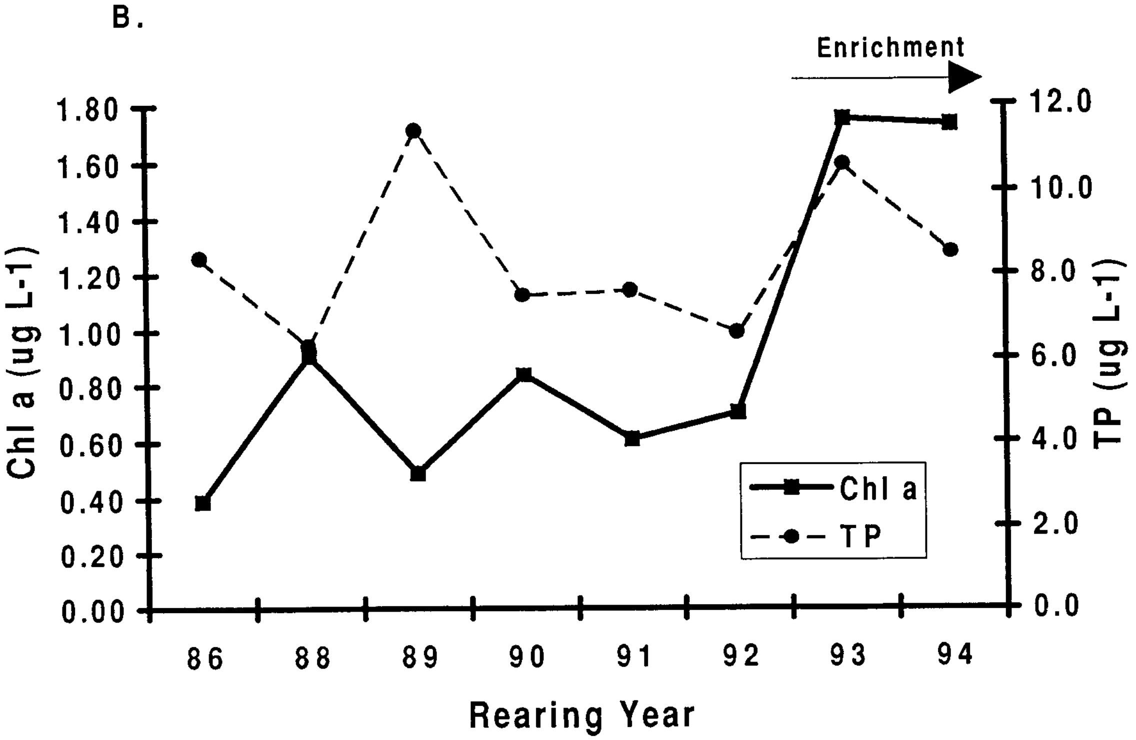


Figure 5. Seasonal changes in chlorophyll *a* (chl *a*) concentration for the 1-m stratum at 3 stations in Coghill Lake during 1994 (A), and seasonal mean chl *a* and total phosphorus (TP) concentrations derived from the 1-m stratum for 1986-94 (B).

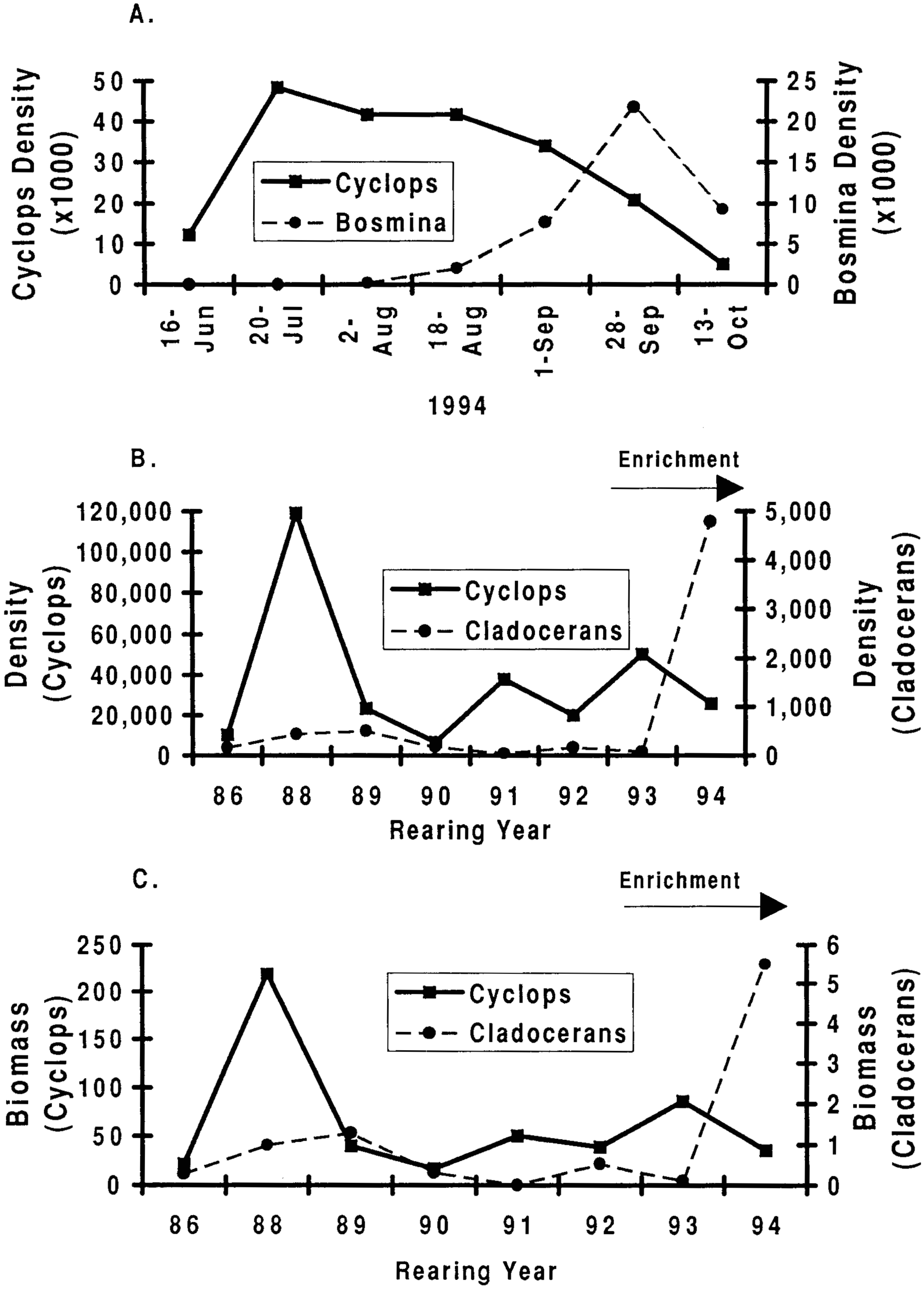


Figure 6. Seasonal changes in *Cyclops* and *Bosmina* densities (number m^{-2}) in Coghill Lake for 1994 (A), and seasonal mean *Cyclops* and cladocera (*Bosmina* and *Daphnia*) density (number m^{-2}) (B) and biomass (mg m^{-2}) (C) for 1986-94.

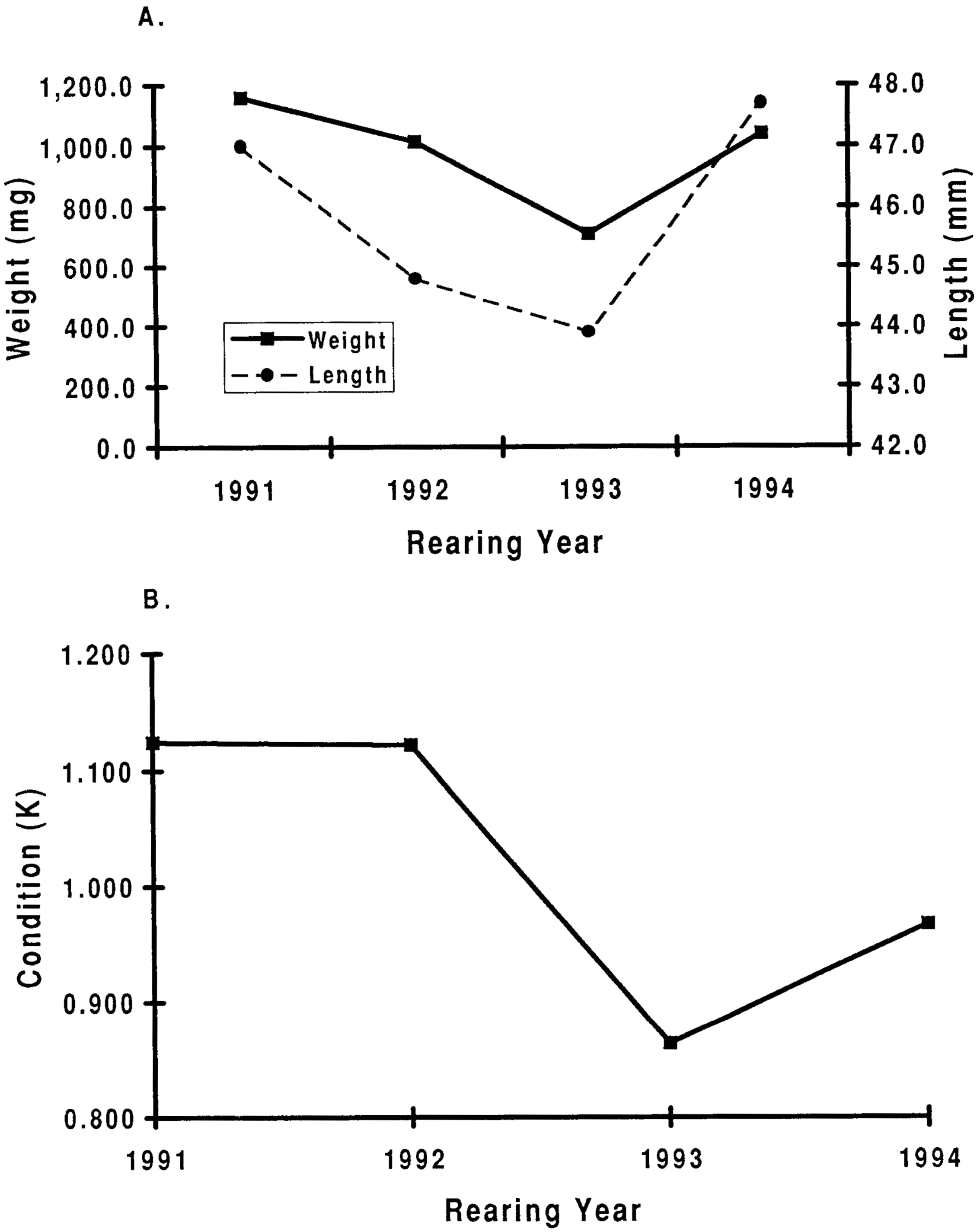


Figure 7. Age-0 sockeye fry mean wet weight and length (A) and fry condition factor based on wet weight (B) for Coghill Lake, 1991-94.

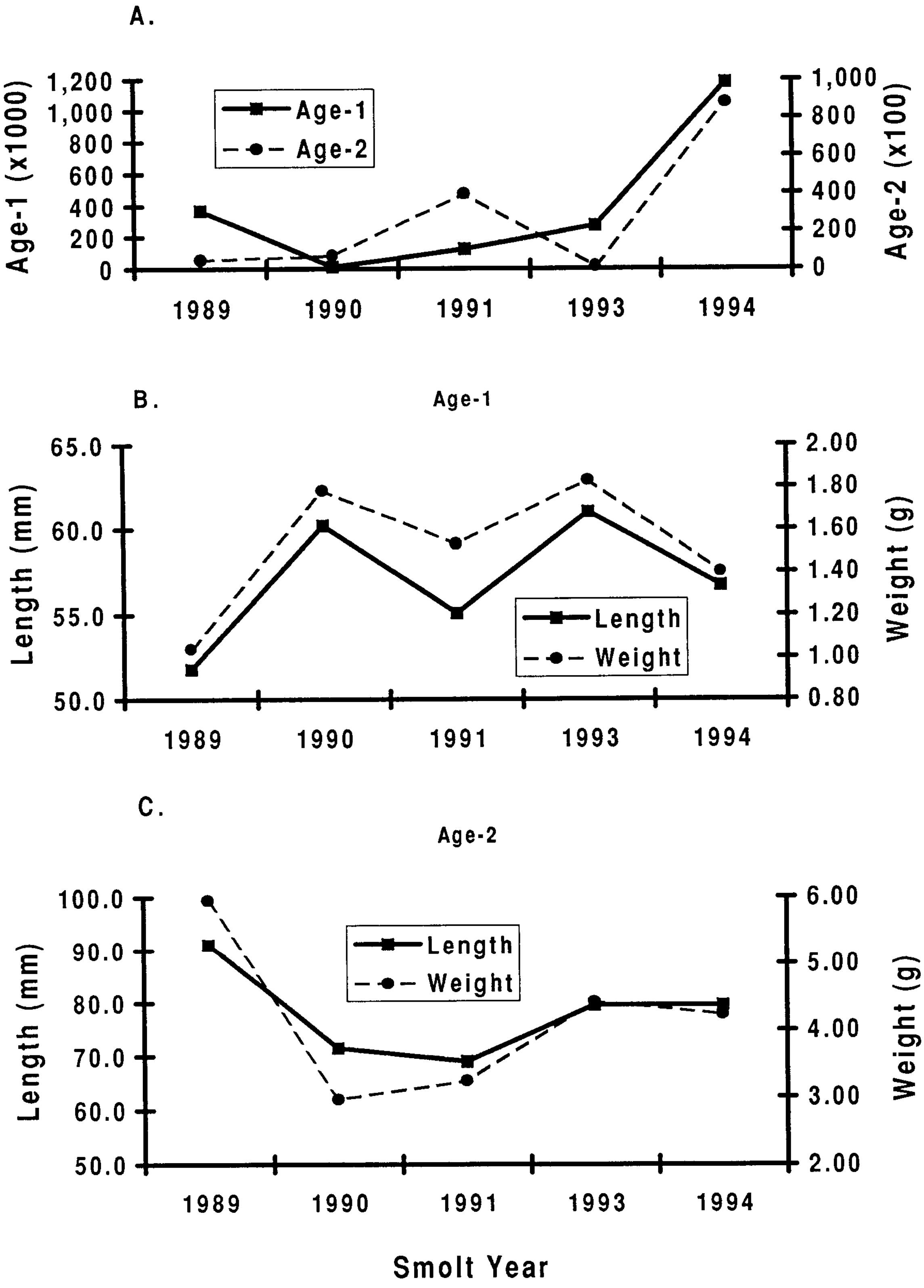


Figure 8. Age-1 and age-2 sockeye smolt production in Coghill Lake for 1989-94 (A), and mean size of age-1 (B) and age-2 smolts (C) for 1989-94.

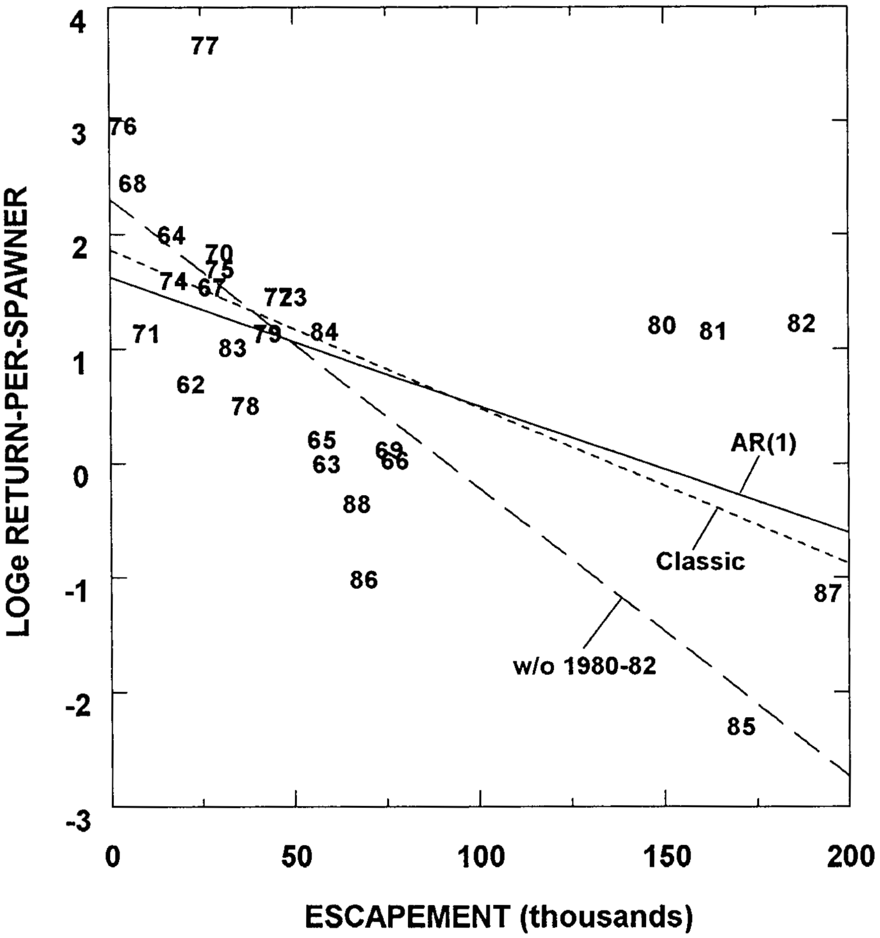


Figure 9. Classic Ricker model of return-per-spawner for Coghill Lake sockeye salmon for brood years 1962-88. Also shown is the first order autoregressive (AR) model which corrects for residual aurocorrelation and the Ricker model without brood years 1980-82.

Appendix A. Summary of general water-chemistry parameters, metals and nutrient concentrations, and algal pigments in Coghill Lake for 1986-94. Data are seasonal mean values and standard deviation (S.D.) derived from the 1-m stratum.

		1986		1988		1989		1990		1991		1992		1993		1994	
Parameter	**Units**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**
Sp. Cond.	μmhos cm^{-1}	63	19	73	11	83	13	75	13	86	12	62	34	77	13	71	9
pH	Units	7.3	0.4	7.2	0.1	7.3	0.2	7.1	0.2	7.2	0.3	6.7	0.6	7.1	0.3	7.0	0.3
Alkalinity	mg L^{-1}	23.8	5.2	17.4	2.0	19.0	1.2	19.3	1.2	18.2	2.6	15.8	8.0	18.3	0.9	18.2	1.9
Turbidity	NTU	4.4	5.3	3.0	2.1	9.7	2.1	5.0	2.1	2.6	0.9	1.8	1.0	7.2	2.0	2.6	0.8
Color	Pt units	6	4	4	3	8	1	5	1	11	2	7	3	4	2	5	3
Calcium	mg L^{-1}	6.6	0.4	na[a]	--	7.1	3.8	8.4	3.8	6.9	0.3	7.7	3.9	7.7	0.5	7.4	0.6
Magnesium	mg L^{-1}	1.0	0.3	na	--	1.3	0.9	1.5	0.9	2.2	1.0	0.6	0.5	1.7	0.5	1.3	0.2
Iron	ug L^{-1}	222	277	141	98	410	130	301	130	148	47	83	49	300	194	93	31
Total-P[b]	μg L^{-1}	8.4	5.8	6.3	2.7	11.4	2.0	7.5	2.0	7.6	3.3	6.6	2.8	10.6	3.7	8.5	4.0
Total filterable - P	μg L^{-1}	7.0	4.2	2.5	0.5	3.1	2.1	2.6	2.1	2.3	0.5	3.6	2.6	2.6	0.8	4.5	4.0
Filterable reactive - P	μg L^{-1}	4.1	2.6	1.4	0.4	2.5	1.6	2.2	1.6	1.9	0.6	1.8	1.3	1.2	0.6	3.0	3.1
Total Kjeldahl - N	μg L^{-1}	49	6.2	48	8	48	12	42	12.4	36	8.9	55	20	77	26	97	31
Ammonia	μg L^{-1}	3.8	3.4	4.1	1.1	1.5	0.3	1.3	0.3	5.0	2.7	4.0	1.2	2.0	1.2	1.9	0.7
Nitrate + nitrite	μg L^{-1}	8.1	8.8	22.7	17.9	27.7	17.5	18.0	17.5	20.0	12.7	18.9	18.0	13.8	10.7	8.2	11.7
Reactive silicon	μg L^{-1}	813	124	710	119	701	237	748	237	710	53	563	280	626	145	430	230
Chlorophyll	μg L^{-1}	0.39	0.32	0.91	0.47	0.49	0.95	0.84	0.95	0.61	0.18	0.70	0.33	1.74	1.05	1.73	1.18
Phaeophytin	μg L^{-1}	0.31	0.16	0.24	0.11	0.21	1.90	0.85	1.90	0.18	0.09	0.27	0.12	0.44	0.19	0.16	0.13

[a] Na = not analyzed.

[b] Uncorrected for turbidity.

Appendix B. Summary of general water-chemistry parameters, metals and nutrient concentrations, and algal pigmnets in Coghill Lake for 1986-94. Data are seasonal mean values and standard deviations (S.D.) derived from the hypolimnion[a].

		1986		1988		1989		1990		1991		1992		1993		1994	
Parameter	Units	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.	Mean	S.d.
Sp. Cond.	µmhos cm^{-1}	29,625	1,702	271	58	311	105	318	93	257	133	116	31	139	25	138	14
pH	Units	7.3	0.1	7.1	0.1	7.0	0.1	7.0	0.1	7.1	0.2	6.9	0.2	6.9	0.1	6.8	0.3
Alkalinity	mg L^{-1}	436.0	103.0	21.9	1.4	22.7	2.3	22.6	1.1	21.0	2.8	20.0	1.2	20.1	1.7	20.4	1.4
Turbidity	NTU	192.5	28.7	1.8	0.2	24.9	30.1	12.5	3.4	3.2	1.7	5.7	5.9	13.2	13.5	3.4	1.8
Color	Pt units	na[b]	--	na	--	8	1	7	2	12	4	7	3	4	2	6	3
Calcium	mg L^{-1}	na	--	na	--	9.7	0.8	10.4	2.5	8.7	1.3	9.8	2.3	8.7	0.9	8.3	0.8
Magnesium	mg L^{-1}	na	--	na	--	5.5	2.3	6.3	2.6	4.8	3.4	1.2	1.1	3.1	0.8	2.5	0.6
Iron	ug L^{-1}	12,518	3,029	71	5	1,051	1,294	667	357	149	94	299	403	550	557	129	77
Total-P[c]	µg L^{-1}	100.4	30.7	4.5	0.5	20.9	21.0	15.9	4.8	5.9	3.3	11.7	13.4	16.5	18.6	5.1	3.0
Total filterable - P	µg L^{-1}	53.9	51.9	2.4	0.1	2.6	0.8	2.6	1.7	1.9	0.9	2.7	1.6	1.6	1.1	2.4	1.5
Filterable reactive - P	µg L^{-1}	39.5	36.2	1.5	0.4	2.3	0.5	2.5	1.3	1.6	0.8	1.6	1.0	1.0	0.8	2.2	1.4
Total Kjeldahl - N	µg L^{-1}	12,822	1,028	39.7	5.4	49	25.8	41.4	5.2	25.1	31	48.4	20.6	56.7	20	41.4	18
Ammonia	µg L^{-1}	21,186	22,107	5.1	1.0	1.4	0.5	1.4	0.4	3.9	2.0	210.4	590.2	2.0	1.1	1.8	1.0
Nitrate + nitrite	µg L^{-1}	4.9	2.7	88.6	22.4	88.3	21.2	83.1	15.2	57.2	21.0	46.7	12.7	52.2	7.9	51.1	10.7
Reactive silicon	µg L^{-1}	4,029	1,263	843	128	818	51	902	217	809	16	743	54	793	99	810	43
Chlorophyll	µg L^{-1}	0.01	0.01	0.27	0.25	0.09	0.05	0.08	0.08	0.13	0.07	0.36	0.34	0.32	0.15	0.22	0.11
Phaeophytin	µg L^{-1}	0.16	0.22	0.13	0.10	0.12	0.07	0.10	0.04	0.10	0.06	0.26	0.13	0.20	0.07	0.09	0.05

[a] Hypolimnetic samples were collected from 60 m (1986), 25 m (1988-91) and 20 m (1992-94).

[b] Na = not analyzed.

[c] Uncorrected for turbidity.

Appendix C. Summary of seasonal mean macrozooplankton density, body size, and biomass by major taxa in Coghill Lake, 1986-94.

Density (number m^{-2})

	1986	1988		1989		1990		1991		1992		1993		1994		
Taxon/Station	A	A	B	A	B	A	B	A	B	A	B	A	B	A	B	D
Cyclops	10,347	112,887	125,772	24,011	22,819	5,175	8,137	39,791	35,881	3,254	36,600	42,992	56,805	18,100	30,536	28,394
Bosmina	88	80	186	531	109	42	308	0	53	0	0	44	136	4,178	5,891	4,204
Daphnia	77	412	212	212	159	0	0	0	35	11	319	0	0	18	0	61
Total	10,512	113,379	126,170	24,754	23,087	5,217	8,445	39,791	35,969	3,265	36,919	43,036	56,941	22,296	36,427	32,659

Body size (mm)

	1986	1988		1989		1990		1991		1992		1993		1994		
Taxon/Station	A	A	B	A	B	A	B	A	B	A	B	A	B	A	B	D
Cyclops	0.78	0.79	0.67	0.68	0.72	0.85	0.84	0.60	0.66	0.71	0.76	0.70	0.72	0.70	0.63	0.81
Bosmina	0.45	0.47	0.41	0.55	na	0.40	0.44	na[a]	na	na	na	0.33	0.34	0.40	0.32	0.36
Daphnia	0.55	0.74	0.74	0.79	0.77	na	na	na	na	0.69	0.95	na	na	0.71	0.71	0.65

Biomass (mg m^{-2})

	1986	1988		1989		1990		1991		1992		1993		1994		
Taxon/Station	A	A	B	A	B	A	B	A	B	A	B	A	B	A	B	D
Cyclops	21.9	246.8	191.4	37.6	41.0	13.2	20.4	48.0	53.8	6.0	73.0	71.0	101.0	30.0	42.0	66.0
Bosmina	0.2	0.2	0.3	0.6	0.0	0.1	0.6	0.0	0.0	0.0	0.0	0.0	0.1	6.0	5.0	5.0
Daphnia	0.1	1.0	0.5	0.6	0.4	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0
Total	22.2	248.0	192.2	38.8	41.4	13.3	21.0	48.0	53.8	6.0	74.0	71.0	101.1	37.0	47.0	71.0

[a] Na indicates not available.