FRED Reports

Limnological and Fisheries Assessment
of Coghill Lake Relative to Sockeye Salmon
(Oncorhynchus nerka) Production and
Lake Fertilization

by
J. A. Edmundson, G. B. Kyle, and M. Willette

Number 118

Alaska Department of Fish & Game
Division of Fisheries Rehabilitation,
Enhancement and Development

Limnological and Fisheries Assessment of Coghill Lake Relative to Sockeye Salmon (*Oncorhynchus nerka*) Production and Lake Fertilization

by
J. A. Edmundson, G. B. Kyle, and M. Willette

Number 118

Alaska Department of Fish and Game
Division of Fisheries Rehabilitation,
Enhancement, and Development

Carl L. Rosier
Commissioner

J. P. Koenings
Director

P. O. Box 25526
Juneau, Alaska 99802-5526

January 1992

TABLE OF CONTENTS

Section | Page

ABSTRACT. 1

INTRODUCTION. 2
  Description of Study Area. 3

METHODS AND MATERIALS 3
  Fish Assessment 3
    Sockeye Escapement and Returns 3
    Sockeye Smolt Abundance, Size and Age. 3
    Hydroacoustic Surveys. 6
  Limnological Assessment 7
    Field Sampling. 7
    Physical Parameters 7
    Water Quality 7
    Nutrients 8
    Phytoplankton 9
    Zooplankton 9

RESULTS AND DISCUSSION 9
  Fish Assessment 9
    Sockeye Escapement and Returns 9
    Sockeye Smolt Abundance, Size and Age. 11
    Juvenile Sockeye Population Estimates and Freshwater Survival. 11
  Limnological Assessment. 15
    Light Penetration. 15
    Temperature and Dissolved Oxygen Regimes. 17
    General Water Quality Parameters. 22
    Metals. 23
    Nutrients. 23
    Phytoplankton. 25
    Zooplankton Abundance, Body Size, and Biomass. 25

EVALUATION. 28

RECOMMENDATIONS. 31

ACKNOWLEDGEMENTS. 32

REFERENCES. 34

LIST OF TABLES

Table		Page
1.	Summary of sockeye salmon escapement, commercial harvest, and total return for Coghill Lake, 1968-1991.	10
2.	Return of sockeye salmon by brood year for the major classes, and the return per spawner (R/S) for Coghill Lake, 1968-1991.	12
3.	Sockeye salmon smolt abundance, size, and age by five-day periods for Coghill Lake, 1989-1991.	13
4.	Estimated freshwater survival of juvenile sockeye for brood years 1987-1989, Coghill Lake.	14
5.	Density of juvenile sockeye (no. per m^3) by depth and and transect for each of the three surveys conducted in Coghill Lake during 1988-1990.	16
6.	Seasonal changes in euphotic zone depth (EZD) and Secchi disk (SD) depth in Coghill Lake during 1986-1990.	18
7.	Range and seasonal mean values for analyzed water quality parameters and nutrients within the mixolimnion (1 m) of Coghill Lake, 1986-1990.	19
8.	Range and seasonal mean values for analyzed water quality parameters and nutrients within the top (25 m; 1989 and 1990) and bottom (25-30 m; 1988) of the chemocline, and in the monimolimnion (60 m; 1986) of Coghill Lake.	19
9.	Macrozooplankton density and body size (mm) for each taxa and station in Coghill Lake, 1986-1990.	26
10.	Comparison of seasonal mean macrozooplankton density and biomass for a variety of sockeye nursery lakes showing the relatively low standing stock of zooplankton in Coghill Lake.	29

LIST OF FIGURES

Figure		Page
1.	Geographical location of Coghill Lake in Prince William Sound.	4
2.	Morphometric map of Coghill Lake showing location of the two (A and B) limnological sampling stations.	5
3.	Seasonal temperature and dissolved oxygen profiles for Station A in Coghill Lake, 1989.	20
4.	Seasonal temperature and dissolved oxygen profiles for Station A in Coghill Lake, 1990.	21
5.	Morphometric map of Coghill Lake showing the location of the proposed zone for fertilizer application.	33

ABSTRACT

Coghill Lake has historically (since 1975) produced returns of sockeye salmon (*Oncorhynchus nerka*) ranging from over a million (1982) to 21,000 (1990), and has averaged 270,000 adults. Since 1987, sockeye returns have steadily declined, and in 1990 and 1991 escapements fell below 10,000. In 1988, limnological and fisheries sampling was initiated to assess freshwater sockeye production. Limnological and juvenile information prior to the decline in adult returns is not available; however, indirect evidence strongly suggests that overescapements may have overgrazed the macrozooplankton community and had a long-term adverse impact on subsequent fry recruitment. This conclusion is based on: 1) lower actual and estimated returns-per-spawner in recent years, 2) adult returns since 1985 have averaged only 7% of the expected based on euphotic volume of the lake, 3) recent smolt outmigrations have averaged only 8% of the expected based on euphotic volume of the lake, and 4) the macrozooplankton biomass has been very low since 1988, and ranks 22 out of 23 compared to other sockeye nursery lakes in Alaska. In addition, the impoverished rearing environment may have caused a reduction in size of smolts emigrating Coghill Lake, which would have reduced the smolt-to-adult survival due to size-dependent mortality. Environmental factors such as the reduction in euphotic zone depth could have caused a reduction in macro-zooplankton biomass and juvenile sockeye growth and survival. However, as environmental factors fluctuate inter- and intra-annually, during the period sampled (1988-1991), we would not have observed the constant low macrozooplankton biomass and consistently small smolt sizes. Although limnological and fisheries information before the decline of sockeye salmon is not available, the combination of large escapements producing lower returns per spawner, the impoverished rearing environment, and poor fish growth and freshwater survival lead us to believe that high escapements have adversely affected the rearing efficiency of Coghill Lake. In this report, we examine juvenile and adult sockeye production and assess the limnology of Coghill Lake relative to the potential for lake fertilization.

INTRODUCTION

Coghill Lake produces the largest sockeye salmon (*Oncorhynchus nerka*) return within the Coghill District of the Prince William Sound commercial fishing management area. The ADF&G Commercial Fisheries Division manages the commercial fishery to achieve an escapement of 40,000-60,000 spawners. Despite management efforts, the total returns (harvest plus escapement) of sockeye salmon to Coghill Lake in the past four years have steadily declined.

Since 1968, annual adult sockeye salmon escapements into Coghill Lake averaged ~65,000; however, escapements have varied from a low of 9,000 to a high of nearly 190,000 fish. In recent years (1980-1987), sockeye salmon escapements were nearly double the escapement goal but adult returns from these brood years were much lower than expected. Kyle *et al.* (1988) has shown that high densities of rearing sockeye juveniles produced from successive large escapements can reduce the forage base (zooplankton biomass). Furthermore, Koenings and Kyle (1991) showed that over-grazed zooplankton populations causes brood-year interactions by reducing the rearing efficiency for ensuing broods. Thus, the recent decline in sockeye salmon production at Coghill Lake has prompted an assessment of the lake's capacity to support rearing sockeye juveniles.

Lake productivity depends to a large degree on the quantity of nutrients (nitrogen and phosphorus) entering the system (Vollenweider 1976; Schindler 1978; Smith 1979). In typical (dimictic) lakes, the replenishment of nutrients in the upper layers occurs during the periods of spring and fall turnover when the lake mixes from top to bottom (Hutchinson 1957; Wetzel 1975; Likens 1985). In contrast, Coghill Lake is meromictic due to the presence of a permanent anoxic layer of saline water (monimolimnion) that begins at a depth of ~30 m and extends to the bottom (Pellissier and Somerville 1987). This perennially stagnant layer prevents nutrients from recycling into the trophogenic zone (Hutchinson 1957; Wetzel 1975). That is, organic material that sinks from the surface is remineralized within the lower strata and then trapped within the dense waters of the monimolimnion resulting in lower primary productivity and zooplankton biomass. As fish yield is related to nutrients through food-chain linkages (Foerster 1968; Brocksen *et al.* 1970; Hanson and Leggett 1982; Koenings *et al.* 1989), continued low escapements may further act to decrease the fertility (nutrients) of Coghill Lake. However, increasing lake fertility through supplemental nutrient loading can stimulate lower trophic level production resulting in greater production of juvenile sockeye and ultimately adult sockeye (LeBrasseur *et al.* 1978; Stockner and Hyatt 1984; Koenings and Burkett 1987; Kyle *et al.* 1991). This report examines sockeye production in Coghill Lake and characterizes lake productivity relative to the potential for enhancement of lower trophic levels through lake fertilization.

Study Site Description-- Coghill Lake (61° 4' N, 147° 54' W) is located in Prince William Sound ~130 km northwest of Cordova (Figure 1). Glacier meltwater from Dartmouth, Muth, and William glaciers that drain into Coghill Lake causes seasonal turbidity. The outlet of the lake empties into the eastern side of Port Wells. Coghill Lake is 7.5 km long and up to 2.7 km wide, has a surface area of 12.7 km^2, a mean lake depth of 46.3 m, a maximum depth of 78 m, and a total volume of 587×10^6 m^3 (Pellissier and Somerville 1984) (Figure 2). Mean annual precipitation is an estimated 330 cm (Anonymous 1979), and as the lake watershed area encompasses 128 km^2, the hydraulic residence time or flushing rate is estimated to be 0.9 yr.

METHODS AND MATERIALS

Fish Assessment

Sockeye Escapement and Returns-- Adult sockeye salmon returning to Coghill Lake are enumerated by the Commercial Fish Division of ADF&G using a weir located in Coghill River (Figure 1). Returning adults are enumerated and sampled each year at the weir for age, size, and sex following procedures described by Crawford and Simpson (1991).

Sockeye Smolt Abundance, Size and Age-- Sockeye salmon smolts migrating from Coghill Lake were enumerated during 1989-1991 using incline-plane traps (Kyle 1983). The traps were operated continuously from early May to early June. Catch efficiencies of the traps were determined by mark and recapture analyses. Each day 40 smolts were

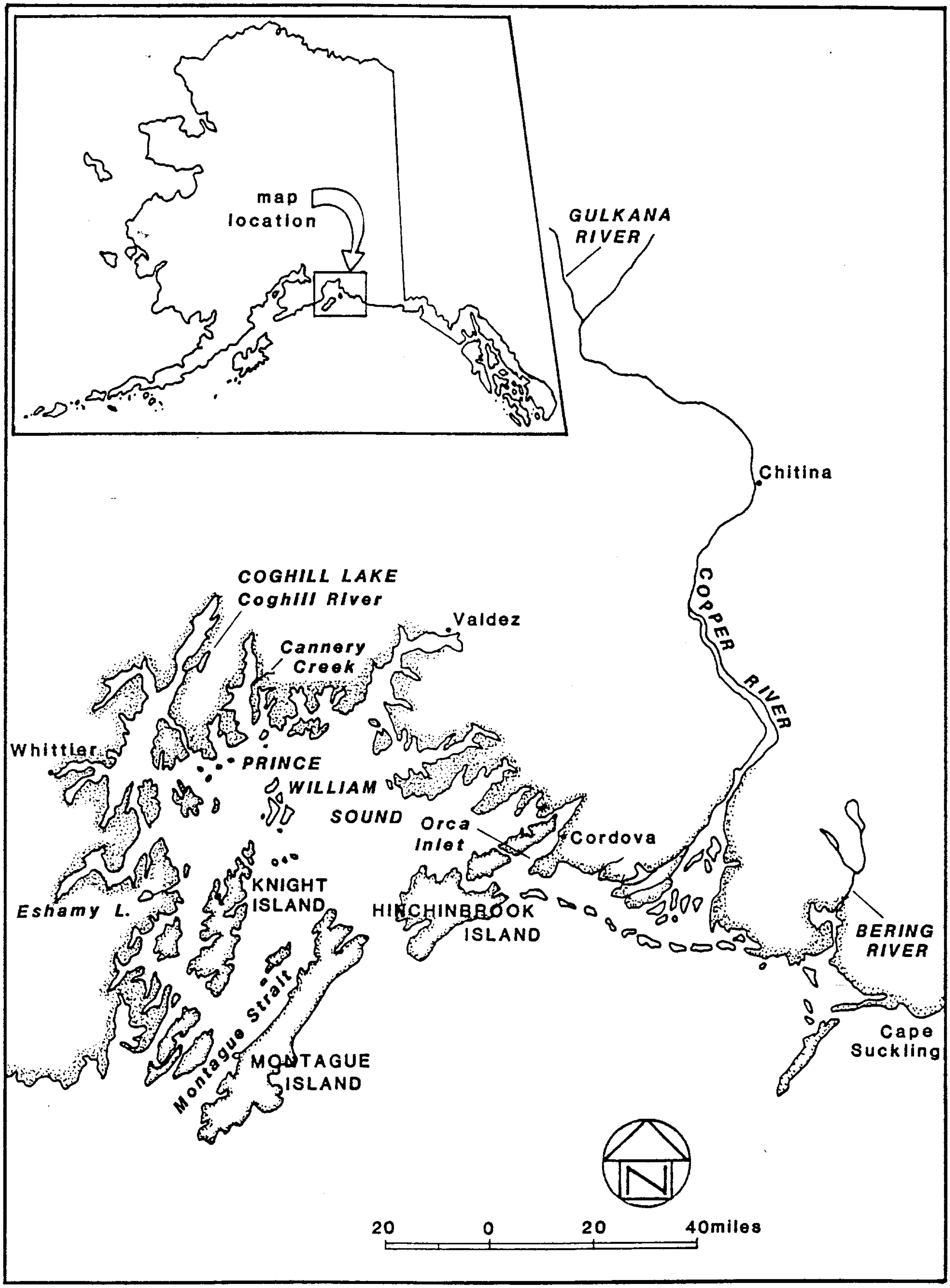

Figure 1. Geographical location of Coghill Lake in Prince William Sound.

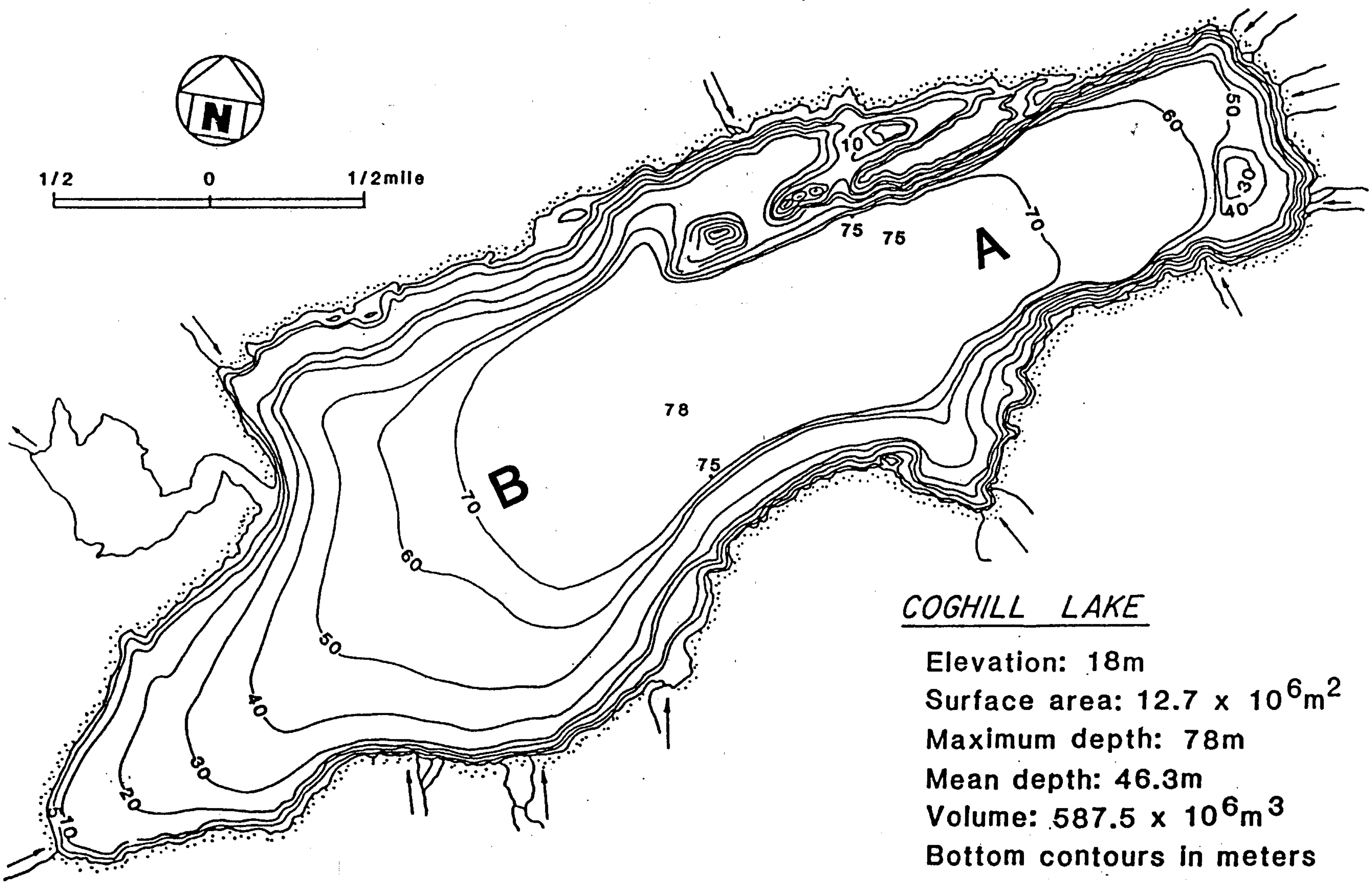

Figure 2. Morphometric map of Coghill Lake showing location of the two (A and B) limnological sampling stations.

anesthetized with MS-222, measured for fork length to the nearest millimeter, and weighed to the nearest 0.1 g. A scale smear was affixed to a glass slide and aged using a microfiche projector.

Hydroacoustic Surveys-- Hydroacoustic surveys were conducted on 01 November 1988, 10 October 1989, and 31 August 1990 to estimate the population and vertical distribution of rearing sockeye juveniles. Data were recorded along 6-10 randomly selected transects that were oriented perpendicular to the longitudinal axis of the lake. All acoustic surveys were done during the darkest period of night, when juvenile sockeye salmon are normally distributed in the upper to middle part of the water column (Narver 1970; McDonald 1973; Eggers 1978; Simpson *et al.* 1981; Nunnallee 1983; Burczynski and Johnson 1986; Levy 1987). In 1988, data were collected using a 420-Khz Biosonics® 105 echo sounder and recorded in digital format on a Beta cassette recorder. In 1989, a 70-Khz Simrad EY-M echo sounder was used and the data was recorded on an analog cassette recorder, and in 1990 the Simrad echosounder was used but data were recorded on a DAT cassette recorder. The 1988 data were analyzed using echo integration; however, fish densities in 1989 and 1990 were low enough to use echo counting techniques. Data collection and analysis are detailed in Kyle (1990). The analysis of recorded hydroacoustic tapes was conducted by Dr. Richard Thorne of BioSonics, Inc.

A 7.5-m long mid-water trawl with a 2 x 2 m opening was used in conjunction with the hydroacoustic surveys to determine species composition and age structure of fish targets. Fish were preserved in 10% formalin for 6 weeks to allow for complete shrinkage, and then measured to the nearest millimeter and weighed (nearest 0.1 g). A scale smear was taken from each fish, affixed to a glass slide, and aged using a microfiche projector.

®Mention of commercial products and trade names does not constitute endorsement by ADF&G, FRED Division.

Limnological Assessment

Field Sampling-- Limnological surveys were conducted at Coghill Lake during June-October during 1986 and 1988-1990. A single mid-lake station was sampled in 1986, after which two permanent sampling locations were established (Figure 2). During 1991, surveys were conducted in July, August, and October; however, analytical data were not completed at the time of this report.

Physical Parameters-- Temperatures and dissolved oxygen concentrations were recorded from the surface to a depth of 40 m using a YSI model-57 meter. Measurements of light penetration (footcandles) were recorded at 1-m increments from the surface to a depth equivalent to 1% of the subsurface light using a Protomatic submarine photometer. The euphotic zone depth (EZD) is the depth to which 1% of the subsurface light (photosynthetically available light [400-700 nm]) penetrates (Schindler 1971). The EZD was calculated as the y-intercept derived by regressing depth against the logarithm of the percent subsurface light. Secchi disk (SD) transparency was determined as the averaged reading (depth) taken by lowering a standard 20-cm disk until it disappears, and then raising the disk until it reappears.

Water Quality-- Water samples were collected from the 1-m stratum, chemocline, and monimolimnion using a non-metallic, opaque Van Dorn sampler. Eight liters of water were collected from each depth, stored (<24 hr) in pre-cleaned polyethylene carboys, transported to Cordova for processing, and then shipped to the Limnology Laboratory in Soldotna for analysis.

Water samples were analyzed for the following parameters as detailed by Koenings *et al.* (1987). Conductivity (μmhos cm^{-1}) was measured with a YSI model-32 conductance meter. Alkalinity levels (mg L^{-1}) were determined by acid titration (0.02 N H_2SO_4) to pH 4.5, using a Corning model-399A specific ion meter. Calcium and magnesium (mg L^{-1}) were determined from separate EDTA (0.01 N) titrations after Golterman (1969), turbidity (NTU) was measured with a HF model-DRT100 turbidimeter, and color (Pt units) was determined with a spectrophotometer. Total iron ($\mu g\ L^{-1}$) was analyzed by reduction of ferric iron with hydroxylamine during hydrochloric acid digestion after Strickland and Parsons (1972).

Nutrients-- All nutrient samples were analyzed by methods detailed by Koenings *et al.* (1987). In general, filterable reactive phosphorus (FRP) was analyzed by the molybdate-blue/ascorbic-acid method of Murphy and Riley (1962), as modified by Eisenreich *et al.* (1975). Total phosphorus was determined using the FRP procedure, after persulfate digestion. Nitrate and nitrite (NO_3 + NO_2) were determined as nitrite following cadmium reduction of nitrate, and total ammonia (NH_3 + NH_4^+) was determined using the phenolhypochlorite methodology after Stainton *et al.* (1977). Total Kjeldahl nitrogen (TKN) was determined as total ammonia following sulfuric acid block digestion (Crowther *et al.* 1980). Total nitrogen was calculated as the sum of TKN and NO_3 + NO_2. Reactive silicon was determined using the method of ascorbic acid reduction to molybdenum-blue after Stainton *et al.* (1977).

Estimation of the yearly phosphorus loading in Coghill Lake was calculated after Vollenweider (1976):

Surface specific loading:

$$Lp(mgP\ m^{-2}\ yr^{-1}) = \frac{[P]^{sp} \times \bar{z}(1 + \sqrt{T_w})}{T_w}$$

Surface critical loading:

$$Lc(mgP\ m^{-2}\ yr^{-1}) = \frac{10 mgP\ m^{-3} \times \bar{z}(1 + \sqrt{T_w})}{T_w}$$

Permissible supplemental P ($mg\ m^{-2}\ yr^{-1}$) loading = $L_c \bullet 90\% - L_p$

Where: $[P]^{sp}$ = spring overturn period total P ($mg\ m^{-3}$)

$\bar{z}$ = mean depth (m)

T_w = water resident time (yr)

10 $mgP\ m^{-3}$ = lower critical phosphorous level.

Phytoplankton-- Water samples (0.5-1.0 L) for chlorophyll a (chl a) analysis were filtered through 4.25-cm GF/F filters to which 1-2 mls of a saturated $MgCO_3$ solution were added just prior to the completion of filtration. The filters were then stored frozen in individual plexislides for analysis. Chlorophyll a analysis followed the fluorometric procedure of Strickland and Parsons (1972). The low-strength acid addition recommended by Riemann (1978) was used to estimate phaeophytin.

Zooplankton-- Replicate bottom-to-surface vertical zooplankton tows were taken using a 0.2-m diameter, 153-μ mesh, conical net. The net was pulled at a constant 1 m s^{-1}, and all organisms were preserved in a 10% neutralized formalin solution. Identification of *Daphnia* followed Brooks (1957), *Bosmina* after Pennak (1978), and the copepods after both Wilson (1959) and Yeatman (1959). Enumeration consisted of counting triplicate 1-ml subsamples taken with a Hansen-Stempel pipette in a 1-ml Sedgewick-Rafter cell. Zooplankton body sizes were obtained by measuring the length to the nearest 0.01 mm of at least 10 individuals along a transect in each 1-ml subsample (Koenings *et al.* 1987). Finally, zooplankter biomass was estimated from an empirical regression between zooplankter body-length and dry weight, and was weighted by organism density (Koenings et *al.* 1987).

RESULTS AND DISCUSSION

Fish Assessment

Sockeye Escapement and Returns-- Since 1968, sockeye escapement into Coghill Lake averaged 65,323 fish and has ranged from a high of 187,263 in 1987 to a low of 8,949 in 1990 (Table 1). During 1980-1987, the sockeye escapement averaged ~125,000 fish or nearly twice the average since 1968. Following the 1988 escapement, sockeye returns have dramatically decreased and for the last two years escapements have been <10,000. Commercial harvest records are available since 1975, and indicate an annual mean harvest of 194,000 sockeye, with a record harvest of 947,431 in 1982 and a low of 12,274 in 1990 (Table 1). Thus, since 1975 the total return has averaged 270,000 sockeye.

Table 1. Summary of sockeye salmon escapement, commercial harvest, and total return for Coghill Lake, 1968-1991.

Year	Escapement	Harvest	Total return
1968	11,800		
1969	81,000		
1970	35,200		
1971	15,000		
1972	51,000		
1973	55,000		
1974	22,333		
1975	34,855	147,849	182,704
1976	9,056	60,493	69,549
1977	31,562	170,778	202,340
1978	42,284	203,522	245,806
1979	48,281	78,800	127,081
1980	142,253	59,116	201,369
1981	156,112	103,055	259,167
1982	180,314	947,431	1,127,745
1983	38,783	38,448	77,231
1984	63,622	94,977	158,599
1985	163,311	350,053	513,364
1986	71,095	400,079	471,174
1987	187,263	416,353	606,616
1988	72,052	83,917	155,969
1989	36,881	108,144	145,025
1990	8,949	12,274	21,223
1991	9,752	15,202	24,954
1968-1991 Mean	65,323	193,558	269,995
1980-1987 Mean	125,344		

Brood-year returns for the five major age classes of sockeye returning to Coghill Lake is presented in Table 2. Prior to broodyear 1978, the return/spawner (R/S) fluctuated from 1 to as high as 40 and averaged just under 10; however, since then the R/S has remained fairly consistent at 3 until 1985. Despite larger escapements during 1980-1987, the R/S were on average 3-fold lower compared to before 1978 when escapements were much lower. Beginning in broodyear 1985 (escapement of 163,000), it appears the R/S has further decreased to below 1. Thus, these data indicate that more spawners do not produce greater returns in Coghill Lake, and irrespective of lower escapements (relaxed overgrazing on zooplankton from reduced fry recruitment), the R/S has not improved.

Sockeye Smolt Abundance, Size, and Age-- The smolt estimates for 1989-1991 were 387,000, 5,800, and 111,000, respectively (Table 3). In 1989 and 1990, smolt sampling ended in late May; however, in 1989 there appeared to be some smolts continuing to emigrate while in 1990 very few were emigrating at the time sampling was terminated. In 1991, a late spring throughout the region (Prince William Sound) delayed the smolt migration as nearly 80% of the estimated population migrated during 04 June - 24 July.

The majority of the smolt population appears to rear only one year prior to emigrating Coghill Lake (Table 3). Age-1 smolt sizes during 1989-1991 ranged from 52-61 mm and 1.0-1.9 g, which is below the minimum average 'threshold size' for sockeye smolts (Koenings and Burkett 1987). In 1990, age-1 smolts were slightly larger, but they were still less than the average threshold weight for age-1 smolts of 2.2 g.

Juvenile Sockeye Population Estimates and Freshwater Survival-- The hydroacoustic survey conducted in the fall of 1988 revealed a juvenile sockeye population estimate of 3,269,000. Based on a 10% survival from potential egg deposition (PED) to spring fry (Foerster 1968), an estimated 27 million spring fry were produced from the 1987 brood year escapement (Table 4). As the 1988 fall fry estimate comprised the majority of total production from the 1987 brood year (100% age-0 caught in townet and <3% of the juvenile sockeye smolts produced reared for more than one year [Table 3]); the total spring-to-fall fry survival is estimated at 12.1% (Table 4). In addition, using a 65% over-winter survival (Kyle

Table 2. Return of sockeye salmon by brood year for the major age classes, and the return per spawner (R/S) for Coghill Lake, 1968-1991.

Brood year	Brood year escapement	Age class 1.1	1.2	1.3	2.2	2.3	Total return	R/S
1968	11,800	0	22,526	108,120	3,219	6,623	137,508	11.7
1969	81,000	0	12,896	60,811	7,908	10,133	91,748	1.1
1970	35,200	0	49,280	158,164	8,803	4,619	220,866	6.3
1971	15,000	115	5,604	32,566	2,782	5,661	46,728	3.1
1972	51,000	0	29,452	164,079	6,691	18,346	218,568	4.3
1973	55,000	0	25,454	203,097	3,332	1,805	233,688	4.2
1974	22,333	455	21,031	76,250	10,499	2,590	111,825	5.0
1975	34,855	NA \a	38,347	136,670	7,713	8,799	191,528	5.5
1976	9,056	90	52,434	99,913	12,717	8,377	173,531	19.2
1977	31,562	1,981	137,083	1,108,256	1,773	1,956	1,251,048	39.6
1978	42,284	656	8,799	51,329	2,139	7,381	70,303	1.7
1979	48,281	270	17,439	105,297	6,351	21,049	150,407	3.1
1980	142,253	162	37,780	344,020	51,572	40,122	473,656	3.3
1981	156,112	436	92,478	355,917	14,590	32,817	496,238	3.2
1982	180,314	155	58,604	546,985	5,829	586	612,159	3.4
1983	38,783	71	11,755	86,810	448	7,213	106,297	2.7
1984	63,622	1,347	64,775	133,744	2,112	1,108	203,086	3.2
1985	163,311	31	1,682	12,951	1,170	562	16,396	0.1
1986	71,095	34	4,372	12,709	61		17,176 \b	0.2
1987	187,263	0	1,596				11,735 \b	0.1
1988	72,052	15						
1989	36,881							
1990	8,949							
1991	9,752							

\a NA denotes not available.

\b Estimated based on historical average age compositions for missing age classes.

Table 3. Sockeye salmon smolt abundance, size, and age by five-day periods for Coghill Lake, 1989-1991.

	1989					1990					1991				
Sample period	Total smolt estimate	Age class	Age comp. (%)	Mean FL (mm)	Mean WT (g)	Total smolt estimate	Age class	Age comp. (%)	Mean FL (mm)	Mean WT (g)	Total smolt estimate	Age class	Age comp. (%)	Mean FL (mm)	Mean WT (g)
06-10 May	33,367	1.0	97.5	52	1.2	931	1.0	76.8	60	1.7	2,419	1.0	87.5	58	1.6
		2.0	2.5	/a	/a		2.0	23.2	76	3.2		2.0	12.5	75	3.6
11-15 May	88,354	1.0	99.5	51	1.0	666	1.0	54.5	60	1.8	3,736	1.0	80.0	61	1.7
		2.0	0.5	/a	/a		2.0	45.5	73	3.0		2.0	20.0	76	3.4
16-20 May	73,901	1.0	100.0	52	1.1	956	1.0	77.3	61	1.9	5,916	1.0	84.4	59	1.6
		2.0	0.0	/a	/a		2.0	22.7	74	3.3		2.0	15.6	74	3.3
21-25 May	83,989	1.0	99.5	52	1.1	1,287	1.0	56.0	59	1.7	5,407	1.0	71.1	58	1.6
		2.0	0.5	/a	/a		2.0	44.0	70	2.8		2.0	28.9	72	3.0
26-30 May	77,181	1.0	97.5	54	1.3	1,949	1.0	61.2	60	1.7	2,471	1.0	74.1	58	1.5
		2.0	2.5	/a	/a		2.0	38.8	72	2.9		2.0	25.9	67	2.4
31 May-04 Jun	30,258	1.0	99.0	53	1.2	NS					2,852	1.0	88.4	55	1.5
		2.0	1.0	/a	/a							2.0	11.6	69	2.8
04 Jun-24 Jul	NS /b					NS					88,109	1.0	71.7	56	1.6
												2.0	28.8	70	3.4
Total	387,050					5,789					110,910				

/a Less than 5 age-2 smolts were sampled per period, and because of the small sample size are not listed.
/b NS denotes sampling was not conducted.

Table 4. Estimated freshwater survival of juvenile sockeye for brood years 1987-1989, Coghill Lake.

Brood year	PED \a	Estimated no. spring fry \b	Estimated no. fall fry \c	Estimated spring-to-fall fry survival (%)	Smolt production Age-1	Age-2	Estimated spring fry-to-smolt survival (%)	Estimated fall fry-to-smolt survival (%)
1987	270,352,000	27,035,200	3,269,000	12.1	383,000	2,100	1.4	11.8
1988	100,807,500	10,080,750	280,500	2.8	3,700	30,000	0.3	12.0
1989	52,337,000	5,233,700	1,550,000	29.6	82,616	NA \d	Incomplete	Incomplete

\a Potential egg deposition = number of females x fecundity.

\b Based on 10% survival (Foerster 1968).

\c Based on hydroacoustic surveys.

\d Not available; age-2 smolts will not migrate until 1992.

unpublished data), the smolt outmigration (1989) would be a projected 2.1 million. However, the 1989 smolt outmigration estimate was only 387,000, or 18% of the projected, and represented a fall fry-to-smolt survival of only 12%. This represents a very low spring fry-to-smolt survival of 1.4% which was well below the 21% expected at optimal rearing capacity (Koenings and Burkett 1987).

For the 1988 brood year, freshwater survivals declined further. That is, the 1989 fall hydroacoustic survey revealed a population of 280,500 juveniles which equates to a spring-to-fall fry survival of 2.8%. In addition, the age composition of age-1 smolts in 1990 (production from the 1988 brood year) was much lower than in 1989 (Table 3), indicating an impoverished rearing environment. Moreover, the estimated spring fry-to-smolt survival was 0.3% and the fall fry-to-smolt survival was 12% for the 1988 brood year. Although the estimated spring fry-to-fall fry survival of the 1989 brood year appears to have increased to 29.6% and is very close to the projected survival based the euphotic volume model (Koenings and Burkett 1987); juvenile sockeye growth as observed from the small age-1 smolt size of 1991 was curtailed. Thus, from the available information, both low freshwater survival and insufficient growth rates (small smolt size) indicate that the rearing environment of Coghill Lake is limiting juvenile sockeye production.

Finally, juvenile sockeye densities were highest for transects (1-5) located in the lower half of Coghill Lake (Table 5). In addition, for all three hydroacoustic surveys conducted during 1988-1990, 46% of the total juvenile sockeye density was distributed within the first depth strata near the surface (2-4 or 6 m), and over 95% was distributed between 2 and 20 m.

Limnological Assessment

Light Penetration-- Coghill Lake receives turbid meltwater from three glaciers, and as such, the most noticeable effect of glacial meltwater intrusion is an increase in turbidity and a decrease in light penetration (Koenings *et al.* 1986; Lloyd *et al.* 1987; Koenings and Edmundson 1991). In Coghill Lake, the euphotic zone depth (EZD) was greatest (mean 11.5 m) during times of minimum glacier melt (June-July), lowest (mean 3.7 m) at maximum glacier melt (September-October), and intermediate (mean 6.0 m) during mid-summer

Table 5. Density of juvenile sockeye (no. per m^3) by depth and transect for each of the three surveys conducted in Coghill Lake during 1988-1990.

	Survey year	Depth interval (m)				
	1988	2-6	6-12	12-18	18-24	>24
	1989	2-4	4-8	8-13	13-18	>18
Tansect	1990	2-4	4-8	8-13	13-18	>18
1	1988	111	144	247	11	0
	1989	3	2	1	1	0
	1990	19	3	1	0	0
2	1988	58	34	19	6	3
	1989	2	2	1	1	1
	1990	26	6	2	2	0
3	1988	57	45	22	9	1
	1989	4	3	2	1	1
	1990	71	9	1	0	0
4	1988	62	66	17	3	2
	1989	4	4	2	1	1
	1990	81	12	2	0	0
5	1988	29	68	3	1	0
	1989	1	2	2	1	0
	1990	91	15	1	0	0
6	1988	2	26	3	2	0
	1989	2	2	1	1	0
	1990	40	6	1	0	0
7	1989	2	2	1	0	0
	1990	16	3	0	0	0
8	1989	2	1	1	0	0
	1990	11	3	1	0	0
9	1989	1	1	1	1	1
	1990	10	2	0	0	0
10	1990	11	4	1	0	0
Distribution by depth interval for all transects (%)		46	30	21	3	1

(August) (Table 6). On a seasonal basis, the EZD averaged 8.6 m in 1986, 9.6 m in 1988 and in 1989 and 1990 decreased to 7.3 m and 5.4 m, respectively. The mean EZD for all years was 7.6 m and the euphotic volume (EZD x lake surface area) equalled 96.5 x 10^6 m^3 or 97 euphotic volume (EV) units, which comprises only 16% of the total lake volume. The Secchi disk (SD) transparency followed the same seasonal trends as the EZD and averaged 2.2 m for all years. The EZD:SD ratio equalled 3.5 which is consistent with other turbid lakes (Koenings and Edmundson 1991).

Seasonal average turbidity levels within the mixolimnion of Coghill Lake ranged from 3-10 NTU; however, during periods of peak glacier run-off (September-October) turbidities reached as high as 26 NTU (Table 7). This phenomena occurs when precipitation combined with glacier melt increases the magnitude of silt loading (Koenings *et al.* 1986; Mayo 1986). Coghill Lake resembles a clearwater lake during early summer as turbidity is less than 5 NTU; however, during late summer (late August - early September) turbidity increases to greater than 5 NTU. Thus, Coghill Lake is defined as a 'semi-glacial' lake (Edmundson and Koenings 1985; Koenings *et al.* 1986).

Temperature and Dissolved Oxygen Regimes-- There was no obvious difference in temperature regimes between the two sampling stations, so temperature profiles from Station A in 1989 (Figure 3) and 1990 (Figure 4) were used to characterize the thermal structure of Coghill Lake. During July and August, Coghill Lake was moderately stratified (i.e. temperatures reached ~15° C within the upper layers of the mixolimnion), cooled steadily to below 5° C near the bottom of the chemocline, and then increased slightly above 5° C near the top of the monimolimnion. Thus, the coldest water occurs within the chemocline, which is due to the fact that the monimolimnion does not undergo mixing during spring or fall turnover. The slightly warmer temperatures below the chemocline are most likely due to anaerobic chemical reactions (Hutchinson 1957; Wetzel 1975). This phenomenon is not unique as similar temperature patterns have been document for other meromictic lakes (Northcote and Johnson 1964; Takahashi *et al.* 1968; Weimer and Lee 1973; Walker 1974; McCoy 1977).

Table 6. Seasonal changes in euphotic zone depth (EZD) and Secchi disk (SD) depth in Coghill Lake during 1986-1990.

Date	Station	EZD (m)	SD (m)
06/01/86	A	17.1	7.5
07/17/86	A	9.8	3.3
09/04/86	A	5.1	1.8
10/16/86	A	2.4	0.5
Mean		**8.6**	**3.3**
06/09/88	A	14.1	6.0
	B	14.3	4.0
07/15/88	A	17.0	3.5
	B	12.0	3.0
09/15/88	A	4.3	1.5
	B	4.4	1.2
10/20/88	A	5.2	1.5
	B	5.3	1.5
Mean		**9.6**	**2.8**
06/05/89	A	11.0	NA\a
	B	11.8	4.0
07/14/89	A	10.9	3.0
	B	11.4	3.0
08/22/89	A	9.3	2.5
	B	8.8	2.5
10/03/89	A	2.0	0.2
	B	2.0	0.2
10/29/89	A	2.5	0.3
	B	3.0	0.3
Mean		**7.3**	**1.8**
06/15/90	A	5.6	1.2
	B	6.1	1.2
07/12/90	A	9.5	1.2
	B	8.4	1.2
08/15/90	A	6.2	1.7
	B	7.9	2.0
09/20/90	A	3.5	0.5
	B	4.3	0.5
10/24/90	A	4.3	0.9
	B	4.4	0.6
Mean		**5.4**	**1.1**

\a NA denotes not available.

Table 7. Range and seasonal mean values for analyzed water quality parameters and nutrients within the mixolimnion (1 m) of Coghill Lake, 1986-1990.

	1986 (n=4)		1988 (n=4)		1989 (n=5)		1990 (n=5)	
Parameter	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Conductivity (umhos/cm)	50-102	63	61-91	74	57-126	83	55-95	75
pH (units)	6.8-8.0	7.3	7.0-7.4	7.2	7.1-7.4	7.3	7.0-7.4	7.1
Alkalinity (mg/L)	20-34	24	15-21	18	17-22	19	18-22	19
Turbidity (NTU)	1-15	4	1-6	3	1-26	10	1.8-8.0	5.0
Color (Pt units)	3-12	6	5-6	6	4-11	8	4-8	5
Calcium (mg/L)	6.1-7.1	6.6	6.5-7.5	7.0	6.1-8.4	7.1	6.2-18.7	8.4
Magnesium (mg/L)	0.7-1.3	1.0	2.3-4.2	3.3	0.6-2.2	1.3	0.6-3.7	1.4
Iron (ug/l)	16-773	222	23-257	141	35-1,035	410	117-520	301
Total -P (ug/L)	2.7-19.3	8.4	3.7-10.8	6.3	4.9-21.4	9.2	4.6-10.7	7.5
Total Filterable -P (ug/L)	2.5-13.8	7.0	1.7-3.2	2.5	2.0-5.1	3.1	1.0-7.3	2.6
Filterable reactive -P (ug/L)	0.7-8.5	4.1	0.7-1.9	1.4	1.8-3.1	2.5	0.6-5.0	2.2
Total Kjeldahl -N (ug/L)	43-58	49	37-61	48	34-65	48.4	25-65	41.8
Ammonia (ug/L)	0.9-10.1	3.8	2.2-5.4	4.1	0.5-4.4	1.5	1-2	1.3
Nitrate + nitrite (ug/L)	3.4-25.2	8.2	5.2-43.9	22.7	3.4-55.9	27.7	<1.0-49.2	18.0
Reactive silicon (ug/L)	591-942	813	566-877	710	468-877	701	507-1,274	748
Chlorophyll a (ug/L)	0.1-1.0	0.3	0.2-1.7	0.9	<0.1-0.7	0.2	0.3-3.5	0.8

Table 8. Range and seasonal mean values for analyzed water quality parameters and nutrients within the top (25 m; 1989 and 1990) and bottom (25-30 m; 1988) of the chemocline, and in the monimolimnion (60 m; 1986) of Coghill Lake.

	1986 (n=4)		1988 (n=4)		1989 (n=5)		1990 (n=5)	
Parameter	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Conductivity (umhos/cm)	27,100-30,800	29,625	191-1,480	793	119-451	311	207-438	318
pH (units)	7.2-7.4	7.3	6.9-7.2	7.1	6.9-7.1	7.0	6.8-7.2	7.0
Alkalinity (mg/L)	20-508	218	21-33	26	21-27	23	21-25	22.6
Turbidity (NTU)	NA \a	--	2-5	4	1.4-68.0	24.9	7.8-16.0	12.5
Color (Pt units)	63-604	331	3-8	5	6-11	8	4 -9	7
Calcium (mg/L)	NA	--	17.2-24.2	20.8	8.8-11.4	9.7	8.4-15.7	10.4
Magnesium (mg/L)	NA	--	22.8-29.8	26.6	1.5-8.8	5.5	3.4-12.1	6.3
Iron (ug/l)	8,668-15,243	12,500	64-284	166	49-3,040	1,051	94-1,149	666
Total -P (ug/L)	57.0-124.3	100.3	4.0-11.8	7.2	3.4-47.9	20.9	9.6-25.7	15.9
Total Filterable -P (ug/L)	4.0-105.0	53.9	1.4-2.5	2.1	1.4-4.5	2.6	1.0-6.3	2.6
Filterable reactive -P (ug/L)	3.4-74.7	39.5	0.6-21	1.2	1.7-3.1	2.3	1.0-5.1	2.5
Total Kjeldahl - N (ug/L)	11,521-13,760	12,822	32-47	41	25-102	49	36-51	41.4
Ammonia (ug/L)	2,742->5,000	>4,436	1.1-5.9	4.1	1.1-2.2	1.4	1.0-2.0	1.4
Nitrate + nitrite (ug/L)	3.4-8.9	4.9	57.1-228.7	131.4	54-117	88	58.7-98.9	83.1
Reactive silicon (ug/L)	2,442-5,048	4,029	665-1,047	892	771-918	818	697-1,349	902
Chlorophyll a (ug/L)	<0.1-0.5	<0.2	0.1-0.3	0.1	<0.1-0.2	<0.1	<0.1-0.3	0.1

\a NA denotes not available.

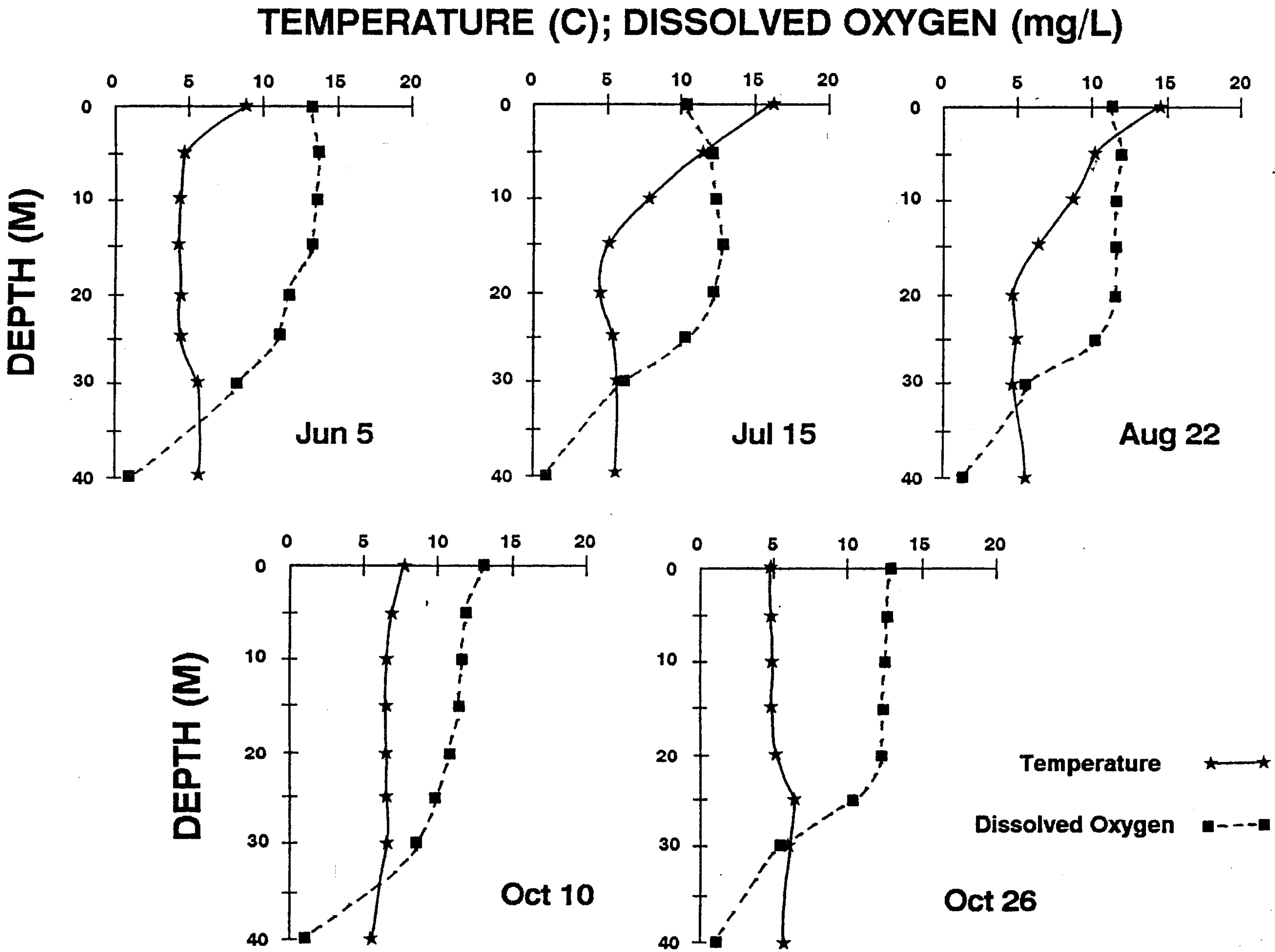

Figure 3. Seasonal temperature and dissolved oxygen profiles for Station A in Coghill Lake, 1989.

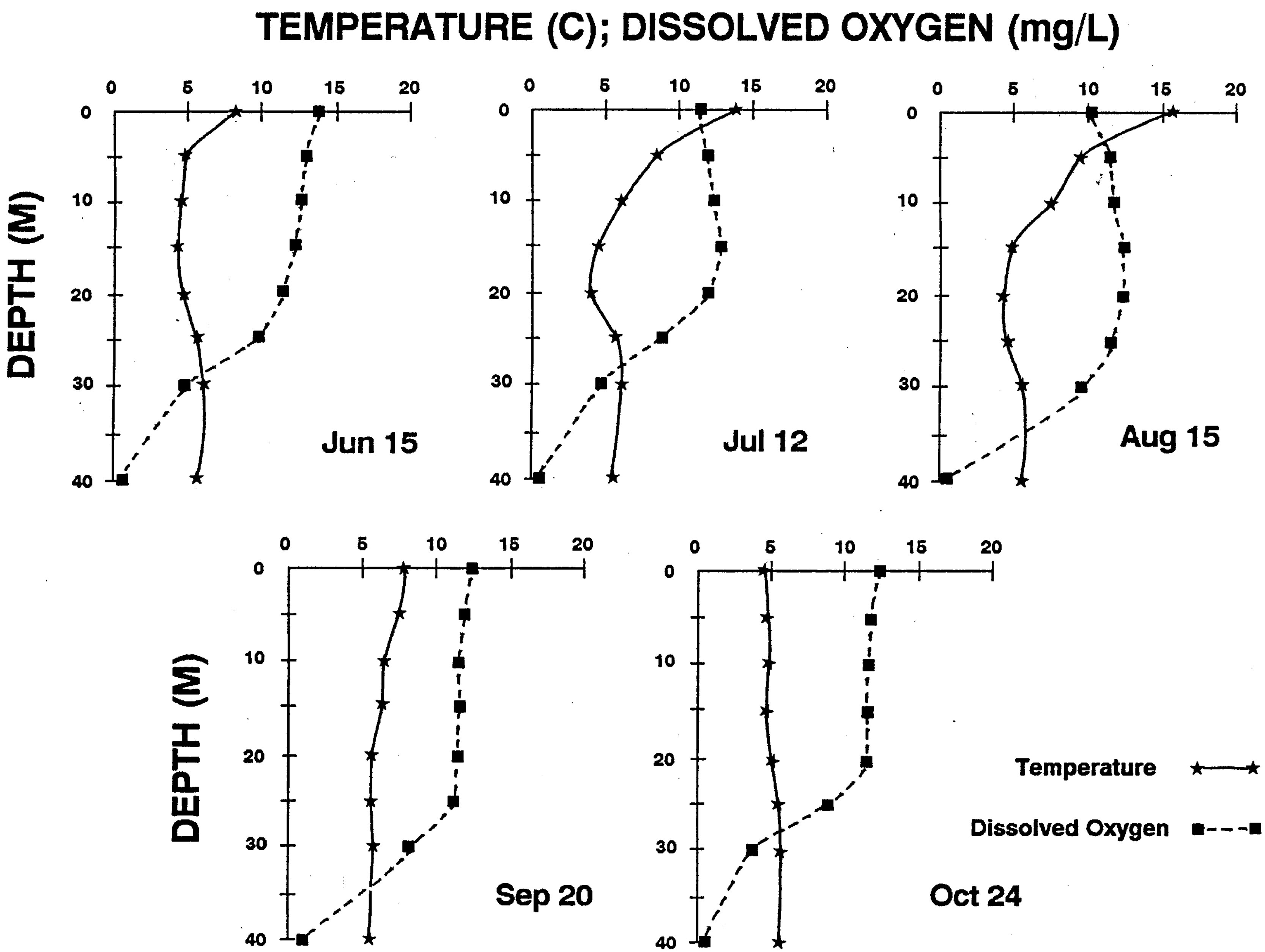

Figure 4. Seasonal temperature and dissolved oxygen profiles for Station A in Coghill Lake, 1990.

The seasonal dissolved oxygen (DO) profiles indicate that Coghill Lake is meromictic (Figures 3 and 4). Specifically, DO concentrations ranged from 10-13 mg L^{-1} above 20 m and were near 100% saturation, but concentrations decreased rapidly to 5 mg L^{-1} (40% saturation) at 30 m. At depths >30 m no DO was found indicating the presence of an anoxic layer referred to as the monimolimnion. This stagnant water mass comprises 45% of the total lake volume. Thus, the portion of water above 20 m mixes and is referred to as the mixolimnion and is separated from the monimolimnion (>30 m) by a chemocline at 20-30 m.

General Water Quality Parameters-- Analytical results derived from the 1-m stratum are used to characterize the mixolimnion (Table 7). Samples collected from the 25 and 30 m strata are used to characterize the chemocline (Table 8); however, data obtained in 1988 reflect conditions near the top of the chemocline (at 25 m), whereas data from subsequent years define the conditions at the bottom of the chemocline (30 m). Results derived from samples collected at a depth of 60 m during 1986 describe the monimolimnion (Table 8). For ease of comparison, the mixolimnion, chemocline, and monimolimnion are discussed here in terms of seasonal mean values except when noted otherwise.

Coghill Lake is a moderately hard water system as conductivity ranged from 63-83 µmhos cm^{-1} in the mixolimnion (Table 7). In contrast, conductivity averaged nearly 30,000 µmhos cm^{-1} in the monimolimnion (Table 8), which is equivalent to ~23‰ or 67% that of seawater. As no vertical mixing extends into the monimolimnion, changes in conductivity occur through the process of diffusion from lower strata (Takahashi *et al.* 1968; McCoy 1977). Thus, conductivity averaged 315 and 793 µmhos cm^{-1} near the top and bottom of the chemocline, respectively. It is this steep density (salinity) gradient which prevents vertical mixing of the monimolimnion during spring and fall turnover and prevents the regeneration of essential nutrients to the surface layers (Hutchinson 1957; Walker 1974; Wetzel 1975).

Alkalinity within the upper layers was moderate compared with other Alaskan lakes as seasonal mean concentrations ranged from 15-34 mg L^{-1} in the mixolimnion (Table 7). Alkalinities were similar within the chemocline, but increased ten-fold (averaged 218 mg L^{-1}) in the monimolimnion (Table 8). The increased alkalinity of the monimolimnion is attributed to the release of carbon dioxide resulting from anaerobic decomposition within the lower strata and lake-bottom sediments. Finally, the pH was uniform and slightly above neutral across all depth strata ranging from 7.0-7.3 units (Tables 7 and 8).

Metals-- Calcium and magnesium levels within the mixolimnion were moderate for Alaskan lakes and ranged from 6.6-8.4 mg L^{-1} and 1.0-3.3 mg L^{-1}, respectively (Table 7). In contrast, calcium and magnesium concentrations averaged ~10 and 6 mg L^{-1}, respectively at the top of the chemocline, but increased to as high as 21 and 27 mg L^{-1} near the bottom of the chemocline (Table 8). Moreover, due to extreme salinity concentrations, calcium and magnesium levels within the monimolimnion exceeded the upper limits of analytical detection (>150 mg L^{-1}). However, calcium and magnesium levels as high as 280 and 840 mg L^{-1}, respectively, have been documented within the monimolimnion of Redoubt Lake in southeast Alaska (McCoy 1977).

In clearwater lakes, under conditions of chemical equilibrium, iron exists primarily as soluble ferric hydroxide (Fe III) in concentrations of <20 µg L^{-1} (Stumm and Lee 1960). In contrast, nearly 90% of the total iron present in turbid glacial lakes is comprised of particulate iron derived from glacial silt (Edmundson and Koenings 1985; Koenings *et al.* 1986). In Coghill Lake, iron concentrations in the mixolimnion ranged from 142-410 µg L^{-1}. Under anaerobic and static conditions, large amounts of ferrous (Fe II) iron are released from the sediments through decomposition. Thus, iron concentrations in the monimolimnion iron averaged 12,500 µg L^{-1}, whereas levels in the chemocline ranged from 166-1,051 µg L^{-1} (Tables 7 and 8).

Nutrients-- Throughout the sampling period, ammonia nitrogen concentrations in Coghill Lake were very low and fairly consistent both within the mixolimnion and chemocline averaging <5 µg L^{-1} (Tables 7 and 8). Nitrate + nitrite nitrogen levels ranged from 8 to 28 µg L^{-1} in the mixolimnion, whereas concentrations were higher in the chemocline (83-131 µg L^{-1}). In contrast, because nitrification in the monimolimnion of Coghill Lake does not occur due to anaerobic conditions, ammonia levels are extremely high (exceed the detection limit of 5,000 µg L^{-1}) and are toxic to fish (Haywood 1983). For example, analysis of multidiluted samples collected in 1991 revealed ammonia concentrations in excess of 10,000 µg L^{-1}. Finally, total Kjeldahl nitrogen (TKN) concentrations (ammonia + organic nitrogen) in the monimolimnion averaged nearly 13,000 µg L^{-1}, but in the mixolimnion and chemocline TKN levels averaged ~50 µg L^{-1}.

The high total phosphorus (TP) concentrations in Coghill Lake (Table 7) are associated with turbidity from glacier meltwater (Koenings *et al.* 1986). That is, 65% of the TP present in glacial lakes is comprised of inorganic particulate phosphorus (IPP) or 'rock phosphate' derived from glacial silt particles (Edmundson and Koenings 1985). In Coghill Lake, TP levels averaged 7.9 µg L^{-1} in the mixolimnion, but ranged from a low of 2.7 µg L^{-1} during minimum glacial run-off (June) to a high of 21.4 µg L^{-1} during the period of increased glacial melt (September). Within the chemocline, TP concentrations were somewhat higher ranging from 3.4-47.9 µg L^{-1} and averaging 14.7 µg L^{-1} (Table 8). In contrast, the TP levels in the monimolimnion were considerably higher and averaged 53.9 µg L^{-1}. The elevated TP concentrations in the monimolimnion are due not only to IPP derived from glacial silt, but also to the accumulation of orthophosphate (filterable reactive phosphorus [FRP]) derived from the mineralization of settling organic material and lake-bottom sediments (Weimer and Lee 1973; Wetzel 1975). Thus, monimolimnetic FRP levels averaged 39.5 µg L^{-1} compared to only 2.0 and 2.6 µg L^{-1} in the chemocline and mixolimnion.

In general, phosphorus (P) loading calculations (Vollenweider 1976) in turbid (>5 NTU) glacial lakes need to account for both turbidity interference (Koenings et al. 1987) and the presence of IPP (Kuenzler *et al.* 1979; Koenings *et al.* 1986). However, in Coghill Lake turbidities were <5 NTU during the spring so TP concentrations were not corrected for these factors. Based on a 5-year average, the P loading rate in Coghill Lake is estimated at 312 mg m^{-2} yr^{-1} and the critical P loading rate is 650 mg m^{-2} yr^{-1}. Thus, the permissible supplemental P loading equals 273 mg m^{-2} yr^{-1}.

Finally, reactive silicon (Si) levels were lowest in the mixolimnion, highest in the monimolimnion, and intermediate in the chemocline as concentrations averaged 743, 4,029, and 871 µg L^{-1}, respectively (Tables 7 and 8).

Phytoplankton-- Chl a levels in the mixolimnion of Coghill Lake were low 0.2-0.9 µg L^{-1} (Table 7) relative to Alaskan clearwater lakes but similar to other Alaskan glacial lakes (Koenings *et al.* 1990; Koenings and Edmundson 1991). Although decreases in light penetration due to inorganic turbidity tend to lessen primary production (Canfield and Bachman 1981; Lambou *et al.* 1982; Hoyer and Jones 1983; Koenings *et al.* 1986), maximum chl a concentrations in the mixolimnion of Coghill Lake reached 3.5 µg L^{-1} in early August of 1990, which indicates that under favorable conditions (e.g. adequate nutrients, sunlight, and temperature) phytoplankton production within the upper layers can be realized. In contrast, as both the chemocline and monimolimnion lie within the aphotic zone where photosynthesis does not occur, chl a concentrations were at or below the detection limit (<0.1 µg L^{-1}).

Zooplankton Abundance, Body Size and Biomass-- The macrozooplankton community in Coghill Lake is comprised of the copepod *Cyclops columbianus*, and two species of cladocerans; *Bosmina longirostris* and *Daphnia longiremus*, the preferred prey of juvenile sockeye salmon (Brocksen *et al.* 1970; Goodlad *et al.* 1974; Hall and Hyatt 1974; Koenings and Burkett 1987; Kyle *et al.* 1988). Seasonal mean total macrozooplankton (TMZ) density averaged 10,500 m^{-2} in 1986, 119,800 m^{-2} in 1988, 24,100 m^{-2} in 1989, and 6,800 m^{-2} in 1990 (Table 9). *Cyclops* populations peaked in late August to early September and comprised 99% of the TMZ. In contrast, both *Bosmina* and *Daphnia* populations appeared sporadically and when combined comprised only 1% of the TMZ densities. The absence of significant numbers of cladocerans is not surprising given the turbid nature of Coghill Lake and the interference by glacial silt particles on feeding and reproduction of cladocerans (Edmundson and Koenings 1985; Koenings *et al.* 1990;). Nonetheless, because of the relatively low turbidity of Coghill Lake, especially in the early season (before August); we would have expected cladoceran densities to comprise greater than 1% of the composition of macrozooplankton. That is, during the four years sampled, *Bosmina* and *Daphnia* densities averaged 177 m^{-2} and 321 m^{-2}, respectively.

The weighted mean body sizes of *Cyclops* were 0.73, 0.81, 0.72, and 0.86 mm in 1986, and 1988-1990, respectively (Table 9). *Bosmina* body sizes ranged from 0.38-0.62 mm and averaged 0.47 mm, which is slightly above the minimum threshold size (0.40 mm) for elective

Table 9. Macrozooplankton density and body size (mm) for each taxa and station in Coghill Lake, 1986-1990.

Year	1986				1988							
Date	09 Jun	17 Jul	04 Sep	16 Oct	09 Jun		15 Jul		06 Sep		20 Oct	
Species/Station	A	A	A	A	A	B	A	B	A	B	A	B
Cyclops columbianus	2,908 (.64)	7,696 (.52)	18,312 (.79)	12,473 (.96)	19,427 (1.17)	11,040 (1.18)	23,415 (.50)	74,841 (.54)	282,378 (.76)	298,832 (.63)	126,327 (.86)	118,376 (.80)
Bosmina longirostris	85 (.52)	0	0	265 (.43)	318 (.47)	743 (.41)	0	0	0	0	0	0
Daphnia longiremus	42 (.72)	0	0	265 (.52)	1,115 (.78)	849 (.74)	0	0	531 (.65)	0	0	0

Table 9 continued. Macrozooplankton density and body size (mm) for each taxa and station in Coghill Lake, 1986-1990.

Year	1989										1990									
Date	05 Jun		14 Jul		22 Aug		03 Oct		26 Oct		16 Jun		12 Jul		15 Aug		20 Sep		24 Oct	
Species/Station	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Cyclops columbianus	96	80	18,312 (.53)	14,761 (.54)	69,533 (.66)	61,040 (.68)	24,416 (.79)	20,435 (.83)	7,696 (.83)	17,781 (.90)	5,255 (.94)	7,245 (.91)	3,742 (.73)	13,854 (.75)	9,713 (.80)	11,677 (.88)	637 (.84)	3,025 (.89)	6,529 (.93)	4,883 (.90)
Bosmina longirostris	0	0	0	16	1,592 (.52)	0	1,062 (.60)	0	0	531	0	0	0	0	0	0	212 (.40)	726 (.50)	0	743 (.38)
Daphnia longiremus	0	0	0	0	0	0	1,062 (.79)	531 (.77)	0	265	0	0	0	0	0	0	0	0	0	0

feeding by sockeye salmon fry (Koenings and McDaniel 1983; Kyle *et al.* 1988). *Daphnia* body sizes ranged from 0.52-0.79 mm and averaged 0.71 mm.

The weighted mean TMZ biomass equalled 22 mg m^{-2} in 1986, increased ten-fold to 220 mg m^{-2} in 1988, and then decreased markedly to 42 mg m^{-2} and 17 mg m^{-2} in 1989 and 1990, respectively. *Cyclops* populations comprised 99% of the TMZ biomass, whereas *Bosmina* and *Daphnia* populations combined averaged <1% (0.7 mg m^{-2}). Finally, a comparison of TMZ density and biomass for a variety of sockeye nursery lakes including glacial lakes reveals that the average standing stock of zooplankton in Coghill Lake ranks 22 out of 23 (Table 10).

EVALUATION

Although limnological and juvenile sockeye information before the decline of sockeye production in Coghill Lake is not available, indirect evidence strongly suggests adverse impacts of large escapements. That is, following an eight-year average (1980-1987) of high sockeye escapements, it appears the macrozooplankton population may have collapsed, and has not recovered despite low fry recruitment from low escapements. The current low zooplankton biomass suggests a period of excessive planktivory or over-grazing (Carpenter *et al.* 1985; Kyle *et al.* 1988) followed by low lake productivity. Although recent (1989-1991) brood-year escapements have been very low (Table 1), the macrozooplankton population has not recovered (Table 9). In addition, macrozooplankton density of samples collected during peak production in 1991 (J. Edmundson pers. comm.[1]) was only 36 mg m^{-2}, indicating continuance of a depressed zooplankton community. The lack of response in the zooplankton community is attributed to: 1) low primary productivity which causes cladocerans the inability to obtain the required energy for successful survival and reproduction because of an inefficient feeding strategy; a phenomenon known to occur in many lake types (Gliwicz 1975 and 1986; Allen 1976; Richman and Dodson 1983; Patalis and Salki 1984; Edmundson and Koenings 1986; Koenings *et al.* 1986), and 2) the slow development of copepods which usually produce only a single generation annually (Carter 1965; Pennak 1978).

---

[1]ADF&G, FRED Division, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669.

Table 10. Comparison of seasonal mean macrozooplankton density and biomass for a variety of sockeye nursery lakes showing the relatively low standing stock of zooplankton in Coghill Lake.

Lake and geographical location \a	Sampled years	Seasonal mean weighted macrozooplankton Density (no./m^2)	Seasonal mean weighted macrozooplankton Biomass (mg/m^2)
Chenik (CI)	87–90	871,677	2,223
Hidden (CI)	81–90	619,203	2,331
Chelatna (CI)	84–85,88–90	409,413	1,313
Chilkat (NSE)	87–90	645,849	1,287
Karluk (Kodiak)	81–91	520,383	1,041
Eshamy (PWS)	81–86,89–90	439,595	972
Packers (CI)\b	81–90	177,815	617
Leisure (CI)	85–90	249,758	398
Skilak (CI)\c	86–91	230,361	556
Hugh–Smith (SSE)\b	81–87	290,404	523
McDonald (SSE)\b	81–90	91,245	297
Bakewell (SSE)\b	83–85,88–90	115,398	221
Frazer (Kodiak)	88–91	147,852	220
Afognak (Kodiak)	87–91	143,241	185
Redoubt (NSE)	84–87,90	137,040	159
Frazer (Kodiak)	85–87	114,086	155
Chilkoot (NSE)	87–90	88,443	145
Crescent (CI)\d	81–82	87,958	145
Tustumena (CI)\c	81–91	41,249	105
Virginia (NSE)	86,88–91	45,318	103
Redoubt (NSE)	82–83	76,818	90
Coghill (PWS)	86,88–91	47,465	79
English Bay (CI)	88–90	53,184	49

\a CI = Cook Inlet; PWS = Prince William Sound; NSE = Northern Southeast; SSE = Southern Southeast.

\b Denotes stained lakes.

\c Denotes glacial lakes.

\d Denotes semi-glacial lakes.

Applying an empirical relationship between euphotic volume (EV) and sockeye salmon production (Koenings and Burkett 1987) to Coghill Lake (97 EV units), indicates the ability to produce 2.2 million threshold size (60 mm; 2.2 g) or 1.1 million optimum size age-1 smolts. However, smolt estimates ranged from 5,800-387,000 during 1989-1991 (Table 3), and on average was 8% of the number expected based on euphotic volume. In addition, age-1 smolts were threshold-size or smaller (Table 3), and based on the available information, in-lake survival was quite low Table 4). Thus, the low number, survival, and small size of sockeye smolts emigrating Coghill Lake indicates an impaired rearing area.

Total sockeye returns (catch and escapement) have fluctuated since 1968 and in recent years, escapements have decreased dramatically (Table 1). In fact, since 1985, adult returns have averaged only 7% of the expected based on euphotic volume. Of the 17 complete brood-year returns since 1968, all six brood-year escapements yielding R/S of 5 or greater were ≤35,000 (Table 2). The greatest R/S (40:1) was achieved from the 1977 escapement of 31,562, and the lowest (1.1) was from an escapement of 81,000. It is evident that although escapements since 1968 have averaged near the escapement goal, wide fluctuations have occurred, and average production (R/S) may have been greater without the highly variable and large escapements.

Furthermore, using a smolt-to-adult survivorship of 12% for threshold size smolts, or 20% for optimal size smolts (Koenings and Burkett 1987), Coghill Lake is forecasted to produce a total of ~250,000 adult sockeye salmon. In addition, Koenings and Burkett (1987) found sockeye escapements in rearing-limited lakes (producing threshold-size smolts) average 800 EV^{-1}; in Coghill Lake that equates to an escapement of ~75,000 sockeye. Thus, the forecasted escapement and total return approximates the historical average escapement and adult return (Table 1); however, the ability of sustaining this level of sockeye production is no longer available and quite possibly is due to the adverse effects of multiple years (1980-1987) of high escapements on the zooplankton community.

Considering density-independent factors such as the relationship between rearing temperatures, food conversion, and growth; it is generally accepted that rearing temperatures between ~5 and 15° C are most favorable for sockeye juveniles (Donaldson and Foster 1941; Rounsefell 1958; Brett et *al.* 1969; Peltz and Koenings 1989). A change in the rearing depth (temperatures) could accompany the increased number of juveniles from large escapements in Coghill Lake and could account for small smolt sizes. However, the vertical distribution of juveniles in Coghill Lake was similar during rearing years 1988-1990, as the majority of the rearing juveniles were above 20 m (Table 5), where rearing temperatures ranged approximately from 5 to 15° C during June-October (Figures 3 and 4). In addition, the consistency in vertical distribution of rearing fry occurred despite five-fold changes in adult escapements during broodyears 1987-1989. Thus, the growth of juvenile sockeye in Coghill Lake does not appear to be inhibited by low rearing temperatures. Additionally, as euphotic zone depth is related to zooplankton biomass (Koenings and Burkett 1987), glacial meltwater intrusion could have reduced light penetration more in some years than in others. However, if substantial variability exists in the amount of glacial input into Coghill Lake, during the sample period (1988-1991) we would not have observed the constant low macrozooplankton biomass (or the consistent small size of smolts).

Finally, without limnological and fisheries information prior to the decline of sockeye salmon in Coghill Lake, the specific cause for the decrease is unknown. However, from empirical and experimental investigations (Kyle et *al.* 1988; Koenings and Kyle 1991), sockeye nursery lakes at rearing limitation can cause excessive planktivory and cause a delayed recovery of over-grazed zooplankton populations. In Coghill Lake, we believe the combination of large escapements producing substantially and consistently lower R/S, the impoverished rearing environment, poor fish growth, and poor freshwater survival have adversely affected the rearing efficiency of Coghill Lake. In addition, it appears from reduced escapements, lake fertility has decreased over what it once was, and from recent sampling the zooplankton has not rebounded despite reduced predation by sockeye fry from smaller escapements.

RECOMMENDATIONS

Ample evidence exists that demonstrates the effectiveness of enhancing lake fertility and sockeye production through lake fertilization (LeBrasseur 1978; Stockner and Hyatt 1984;

Stockner 1985; Kyle *et al.* 1991). For Coghill Lake we recommend a lake fertilization program for one sockeye life cycle (5 years) to elevate lake productivity until once again adult spawners are numerous enough to significantly contribute to nutrient loading. The recent loading of phosphorus into Coghill Lake has averaged 312 mg m^{-2}. This level of loading is 273 mg m^{-2} less than the critical load (Vollenweider 1976) necessary for full productivity potential. In addition, to maintain an atomic ratio of nitrogen to phosphorus of 18:1 for desired phytoplankton production, an estimated 2,273 mg m^{-2} of nitrogen should be added. To achieve these nutrient loading rates, we recommend the addition of 23 tons of a liquid product (20-5-0) containing 20% nitrogen and 5% phosphorus and 31 tons of 32-0-0 comprising of equal portions of ammonium, nitrate-nitrite, and organic nitrogen. The application zone would be basically the middle third of the lake comprising an area of 3.9 km^2 (Figure 5). The 20-5-0 fertilizer would be added during mid June to August 1, and the 32-0-0 would be added from August 1 to early September. Finally, limnological surveys should be conducted every 3-4 weeks during June-October, and smolt enumeration and sampling should be conducted to assess changes resulting from lake fertilization. Also, careful balancing of juvenile recruitment (through less variable and appropriate escapements) with the forage base will yield a sustainable, and on the long-term a higher level of smolt production, and ultimately, a consistently higher adult return.

ACKNOWLEDGEMENTS

We thank the Commercial Fish Division of ADF&G in Cordova for providing adult return and harvest data. In addition, the U. S. Forest Service provided partial funding for data collection. Finally, we thank staff of FRED Division (ADF&G) in Cordova for data collection and staff of the Limnology Laboratory in Soldotna for analysis of water and zooplankton samples.

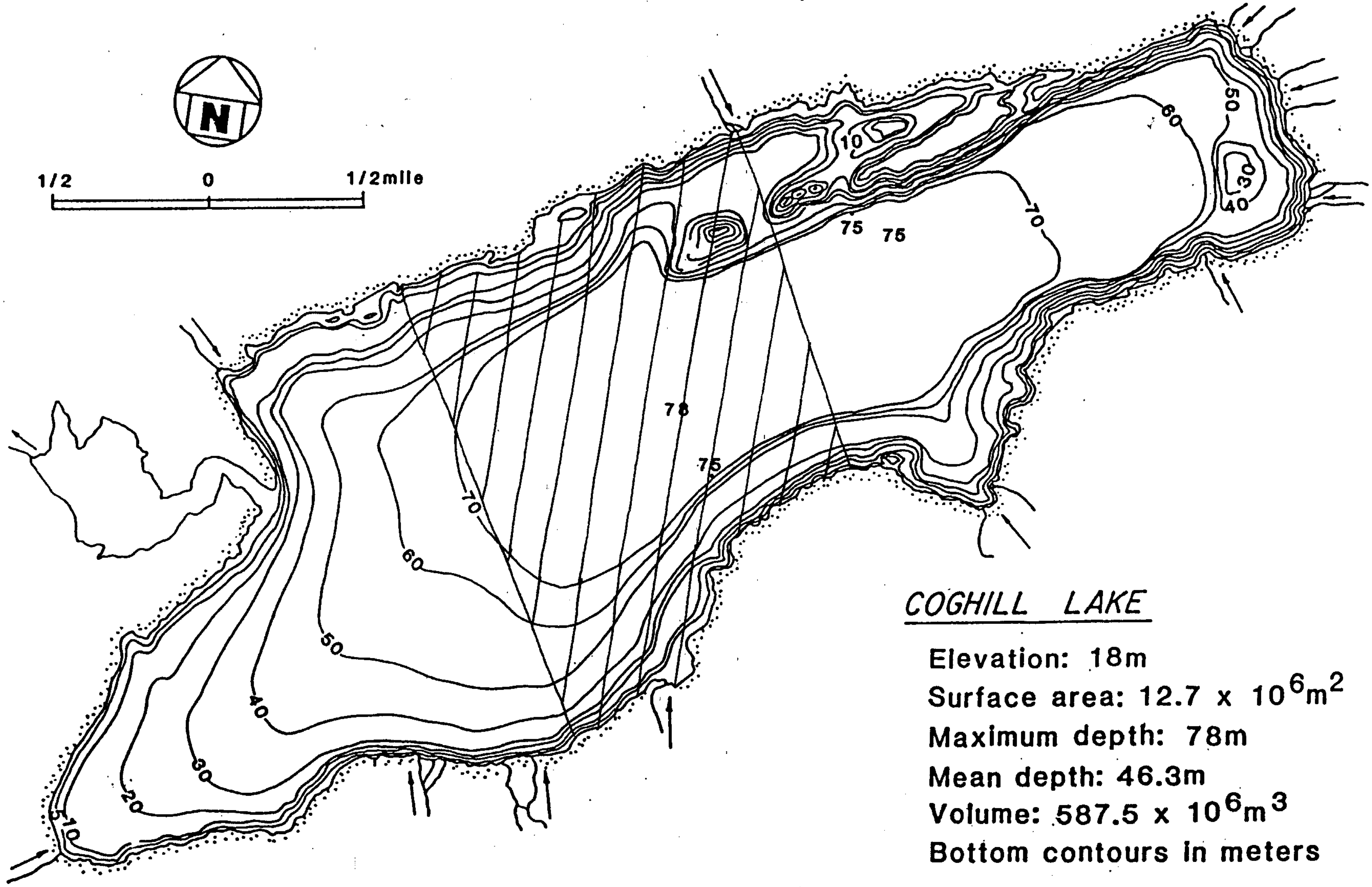

Figure 5. Morphometric map of Coghill Lake showing the location of the proposed zone for fertilzer application.

REFERENCES

Anonymous. 1979. Water resources atlas. U. S. Forest Service - Region 10. Juneau, Alaska.

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

Brett, J. R., J. E. Shelbourn, and C. T. Shoup. 1969. Growth rate and body composition of fingerling sockeye salmon (*O. nerka*), in relation to temperature and ration size. J. Fish. Res. Bd. Can. 26:2363-3294.

Brocksen, R. W., G. E. Davis, and C. E. Warren. 1970. Analysis of trophic processes on the basis of density-dependent function. *In* J. A. Steel [ed.] Marine food chains. Oliver and Boyd, Edinburgh. p. 468-499.

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

Burczynski, J. J. and R. L. Johnson. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43:1776-1788.

Canfield, D. E. Jr. and R. W. Bachman. 1981. Prediction of total phosphorus concentrations, chlorophyll a, and Secchi depths in natural and artificial lakes. Can. J. Fish. Aquat. Sci. 38:414-423.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience. 35(10):634-638.

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

Crawford, D. and E. M. Simpson. 1991. Catch and escapement statistics for Copper River, Bering River, and Prince William Sound, 1988. Alaska Department of Fish and Game Technical Fishery Report 91-06. 193 p.

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.

Donaldson, L. J. and F. J. Foster. 1941. Experimental study of the effects of various water temperatures on the growth, food utilization, and mortality rates of fingerling sockeye salmon. Trans. Am. Fish. Soc. 70:339-346.

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

Edmundson, J. M. and J. P. Koenings. 1986. The influence of suspended glacial particles on the macro-zooplankton community structure within glacial lakes. Alaska Department of Fish and Game. FRED Division Report Series 67:22 p.

Eggers, D. M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnol. Oceanogr. 23:43-53.

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

Foerster, R. E. 1968. The sockeye salmon, (*Oncorhynchus nerka*). Fish. Res. Bd. Can. Bull. 162:422 p.

Gliwicz, Z. M.. 1975. Effect of zooplankton grazing on photosynthetic activity and composition of phytoplankton. Verh. Internat. Verein Limnol. 19:1490-1497.

Gliwicz, Z. M. 1986. Suspended clay concentration controlled by filter-feeding zooplankton in a tropical reservoir. Nature 3323:330-332.

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

Goodlad, J. C., T. W. Gjernes, and E. L. Brannon. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Bd. Can. 31:871-892.

Hall, K. J. and K. D. Hyatt. 1974. Marion Lake (IBP) - from bacteria to fish. J. Fish. Res. Board Can. 31:893-911.

Hanson, J. M. and W. C. Leggett. 1982. Empirical prediction of fish biomass and yield. Can. J. Fish. Aquat. Sci. 39:257-263.

Haywood, G. P. 1983. Ammonia toxicity in teleosts fishes: a review. Can. Tech. Rep. Fish. Aquat. Sci. No. 1177. 35 p.

Hoyer, M. V. and J. R. Jones. 1983. Factors affecting the relation between phosphorus and chlorophyll a in midwestern reservoirs. Can. J. Fish. Aquat. Sci. 40:192-199.

Hutchinson, G. E. 1957. A Treatise on Limnology: Vol. I. Geography, Physics and Chemistry. John Wiley and Sons, New York, NY.

Koenings, J. P. and R. D. Burkett. 1987. The production patterns of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan Lakes. *In* H. D. Smith, L. Margolis, and C. C. Woods [eds.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96 p.

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. 1991. Collapsed populations and delayed recovery of zooplankton in response to heavy juvenile sockeye salmon (*Oncorhynchus nerka*) foraging. Proceedings of the international symposium on biological interactions of enhanced and wild salmonids. *In* review. Spec. Publ. Can. J. Fish. Aquat. Sci.

Koenings, J. P. and J. McDaniel. 1983. Monsoon and Dickey: two phosphorus-rich brown-water lakes with little evidence of vertebrate predation pressure on the zooplankton community. Alaska Department of Fish and Game, FRED Division Report Series 21: 37 p.

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

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

Koenings, J. P., R. D. Burkett, M. H. Haddix, G. B. Kyle, and D. L. Barto. 1989. Experimental manipulation of lakes for sockeye salmon (*Oncorhynchus nerka*) rehabilitation and enhancement. Alaska Department of Fish and Game, FRED Division Report Series 96:18 p.

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

Kuenzler, E. J., D. W. Stanley, and J. P. Koenings. 1979. Nutrient kinetics of phytoplankton in Pamlico River, North Carolina. University of North Carolina. Water Resources Institute Report No. UNC-WRRI-79-139. 163 p.

Kyle, G. B. 1983. Crescent Lake sockeye salmon (*Oncorhynchus nerka*) smolt enumeration and sampling, 1982. 1983. Alaska Department Fish and Game, FRED Division Report Series No. 17:24 p.

Kyle, G. B. 1990. Summary of acoustically-derived population estimates and distributions of juvenile sockeye salmon (*Oncorhynchus nerka*) in 17 nursery lakes of southcentral Alaska, 1982-1987. Alaska Department of Fish and Game. FRED Division Report Series 104:47 p.

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. M. Edmundson. 1991. An overview of Alaska lake-rearing salmon enhancement strategy: nutrient enrichment and juvenile stocking. p. xx-xx. *In* A. Milner and M. Oswood [eds.] Alaska Freshwaters. *In* preparation. Springer-Verlag. New York, NY.

Lambow, V. W., S. C. Hern, W. D. Taylor, and L. R. Williams. 1982. Chlorophyll, phosphorus, Secchi disk, and trophic state. Water Resour. Bull. 18:807-813.

Likens, G. E. [ed.]. 1985. An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer-Verlag. New York, NY. 516 p.

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.

Levy, D. A. 1987. Review of the ecological significance of diel vertical migrations by juvenile sockeye salmon (*Oncorhynchus nerka*). p. 44-52. *In* H.D. Smith, L. Margolis, and C. C. Wood [eds.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96 p.

Lloyd, D. S., J. P. Koenings, and J. D. LaPerriere. 1987. Effects of turbidity in fresh waters of Alaska. North Amer. J. Fish. Mang. 7:18-33.

Mayo, L. R. 1986. Annual runoff rate from glaciers in Alaska; a model using the altitude of glacier mass balance equilibrium. p. 509-517. *In* D. L. Kane [ed.] Proceedings: Cold Regions Hydrology American Water Resources Assoc. Bethesda, MD.

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

McDonald, J. 1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*), at Babine Lake, B. C. Canada. Fish. Res. Bd. Can. Tech. Rep. No. 378. 55 p.

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

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon on the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Bd. Can. 27:281-316.

Northcote, T. G. and W. E. Johnson. 1964. Occurrence and distribution of sea water in Sakinaw Lake, British Columbia. J. Fish. Res. Bd. Can. 21:1321-1324.

Nunnallee, E. P. 1983. Scaling of an echo integrator using echo counts, and a comparison of acoustic and weir count estimates of a juvenile sockeye salmon population. FAO Fish. Res. 300:261-268.

Patalis K. and A. Salki. 1984. Effects of impoundment and diversion on the crustacean plankton of Southern Indian Lake. Can. J. Fish. Aquatic. Sci. 41:613-637.

Pellissier, R. F. and M. A. Somerville. 1984. Field data summary for Copper River and Prince William Sound lake investigations, 1984. Prince William Sound Regional Aquaculture Association, Cordova, Alaska. Annual contract report. 229 p.

Pellissier, R. F. and M. A. Somerville. 1987. Field data summary for Copper River and Prince William Sound lake investigations, 1985. Prince William Sound Regional Aquaculture Association, Cordova, Alaska. Annual contract report. 149 p.

Peltz L. R. and J. P. Koenings. 1989. Evidence for temperature limitation of juvenile sockeye salmon, *Oncorhynchus nerka*, growth in Hugh Smith Lake, Alaska. Alaska Department of Fish and Game. FRED Div. Rep. Ser. No. 90. Juneau, Alaska. 26 p.

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

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

Richman, S. and S. I. Dodson. 1983. The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. Limnol. Oceanogr. 28(5):948-956.

Rounsefell, G. A. 1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. Fish. Bull. 58:83-169.

Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's fresh waters. Limnol. Oceanogr. 23:478-486.

Simpson, K. L., L. Hop Wo, and I. Miki. 1981. Fish surveys of 15 sockeye salmon (*Oncorhynchus nerka*) nursery lakes in British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. No. 1022. 87 p.

Smith, V. H. 1979. Nutrient dependence of primary productivity in lakes. Limnol. Oceanogr. 24:1051-1064.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of fresh water, 2nd ed. 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. p. 198-215. *In* H.D. Smith, L. Margolis, and C.C. Woods [eds.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish Aquat. Sci. 96 p.

Stockner, J. G. and K. D. Hyatt. 1984. Lake fertilization: state of the art after 7 years of application. Can. J. Fish. Aquat. Sci. 1324:33 p.

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

Stumm, W. and G. F. Lee. 1960. The chemistry of aqueous iron. Schweizererische Zeitschrift Fur Hydrologie Revue Suissed - Hydrologie. 22:295-319.

Takahashi, T., W. Broecher, Y. H. Li, and D. Thurber. 1968. Chemical and isotopic balances for a meromictic lake. Limnol. Oceanogr. 13:272-292.

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

Walker, K. F. 1974. The stability of meromictic lakes in central Washington. Limnol. Oceanogr. 19:209-222.

Weimer, W. C. and G. F. Lee. 1973. Some considerations of chemical limnology of meromictic Lake Mary. Limnol. Oceanogr. 18:414-424.

Wetzel, R. G. 1975. Limnology. Saunders.

Wilson, M. S. 1959. Calanoida. p. 738-794. *In* W. T. Edmondson [ed.] Fresh-water biology, 2nd. ed. John Wiley and Sons. New York, NY.

Yeatman, H. C. 1959. Cyclopoida. p. 795-815. *In* W. T. Edmondson [ed.] Fresh-water biology, 2nd. ed. John Wiley and Sons, New York, NY.