Regional Information Report No. 2A02-08

SOCKEYE SALMON PRODUCTION RELATIVE TO CHANGES IN REARING CAPACITY OF CRESCENT LAKE, UPPER COOK INLET

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J. M. Edmundson and J. A. Edmundson

Alaska Department of Fish and Game
Division of Commercial Fisheries
333 Raspberry Road
Anchorage, Alaska 99518-1599

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Central Region
333 Raspberry Road, Anchorage, Alaska 99518-1599

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AUTHORS

John M. Edmundson is a fishery biologist for Central Region Limnology, Division of Commercial Fisheries, Alaska Department of Fish and Game, 43961 Kalifornsky Beach Road, Suite B, Soldotna, Alaska 99669.

Jim A. Edmundson is the research project leader for Central Region Limnology, Division of Commercial Fisheries, Alaska Department of Fish and Game, 43961 Kalifornsky Beach Road, Suite B, Soldotna, Alaska 99669.

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ABSTRACT

Edmundson, J. M. and J. A. Edmundson. Sockeye salmon production relative to changes in rearing capacity of Crescent Lake, upper Cook Inlet. Alaska Department of Fish and Game, Division of Commercial Fisheries, Central Region, Regional Information Report No. 2A02-08, Anchorage, Alaska.

Beginning in the mid 1980s and through much of the 1990s, production of the Crescent River sockeye (*Oncorhynchus nerka*) salmon declined as evidenced by lower adult returns and fewer adult recruits produced per spawner (RPS). For brood years 1984-1988 and 1990, RPS values fell below replacement. Concern over the decline in productivity initiated limnological studies in 1996 to determine whether sockeye salmon production was related to variability in changing conditions of the major nursery lake (Crescent Lake) of this system. The escapement goal range was lowered in 1998 from 50,000-100,000 to the current 25,000-50,000 range in part based on the low density of cyclopoid (*Cyclops scutifer*) copepods, the primary food resource (zooplankton) for rearing sockeye salmon juveniles, and an apparent increase in water column turbidity. Since then (1998), turbidity has lessened and the euphotic zone depth has increased, but copepod abundance has not. However, sockeye salmon escapements exceeded the escapement goal in both 1999 (69,000), 2000 (57,000), and 2001 (78,000). Therefore, we are uncertain whether reduced *Cyclops* abundance is due to top-down or over-grazing effects by rearing sockeye juveniles or from bottom-up effects of reduced primary production associated with increasing turbidity or a combined effect. Nonetheless, both mechanisms can serve to reduce sockeye salmon productivity. Based on turbidity levels and amount of food resources for rearing sockeye salmon juveniles in Crescent Lake, we feel that the current escapement goal of 25,000-50,000 spawners should be maintained because it provides a good balance between fry abundance and the quantity of available forage.

KEY WORDS: sockeye salmon, *Oncorhynchus nerka*, limnology, escapement goal, Upper Cook Inlet, Crescent River, Crescent Lake, Alaska

INTRODUCTION

The Crescent River system is an important producer of sockeye salmon (*Oncorhynchus nerka*) in the upper Cook Inlet (UCI) area of southcentral Alaska. Annual runs for this system exceed 200,000 in some years (Fox and Shields 2000). As such, Crescent River supports economically viable commercial set and drift gillnet fisheries. Like many sockeye salmon stocks, there is a great deal of inter-annual variability in the size of the run that is usually attributed to changes in ocean and freshwater habitat conditions. While nearly all of the mortality of a salmon brood occurs during their freshwater life phase, it is most often assumed that the variation in adult returns is largely due to changing ocean conditions (Beamish and Boullion 1993; Hare and Francis 1995; Mantua et al. 1997). However, Bradford (1995) showed that the annual variability in adult returns of Pacific salmon is partitioned about equally between the freshwater and marine life histories.

Commercial catches of Crescent River sockeye salmon increased dramatically from about the late 1970s to the mid 1980s. However, from the mid 1980s through much of the 1990s, system productivity declined as indexed by lower adult returns. Over the past ten years, total returns averaged about 70,000 or approximately one-quarter of the maximum historical returns. More importantly, the number of adult recruits produced per spawner (RPS) declined markedly during this time period and for brood years 1984-1988, RPS values fell below replacement (i.e., where 1 spawner produces 1 recruit). Concern by Alaska Department of Fish and Game (ADF&G) over the decline in productivity initiated limnological studies in 1996 to determine whether sockeye salmon production was related to variability in conditions of the major nursery lake (Crescent Lake) of this system. In 1998, following two years of lake studies, the escapement goal range was lowered from 50,000-100,000 spawners to the current 25,000-50,000 range in part based on the low density of cyclopoid copepods (*Cyclops*), the primary food resource (zooplankton) for rearing sockeye salmon juveniles, and an increase in glacial turbidity (Fried 1999).

Since the previous (1999) UCI Board of Fisheries (BOF) action concerning the escapement goal, limnological investigations have continued on Crescent Lake to further assess both environmental conditions and the magnitude of the forage base (cyclopoid copepods) for rearing sockeye salmon juveniles. However, since 1999 sockeye salmon escapements exceeded the revised goal: 1999 (69,000), 2000 (57,000), and 2001 (78,000). The strength of the run in the past couple of years has led some to question the rationale or evidence for the recent (1999) decision to lower the escapement goal. That is, perhaps the observed increase in turbidity and low plankton abundance represented short-term changes in lake conditions rather than any fundamental decrease in freshwater rearing capacity for sockeye salmon juveniles. In addition, it has been suggested lowering the escapement goal could lead to a shortage of essential marine-derived nutrients because of too few spawners causing productivity to further decline. Unfortunately, there is no limnological data corresponding to the decline in total returns and RPS that began in the mid 1980s making it difficult to infer potential freshwater causal mechanisms for the decrease in sockeye salmon productivity. Nonetheless, limnological (habitat) information can be useful in assessing the rearing capacity relative to juvenile sockeye salmon production (Koenings and Burkett 1987; Koenings and Kyle 1997; Edmundson and Mazumder 2001; Mazumder and Edmundson submitted) and to evaluate escapement goals (Schmidt et al. 1998).

Our recent limnological studies (1996-2000) of Crescent Lake, however, were not the first. In 1979, limnological and juvenile fisheries investigations were conducted on Crescent Lake as part of an ADF&G statewide lake inventory program, and to determine the feasibility of nutrient enrichment for purposes of enhancing sockeye salmon production (Koenings et al. 1985). Their studies (1979-1982) revealed that Crescent Lake was a glacially influenced system with seasonally variable turbidity levels caused by glacial meltwater intrusion. It has been shown that even small increases in turbidity (i.e., 5 nephelometric turbidity units, NTU) from suspended glacial silt particles significantly decrease light penetration (Lloyd et al. 1987; Koenings and Edmundson 1991), lower water column temperatures (Edmundson and Mazumder 2002), alter nutrient (phosphorus) regimes and decrease primary production (Edmundson and Carlson 1998), limit macrozooplankton abundance and species diversity (Koenings et al. 1990), and reduce fish yield (Koenings et al. 1986). In part because of its glacial nature and its attendant effects on lacustrine productivity, Crescent Lake was not considered a viable candidate for lake fertilization. In addition, interest in sockeye salmon enhancement and opportunities for funding further limnological work waned at about the time lands bordering much of the lake and surrounding watershed were incorporated into the U.S. Department of Interior, Lake Clark National Park and Preserve. Thus, in 1983 ADF&G discontinued limnological investigations of Crescent Lake.

Although we lack a long time series of consistent limnological data for Crescent Lake, we can make some comparisons in lake rearing conditions between the early 1980s and the more recent period (1996-2000). In this report, we evaluate the salient information on environmental conditions, nutrients, and macrozooplankton abundance relative to the rearing capacity for sockeye salmon juveniles in Crescent Lake. We focus on the distinct temporal differences in turbidity and cyclopoid abundance and biomass between the early and late surveys and make some inferences relative to the observed patterns in sockeye salmon stock and recruitment. Finally, we provide an analysis of limnological and fisheries data to determine the optimum escapement goal for the Crescent River sockeye salmon stock.

Description of Study Site

Crescent Lake (60° 22’ N, 152° 59’ W) is situated in a steep mountain valley at an altitude of 183 meters and drains via the Crescent River for about 60 kilometers into the west side of Cook Inlet (Figure 1). The Crescent River watershed encompasses about 300 km^2. Crescent Lake proper is approximately 10 km long and 2 km wide and consists of a relatively broad, flat basin with a mean depth of 23 meters and a maximum of about 31 meters (Spafard and Edmundson 2000). Bathymetric contours and limnological sampling station locations (A, B, C) are shown in Figure 2. Annual water residence time or flushing rate is estimated to be 0.7 to 0.8 years (Koenings et al. 1985). Crescent Lake is classifies as semi-glacial (Koenings et al. 1986) with periodic inflows of glacially turbid water that can raise turbidity levels as high as 30 NTU. The most turbid conditions occur in the fall at the time of heaviest precipitation. Two major inlet streams, one mid lateral and one at the upper end, feed the lake, with the-mid lake tributary being the most turbid.

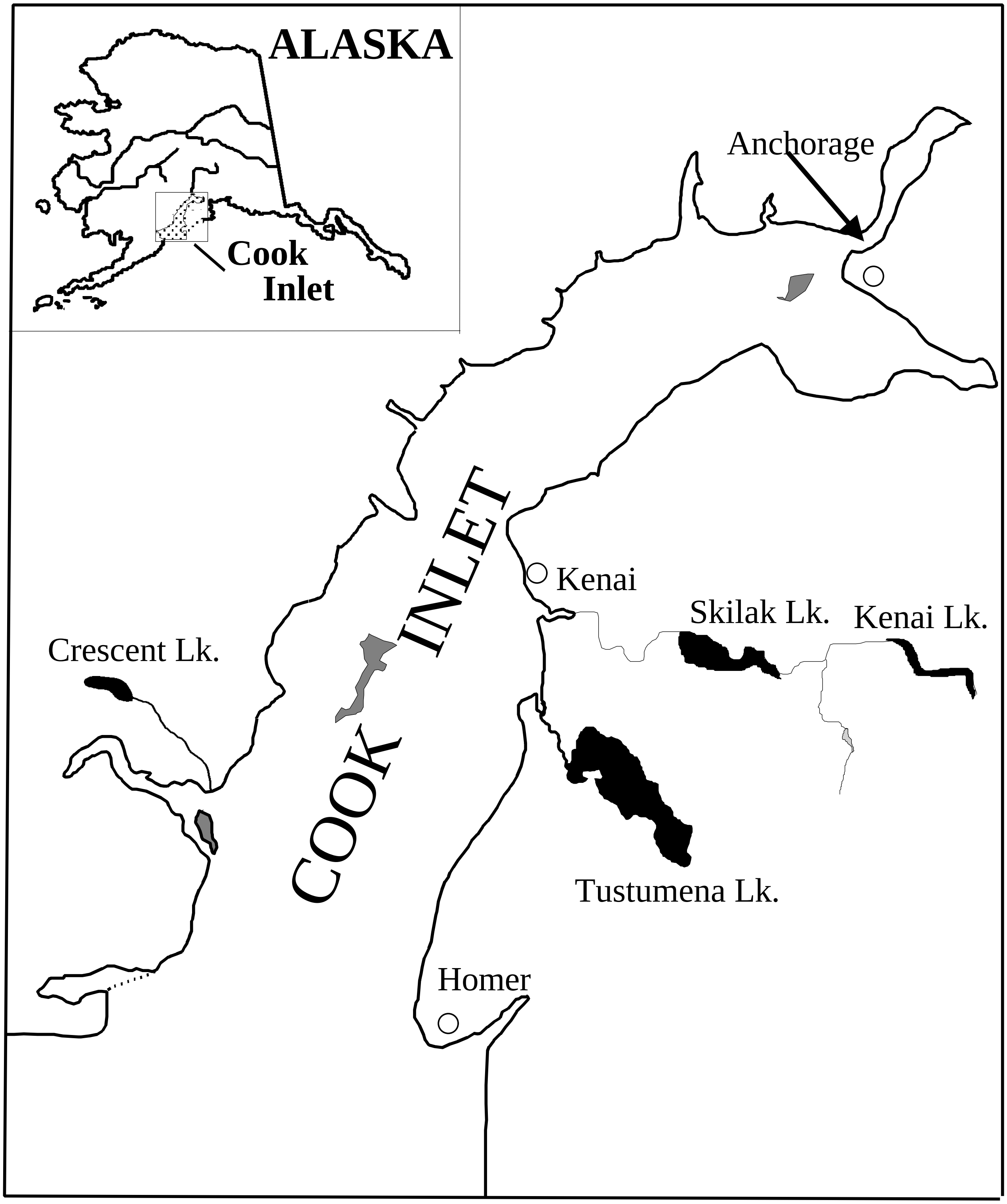

Figure 1. Geographic location of Crescent Lake in relation to upper Cook Inlet.

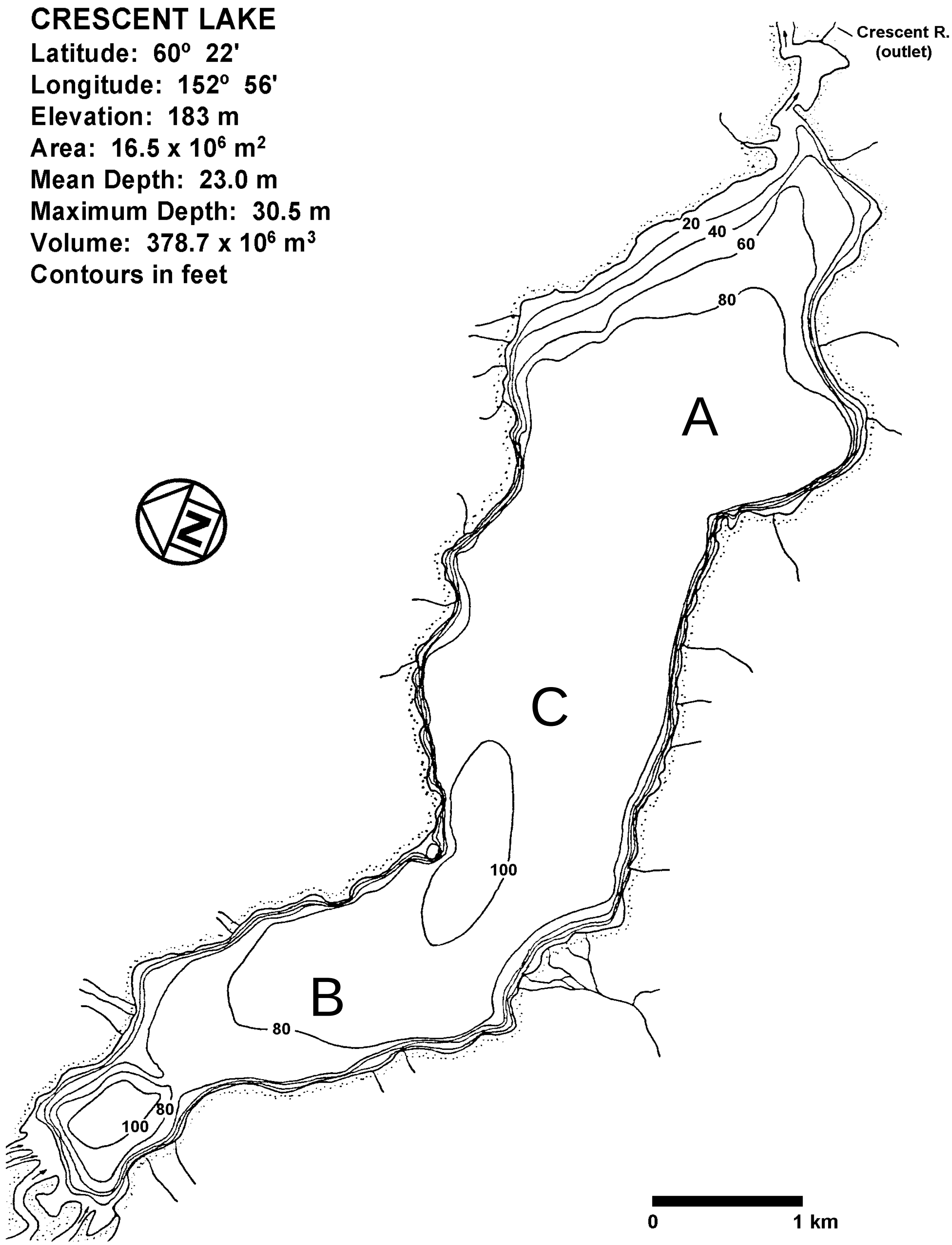

Figure 2. Bathymetric map of Crescent Lake showing locations of the limnological sampling stations (A, B, C).

METHODS

Sockeye Salmon Data

Sockeye salmon escapement, harvest (catch) and total return (escapement + catch) by year of return were available from 1970-2001 (Tobias and Tarbox 2000); and for adult sockeye salmon returns by brood year (year of spawning) the data were complete for 1970-1994. We described spawner-recruit (S-R) data for Crescent River using a classic Ricker (1975) recruitment curve by transforming the equation $R = aS[\exp]^{-bS}$ into the form, $ln\ R/S = a\text{-}bS$, and treating it as a linear regression, where R = total returns, S is the number of spawners, and a and b are the productivity (y-intercept) and density dependent parameters (slope), respectively (Hilborn and Walters 1992). We also examined S-R data using a Markov transition probability table as described by Hilborn and Walters (1992). We constructed a table using a discrete interval of 20,000 spawners that was offset by 10,000 fish. We then computed mean spawner abundance, adult recruits, yield, and number of recruits produced per spawner (RPS) for each spawner interval.

Sockeye Salmon Carrying Capacity

We estimated carrying capacity, expressed as predicted smolt biomass (SB), for juvenile sockeye salmon using euphotic volume (Koenings and Burkett 1987), euphotic zone depth (Edmundson and Carlson, unpublished data), and total macrozooplankton biomass (Koenings and Kyle 1997) models. The three model equations are as follows:

Euphotic Volume (EV): SB (000's kg) = $-4.31 + 0.0147 \times EV$ (units) (1)

Euphotic Zone Depth (EZD): $ln\ SB$ (000s kg km^{-2}) = $-5.45 + 0.095 \times EZD$ (m) (2)

Zooplankton Biomass (ZB): SB (kg km^{-2}) = $-68.9 + 2.07 \times ZB$ (mg m^{-2}) (3)

To assess the magnitude of zooplanktivory or grazing pressure in Crescent Lake, we made the assumption that the number of spawners was proportional to fry recruitment. We then devised a composite index of grazing pressure based on spawner density and macrozooplankton community characteristics. Our index of grazing pressure was simply computed as the escapement per unit of lake area or spawner density (Nr. km^{-2}) divided by the seasonal mean areal zooplankton biomass (kg km^{-2}) estimate. Thus, the grazing pressure index is expressed as the number of spawners per unit standing stock of macrozooplankton (Nr. kg^{-1}). We assumed that high values are associated with increased grazing pressure or conversely low values reflect low sockeye planktivory. For comparative purposes, we also computed the grazing pressure index for 16 other Alaskan sockeye nursery lakes. Like the Crescent Lake early and late data sets, the grazing pressure index for the other lakes was calculated using only the brood year escapements in which we had corresponding zooplankton data from the subsequent rearing year.

Limnological Sampling and Laboratory Analysis

During 1996-2000, ADF&G Central Region Limnology (CRL) staff collected physical, chemical, and biological samples from Crescent Lake. For the most part, surveys were conducted once per month during the ice-free period (June-October) and we sampled from three sites representative of the entire lake basin (Figure 2). All sampling was conducted from a float-equipped aircraft after mooring to an anchored buoy. Underwater irradiance (light penetration) was measured with an International Light or Li-Cor submarine photometer equipped with a cosine corrected sensor. We calculated light extinction coefficients (K_d), the rate (m^{-1}) at which light dims with increasing depth, according to Kirk (1994). The euphotic zone depth (EZD), the depth equivalent to 1% of the subsurface light, was computed using the method in Koenings et al. (1987) as modified by Edmundson et al (2000). The euphotic volume was estimated as the product of EZD and lake surface area, where 1 million cubic meters of euphotic volume (EV) is equal to 1 EV unit (Koenings and Burkett 1987). We used a standard Secchi disk to measure water clarity. Vertical temperature profiles were measured from the surface to the maximum depth at each sample station using either an YSI model oxygen meter equipped with a thermistor or with a Hydrolab instrument. We also estimated the length of the growing season, defined as the number of days between spring and fall 4°C isothermy, by plotting temperature of the 1-m stratum (averaged across stations) by day of year after pooling the data across all 4 sample years. These data were then fitted with a 3rd order polynomial curve, where the respective x-intercepts of the polynomial regression represent spring and fall 4°C isothermy (Edmundson and Mazumder 2002).

We collected bulk water samples from depths of 1 and 25 m for analysis of general water chemistry, nutrients, and algal biomass using an 8-L van Dorn bottle. All water testing was performed at the ADF&G CRL laboratory in Soldotna. Conductivity was measured with a YSI conductance meter and pH was measured with an Orion model 420A pH meter. Alkalinity was determined by acid (0.02 N H_2SO_4) titration to pH 4.5 units. Turbidity, expressed as nephelometric turbidity units (NTU), was measured with a HF model 00B meter, and color was determined on a filtered (GFF) sample by measuring the spectrophotometric absorbance at 400 nm and converting to equivalent platinum cobalt (Pt) units. Calcium and magnesium were determined from separate EDTA (0.01 N) titrations, and total iron was analyzed by reduction of ferric iron with hydroxylamine during hydrochloric acid digestion. Reactive silicon was determined using the method of ascorbic acid reduction to molybdenum blue. Filterable reactive phosphorus (FRP) was analyzed by the molybdenum blue/ascorbic acid reduction procedure as modified by Eisenreich et al. (1975). Total phosphorus (TP) utilized the FRP procedure after acid- persulfate digestion. Nitrate + nitrite was analyzed as nitrite following cadmium reduction, and total ammonia utilized the phenylhypochlorite methodology. Total Kjeldahl nitrogen (TKN) was determined as ammonia following acid-block digestion. We computed total nitrogen (TN) as the sum of TKN and nitrate + nitrite.

For analysis of chlorophyll *a* (chl *a*), we filtered 1-2 L aliquots of each water sample through a GFF filter to which we added 2 ml of $MgCO_3$ just prior to completion of the filtration process. Individual filters were stored frozen in separate Plexiglas slides until analyzed. We extracted algal pigments by grinding the filters with a Teflon pestle in 90% acetone and refrigerating (4°C) the slurry in the dark for 2 hr. Following acetone extraction, the slurry was centrifuged and the supernatant was decanted and brought volume with 90% acetone. Chl *a* concentration was determined using a calibrated (Sigma Co. chl *a* standards Turner model 112 flurometer.

We collected macrozooplankters using a 0.5-m diameter, 153 μm meshed, conical plankton net. Vertical tows were made from one meter above the bottom to the surface and the contents were preserved in 10 % buffered formalin. Macrozooplankters were identified to species, enumerated from triplicate subsamples, and sized (length) to the nearest 0.02 mm in the lab using a 70× power dissecting scope. Counts were converted to areal (Nr. m^{-2}) and volumetric (Nr. m^{-3}) zooplankton density estimates. We also estimated macrozooplankton biomass, areal (mg m^{-2}) and volumetric (mg m^{-3}), using species-specific wet length to dry weight regression formulae (Koenings et al. 1987).

Data Analysis

Koenings et al. (1985) reported the limnological information from the 1979-1982 surveys, so we have not reiterated that data in detail here. For our descriptive purposes, we averaged recent data (1996-2000) for general water chemistry, nutrients, and algal pigments across all three stations (A-C) and four the sample years. We did, however, use analysis-of-variance (ANOVA) followed by Tukey's post-hoc comparisons to test for differences in water chemistry, nutrient concentrations, and algal pigment levels between stations and between the early (1979-1982) and late (1996-2000) periods. Because station C was sampled only during the later period, this station was excluded from our ANOVA testing. Least squares regression analysis was used to test the functional relationship between two variables (Neter et al. 1990). All tests were conducted at $\alpha = 0.05$, and statistical analyses were facilitated using SYSTAT version 9 (SPSS 1999).

RESULTS

Stock and Recruitment Patterns

During 1979-2000, annual sockeye salmon returns (catch + escapement) for Crescent River ranged from 44,000 (1994) to 309,000 (1985) and averaged 122,600 (Figure 3). The highest returns (greater than 140,000) occurred from 1983-1988. However, between 1985 and 1991, production of Crescent River sockeye salmon declined substantially and over the next five years (1992-1996) remained relatively low (less than 70,000). Although the total return increased slightly since then (1999-2001), catch and escapement levels were only about one-quarter that of peak sockeye salmon production. For brood years 1979-1994, the Ricker compensatory spawner-recruit (S-R) model was significant (P=0.024), but S accounted for only 30% of the variance in the natural logarithm (*ln*) of R/S (Figure 4). In addition, although the Ricker regression function was statistically significant, the slope was highly influenced by just three

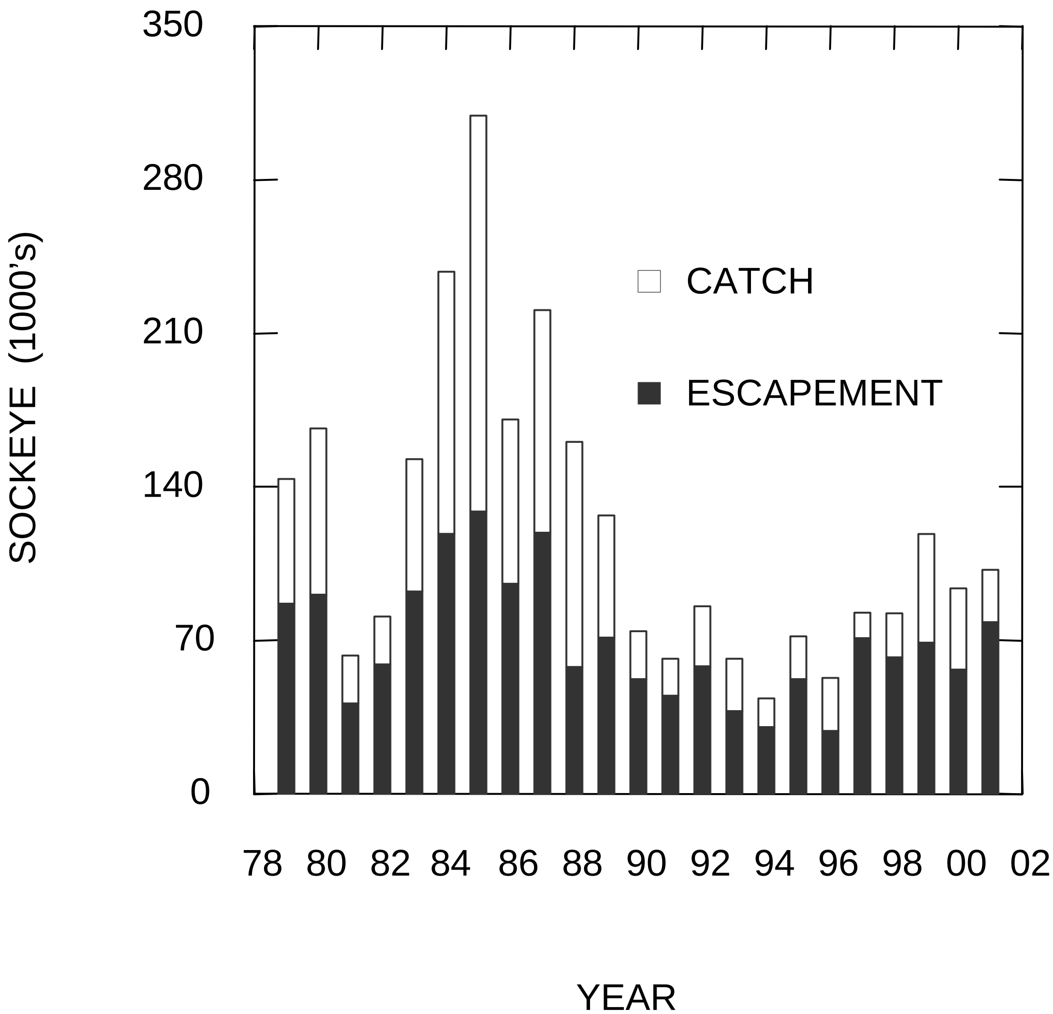

Figure 3. Harvest and escapement of sockeye salmon to Crescent Lake, 1979-2001.

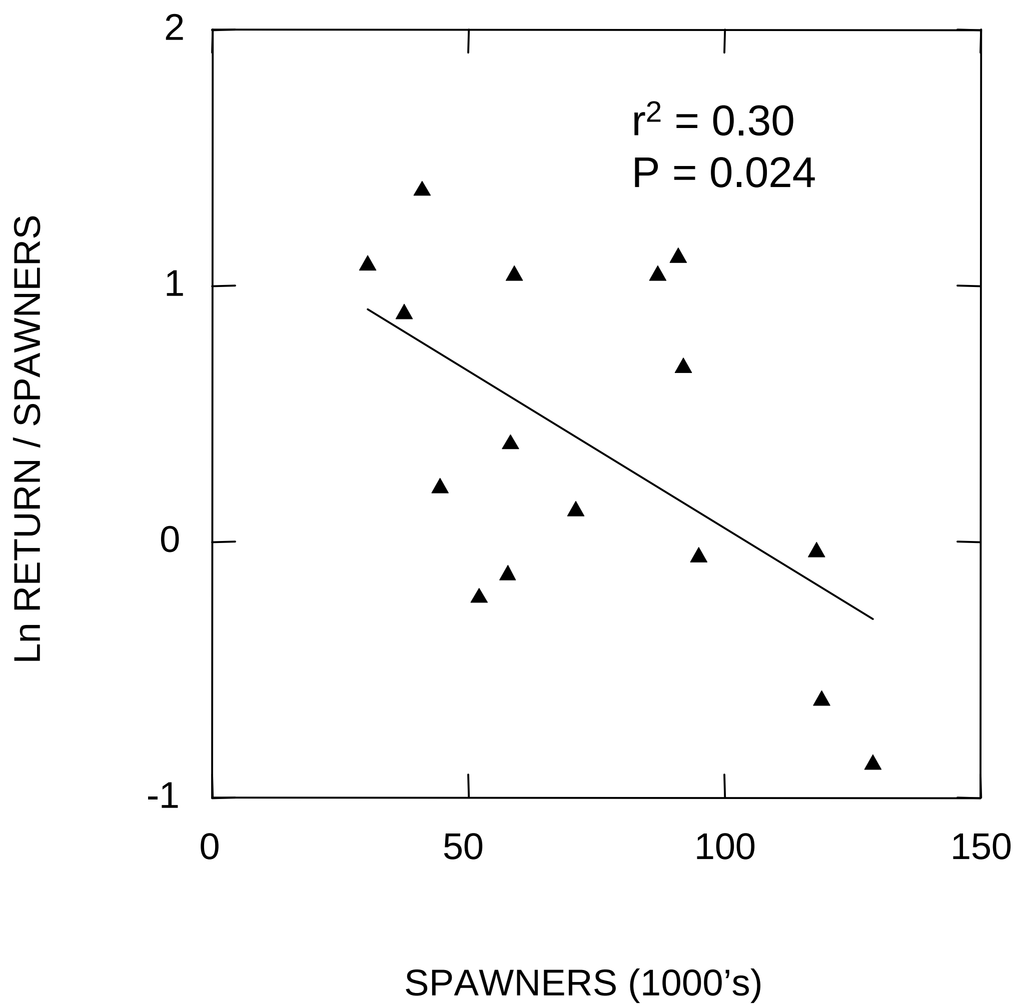

Figure 4. The relationship between the number of sockeye salmon spawners and the natural logarithm (ln) of recruits per spawner in Crescent Lake.

data points corresponding to the 1984, 1985, and 1987 escapements, each of which exceeded 100,000 fish. Nonetheless, based on this Ricker model, the estimated number of spawners to maximize yield (S_{MSY}) was 43,700 and the predicted number of recruits at S_{MSY} was 91,200.

Over all brood years (1979-1994), sockeye salmon recruitment ranged from 41,000 to 275,000 and averaged 114,900; however, for brood years 1979-1991, recruitment steadily declined from 275,000 to 41,000 (Figure 5A). More importantly, in six of those years (1984-1998, 1990), RPS values fell below replacement (Figure 5B). A summary of Markov probability matrices suggested that the highest surplus yield (89,000-106,000) occurred while spawner abundance was in the range of 70,000-110,000 fish, whereas escapements exceeding 100,000-130,000 produced negative yields (Table 1). However, high yields (56,000-61,000 on average) also resulted from escapements of 20,000-50,000; i.e. from fewer spawners. The highest productivity, as reflected by RPS values (2.7), was obtained under the lowest escapements (20,000-50,00 on average) and not from escapements that produced on average the highest yield (mean RPS = 2.0).

Juvenile Sockeye Salmon Rearing Habitat

The limnetic macrozooplankton community of Crescent Lake is simple and consists of a single copepod species, *Cyclops scutifer*. For comparative purposes, we hereafter refer to the 1979-1982 and 1996-2000 rearing years as the early and late periods, respectively. Limnological data are not available for the 1983-1995 rearing years. Over all sample years, seasonal mean *Cyclops* densities ranged from 9,249 to 106,698 Nr.m^{-2}; however, densities were about five times higher (ANOVA, P<0.001) on average in the 1980s (104,000 Nr. m^{-2}) compared to the 1996-2000 rearing years (18,500 Nr. m^{-2}) (Figure 6A). *Cyclops* abundance was lowest in 2000 and represented only 9% of the highest mean density of the nine-year time series. For the early period, *Cyclops* biomass estimates were available for only two years (1981 and 1982). During 1981-1982 and 1996-2000, seasonal mean biomass of *Cyclops* ranged from 23 mg m^{-2} to 219 mg m^{-2} and averaged 79 mg m^{-2} (Figure 6B). Biomass was four times higher in the early period (mean 173 mg m^{-2}) compared to the late period (mean 41 mg m^{-2}). This difference in the average standing crop of *Cyclops* between the early and late sampling periods represented nearly an 80% reduction in the magnitude of the forage base for rearing sockeye juveniles. The seasonal mean body size (length) of *Cyclops* ranged from 0.67 to 0.96 mm and averaged 0.79 mm (Figure 6C). Body size was relatively inconsistent from year to year, but we found no obvious temporal (inter-annual) pattern within or between the early and late periods. Finally, the temporal (seasonal) development of *Cyclops* abundance differed between the early and late periods. For instance, in the early 1980s peak densities occurred in August; however, during 1996-2000, *Cyclops* populations were most abundant in July (Figure 7).

During 1996-2000, the underwater light climate of Crescent Lake was extremely variable in response to changes in the amount of inorganic turbidity. We found that turbidity levels within the 1-m stratum exhibited an order of magnitude change (3-30 NTU). As expected, there was a strong (r^2=0.85; P<0.001) positive, linear relationship between the light extinction coefficient (K_d) and turbidity (Figure 8A) indicating suspended glacial silt particles are the principle light-

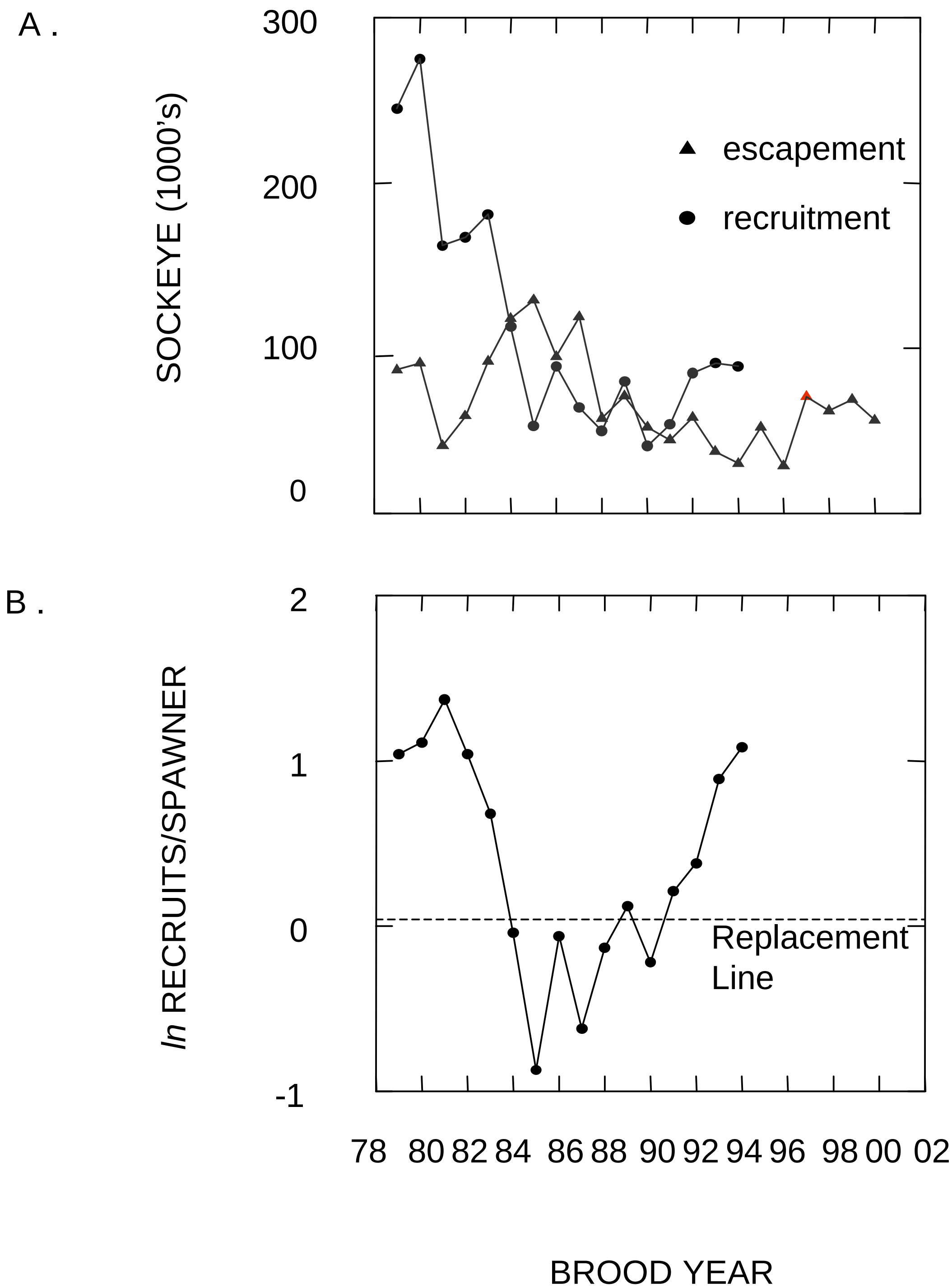

Figure 5. (A) Sockeye salmon spawner and recruitment from brood year and (B) natural logarithm (ln) recruit per spawner by brood year.

Table 1. Summary of results from two Markov transition probability tables of Crescent River sockeye salmon spawner-recruit data, 1970-1994. Each table was based on a spawner abundance interval of 20,000 fish and the tables were offset by 10,000 fish.

Spawner Interval x 1000	N	Mean Spawners	Mean Recruits	Recruits/ Spawner	Mean Yield
20 - 40	2	33,956	90,000	2.70	56,045
30 - 50	4	38,353	99,000	2.64	60,647
40 - 60	6	52,104	93,167	1.86	41,063
50 - 70	4	56,781	85,750	1.50	28,970
60 - 80	1	71,064	80,000	1.13	8,936
70 - 90	2	79,032	162,500	1.98	83,468
80 - 100	4	91,250	197,500	2.19	106,250
90 -110	3	92,667	181,667	1.98	89,000
100 - 120	2	118,500	88,500	0.75	-30,000
110 -130	3	122,000	76,667	0.64	-45,333

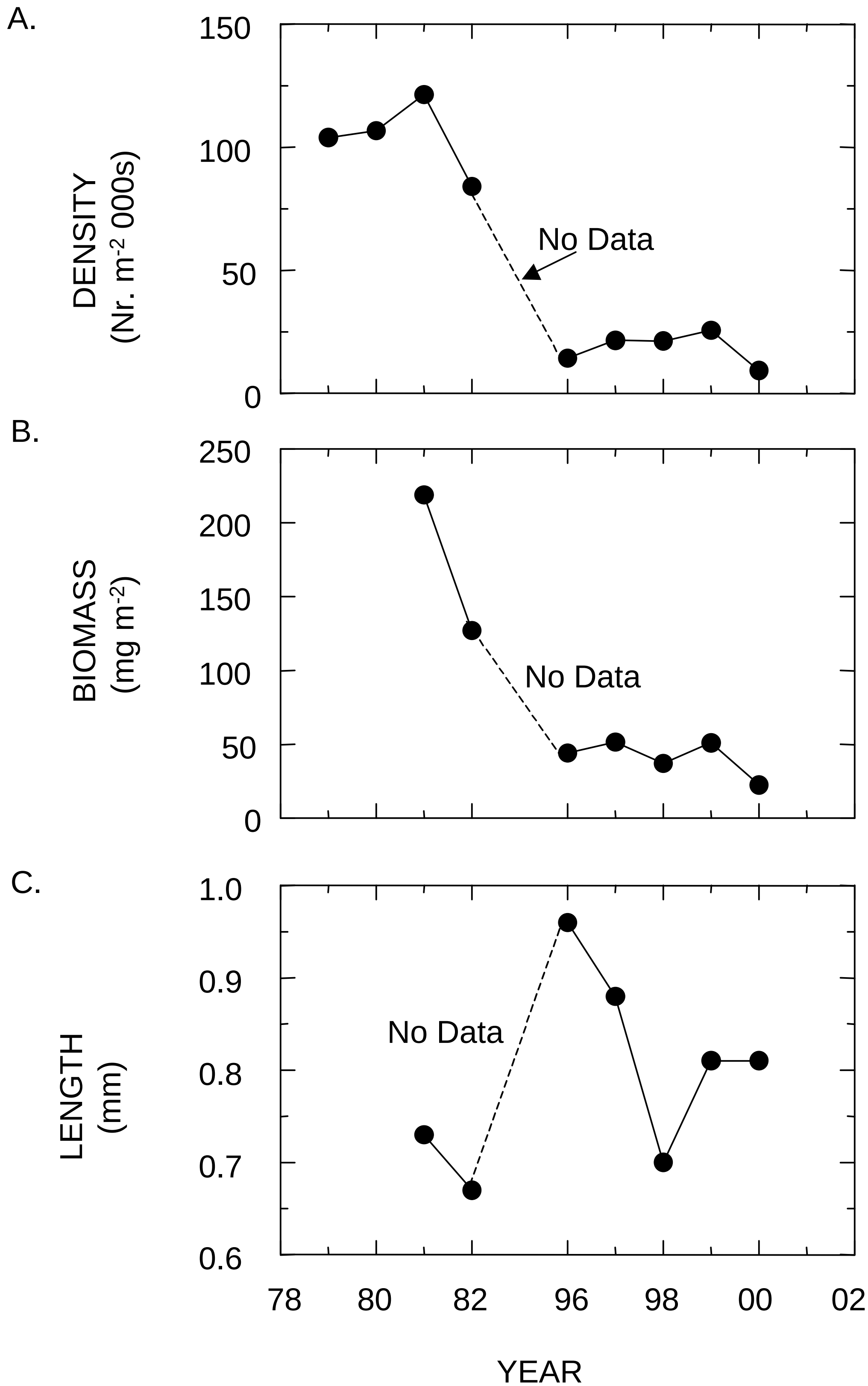

Figure 6. Inter-annual changes in (A) mean *Cyclops* density, (B) biomass and (C) body length from Crescent Lake, 1979-1982 and 1996- 2000. No zooplankton data are available for the 1983-1995 rearing years.

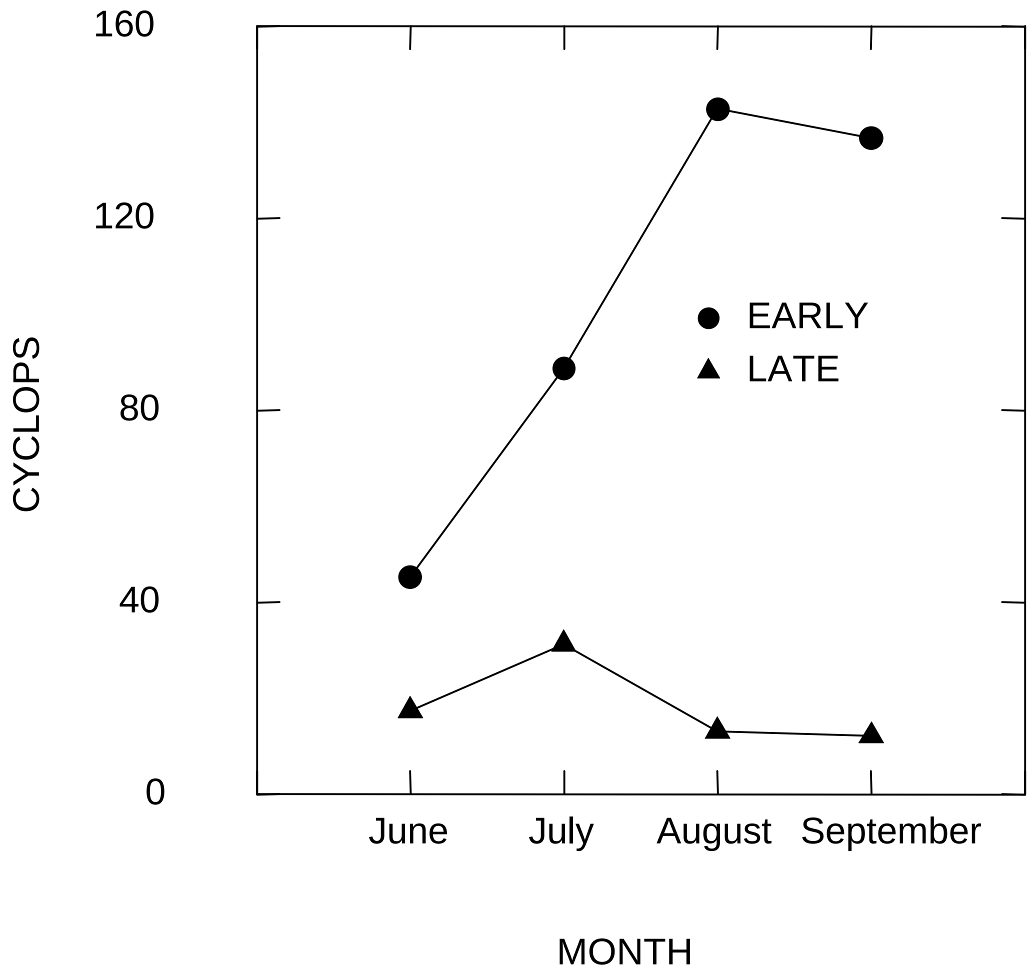

Figure 7. Monthly mean Cyclops densites (Nr. m^{-2} x 10^{3}) for the early (1979 - 1982) and late (1996 - 2000) periods.

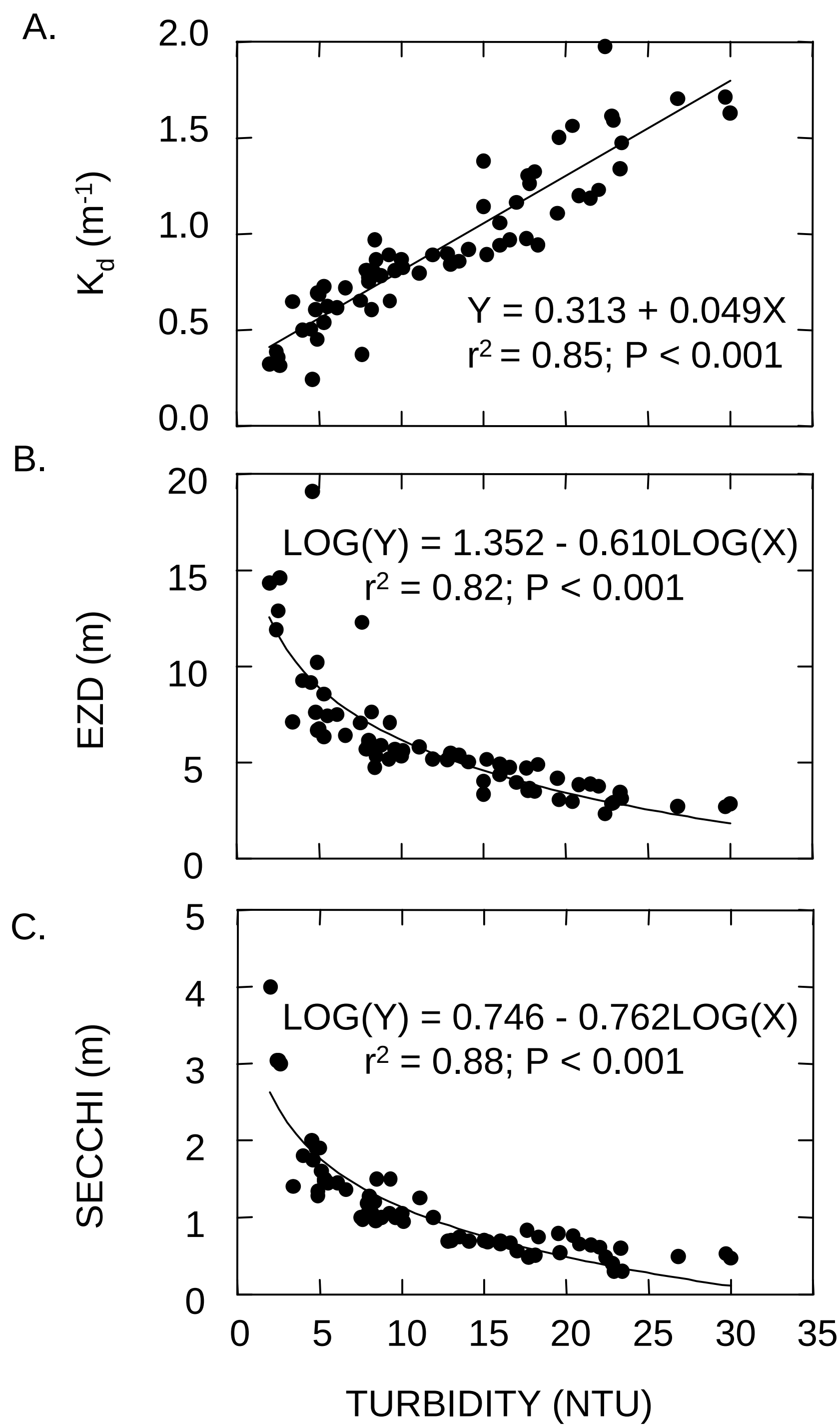

Figure 8. Relationships between turbidity and (A) light extinction coefficient (K_d), (B) euphotic zone depth (EZD), and (C) secchi depth for Crescent Lake, 1996-2000.

attenuating component in this lake. K_d values ranged from 0.25 (relatively clear) to 2.00 (very turbid) and averaged 0.93. In addition, euphotic zone depth (EZD) was inversely related (r^2 = 0.88, P<0.001) to turbidity and this relationship conformed to a log-linear function (Figure 8B). Over the four years sampled, EZD ranged from about 2 to 20 m and averaged 6.1 m. Secchi depths ranged from less than 1 to 4 m (Figure 8C), and like EZD they were negatively related to turbidity (r^2=0.82; P<0.001) in a curvilinear fashion.

Although we lack turbidity measurements for Crescent Lake for the early years of sampling, measurements of light penetration (e.g., EZD) were available. Because of the strong correlation between turbidity and EZD, we examined turbidity effects between the early and late sampling periods using EZD as a proxy variable. During 1979-1982, mean EZD was fairly consistent and ranged from 6.9 to 8.1 m (Figure 9). Based on our EZD-turbidity regression as described above, the corresponding turbidity levels associated with these EZD estimates averaged about 6 NTU. In contrast, mean turbidity during 1996 (17.7 NTU) and 1997 (19.3 NTU) increased three-fold and the EZD averaged approximately 4 m in these two years. Over the next three years, turbidity levels in Crescent Lake decreased substantially to about 8 NTU and light penetration increased. During 1998-2000, for example, mean EZD ranged from 6.6 to 7.2 m, which was similar to the estimated light penetration of the early 1980s.

Vertical temperature profiles in mid-summer (late July – early August) revealed that Crescent Lake did not undergo thermal stratification during the open water period, at least for any prolonged of time (Figure 10). Maximum surface temperatures reached as high as 15°C in 1979; however, maximum temperatures typically ranged between 10 and 12°C. Results of ANOVA suggested no significant difference (P=0.441) in average surface (1-m) water temperatures between the early (1979-1983) and late (1996-2000) survey periods. To assess the growing season pattern of Crescent Lake, we pooled the temperature data for the 1-m stratum across all sample years and then fit a quadratic regression model to the scatter plot of temperature against day of year (Figure 11). The respective x-intercepts, where y = 4°C, indicated Crescent Lake achieved spring 4°C isothermy by about 02 June (day 154) and reached fall 4°C isothermy by 15 October (day 289). The projected day of maximum heat content was 07 August (day 220). Thus, the estimated average duration of the growing season (289 minus 154) was 135 days or about 4 ½ months.

We compared general water chemistry, nutrient concentrations, and algal pigment levels between stations and between the early and late sampling periods (Table 2). Results of ANOVA suggested no difference (P>0.05) in general water chemistry or nutrient levels between stations A and B; however, chlorophyll *a* concentrations were on average 0.10 μg L^{-1} lower (P=0.033) at station B, closer to the glacier input, than station A (toward the outlet). Low algal biomass levels, as indexed by chlorophyll *a* values less than 1 μg L^{-1}, and total phosphorus (TP) concentrations of less than 10 μg L^{-1} (after correcting TP for turbidity interference) are consistent with a highly oligotrophic system. There were significant differences between the early and late periods as suggested from results of ANOVA: conductivity and alkalinity were higher during the later sample years than the early years, whereas calcium and magnesium were lower. However, we view these small differences to have little biological meaning, at least in relation to sockeye salmon production. During 1996-2000, total iron (mean 3.69 mg L^{-1}) averaged about 1 mg L^{-1} (or 1,000 μg L^{-1}) higher (P<0.001) than the 1979-1982 period (mean 2.65 mg L^{-1}), which

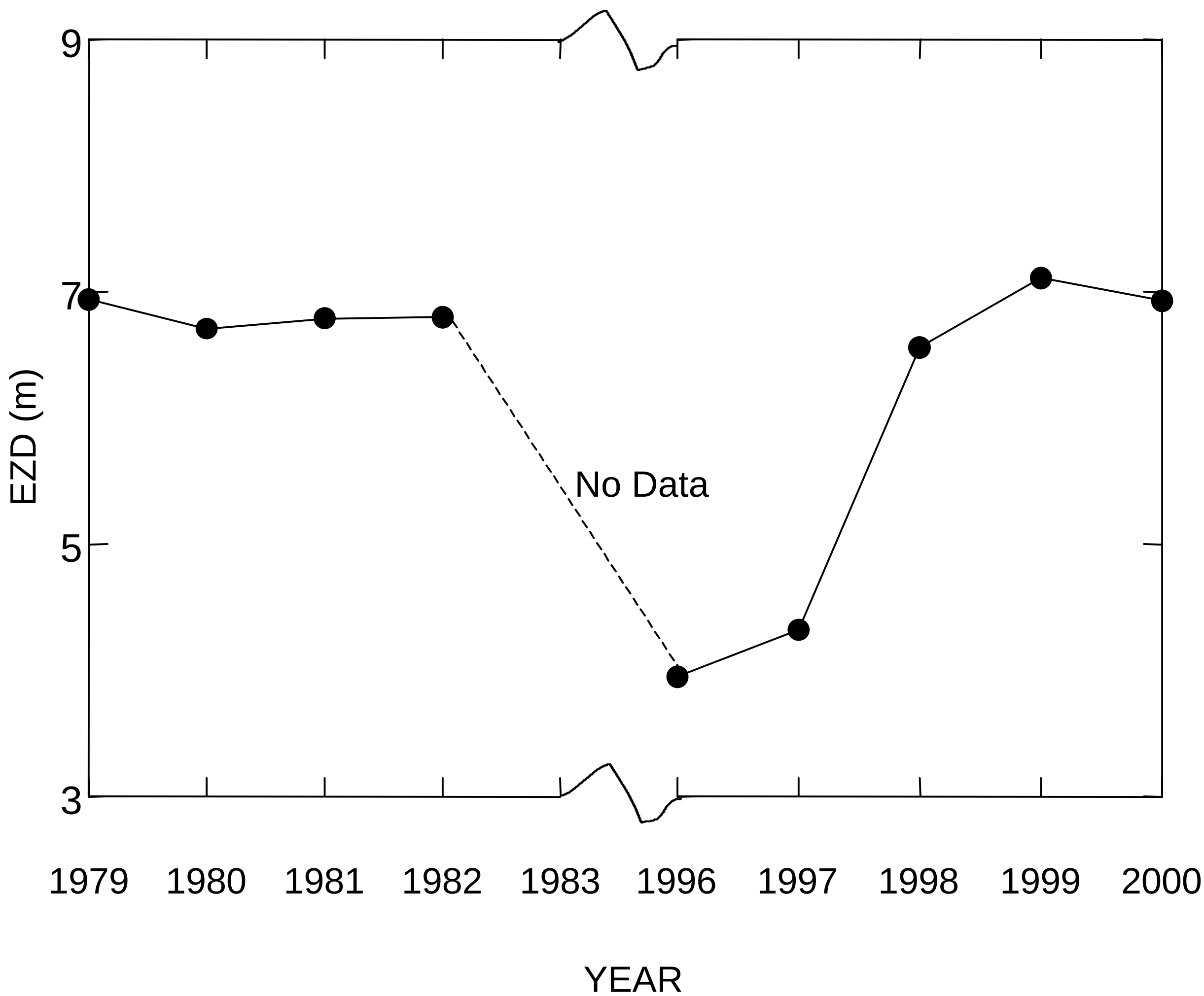

Figure 9. Interannual mean euphotic zone depth (EZD) in Crescent Lake, 1979-1982 and 1996-2000.

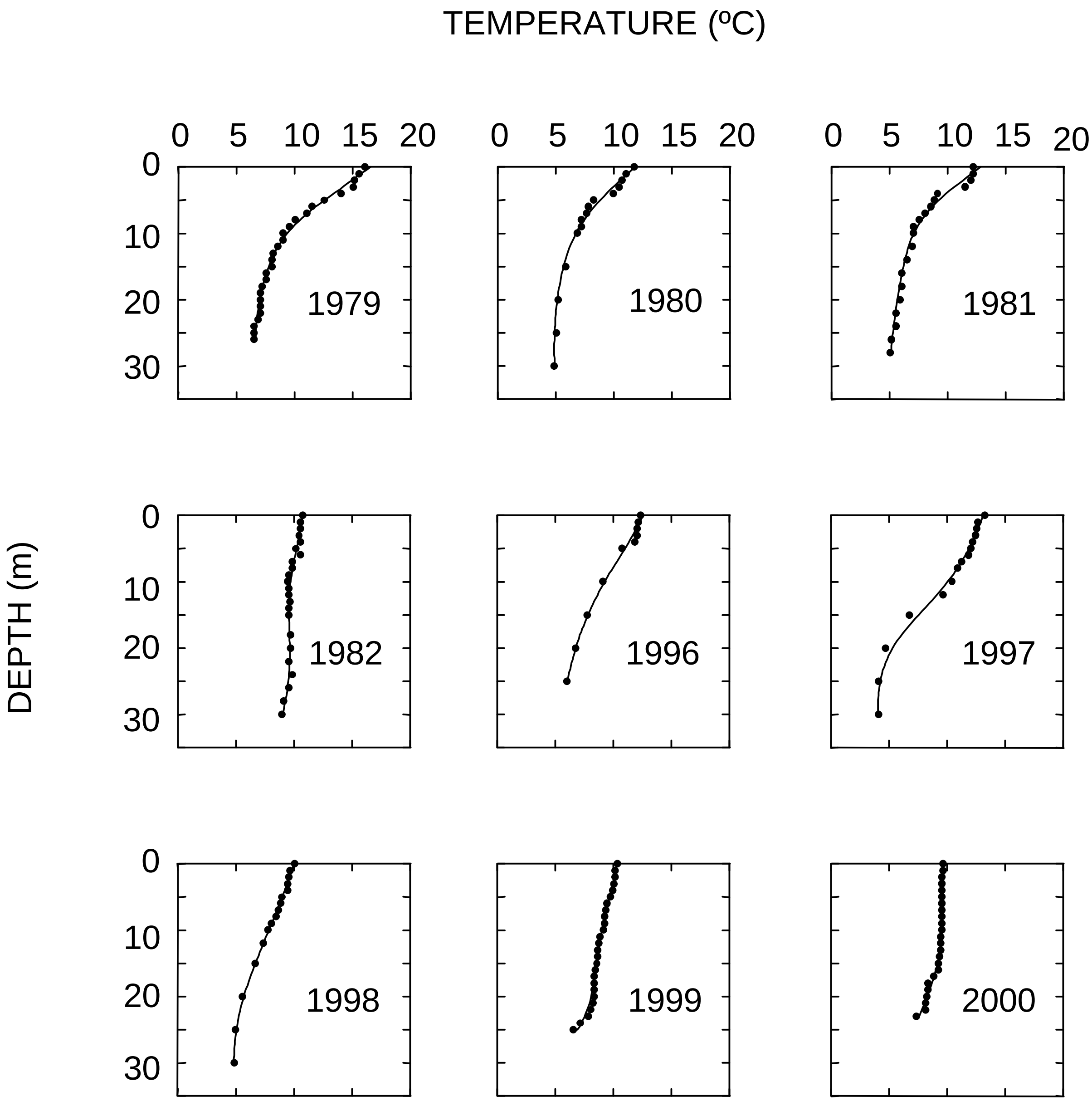

Figure 10. Vertical temperature profiles during time of maximum heat content (July and August) for Crescent Lake, 1979-1982 and 1996-2000.

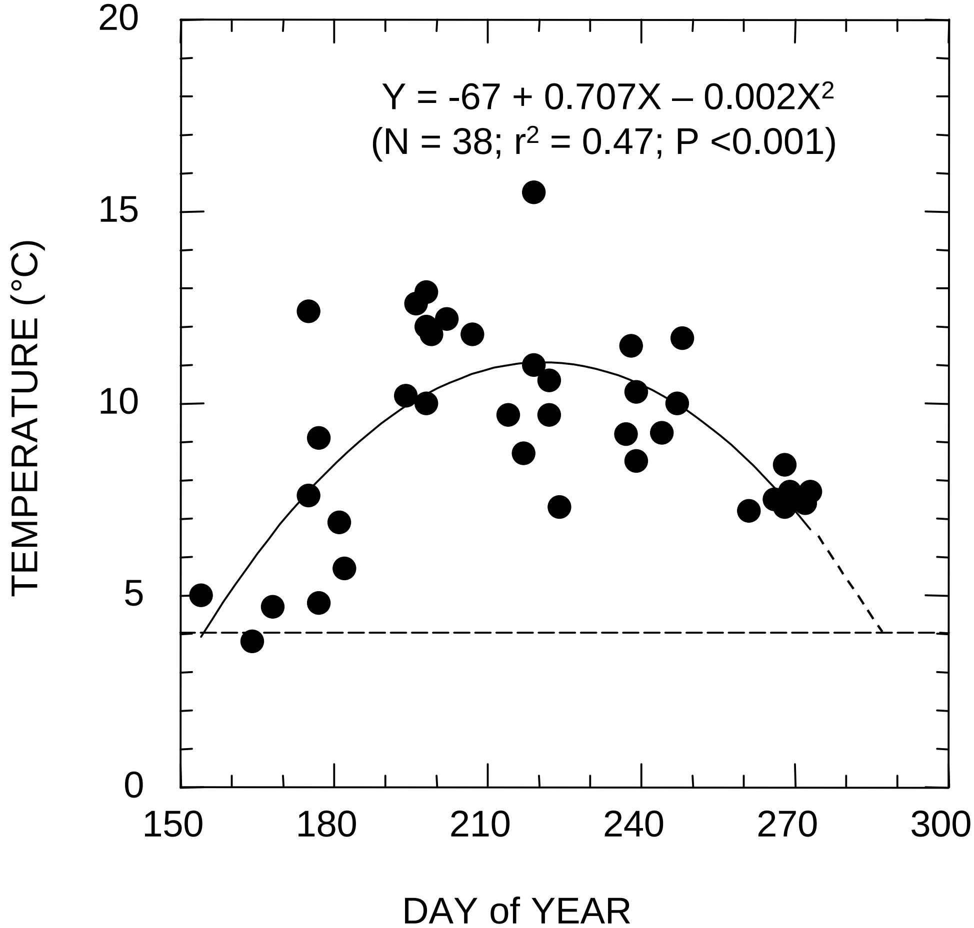

Figure 11. Plot of temperature at 1-m during the ice-free season for Crescent Lake. Data are pooled across sampled years (1979-1983, 1996-2000) and fitted to a quadratic model. Where the fitted line intersects the 4°C axis (dashed line) are the start and end of the growing season, the interval between is the estimated duration of the growing season.

Table 2. Comparison of mean water quality variables by stations (A + B) and by period, early (1979-1982) and late (1996-2000).

Variable	Unit of Measure	Station Mean A	Station Mean B	P-value	Period Mean Early	Period Mean Late	P-value
Conductivity	µmhos cm^{-1}	26.30	26.20	0.782	23.90	27.70	< 0.001
pH	Units	6.70	6.70	0.652	6.70	6.70	0.870
Alkalinity	mg L^{-1}	10.40	10.20	0.408	10.00	10.50	0.028
Turbidity	NTU	9.90	10.80	0.016	2.43	13.00	< 0.001
Calcium	mg L^{-1}	3.90	3.90	0.759	4.10	3.80	0.011
Magnesium	mg L^{-1}	0.34	0.31	0.115	0.40	0.30	0.008
Iron	mg L^{-1}	3.30	3.30	0.984	2.65	3.69	< 0.001
Total phosphorus	µg L^{-1}	11.50	12.70	0.054	10.00	13.40	< 0.001
Total filterable phosphorus	µg L^{-1}	2.40	2.30	0.839	2.40	2.30	0.692
Filterable reactive phosphorus	µg L^{-1}	1.90	2.10	0.112	1.90	2.10	0.163
Total nitrogen	µg L^{-1}	233.00	238.00	0.514	271.00	214.00	< 0.001
Kjeldahl nitrogen	µg L^{-1}	45.00	49.00	0.341	47.00	47.00	0.987
Ammonia	µg L^{-1}	9.50	7.10	0.060	8.10	8.50	0.733
Nitrate + nitrite	µg L^{-1}	188.00	188.00	0.997	224.00	170.00	< 0.001
Reactive silicon	µg L^{-1}	2243.00	2242.00	0.961	2208.00	2263.00	0.022
Chlorophyll *a*	µg L^{-1}	0.51	0.41	0.033	0.42	0.48	0.143
Phaeophytin	µg L^{-1}	0.23	0.20	0.182	0.17	0.25	0.008

represented a 40% increase. In addition, results of ANOVA suggested TP levels were about 30% higher ($P<0.001$) in the later years compared to the early years. On the other hand, inorganic nitrogen (i.e., nitrate + nitrite) concentrations were 25% lower ($P<0.001$), yet total Kjeldahl nitrogen (organic nitrogen + ammonia) was not significantly different ($P=0.987$) between the two periods.

Sockeye Salmon Carrying Capacity

We applied our current (1996-2000) mean estimates ($\bar{X}$) of euphotic volume (EV), euphotic zone depth (EZD) and total macrozooplankton biomass (ZB) for Crescent Lake to the existing carrying capacity (smolt biomass) models for Alaskan sockeye salmon as shown below:

Model	$\bar{X}$	Smolt (kg)	Smolt (Nr.) [a]	Adult recruits [b] (Nr.)	Spawners [c] (Nr.)	Harvest (Nr.)
EV	102 units	10,680	3.8 million	458,000	160,000	298,000
EZD	8.1 m	8,290	2.9 million	355,000	124,000	231,000
ZB	41 mg m^{-2}	264	94,000	11,000	4,000	7,000

[a] Conversion of smolt biomass to smolt abundance assumes 2.8 g smolt (Koenings et al 1985).
[b] Adult recruits based on 12% smolt-to-adult survival (Koenings and Kyle 1997).
[c] Optimum spawners based on 35% of total return (Koenings and Burkett 1987).

Both EV and EZD models predicted similar sockeye salmon production levels that were about 2-3 times higher than the system average. In contrast, based on current zooplankton biomass, the predicted sockeye salmon production is only 3% of that estimated using the EV and EZD carrying-capacity models.

During our 1996-2000 studies, sockeye salmon escapements averaged approximately 3,200 per square kilometer of lake surface area (Table 3). In comparison, spawner density (Nr. km^{-2}) during the early study period (1981-1982) was somewhat lower and averaged 2,500. However, the average grazing pressure index (spawner density/zooplankton biomass density) was 3 times higher (64) in recent years compared to the early 1980s (21). In other systems, the grazing index ranged from more than 800 to less than 2. The grazing pressure index for 17 Alaskan lakes fell into three levels of grazing pressure: 1) less than 10 (low), 2) 10-50 (moderate), and 3) greater than 50 (high). Thus, based on escapement levels and food resources (*Cyclops* biomass) during the early 1980s, we considered Crescent Lake to have had a more moderate grazing pressure. In contrast, based on the recent (1996-2000) spawner densities and low zooplankton biomass, we considered the current grazing pressure in Crescent Lake to be relatively high.

Table 3. Comparison of mean spawner abundance, spawner density, zooplankton biomass and the grazing pressure index for 17 sockeye nursery lakes.

Lake	Typology	Area (A) (km^2)	Brood years	Mean spawner abundance (P) (Nr.)	Mean spawner density (P/A) (Nr. km^{-2})	Zooplankton biomass (ZB) (kg km^{-2})	Grazing pressure index (P/A)/(ZB) (Nr. kg^{-1})
Desire	Clear	1.8	1980,1996	13,200	7,333	17	822.8
Falls	Stained	0.9	1981-1984	2,061	2,172	51	105.9
Frazer	Clear	16.6	1984-1986	221,963	13,371	149	104.0
Chilkoot	Glacial	7.0	1986-1990; 1994-1999; 1999	51,268	7,311	115	96.2
Coghill	Glacial	12.7	1987-1997	52,199	4,119	91	89.6
Crescent	Glacial	16.5	1996-2000	69,350	3,212	50	64.2
Delight	Clear	2.8	1980;1996	8,850	3,161	102	37.2
Redoubt	Stained	12.9	1982-1984; 1989-1995;	27,174	2,115	122	35.4
Crescent	Glacial	16.5	1981-1982	41,213	2,498	118	21.2
Karluk	Clear	39.4	1980-1993	601,997	16,370	1,125	17.3
Big	Clear	12.1	1984	75,071	15,785	1,021	15.5
Skilak	Glacial	99.0	1985-1998	422,571[a]	4,268	485	9.5
Eshamy	Clear	3.6	1980;1984 1988-1994	29,599	9,503	1,701	7.0
Auke	Stained	0.9	1985;1989-1991	2,889	3,140	462	6.9
Tustumena	Glacial	294.5	1980-1998	217,048[b]	734	119	6.8
Kook	Stained	2.4	1994	1,817	755	241	3.1
Ugashik	Clear	381.7	1996-1998	854,954	1,931	1,048	1.9
Becharof	Clear	1142.0	1996-1998	1,103,614	961	767	1.3

[a] The abundance was adjusted to reflect the proportion of spawners to Skilak Lake to the total number of Kenai River mainstem spawners based on fall fry abundance (hydroacoustic) estimates.

[b] A portion of the spawner abundance was back calculated from the number of stocked (spring) fry using standard freshwater survival estimates.

[c] Fry grazing pressure on the forage base produced from a brood year (Y) occurrs during rearing year (Y+1). Zooplankton biomas estmates were calculated from rearing year (Y+1).

DISCUSSION

Sockeye Salmon Production Relative to Limnological Conditions

Since 1979-1982, Crescent Lake has experienced increased turbidity and decreased light penetration (Figure 9). One explanation for the higher turbidity may be due to warmer regional climatic conditions, which would likely increase glacier melt (Edmundson and Mazumder 2002). Cold glacier meltwater entering a lake basin at depth tends to reduce water column temperatures (Edmundson and Mazumder 2002). However, water column temperatures of Crescent Lake were not noticeably warmer during 1996-2000 compared to those of about two decades ago (Figure 10). On the other hand, turbidity is a function not only of the magnitude of silt loading, but also of the particle size distribution (Edmundson and Koenings 1985; Koenings et al. 1986). Smaller, planer silt particles scatter light more effectively and increase turbidity more so than particles having a smaller surface-to-volume ratio. The portions of the glaciers that are melting today, which feed turbid meltwater into Crescent Lake (Figure 2), may contain a different composition of silt particles than the meltwater of the early 1980s. Consequently, the observed recent increases in turbidity that occurred in Crescent Lake may have more to do with a smaller size distribution of inorganic silt particles rather than just the amount of silt input.

Another possible explanation for the increased turbidity in Crescent Lake, at least in the short term, was the 1989-1990 volcanic eruptions of nearby Mt. Redoubt volcano (AVO 1990). Eicher and Rounsefell (1957) related that in several sockeye-producing lakes on Afognak Island that were affected by heavy ash fallout from the 1912 Mt. Katmai eruption were all but devoid of fry forage. They further suggested that adult returns from broods that reared in these lakes under those very adverse (turbid) conditions were relatively small and it took about nine years for returns to recover to pre-eruption levels. Crescent Lake, which lies at the base of Mt. Redoubt, undoubtedly experienced significant ash deposition from 1989-1990 volcanic events. This could have greatly increased turbidity levels either through increased ice melting or ash fallout, thereby reducing primary production and decreasing salmon productivity. We have no limnological information for years when the effects of ash deposition would have been greatest, but as we have shown, turbidity levels were significantly higher in 1996 and 1997, about twice as much.

While we are uncertain as to the causal mechanisms for the changing turbidity, we are certain that the euphotic volume or productive capacity for photosynthetic algae of Crescent Lake was much smaller (about ½) in recent years, particularly in 1996 and 1997 (Figure 9), compared to the early 1980s. Although we do not know whether turbidity in Crescent Lake was increasing during the intervening years between the early (1979-1982) and late (1996-2000) periods, turbidity in nearby Skilak Lake has increased since the mid 1980s (Edmundson and Todd 2001). In addition, we do know that during this time the productivity of Crescent Lake sockeye, as reflected by RPS values, was also decreasing (Figure 5B). Thus, we infer that the decline in sockeye productivity was associated, at least in part, to accelerated glacier melt or the nature of the meltwater intrusion and its attendant effects on turbidity.

It has been suggested that nutrients released from salmon carcasses are important in sustaining salmon productivity (Stockner 1987; Cederholm 1989; Kline et al. 1993; Finney et al. 2000).

Although sockeye salmon escapements in Crescent Lake began to decline substantially in the mid 1980s, we do not believe that lacustrine productivity and sockeye production (RPS) were negatively affected by a lack of carcass nutrients from too few spawners. For example, total phosphorus was somewhat higher in concentration during 1996-2000 compared to 1979-1982 (Table 2). However, it has also been demonstrated that primary production in glacial lakes is largely a function of light penetration and not nutrients (Koenings and Edmundson 1991; Edmundson and Carlson 1998). Moreover, in glacial lakes, the total phosphorus (and iron) pool is largely derived from inorganic silt; however, this source is mostly biologically unavailable; i.e. rock phosphorus (Edmundson and Koenings 1985; Edmundson and Carlson 1998). Koenings et al. (1985) showed the phosphorus cycling in Crescent Lake was tightly coupled with seasonal fluctuations in turbidity. Thus, the higher phosphorus (and iron) concentrations during 1996-2000 are the result of increased turbidity from suspended glacial silt particles. Although, inorganic nitrogen (nitrate + nitrite) levels were lower in recent years than the early 1980s (Table 2), we do not believe nitrogen is limiting productivity of plankton more so now than before. Total nitrogen levels in Crescent Lake were about twice the concentration as in clear lakes that support rearing sockeye salmon juveniles (Edmundson and Carlson 1998). In addition, it is phosphorus, not nitrogen that is the primary nutrient limiting phytoplankton production in oligotrophic lakes in Alaska (Edmundson and Carlson 1998). Thus, the observed decline in sockeye salmon production in Crescent Lake is probably unrelated to changes in nutrient (phosphorus and nitrogen) levels.

It has also been shown that inorganic turbidity from suspended glacial silt particles lowers areal zooplankton abundance and biomass and reduces species diversity (Edmundson and Koenings 1985; Koenings et al. 1990). Simply put, glacial lakes have lower zooplankton production on average than clear lakes. In addition, the size distribution of inorganic glacial silt largely overlaps that of the phytoplankton. The mixture of particles consumed by zooplankton through filter feeding is therefore of relatively low nutritional value. As a result, glacial lakes cannot support abundant populations of filter-feeding cladocerans such as *Daphnia* (Koenings et al. 1990), which have higher nutritional requirements than copepods like *Cyclops*. In Crescent Lake, the observed decrease in the abundance of *Cyclops* (Figure 6A-B) could have occurred because of higher turbidity and decreased euphotic volume, which reduced the photosynthetic capacity of the water column and lowered phytoplankton biomass. However, there was no significant difference in mean chlorophyll *a* concentration between the early and late periods (Table 2). Nonetheless, chlorophyll *a* concentrations were near our analytical detection limit making it difficult to infer whether there was a change in algal biomass levels in Crescent Lake.

We also know that fry growth, size at age, and survival of sockeye salmon in freshwater decreases with increasing fish density (Foerster 1968; Burgner 1987; Reiman and Meyers 1992; Edmundson and Mazumder 2001). In addition, high fry densities can lead to predator induced behavioral changes in the zooplankton community resulting in reduced forage availability (Schmidt et al. 1995). We considered heavy grazing pressure by rearing sockeye salmon juveniles on the zooplankton forage base as another reason for the observed decline in sockeye production. For example, although turbidity was much higher in 1996 and 1997, it has since lessened and light penetration has increased (Figure 9). Yet, *Cyclops* populations have not recovered at all to the densities observed in the early years (Figure 6A-B). Consecutive years of high escapements have been attributed to declines in sockeye salmon production in other

Alaskan lakes through overgrazing of the zooplankton forage base (Kyle et al. 1988; Edmundson et al. 1992; Koenings and Kyle 1997; Schmidt et al. 1994, Schmidt et al. 1995; Mazumder and Edmundson submitted). During 1984-1987, sockeye escapements in Crescent Lake exceeded the escapement goal (50,000-100,000) in three of the four years (Figure 5A) and recruitment (RPS) from these brood years was less than replacement (Figure 5B). Studies of Alaskan lakes have also shown that the macrozooplankton community may take several years to recover from the effects of high planktivory from stocking too many fry or by recruitment from large escapements (Kyle 1996; Edmundson et al. 1992; Schmidt et al. 1995; Koenings and Kyle 1997). Moreover, recovery in terms of abundance may take even longer for zooplankton populations composed mainly of copepods, which have a protracted reproductive strategy, compared to cladocerans. Cladocerans can produce many broods within a single season (Pennak 1978). In comparison, Schmidt et al. (1995) demonstrated that *Cyclops* has a two-year life history in nearby Skilak Lake, another glacial system that produces large runs of sockeye salmon. We do not know how long zooplankton populations have been depressed in Crescent Lake, but the decrease in turbidity and increase in light penetration, and presumably higher phytoplankton production over the past couple of years, did not result in greater densities or biomass of *Cyclops*.

In Crescent Lake, the current escapement goal (25,000-50,000) initiated in 1998 (Fried 1999) was exceeded in 1999, 2000, and 2001 (Figure 3). As we have shown, although turbidity lessened and light penetration increased in those years (Figure 9), *Cyclops* densities did not (Figure 6A-B). In addition, per capita food availability for sockeye salmon fry was considered high relative to other sockeye salmon nursery lakes (Table 1). That is, the average grazing pressure index was three times higher (64) in recent years than it was in the early 1980s (21) suggesting a less efficient balance between predator and prey. Nonetheless, we are unsure if zooplankton abundance in Crescent Lake is now trapped at low levels because of a decrease in trophic status (higher turbidity) which made an inherently unproductive glacial environment even more severe, or from excessive grazing due to high fry densities, or a combination of both "bottom-up" and "top-down" effects. What is clear is that sockeye salmon fry must cope with not only a reduced forage base but they also face metabolic restrictions of feeding and growth due to limited temperatures (Brett 1971). The combined effects of limited food resources (zooplankton biomass), high fry densities (increased competition) and cold rearing temperatures result in slower growth rates and greater mortality of sockeye salmon juveniles in freshwater (Edmundson and Mazumder 2001). Indeed, even under the more favorable rearing conditions (less turbidity and more zooplankton) such as occurred in the early 1980s, Crescent Lake produced small, threshold-sized (~2 g) smolts (Koenings et al. 1985), which on average tend to have poorer marine survival (12%) than larger (4-5 g) smolts (21%) (Koenings and Burkett 1987; Geiger et al. 1991).

CONCLUSIONS AND RECOMMENDATIONS

Having reviewed all the pertinent data available to us concerning production of the Crescent River sockeye salmon stock, consideration may be given to the current escapement goal (25,000-50,000). Several important findings have been presented to help indicate what the optimum number of spawners should be. Collectively, results (S_{MSY}) of our Ricker analysis (Figure 4) and tabular summary of escapements and yield (Table 1) suggest an optimum escapement level for Crescent River sockeye salmon in the range of 20,000-40,000. This is in good agreement with the average spawner abundance (41,200) and associated per capita food resource availability as reflected by a low to moderate grazing pressure index (Table 3). On the other hand, surrogates of primary productivity (i.e., EV and EZD) did not seem to summarize very well the carrying capacity of sockeye salmon in Crescent Lake. For instance, the predicted number of adult recruits from these indices is 3-4 times higher than the actual peak returns for the system. In addition, sockeye salmon production based on existing zooplankton biomass (ZB model) is only about 5% of the size of the highest returns. However, what this does imply is that the former escapement goal (50,000-100,000) was probably too high and given the observed decline in RPS, lake- rearing capacity was exceeded by top-down control of the zooplankton community. It may be argued that the unusually low RPS values observed in the mid 1980s may have been be an anomaly or related more to changing ocean conditions (Beamish and Bullion 1993; Hare and Francis 1995; Mantua et al. 1997), but low productivity may also suggest that freshwater survival decreased as a function of high fry abundance and heavy grazing on *Cyclops*. Compensatory (density dependent) fits to the spawner-recruit data were possible (Figure 4) and this seems to support the evidence about the dramatic differences in zooplankton food supplies available to rearing sockeye salmon juveniles between the early and late periods. It is clear from our estimates that there was much less zooplankton food available for each juvenile during 1996-2000 compared to 1979-1982, around one-third as much (Table 3). Thus, from the data just reviewed the current escapement goal of 25,000 to 50,000 provides a more efficient match between fry density and zooplankton standing crop.

We support maintaining the current sockeye salmon escapement goal for Crescent River for at least a few more years. If the goal is consistently met, we propose that the abundance of cyclopoid copepods will increase under relaxed grazing pressure, fry growth and survival will improve, and sockeye salmon productivity will increase. Unfortunately, funding for continued limnological investigations has been terminated due to fiscal constraints. It will be impossible to ascertain future feeding capacities for juvenile sockeye salmon in Crescent Lake in response to turbidity and fish density. Thus, we will have to assess the productivity of this stock by trends in escapement and harvest or RPS values. However, the latter gives information only on total mortality across the freshwater and ocean life history components. Such rough and approximate comparisons of sockeye salmon productivity do not allow us to see if the effects of changes in lake rearing capacity, in terms of quantity and quality, underlie the changes in recruitment and surplus yield. The lesson to be learned here is that, despite some uncertainty in the underlying mechanisms controlling zooplankton and fry recruitment in Crescent Lake, concomitant information about habitat (limnological) conditions along with spawner-recruit data can facilitate fishery management objectives such as determining the number of spawners to maximize yield and to have a good sustainable fishery (Schmidt et al. 1997).

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